PHYLOGENY OF THE MOSASAURINAE (SQUAMATA: MOSASAURIDAE) WITH DESCRIPTIONS AND FUNCTIONAL MORPHOLOGY OF NEW AND EXISTING MOSASAURINES

by

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To Maddy

ABSTRACT

Mosasaurs were giant marine squamates that inhabited all of the world's oceans approximately 93 to 65 Million Years Ago. The subfamily Mosasaurinae is one of the most diverse groups, including the robust-toothed Globidensini and the ichthyosaur-like members of the Plotosaurini (*Plotosaurus* + *Mosasaurus*). *Eremiasaurus heterodontus*, a new mosasaurine from the Maastrichtian of Morocco, is described and added to a comprehensive phylogenetic analysis of the Mosasaurinae. *Eremiasaurus heterodontus* is recovered as the sister taxon to the Plotosaurini, but possesses features previously considered to be globidensine synapomorphies. As a result, the Globidensini may no longer be considered monophyletic. The cranial anatomy of *Plotosaurus bennisoni* is also redescribed to highlight a trend towards an increasing level of aquatic adaptation of the skulls of derived mosasaurines. These findings challenge the conventional dichotomy of plotosaurine and globidensine mosasaurs and the evolutionary trends within the Mosasaurinae

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Institutional Abbreviations

CM, Canterbury Museum, Christchurch, New Zealand

LACM/CIT, Natural History Museum of Los Angeles County, Los Angeles (former California Institute of Technology collection)

IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium

MNHN, Muséum National d'Histoire Naturelle, Paléontologie, Paris, France

NHMM, Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands

NHMUK, The Natural History Museum, London, UK

OCP DEK/GE, Office Chérifien des Phosphates, Collection de Paléontologie, Centre Minier de Khouribga, Morocco

RFWUIP, Institut für Paläontologie Rheinische Friedrich-Wilhelms-Universität, Bonn, Germany

UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Canada

UCMP, Museum of Paleontology, University of California, Berkeley.

Anatomical Abbreviations

The reader is referred to the figure captions for the anatomical abbreviations that are specific to each figure.

CHAPTER ONE

GENERAL INTRODUCTION

INTRODUCTION TO THE MOSASAURINAE

The superfamily Mosasauroidea represents a diverse group of marine squamates that achieved gigantic proportions and worldwide distributions by the end of the Maastichtian (Late Cretaceous), roughly 65 Million Years Ago (Russell, 1967; Caldwell and Palci, 2007). The earliest mosasauroids are best known from upper Cenomanian (approximately 93 Million Years Ago) deposits of Croatia and were comparatively small semi-aquatic lizards (Carroll and DeBraga, 1992; Dutchak and Caldwell, 2006, 2009). In a relatively short period, mosasauroids became much larger and were obligatorily aquatic, as is indicated by their large rudder-like paddles and the loss of sacral attachments (Bell and Polcyn, 2005; Caldwell and Palci, 2007).

Although the systematics of the Mosasauroidea (Aigialosauridae + Mosasauridae) and the relationships of the early semi-aquatic aigialosaurids to the paddle-bearing mosasaurids (sensu Bell, 1997) are still debated (Bell and Polcyn, 2005; Caldwell and Palci, 2007; Caldwell and Dutchak, 2009) three major groups are thought to represent separate radiations within the Mosasauridae: the parafamily ‘Russellosaurina’, the Halisauromorpha and the Mosasaurinae (Bell and Polcyn, 2005). The Mosasaurinae are a diverse assemblage of mosasaurs that are all more closely related to *Dallasaurus turneri* than to any other mosasaurid (Fig. 1–1; Bell and Polcyn, 2005). All mosasaurines, including the terrestrial limb-bearing *D. turneri*, possess (1) a deep coronoid buttress of the surangular; (2) short median frontal flanges that invade the dorsal surface of the parietal table and (3) fused haemal arches in the caudal vertebral region (Bell and Polcyn, 2005). The cladistic definition of the Mosasaurinae according to Bell and Polcyn (2005) is complicated by the inclusion of the 'aigialosaur'-grade *D. turneri* within the Mosasaurinae without providing a revised diagnosis of the Mosasauridae or the Mosasaurinae (Bell and Polcyn, 2005; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009). Furthermore, the intrarelationships of the Mosasaurinae remain uncertain, having changed significantly since Russell's (1967) first attempt to systematize the mosasaurines.

Russell (1967) expanded the composition of the Mosasaurinae from Williston (1895), initially only consisting of *Clidastes* and *Mosasaurus*, to include several additional taxa that were grouped into three tribes: the Mosasaurini (*Mosasaurus*, *Clidastes*, *Liodon*), the Globidensini (*Globidens*) and the Plotosaurini *(Plotosaurus*, *Taniwhasaurus*). *Taniwhasaurus* has since been recognized by many authors (e.g., Caldwell et al., 2008; Fernandez and Martin, 2009) to be a close relative of *Tylosaurus* (and thus a member of the 'Russellosaurina' of Bell and Polcyn, 2005), which would have made *Plotosaurus* the sole member of the Plotosaurini. Additionally, the genus '*Liodon*' has remained poorly defined since the original description by Gaudry (1892) and is now considered a nomen dubium (Schulp et al., 2008). The first major change to the systematics of the Mosasaurinae, however, did not occur until Bell (1993; 1997) presented the first phylogenetic analysis of North American and Adriatic mosasauroids. While the phylogeny presented in Bell (1997) was largely consistent with Russell (1967), two major changes to the ingroup composition of the mosasaurinae were proposed: (1) *Plesiotylosaurus* and *Prognathodon* were no longer allied with the plioplatecarpines (sensu Russell, 1967), but rather with *Globidens*, expanding the definition and ingroup composition of the Globidensini, and (2) *Mosasaurus* was considered to be more closely related to *Plotosaurus* than to *Clidastes*. The phylogeny of Bell (1997) was thus the first to propose a dichotomy between two major groups of derived mosasaurines: the Globidensini (now consisting of *Globidens*, *Plesiotylosaurus* and *Prognathodon*) and the Plotosaurini (*Mosasaurus* and *Plotosaurus*). *Clidastes* was removed from the Plotosaurini (sensu Bell, 1997) and in all phylogenies that have used the dataset of Bell (1997), or the modified dataset of Bell and Polcyn (2005) has been recovered as a paraphyletic grade of basal mosasaurines (Fig. 1–1A).

Numerous authors have since recovered similar topologies of the Mosasaurinae (Christiansen and Bonde, 2002; Dortangs et al., 2002; Caldwell and Palci, 2007), but many of the phylogenies presented subsequent to, and including Bell (1997), have failed to recover a monophyletic *Prognathodon* (Fig. 1–1A). Such finer-scale resolution of the relationship of *Prognathodon* to the other globidensines has been attempted by Christiansen and Bonde (2002), Dortangs et al. (2002) and Schulp (2006), using additional species of *Prognathodon* (Fig. 1–1B), but not without greatly modifying the original dataset from Bell (1997). Christiansen and Bonde (2002) and Schulp (2006) presented topologies based on a reduced dataset that excluded postcranial characters, while Dortangs et al. (2002) restricted their analysis to mosasaurine taxa, using *Clidastes* as an outgroup. Caldwell and Palci (2007) were the last to use the dataset of Bell (1997) in its entirety, but suggested that many of the original characters were uninformative or poorly constructed. Of particular concern was the high percentage of characters concerning the quadrate, a bone that is considered to be diagnostic for many mosasaur taxa (Lingham-Soliar, 1995; Bell, 1997; Lindgren and Schulp, 2010). Caldwell and Palci (2007) deleted several characters concerning finer-scale features of the quadrate and produced a similar topology of the mosasaurine taxa to Bell and Polcyn (2005), where *Prognathodon* was again paraphyletic (Fig. 1–2).

The globidensines are consistently united by characters associated with their unusually robust quadrates and the possession of stout, highly ornamented tooth crowns; both features presumably evolving to resist the higher compressive forces associated with hard-biting (Bell, 1997; Christiansen and Bonde, 2002; Schulp, 2005; Schulp, 2006). Conversely, identifying characters that differentiate globidensine taxa from each other has proven to be difficult, because many of the characters from Bell (1997) fail to account for gradational variation in dental features that have been used to distinguish *Prognathodon* from the other globidensines. This has resulted in a high percentage of inconsistencies in the character state assignments for *Prognathodon* (Christiansen and Bonde, 2002; Dortangs et al., 2002; Schulp, 2006; Schulp et al., 2006) and highlights a need to re-evaluate these characters and their phylogenetic utility, as was done for the quadrate characters that Caldwell and Palci (2007) deemed uninformative.

Problems of phylogeny and taxonomy also plague the second group of derived mosasaurines. *Mosasaurus* and *Plotosaurus* together form a monophyletic

Plotosaurini, which is supported by Bell (1997) and subsequent authors (Fig. 1–2; Dortangs et al., 2002; Caldwell and Palci, 2007). The relationship of *Plotosaurus* to the constituent species of *Mosasaurus*, however, remains contentious. Bell (1997) recognized this issue and noted that *Mosasaurus* is paraphyletic (Figs. 1–1A, 1–2), electing to use the name Plotosaurini for the clade consisting of (*Mosasaurus* + *Plotosaurus*) and abandoned the use of the name Mosasaurini from Russell (1964). This proves to be particularly problematic, because all higher-ranked taxa including the type genus *Mosasaurus* are named following the principles of Linnean nomenclature, except for this tribe. Furthermore, no formal diagnosis for the Plotosaurini has been provided since Russell (1967), when the group consisted solely of *Plotosaurus*. A revised diagnosis for this clade would involve re-characterization of the anatomy of its constituent species, which has been done for some, but not all plotosaurine taxa (Lingham-Soliar, 1995; Mulder, 1999). Lindgren et al. (2008) redescribed the post-cranial anatomy of *Plotosaurus*, but a redescription of the cranial anatomy of this unusual mosasaurine has not been undertaken. A detailed anatomical review of the skull of the holotype of *Plotosaurus bennisoni* is of particular importance not only for characterizing its anatomy for more detailed comparisons with species of *Mosasaurus*, but also because of its implications for understanding more about the adaptations of derived mosasaurines to an increasingly pelagic lifestyle (Lindgren et al., 2007).

Since Camp's (1942) original description of *Plotosaurus*, this taxon has been recognized as one of the best suited for life as an obligatorily aquatic squamate. Following Camp's assertions, Lindgren et al. (2007) provided a detailed account of the suite of anatomical changes that characterized the transition from a serpentine ambush predator to a fish-like open water cruiser. A restriction of the zygapophyses to the anterior-most trunk region, the development of long hyperphalangic paddles and a large two-lobed caudal fin were among the features that Lindgren et al. (2007) postulated evolved in *Plotosaurus* as a result of a dramatic change in mosasaur predatory behavior. The features outlined by Lindgren et al. (2007) only concerned the postcranial skeleton and did not explore the potential for such dramatic changes in the skull of *Plotosaurus*, despite its ichthyosaur-like appearance (Bell, 1997; Lindgren et al., 2007; Lindgren et al., 2008). Such a description and functional analysis of the cranial anatomy of this mosasaur could provide great insight into the evolution of the most aquatically adapted of the mosasaurines.

Introduction to Chapter Two

A new mosasaur, *Eremiasaurus heterodontus* gen. et sp. nov., from the Maastrichtian phosphates of Morocco is described based on a nearly complete skull, vertebral column and isolated appendicular elements. This description not only adds to the diversity of mosasaurines from Morocco, but also bridges the morphological gap between the Globidensini and the Plotosaurini. The phylogenetic and evolutionary implications for the presence of a mosasaur that possesses both globidensine and plotosaurine synapomorphies are explored and the suite of dental and quadrate characters that currently support globidensine monophyly are criticized. Lastly, the significance of a *Plotosaurus*-like caudal anatomy in *Eremiasaurus heterodontus* is addressed.

Introduction to Chapter Three

The cranial anatomy of *Plotosaurus bennisoni* from the Maastrichtian Moreno Formation of central California is redescribed in Chapter Three. New anatomical observations following Camp's (1942) original description of *Plotosaurus* are made based primarily on the holotype skull of *P. bennisoni*, but also on referred material of *P. bennisoni* and *P. tuckeri*, which has since been synonymized with the former taxon (Lindgren et al., 2008). Comparisons with other mosasaur taxa are framed in the context of modern views of mosasaurine phylogeny (e.g. Bell and Polcyn, 2005; Caldwell and Palci, 2007). Comparisons between *Mosasaurus hoffmanni*, *M. missouriensis* and *Plotosaurus* are based on observations of the holotypes of the three species as well as the anatomical descriptions of these taxa provided by Goldfuss (1845), Camp (1942) and Lingham-Soliar (1995). This redescription of the cranial anatomy of *Plotosaurus* serves as the basis for the evolutionary and biomechanical hypotheses made in the following chapter.

Introduction to Chapter Four

Evolutionary and functional hypotheses for the development of a long snout and other unusual features of *Plotosaurus* are presented in Chapter Four. The significance of an elongate snout, high degree of tooth interdigitation and the suite of osteological features that would have restricted intracranial and intramandibular mobility in *Plotosaurus* are investigated in detail. Based on these observations, *Plotosaurus* likely possessed an akinetic skull, similar to what previous authors have reported (Russell, 1964; Callison, 1967; Lingham-Soliar, 1995). Furthermore, mobility at the intramandibular joint was likely impeded and the ability of the quadrate to rotate about the suspensorium (streptostyly) is deemed to have been completely lost (contra Camp, 1942; Russell, 1964; Callison, 1967). It is concluded that the loss of streptostyly, intracranial kinesis and intramandibular mobility can be best attributed to a specialization for piscivory in *Plotosaurus* and not to a need to cope with increased bite forces as in other akinetic mosasaurines (Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995).

FIGURE 1–1. Two recent phylogenies of the Mosasaurinae. **A**, the Mosasaurinae as depicted in one of three equally most parsimonious trees of 412 steps from Bell and Polcyn (2005) using 41 taxa and 142 characters (CI = 0.430, RI = 0.757). Modified from Bell and Polcyn (2005:fig. 7). **B**, the Mosasaurinae as depicted in the Nelsen concensus tree of three equally most parsimonious trees of 212 steps (CI = 0.44, RI = 0.76) from Christiansen and Bonde (2002) using 80 cranial characters and 33 taxa. Modified from Christiansen and Bonde (2002:fig. 7).

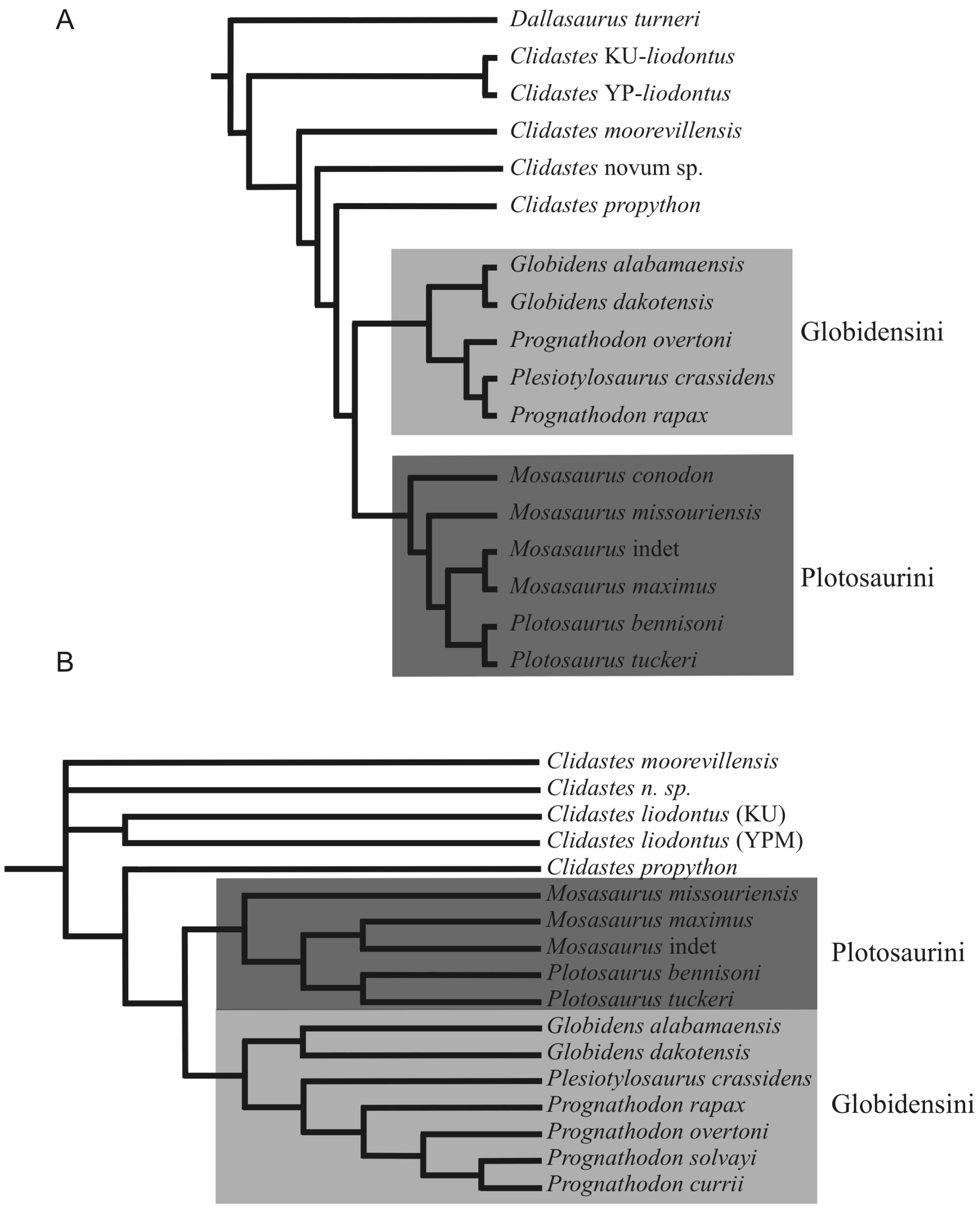
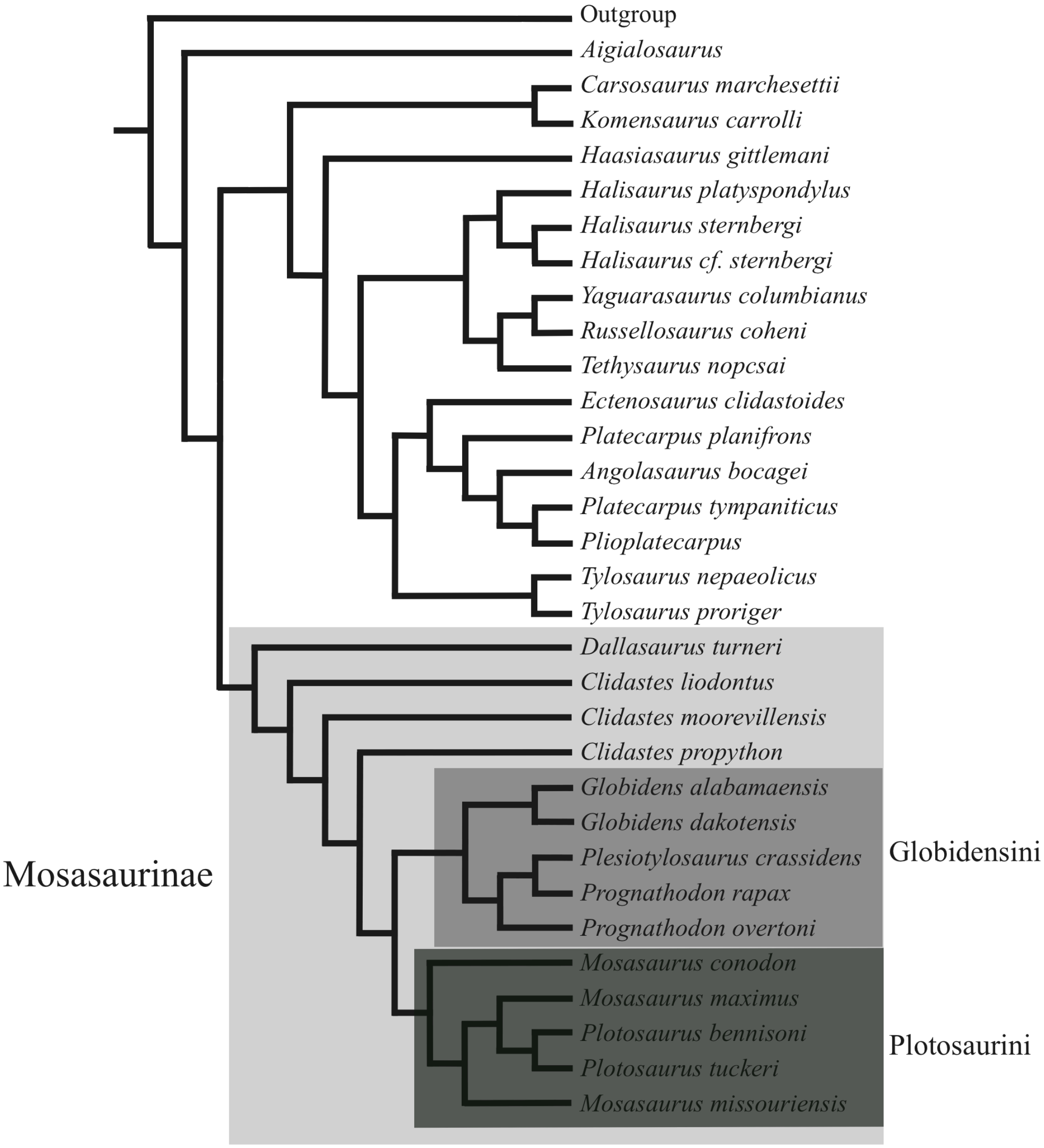

A
Dallasaurus turneri
Clidastes KU-liodontus
Clidastes YP-liodontus
Clidastes moorevillensis
Clidastes novum sp.
Clidastes propython
Globidens alabamaensis
Globidens dakotensis
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Globidensini
Mosasaurus conodon
Mosasaurus missouriensis
Mosasaurus indet
Mosasaurus maximus
Plotosaurus bennisoni
Plotosaurus tuckeri
Plotosaurini
B
Clidastes moorevillensis
Clidastes n. sp.
Clidastes liodontus (KU)
Clidastes liodontus (YPM)
Clidastes propython
Mosasaurus missouriensis
Mosasaurus maximus
Mosasaurus indet
Plotosaurus bennisoni
Plotosaurus tuckeri
Plotosaurini
Globidens alabamaensis
Globidens dakotensis
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Prognathodon solvayi
Prognathodon currii
Globidensini

FIGURE 1–2. The preferred topology of Caldwell and Palci (2007) after deleting or modifying several characters (8, 15, 53-55, 57-60 and 62) from Bell and Polcyn (2005) and reducing the number of terminal taxa to 31 (CI = 0.48, RI = 0.73, TL = 351). Modified from Caldwell and Palci (2007:fig. 8b).


Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Halisaurus platyspondylus
Halisaurus sternbergi
Halisaurus cf. sternbergi
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
Ectenosaurus clidastoides
Platecarpus planifrons
Angolasaurus bocagei
Platecarpus tympaniticus
Plioplatecarpus
Tylosaurus nepaeolicus
Tylosaurus proriger
Dallasaurus turneri
Clidastes liodontus
Clidastes moorevillensis
Clidastes propython
Globidens alabamaensis
Globidens dakotensis
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Mosasaurus conodon
Mosasaurus maximus
Plotosaurus bennisoni
Plotosaurus tuckeri
Mosasaurus missouriensis
Mosasaurinae
Globidensini
Plotosaurini

LITERATURE CITED

Bell, G. L., Jr. 1993. A phylogenetic revision of North American and Adriatic Mosasauroidea (Squamata). Unpublished Ph.D thesis, University of Texas at Austin, 293 pp.

Bell, G. L., Jr. 1997. Chapter 11. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293–332 in J. M. Callaway, and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bell, G. L., Jr., and M. J. Polcyn. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). Netherlands Journal of Geosciences 84:177–194.

Caldwell, M. W., and A. Palci. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. Journal of Vertebrate Paleontology 27:863–880.

Caldwell, M. W., T. Konishi, I. Obata, and K. Muramoto. A new species of *Taniwhasaurus* (Mosasauridae, Tylosaurinae) from the Upper Santonian-Lower Campanian (Upper Cretaceous) of Hokkaido, Japan. Journal of Vertebrate Paleontology 28:339–348.

Callison, G. 1967. Intracranial mobility in Kansas mosasaurs. The University of Kansas Paleontological Contributions 26:1–15.

Camp, C. L. 1942. California Mosasaurs. Memoirs of the University of California 13:1–68.

Camp, C. L. 1951. *Plotosaurus*, a new generic name for *Kolposaurus* Camp, preoccupied. Journal of Paleontology 25:822.

Carroll, R. L., and M. DeBraga. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. Journal of Vertebrate Paleontology 12:66–86.

Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22:629–644.

Dortangs, R. W., A. S. Schulp, E. W. A. Mulder, J. W. M. Jagt, Peeters, H. H. G., de Graaf, D. Th. 2002. A large new mosasaur from the Upper Cretaceous of the Netherlands. Netherlands Journal of Geosciences 81:1–8.

Dutchak, A. R., and M. W. Caldwell. 2006. Redescription of *Aigialosaurus dalmaticus* Kramberger, 1892, a Cenomanian mosasauroid lizard from Hvar Island, Croatia. Canadian Journal of Earth Sciences 43:1821–1834.

Dutchak, A. R., and M. W. Caldwell. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. Journal of Vertebrate Paleontology 29:437–452.

Fernandez, M. S., and J. E. Martin. 2009. Description and phylogenetic relationships of *Taniwhasaurus antarcticus* (Mosasauridae, Tylosaurinae) from the upper Campanian (Cretaceous) of Antarctica. Cretaceous Research 30:717–726.

Gaudry, A. 1892. Les pythonomorphes de France. Mémoires de la Société Géologique de France (Paléontologie) 10: 13 + iv pp.

Goldfuss, A. 1845. Der Schädelbau des *Mosasaurus*, durch Beschreibung einer neuen Art dieser Gattung erläutert. Nova Acta Academiae Caesar Leopoldino-Carolinae Germanicae Natura Curiosorum 21:173–200.

Lindgren, J., J. W. M. Jagt, and M. W. Caldwell. 2007. A fishy mosasaur—the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. Lethaia 40:153–160.

Lindgren, J., M. W. Caldwell, and J. W. M. Jagt. 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). Journal of Vertebrate Paleontology 28:1043–1054.

Lindgren, J., and A. S. Schulp. 2010. New material of *Prognathodon* (Squamata: Mosasauridae), and the mosasaur assemblage of the Maastrichtian of California, U.S.A. Journal of Vertebrate Paleontology 30:1632–1636.

Lingham-Soliar, T., and D. Nolf. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 59:137–190.

Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, upper Maastrichtian of the Netherlands.

Philosophical Transactions of the Royal Society of London B347:155–180.

Lingham-Soliar, T., and D. Nolf. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 59:137–190.

Mulder, E. W. A. 1999. Transatlantic latest Cretaceous mosasaurs (Reptilia, Lacertilia) from the Maastrichtian type area and New Jersey. Geologie en Mijnbouw 78:281–300.

Russell, D. A. 1964. Intracranial mobility in mosasaurs. Peabody Museum of Natural History, Yale University, Postilla 86:1–19.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs (Reptilia, Sauria). Peabody Museum of Natural History, Yale University, Bulletin 23:1–241.

Schulp, A. S. 2005. Feeding the mechanical mosasaur: what did *Carinodens* eat? Netherlands Journal of Geosciences 84:345–357.

Schulp, A. S. 2006. A comparative description of *Prognathodon saturator* (Mosasauridae, Squamata), with notes on its phylogeny; pp. 19–56 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. L. Jacobs, M. L. Morais, and T. da S. Tavares. 2006. New mosasaur material from the Maastrichtian of Angola, with notes on the phylogeny, distribution and palaeoecology of the genus *Prognathodon*: pp. 57–67 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. J. Jacobs, and M. L. Morais. 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon* in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:1–12.

CHAPTER TWO

A NEW MOSASAURINE FROM THE MAASTRICHTIAN (U. CRETACEOUS) PHOSPHATES OF MOROCCO AND THE IMPLICATIONS FOR THE SYSTEMATICS OF THE MOSASAURINA[1]

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INTRODUCTION

Mosasaurs were a diverse and successful group of secondarily marine lizards that achieved a global distribution in the world's oceans and seas during the Late Cretaceous (Russell, 1967). Their dietary specializations, particularly during the Maastrichtian, illustrate their success as apex predators in marine habitats (Lindgren et al., 2007; Bardet et al., 2008). During the Late Cretaceous, the western regions of Morocco were flooded by the expanding Atlantic Ocean during global eustatic sea level rise that led to a number of recognized local, transgressive events (Gheerbrant et al., 2003; Noubhani, 2010). The relatively shallow and warm waters marked the southern extent of the Tethys Sea and the Cretaceous Tethyan Phosphogenic Zone, forming a platform margin rich in organic matter (Gheerbrant et al., 2003; Noubhani, 2010). Presumed upwellings and great quantities of organic matter resulted in a high level of productivity that has been linked to extensive phosphate sedimentation, particularly in the west of Morocco (Gheerbrant et al., 2003; Bardet et al., 2010; Noubhani, 2010). Within these phosphate deposits, large numbers of marine reptile fossils have been recovered, the most abundant of which are the remains of mosasaurs (Arambourg, 1952; Bardet et al., 2004; 2005a; 2005b; 2008; 2010).

In this study we describe a new mosasaur from the Maastrichtian phosphates of the Oulad Abdoun Basin in Morocco. The holotype is represented by two syntypes (article 73.2 of the ICZN) that are: 1) a nearly complete skeleton

(UALVP 51744) including a complete skull, a nearly complete vertebral column, portions of the pectoral and pelvic girdles and isolated hind limb elements; and 2) a complementary skeleton (OCP DEK/GE 112) including an almost complete skull and most of the vertebral column. As OCP DEK/GE 112 is currently under final mechanical preparation, only UALVP 51744 is described here, while OCP DEK/GE 112 will be the subject of a paper by Bardet, LeBlanc, Caldwell et al. The anatomy of this unique mosasaur not only adds to the current knowledge regarding the diversity and degree of dietary specializations mosasaurs exhibited during the Maastrichtian in Morocco, but also provides insight into the interrelationships of two major groups of mosasaurines: the Plotosaurini Russell, 1967, and the Globidensini Russell, 1967.

GEOLOGICAL CONTEXT

Commercially viable concentrations of phosphates in Morocco have been known since 1917, and have been extensively mapped for mining purposes since the foundation of the Office Chérifien des Phosphates (OCP) in 1920 (Bardet et al., 2010). The phosphates of Morocco are part of the much larger Mediterranean Tethyan Phosphogenic Province, which extends from the Pernambuco Province of Brazil through North Africa and into the Middle East (Christiansen and Bonde, 2002; Bardet et al., 2008; Bardet et al., 2010). The phosphate successions of Morocco, however, span the largest interval of any of these occurrences, from Maastrichtian (Late Cretaceous) to Lutetian (Middle Eocene) times with apparent continuity (Bardet et al., 2010; Noubhani, 2010). The phosphate successions in the region are exposed along five main basins across northern and central Morocco. From northeast to southwest, these are the Oulad Abdoun, Ganntour, Meskala, Sous and Oued Eddahab basins (Bardet et al., 2010; Noubhani, 2010). Of these, the 1700 km^2 Ganntour Basin, situated North of Marrakech and the 9000 km^2 Oulad Abdoun Basin, Southeast of Casablanca (Fig. 2–1A), are the two most productive areas for industrial mining, possessing abundant exposures of soft, unconsolidated phosphorite (Noubhani, 2010).

Accurate dating of the Moroccan phosphate deposits has been problematic since Arambourg's first attempt at using vertebrate biostratigraphic markers in 1952 (Bardet et al., 2010). A lack of invertebrate and floral biostratigraphic markers from the Oulad Abdoun Basin and lateral facies heterogeneity make the use of vertebrate remains the most reliable option for correlation within, and across, adjacent basins (Arambourg, 1952; Bardet et al., 2010). Informal names for the soft and hard phosphatic layers have been given to the horizons that are exploited in the Oulad Abdoun Basin, all of which bear the name 'Couche' (= bed) with roman numerals (CIII, Maastrichtian to CI, Ypresian), based on their stratigraphic positions and vertebrate fossil content (see Bardet et al., 2005b; 2010).

The Maastrichtian phosphate deposits of the Oulad Abdoun Basin, particularly in the Sidi Daoui area near the city of Oued Zem (Fig. 2–1B), are condensed to a 2-5 meter thick Lower and Upper Couche III directly underlying Danian strata (Bardet et al., 2008). Here, Couche III is divided into a basal bonebed (BBB), a lower grey phosphatic layer (Lower Couche III = LCIII) and a highly fossiliferous upper yellow phosphatic layer (Upper Couche III = UCIII) (Fig. 2–1C). These horizons are late, but not latest, Maastrichtian in age, according to their selachian fauna (Cappetta, 1987). Couche III is known for its abundance of vertebrate remains, particularly isolated teeth of mosasaurids and several fairly complete and articulated mosasaurid specimens (Arambourg, 1952; Bardet et al., 2010). Isolated teeth of the selachians *Cretolamna maroccana* Arambourg, 1935, *Schizorhiza stromeri* Weiler, 1930, and *Rhombodus binkhorsti* Dames, 1881, were recovered from the matrix surrounding UALVP 51744 (A. LeBlanc, pers. obs.). The occurrence of these taxa is indicative of a provenance from Couche III of the phosphatic series. More specifically, the soft, yellow, phosphatic sand is most similar to Upper Couche III of the phosphatic successions of the Oulad Abdoun Basin (N. Bardet, pers. obs.), which is upper Maastrichtian. Similarly, OCP DEK/GE 112 was recovered the Upper Couche III of the Sidi Daoui area (N. Bardet, pers. obs.) and supports a Maastrichtian age for *E. heterodontus* (Arambourg, 1952; Cappetta, 1987).

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

MOSASAURIDAE Gervais, 1853

MOSASAURINAE Gervais, 1853

EREMIASAURUS gen. nov.

Type Species—*Eremiasaurus heterodontus*, sp. nov.

Etymology—From the Greek *eremia* (masc., desert) and *sauros* (masc., lizard), referring to the arid climate in present day Morocco where this marine reptile was recovered.

Diagnosis—As for type and only species.

EREMIASAURUS HETERODONTUS, sp. nov.

(Figs. 2–7)

Etymology—From the Greek *heteros*- (different) and *odontos* (tooth), referring to the dramatic change in tooth shape between anterior, middle and posterior marginal dentition as well as in the pterygoid tooth row.

Syntypes—UALVP 51744: skull, vertebral column, isolated ribs, left scapula, coracoid and humerus, left and right ischia and ilia, femur, tibia, fibula, isolated tarsal, metatarsal and phalangeal elements; OCP DEK/GE 112: skull and nearly complete vertebral column.

Type Locality—Upper Couche III (upper Maastrichtian) of Sidi Daoui area, Oulad Abdoun Basin, Morocco.

Diagnosis—Apomorphies of taxon: pterygoid teeth become increasingly curved posteriorly; pronounced heterodonty, anterior marginal teeth straight and conical, middle dentition composed of laterally compressed blade-like teeth with anterior and posterior serrated carinae, posterior teeth asymmetrically expanded anteriorly, producing highly convex anterior surfaces in lateral view; tooth enamel surfaces smooth; upper and lower teeth interdigitate tightly in anterior region of the snout, leaving interdental pitting of the bone between adjacent tooth crowns; interdental spaces decrease posteriorly in maxillae and dentaries; pygal series long, composed of 20 pygal vertebrae; intermediate caudal series short, composed of 10 vertebrae. Differing from *Mosasaurus* and *Plotosaurus* in having: quadrate infrastapedial and suprastapedial processes fused; pterygoid teeth large, approaching size of middle marginal dentition; glenoid condyle of humerus gently domed; phalangeal elements long and thin, with only moderately expanded epiphyses. Differing from *Prognathodon* and *Plesiotylosaurus* in having: premaxilla internarial bar with dorsal keel; large frontal narial embayments; prefrontals excluded from border of external nares; surangular articular lateral sutural trace straight; retroarticular process inflected almost 90 degrees; quadrate ala thin, with groove along lateral alar rim.

DESCRIPTION AND COMPARISONS

General

UALVP 51744 consists of a well-preserved skull, a nearly complete vertebral column, and several of the hind and forelimb elements, all preserved in a series of eight blocks (Fig. 2). The total length of the skeleton is approximately 4.5 meters; however the absence of several dorsal vertebrae suggests the body length was closer to five meters. The total skull length measured from the tip of the premaxillary rostrum to the posterior corner of the right squamosal is 63.5 cm. Using the body size estimation method outlined by Christiansen and Bonde (2002), which incorporates proportions of the skull relative to the total body length, the estimated total length of *E. heterodontus* is between 4.5 and 5.5 meters. The skull has been crushed so that the snout curves to the right side, which has resulted in the bulk of the cranial elements being disarticulated and broken apart on the left side of the skull. The right side, however, is better preserved. The vertebral column is rotated at several points, preserving vertebrae in various views. The anterior and mid-dorsal vertebrae are preserved with their ventral surfaces exposed, while the posterior dorsal and pygal vertebrae are preserved in dorsal view. The vertebrae of the caudal series are all preserved in lateral view. Portions of the appendicular skeleton are also preserved in association with the vertebral column. Of the elements of the pectoral girdle and forelimb, the left scapula, proximal portion of the coracoid, and most of the humerus are present. Both of the pelvic girdles, as well as portions of the right hind limb, are identifiable in UALVP 51744.

Skull and Mandible

Premaxilla—The premaxilla is preserved in close to natural position, although it has rotated slightly towards the right, making the outline of the premaxillo-maxillary suture difficult to trace on the left side (Fig. 2–3A, B). The premaxillary rostrum is short and conical in dorsal view, and extends anteriorly by less than the length of an alveolar space. The dorsal surface of the dentigerous portion of the premaxilla is gently convex and has a low, rounded mid-dorsal keel similar to those in *Mosasaurus* Conybeare, 1822, *Plotosaurus* Camp, 1951, and *Prognathodon kianda* Schulp et al., 2008. It is flanked on either side by several small neurovascular foramina (Camp, 1942; Lingham-Soliar, 1995; Schulp, 2008). The outline of the dorsal surface of the premaxilla is narrow and pointed anteriorly, similar to *Mosasaurus* and *Plesiotylosaurus* Camp, 1942, although there is no long extension of the edentulous rostrum as there is in the latter genus (Lingham-Soliar, 1995; Lindgren, 2009). Parts of the left posterior and right anterior premaxillary teeth are preserved; they are straight and conical with smooth enamel surfaces. Both of these crowns have been displaced slightly and are directed further laterally than they would have been in life (Fig. 2–3A, B). Based on the presence of a small pit anterior to the first dentary tooth on either side of the dentary, as well as the position of the first premaxillary alveolus, it can be inferred that the premaxillary teeth did not protrude anteriorly, but instead pointed straight ventrally. The anterior-most portion of the maxilla has been displaced forward and obscures the premaxillary-maxillary suture on the left side (Fig. 2–3A, B). The left premaxillary teeth and first maxillary tooth have shifted one tooth position posteriorly relative to the dentary. This gives the appearance of a dentary that protrudes further than the premaxilla and gives a short and steep profile to the premaxillary-maxillary suture, the latter being a characteristic of the genus *Prognathodon* (Schulp, 2006). This suture is instead best viewed from the right side. The suture extends posterodorsally from the ventral border of the premaxilla at a shallow angle (Figs. 2–4A, B, 2–5), creating a low and slender lateral maxillary profile similar to *Mosasaurus* (Lingham-Soliar, 1995). The suture terminates posteriorly at a point just anterior to the midline of the fourth maxillary tooth, and is relatively longer than in most species of *Prognathodon* and much shorter than in *Mosasaurus* and *Plesiotylosaurus* (Camp, 1942; Russell, 1967; Schulp, 2006; Lindgren, 2009). Posterior to the premaxillo-maxillary suture terminus, the internarial bar is laterally constricted and has a prominent median dorsal keel extending along the posterior half (Fig. 2–3A, B). The internarial bar is triangular in cross-section.

Maxilla—The maxilla is long and slender. At the posterior terminus of the premaxillary-maxillary suture, the depth of the maxilla is 5.8 cm and the length from this point to the anterior border of the maxilla is 9.6 cm. Nutritive foramina line the lateral surface of the maxilla and become larger posteriorly. These foramina are situated approximately 2 cm dorsal to the maxillary tooth row. A second row of smaller and more sparsely distributed foramina lines the dorsolateral surface of the maxilla. At a point above the tenth maxillary tooth, a projection of the maxilla extends posterodorsally to overlap the prefrontal (Figs. 2–4A, 2–5). Although these processes are badly crushed on both sides, the extent of the overlap of the maxillae over the prefrontals can be inferred based on the presence of a distinct groove along the anterodorsal border of the right prefrontal. This groove marks the contact with the posterodorsal wing of the right maxilla and suggests that this process overlapped the prefrontal so that the prefrontal was excluded from the external narial opening in dorsal view. The exclusion of the prefrontal from the posterolateral border of the external naris is also seen in *Plotosaurus*, *Ectenosaurus* Russell, 1967, and *Tylosaurus* Marsh, 1872, (Camp, 1942; Russell, 1967). The maxilla does not extend posterior to the last maxillary tooth, above which is situated the contact with the horizontal ramus of the jugal.

The left and right maxillae each preserve 13 tooth positions. The anterior three teeth resemble those of the premaxilla and are long, straight and conical, teardrop-shaped to round in cross section, and possess only anterior serrated carinae. These teeth interdigitate with those from the dentary and are accommodated in small pits between adjacent dentary teeth when the jaws are closed (Fig. 2–4A, B). This interdental pitting is also found along the dental margin of the maxilla. This pitting is also seen in *Goronyosaurus* Azzaroli et al., 1972, where the pits are much deeper and persist further down the length of the jaws (Lingham-Soliar, 1991). They also occur in *Mosasaurus hoffmanni* Mantell, 1829 (A. LeBlanc, pers. obs.), *M. lemonnieri* Dollo, 1894, (A. LeBlanc, pers. obs.) and '*Liodon*' *mosasauroides* Gaudry, 1892, (A. LeBlanc pers. obs.), although the interdental pits generally disappear posterior to the fifth dentary tooth in these taxa. The fourth to ninth maxillary teeth become progressively more laterally compressed and are slightly curved (Figs. 2–3, 2–4). These crowns are blade-like, bicarinate with a 180-degree intercarinal angle, and are much longer anteroposteriorly than in the anterior dentition. The enamel surfaces are smooth with faint traces of facets extending up to two-thirds the height of a given tooth crown. Additionally, the anteroposterior expansion of the tooth crown leaves little room between adjacent teeth, and, by the seventh maxillary tooth, the interdental pits are absent. At this point, the maxillary and dentary teeth no longer interdigitate, but shear past one another such that the maxillary teeth conceal the lower teeth in lateral view when the jaws are closed (Figs. 2–3, 2–4). The tenth to thirteenth maxillary teeth are also bicarinate, but exhibit much less lateral compression and are also asymmetrically expanded anteriorly. As a result, the anterior surfaces of these teeth are convex in lateral view. These crowns are also flared at their bases and have smooth enamel surfaces.

Jugal—Both jugals are preserved; however the vertical rami of both elements are concealed by other bone fragments. The right jugal is the most complete and exhibits a long horizontal ramus (Fig. 2–4A). A small posteroventral process is present at the junction between the horizontal and vertical rami. The two rami of the jugal diverge at about a 90-degree angle.

Pterygoid—The pterygoids are not visible, but a row of pterygoid teeth is exposed between the left and right splenials (Fig. 2–4C). The row consists of five teeth and one isolated, but associated pterygoid tooth. The isolated tooth belongs to the same pterygoid tooth row, based on identical curvature of the crowns. The pterygoid teeth are long, approaching the sizes of the posterior marginal teeth, but are significantly smaller than the middle marginal crowns. The anterior two teeth are slender, straight and conical, while the last three become progressively smaller and more curved. The isolated pterygoid tooth is smaller than the marginal dentition, has an expanded base of the crown and is curved posteromedially. The marked degree of heterodonty in the pterygoid dentition reflects similar changes in the marginal teeth, where the crowns become smaller, more bulbous and curved further posteriorly. Additionally, the cross-sectional areas of the pterygoid tooth bases in *E. heterodontus* do not become any larger anteriorly, contrary to what would be expected for any species of *Prognathodon* (Lingham-Soliar and Nolf, 1989; Schulp, 2006; Schulp et al., 2008).

Prefrontal—Both prefrontals are preserved near their natural positions. The prefrontal is a robust bone that forms the anterodorsal border of the orbit. The lateral surface of the prefrontal is concave and possesses a broad, flat dorsal surface for contact with the overlapping frontal and maxilla. A large and rounded triangular supraorbital process extends from the posterodorsal surface of the prefrontal (Figs. 2–3A, 2–4A), similar to other members of the Mosasaurinae (Russell, 1967). The extent of the contact of the prefrontal with the postorbitofrontal is difficult to determine, because the left postorbitofrontal has been lost. It seems likely that there was contact between these two elements however, because the right postorbitofrontal is still situated near the posterior end of the prefrontal (Fig. 2–4). This condition is most similar to *Mosasaurus missouriensis* Harlan, 1834, and *M. lemonnieri* Dollo, 1889, where the contact between the postorbitofrontal and the prefrontal is minimal, but enough to exclude the frontal from the dorsolateral border of the orbit (Fig. 2–5).

Postorbitofrontal—Only the right postorbitofrontal is identifiable. The dorsal surface of the element is well exposed due to displacement of the overlying frontal (Fig. 2–4A). Matrix and fragments of the parietal and frontal conceal the medial process of the postorbitofrontal. Faint traces of a gently curving border along the anterodorsal surface of the element represent the contact with the frontal, placing the postorbitofrontal in contact with the posterior-most extensions of the prefrontal. The dorsal surface of the postorbitofrontal forms a triangle, with the lateral point of the bone being the small, posterolaterally directed ventral process, which would have contacted the jugal. Although only the anterior portion of the squamosal ramus is intact, the postorbitofrontal must have extended to the posterior end of the temporal arcade (Fig. 2–4A, B).

Frontal—The dorsal surface of the frontal has broken into three fragments and is damaged along the fronto-parietal suture, concealing the position and size of the parietal foramen (Fig. 2–3A). The width of the frontal is also difficult to determine. In dorsal view, the frontal would have been triangular to sub-rectangular and slightly anteroposteriorly longer anteroposteriorly than it is wide. The anterolateral process encircling the external narial opening has been broken. The left anterolateral process has been pushed underneath the main body of the frontal and would have bordered a significant portion of the posterior end of the external naris (Fig. 2–3A), similar to the state in *Plotosaurus* (Camp, 1942). The anterior extent of the anteromedial process of the frontal is difficult to determine. A low and rounded median dorsal keel extends from the anterior end of the frontal to approximately its mid-length.

The lateral border of the frontal is preserved on the right side (Fig. 2–4A). The lateral border is straight, with no signs of a supraorbital expansion sensu Bell (1997), and extends straight posteriorly from the anterolateral process of the frontal to the frontal ala, which forms the posterolateral corner of the bone. The frontal ala is broad, rounded and projects laterally. The posterior portion of the frontal is best preserved on the left side, but is still fragmentary. Medial to the frontal ala, the posterior border of the frontal extends further posteriorly and forms a median sutural flange, which overlaps the anterior surface of the parietal table. The posterior extent of this flange is difficult to determine, because the borders of the parietal foramen are not visible.

Parietal—The parietal is highly fragmented and distorted. Portions of the postorbital processes of the parietal are only preserved on the left side of the skull (Fig. 2–3A). Without the preservation of the pineal foramen, it is difficult to determine the posterior extent of the left overlapping flange of the parietal or its proximity to the lateral border of the foramen. Posteriorly, the parietal table has been pushed underneath the postorbital process. The parietal table is narrow and rectangular in dorsal view, with two parallel ridges running along the dorsolateral edges. Posteriorly, the parietal rami diverge at less than a 90-degree angle and become dorsoventrally compressed further distally. Unfortunately, many elements of the temporal arcade have been thrust on top of the suspensorial rami, concealing the nature of their contact with the supratemporal.

Squamosal—Only the right squamosal is readily identifiable (Fig. 2–4A). It is preserved close to its natural position. A thin, deep groove in the dorsal surface of the element marks the posterior extent of the postorbitofrontal. Posterior to this groove, the squamosal expands mediolaterally and possesses a broad, flat medial face for contact with the supratemporal, which is poorly preserved. The posteroventral surface of the squamosal is concave and articulates with the distal end of the suprastapedial process of the quadrate.

Supratemporal—Only the distal tip of the right supratemporal is identifiable. It is preserved in contact with the most distal portion of the quadrate suprastapedial process (Figs. 2–4A, 2–5). This portion of the supratemporal extends further posteriorly along the dorsal surface of the quadrate than the squamosal and wraps around the distal tip of the suprastapedial process to brace it posteriorly.

Quadrate—The ventral half of the left quadrate is preserved in anterior view. The mandibular condyle is wider mediolaterally than long anteroposteriorly, and is gently domed (Fig. 2–3A). A small anterior extension of the articular surface for the mandibular condyle is present on the anteroventral surface of the quadrate. The right quadrate is more complete and is preserved in lateral view, close to natural position (Figs. 2–4A, 2–5, 2–6). The dorsoventral height of the quadrate shaft is approximately 12 cm, exceeding the mediolateral width of the mandibular condyle. Halfway up the length of the quadrate shaft, a large pedestal-like infrastapedial process extends posterodorsally from the main shaft at an acute angle (Figs. 2–5, 2–6A, B). The infrastapedial process originates high on the quadrate shaft when compared to other species with large pedestal-like infrastapedial processes. The ventral portion of the quadrate is therefore elongate between the base of the infrastapedial process and the mandibular condyle, similar to *Plesiotylosaurus* and *Prognathodon saturator* Dortangs et al., 2002, (Konishi, 2008; Lindgren, 2009), but differing markedly from the stout dimensions of the quadrates of most other species of *Prognathodon* (Russell, 1967; Lingham-Soliar and Nolf, 1989; Schulp et al., 2008). This large process contacts the distal tip of the descending suprastapedial process and the two were fused. The two processes enclose the quadrate meatus in a similar fashion to that seen in *Prognathodon*, where the site of contact is a broad and flat plate formed by expanded distal portions of the infrastapedial and suprastapedial processes (Schulp, 2006; Konishi, 2008). The tympanic notch is relatively small.

The posterior surface of the suprastapedial process is exposed adjacent to the contact with the supratemporal. This surface bears an elliptical fossa, which was likely a point of insertion for the *M. depressor mandibulae* (Fig. 2–6A; Russell, 1967). Fragments from the main shaft of the quadrate conceal any traces of the ascending alar crest on the posterolateral surface of the quadrate below the infrastapedial process. Several segments of the ala are still preserved in contact with the shaft and show that the ala extended ventrally to the border of the mandibular condyle and dorsally to the dorsolateral border of the suprastapedial process. Two fragments preserve the natural lateral border of the quadrate ala. A distinct groove is present throughout the length of this border as in *Plotosaurus* and *Mosasaurus* (Figs. 2–5, 2–6C; Camp, 1942; Russell, 1967).

Basioccipital and Basisphenoid—The left basioccipital tuber and the left half of the occipital condyle are preserved. The posterior-most extension of the basisphenoid encircles the basioccipital tuber ventrolaterally (Fig. 2–3A). The basioccipital tuber projects ventrolaterally and is long.

Dentary—Both dentaries are well preserved and each possesses fifteen teeth. The pattern of heterodonty in the lower dentition mirrors that of the premaxilla and maxillae. The first five teeth are straight and conical and each has only a single serrated anterior carina. The sixth to ninth teeth are more laterally compressed and blade-like, and each has a serrated carina on the anterior and posterior borders of the tooth. These tooth crowns are also more convex along their lingual surfaces than along their labial sides. The tenth to fifteenth teeth are more bulbous and curved, and still possess two carinae with an intercarinal angle of 180 degrees. There are small depressions along the dental margin between adjacent teeth, which disappear posterior to the eighth dentary tooth position (Figs. 2–3, 2–4, 2–5).

The lower jaws are slender in comparison to the sizes of the teeth housed along the dentary. The anterior seven tooth crowns are nearly as tall as the dentary is deep, but this ratio becomes much lower as the tooth crowns become smaller posteriorly and the dentary becomes deeper. The dorsal margin of the dentary is slightly convex in lateral view. This convexity is not as pronounced as in most species of *Prognathodon* (Lingham-Soliar and Nolf, 1989; Schulp, 2006) and is instead more similar to that in *Mosasaurus* (e.g. IRSNB R1224) and *Prognathodon kianda* (Schulp et al., 2008). Anterior to the first tooth position a small projection of the dentary extends anteriorly as far as the tip of the premaxillary rostrum. At its anterior tip, the dentary possesses a small depression anterior to the first dentary tooth, which housed the tip of the first premaxillary tooth. A line of large neurovascular foramina extends the length of the lateral surface of the dentary. There is no edentulous space posterior to the last dentary tooth, and there is no posterior indentation in the lateral surface of the dentary as there are in *Prognathodon*.

Coronoid—The right coronoid is virtually complete and is preserved in contact with the surangular (Fig. 2–4). The coronoid is a large element that straddles an anteriorly ascending coronoid buttress of the surangular. The anterior end of the coronoid contacts the posterodorsal extremity of the dentary, as the tip of the coronoid is situated close to the last dentary tooth on both sides (Fig. 2–5). The anterolateral wing of the coronoid has a smooth anterior margin, and lacks a distinct notch surrounding the surangular foramen as in *Prognathodon* or *Mosasaurus*. The coronoid bears a large vertically oriented posterior process, which gives the dorsal margin of the bone a nearly 90-degree angle between the horizontal anterior end and the vertical posterior wing (Fig. 2–4A, B). This elaboration of the posterior process is similar to that seen in *Mosasaurus* and *Prognathodon* (Russell, 1967) and contributes to a deep lateral profile to the posterior mandibular unit. The posterior wing of the coronoid is well developed. Based on the exposed sections of the medial wing of the left coronoid, it can be assumed that the descending medial portion of the coronoid was extensive, although the presence of contact with the angular cannot be determined.

Splenial—The left and right splenials are preserved along the posteroventral margins of the dentaries. The posteromedial surface of the left splenial is visible on the right side of the skull (Fig. 2–4A). The left splenial is still in close contact with the angular, while the right splenial and angular have separated, exposing the concave articular surface on the posterior end of the splenial. Both splenials are exposed in lateral view along the posterior one-third of the length of the dentaries, roughly to a point ventral to the eleventh dentary teeth.

The concave articulations with the angular are elliptical in cross-section with the long axis oriented dorsoventrally.

Angular—The angulars are exposed along the ventrolateral border of the post-dentary complex. The right angular is only visible in lateral view and appears to have undergone significant remodeling as a result of pathology, possibly associated with similar damage to the right surangular (Fig. 2–4A, B). The left angular is fragmented in lateral view, but the medial surface of the bone is visible from the right side. The medial wall of the angular rises steeply behind its convex anterior surface, which articulates with the splenial. Most of the medial surface of the angular is concealed by the right surangular, however, and the presence or absence of contact between the medial wing of the coronoid and the ascending medial process of the angular cannot be determined.

Surangular—Tracing the dorsal border of the surangular anteriorly from the glenoid, a thin, high wall of the surangular rises steeply to form the coronoid buttress, which is straddled by the posterior wing of the coronoid (Fig. 2–4A, B). The relative size of the coronoid buttress is most similar to the states in *Mosasaurus*, *Plotosaurus* and *Prognathodon* (Camp, 1942; Russell, 1967). This large dorsal expansion of the surangular gives the postdentary complex a deep, triangular outline in lateral view. The surangular-articular suture extends posteriorly from the glenoid fossa, and then descends along the ventral margin of the postdentary complex before being concealed from view on both sides of the skull. Along the anteroventral corner of the surangular on the right side, there are three punctures. All have rounded edges, which indicate some degree of healing and remodeling of the bone tissue (Fig. 2–4B). The posterior-most puncture is 3.2 cm wide, followed by two much smaller depressions 4.5 cm farther anteriorly. Ventral to the anterior two excavations lies the right angular, which also appears to have undergone extensive bone remodeling.

Articular—The articulars form broad rectangular extensions of the lower jaws behind the glenoid fossae (Figs. 2–3, 2–4). In lateral view, the left retroarticular process is rotated 90 degrees relative to the orientation of the other postdentary elements. The dorsal surface of the retroarticular process is marked with several neurovascular foramina and is rugose, marking insertions of the abductor musculature of the lower jaws.

Hyoid—A thin rod of bone underneath the right surangular extends anteriorly approximately 20 cm (Fig. 2–4A). At its posterior end, the bone is slightly expanded. This element does not articulate with any portions of the posterior mandibular unit and is interpreted as part of the hyoid apparatus. Portions of the hyoid apparatus are rarely recovered in mosasaurs.

Vertebral Skeleton

Atlas/Axis—Of the four elements of the atlas vertebra, only the left neural arch and the intercentrum are visible (Fig. 2–3A). The atlantal neural arch is preserved in lateral view, exposing only the anterior-most portion of the condylar articulation. A notch in the anterior border of the neural arch separates the condylar articulation surface from the ascending atlas synapophysis. This synapophysis is robust, becoming fan-shaped as it extends further dorsally.

Although the posterior terminus of the atlas is poorly preserved, the base of the posteriorly-directed synapophyseal process is still identifiable. This process was well-developed and would have extended posteroventrally past the articular surface of the atlas centrum. The atlas intercentrum is a stout, prismatic element that forms the ventral border of the condylar articulation (Russell, 1967). It is preserved in lateral view on the left side of the skull. The intercentrum has parallel anterior and posterior borders and a sloped anterior surface for articulation with the occipital condyle.

The axis is preserved in close association with the atlas, but has been distorted and crushed so that only the general outline of the vertebra is identifiable on the left side (Fig. 2–3A). Fragments of bone found ventral to the remains of the axis centrum may represent the axis intercentrum and hypapophyseal peduncle.

Third (C3) to Seventh (C7) Cervical Vertebrae—The third and fourth cervical vertebrae are in the block housing the skull (Figs. 2–3A, 2–4A), while the fifth to seventh cervicals are in the second block, along with the anterior-most dorsal vertebrae (Fig. 2–7 A, B). The third to sixth cervical vertebrae are preserved in lateral view, while the last cervical is preserved in ventral view. All cervicals possess hypapophyses (sensu Russell, 1967), except the seventh, which possesses a ventromedian ridge extending the length of the centrum, terminating posteriorly as a small protuberance. Cervical 3 is the best preserved of the cervicals and possesses large, steeply inclined prezygapophyses for articulation with the axis and a large hypapophysis. The neural spine is tall and straight. C5 and C6 possess large prezygapophyses and tall synapophyses (Fig. 2–7A). The posterior cervical centra are as large as the centra of the anterior dorsal vertebrae. The presence or absence of zygosphenes and zygantra is impossible to verify given the current state of preparation.

Dorsal Vertebrae—The eighth vertebra is the first to lack any trace of a hypapophysis or ventromedian ridge, and is thus interpreted as the first in the dorsal series (Fig. 2–7A). There are 19 articulated and two isolated vertebrae attributable to the dorsal region. The fourth dorsal vertebra is exposed in lateral view. This vertebra retains large prezygapophyses and has synapophyses that do not equal the dorsoventral height of the centrum. The centra of the anterior dorsal vertebrae are longer than they are wide and possess equidimensional anterior and posterior surfaces. The condylar and cotylar surfaces are not inclined in lateral view.

The anterior-most dorsal vertebra from the third block does not have the same orientation as the last vertebra from the second block (Fig. 2–2A, B), suggesting there are vertebrae missing between the fourth and ‘fifth’ dorsal vertebrae. Furthermore, there is a drastic change in the size and number of associated ribs on the third block. Ribs are numerous and large on the second block, whereas the few ribs in the third block are short and slender. These smaller ribs originate posterior to the sternum and true thoracic vertebrae. The same disparity can be seen between blocks four and five, suggesting several vertebrae may be missing from the mid- and posterior dorsal regions as well (Fig. 2–2B). Nevertheless, the posterior dorsal centra remain longer than they are high and wide. The centra of the posterior dorsal vertebrae are also proportionately longer than those of the anterior dorsal vertebrae. Posterior dorsal vertebrae have synapophyses that are directed more ventrolaterally than those from the anterior dorsal series, where they appear to project laterally and even dorsolaterally in the anterior-most dorsal vertebrae.

Pygal Vertebrae—Pygal vertebrae are identified as those centra associated with the sacral region and base of the tail, bearing elongate transverse processes in the place of short and robust synapophyses, while also lacking haemal arches (Russell, 1967). There are twenty pygals (Fig. 2–2B). Few mosasaurs have over ten pygal vertebrae (Russell, 1967) and of these, only *Plotosaurus bennisoni* has a longer pygal series (27-38 sensu Camp, 1942; Lindgren et al., 2007). Although *Mosasaurus conodon* was described as possessing only eight pygal vertebrae (Russell, 1967), Dollo (1892) reported twelve pygals for a fairly complete specimen of *M. lemonnieri*, while Caldwell and Bell (2005) identified a minimum of eleven pygals for *M. missouriensis*. In addition, Lingham-Soliar (1994) reported a specimen of *Plioplatecarpus marshi* with a pygal count of fifteen.

The first in this series has transverse processes closely associated with a deformed and poorly preserved centrum (Fig. 2–2B). Pygal vertebral centra are not as elongate as those from the posterior dorsal series and also possess noticeably shallower condylar and cotylar surfaces. In anterior or posterior view, these centra have sub-triangular articular faces as a result of the extension of the transverse processes from the ventrolateral borders of the centra. Although their anteroposterior lengths are reduced, the pygal centra are still longer than they are tall. In comparison to other mosasaurs with high pygal counts, the ratio of centrum length to centrum height is much higher for *E. heterodontus* than in *Plioplatecarpus marshi* and *Plotosaurus* (Lingham-Soliar, 1994; Lindgren et al., 2007). The dimensions of the pygal centra in *E. heterodontus* most closely resemble those of *Mosasaurus hoffmanni* (e.g. MNHUK 42946) and *Plioplatecarpus primaevus* Russell, 1967, where pygal vertebrae are nearly equidimensional in lateral view instead of showing significant posterodorsal compression as they do in *Plioplatecarpus marshi*, *Prognathodon solvayi*, *P. saturator* and *Plotosaurus* (Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1994; Schulp, 2006; Lindgren et al., 2007). The anterior sixteen pygal vertebrae all bear elongate and robust transverse processes, the bases of which comprise nearly 80% of the length of the ventrolateral margin of each associated centrum. The posterior four pygal vertebrae are smaller and have short and slender transverse processes with thinner bases, similar to those of the adjacent intermediate caudal vertebrae. No neural spines are preserved from this series.

Intermediate Caudal Vertebrae—Ten vertebrae retain transverse processes and possess haemal arches (Figs. 2–2B, 2–8), here termed intermediate caudals sensu Russell (1967). The first four intermediate caudals possess transverse processes developed to the same degree as those from the posterior pygal series, but also have paired ventral excavations in the centra for fused haemal arches. The remaining six intermediate caudals have reduced transverse processes and have haemal arches that project posteroventrally at a shallow angle from the centra. The centra of the intermediate caudal vertebrae are equidimensional in lateral view (Fig. 2–8A, B). The neural spines are recumbent in the anterior five vertebrae of this series, are vertical in the proceeding three vertebrae, and procumbent in the posterior two (Fig. 2–8A, B).

Terminal Caudal Vertebrae—The remaining twenty-eight vertebrae lack transverse processes and possess elongate haemal spines. A few vertebrae are missing from the posterior end of the tail, but the majority of the series is preserved. The haemal spines project from the centra at higher angles than those from the intermediate caudal region and are at least 1.5 times longer than their associated neural spines are tall. The orientations of the neural spines shift from procumbent in the anterior seven vertebrae, to vertical in the next two, and finally recumbent in the remainder of the series (Fig. 2–8). This creates a broad, sweeping fan of neural spines similar to that of *Clidastes* Cope, 1868, *Mosasaurus* and *Plotosaurus* (Russell, 1967; Lindgren et al., 2007), interpreted as the root of a dorsal caudal fin (Fig. 2–8C; Lindgren et al., 2007; Lindgren et al., 2010). In the same region of the terminal caudal series, the tail is ventrally deflected, similar to *Plotosaurus* (Fig. 2–8; Lindgren et al., 2007). Lindgren et al. (2007, 2010) demonstrated that the ventral curve of the caudal segment occurs near the anterior end of the terminal caudal series in *Plotosaurus* and *Platecarpus*, where the ratio of dorsal to ventral centrum length is highest. In *Eremiasaurus heterodontus*, the curve begins at the tenth intermediate caudal vertebra and becomes most pronounced in the anterior six terminal caudals (Fig. 2–8). The ratio of dorsal centrum length to ventral centrum length is highest in this region, suggesting that the greatest degree of the tail bend occurs in the anterior portion of the terminal caudal series.

Appendicular Skeleton

Scapula—The left scapula is preserved on the second block. The scapula is in contact with the proximal portion of the coracoid and the humerus (Fig. 2–7A). The scapula and coracoid appear to be tightly sutured anterior to the glenoid fossa. The posterolateral facet forming the dorsal half of the glenoid fossa is approximately equal in size to the adjoining facet on the posterodorsal corner of the coracoid. Posterior to the glenoid fossa, the posterior margin of the scapula extends dorsally before expanding to form the posterior margin of the scapular blade, similar to *Clidastes* (Russell, 1967). Several large thoracic ribs conceal the dorsal margin of the scapular blade from lateral view, obscuring the arc formed by the dorsal edge of the scapula. The anterior border of the scapular blade is fragmented, but the outline of the anterior portion of the scapular blade is straight and horizontal. The lateral face of the scapula is broad, smooth and flat.

Coracoid—The left coracoid is broken away dorsal to the coracoid foramen and thus does not allow for any inference as to the size of the coracoid relative to the scapula (Fig. 2–7A). The coracoid forms a subequal portion of the glenoid fossa, the surface of which is obscured by the glenoid condyle of the humerus. The posterior border of the coracoid is concave in front of the glenoid fossa, suggesting the neck of the coracoid was constricted, similar to *Clidastes* (Russell, 1967).

Humerus—The left humerus is exposed in lateral view (Fig. 2–7A). The proximal end of the humerus is well preserved. A domed glenoid condyle is distinctly separated from a pronounced postglenoid process, which is directed posterodorsally. The postglenoid process does not extend further than the glenoid condyle. The humeral mid-shaft is slightly constricted as in *Clidastes* (Russell, 1967; Bell, 1997). The humerus also resembles that of *Clidastes* in being of subequal height and width. In contrast, the humeri of *Mosasaurus* and *Plotosaurus* are wider than they are high (Bell, 1997). The distal end of the humerus is weathered, resulting in the loss of the radial and ulnar facets as well as the entepicondylar and ectepicondylar processes.

Ilium—The right ilium is preserved in contact with the ischium and the proximal portion of the pubis. The left ilium is preserved as an impression, in close association with the complete left ischium (Fig. 2–2B). Like all mosasaurids, the iliac crest is reduced to an anteriorly sloping cylindrical process (Russell, 1967). The right iliac process is draped over the sixteenth and seventeenth pygal vertebrae, while the remains of the right ilium are preserved adjacent to the anterior six pygal vertebrae (Fig. 2–2B, 2–9A). The distal end of the ilium is expanded and bears anteroventral and posteroventral facets for articulation with the pubis and ischium respectively. Despite being well-preserved, the distal end of the right ilium is rotated such that only the medial surface is exposed, and the shape of the acetabular facet is unknown.

Ischium—The left ischium is the more complete of the two and is preserved in lateral view. The proximal head is weathered and does not preserve the acetabular facet. A prominent, ischiadic tubercle projects from the posterodorsal portion of the shaft of the ischium. This tubercle is separated from the proximal head of the bone by an elongate neck, similar to *Tylosaurus* (Russell, 1967). The distal end of the ischium is more expanded anteromedially than the proximal head. Overall, this gives the impression that the ischium is bowed posteriorly at the mid-point of the shaft. The degree of anteromedial expansion of the distal end of the ischium is most similar to *Tylosaurus* (Russell, 1967). The right ischium remains in contact with the ilium, although only the proximal head of the ischium is preserved. It can be differentiated from the right pubis by a lack of a pubic foramen. The shape of the articular surface of the ischium is not discernable.

Femur—The single, apparently left, femur is preserved in association with a tibia and fibula on the left side of the posterior pygal region (Figs. 2–2B, 2–9A). The femur is an 11.7 cm-long dumbbell-shaped element, with a constricted diaphysis (Fig. 2–9B). The proximodistal length of the femur is more than three times the width of the bone at its most constricted point. The element is more elongate and slender than those of *Plotosaurus* or *Mosasaurus* (Russell, 1967; Lindgren et al., 2008), but bears some resemblance to the femur of *Clidastes liodontus* Merriam, 1894 (Fig. 2–9C; Russell, 1967:fig. 60). The distal end of the femur bears a small, flat fibular facet, which is located anterior to the larger facet for contact with the tibia (Fig. 2–9B). The inverted orientation of these contact surfaces suggests that the femur is preserved in flexor aspect.

Tibia—The left tibia is nearly complete and is preserved in flexor aspect (Figs. 2B, 9A, B). It is a rectangular element, longer proximodistally than anteroposteriorly. The posterior border of the tibial shaft is constricted and concave medially, forming the anterior border of the crural foramen (Fig. 2–9B). The posterior portion of the diaphysis is constricted to a greater extent than in *Clidastes* (Fig. 2–9C; Russell, 1967:fig. 60), but to a lesser degree than in *Mosasaurus lemonnieri* (Fig. 2–9D; pers. obs.). A large anterior flange originates from both the proximal and distal ends to give the tibia its rectangular outline. Dollo (1892:fig. 1–5) figured this flange as originating from the proximal and distal ends of the tibia in *Mosasaurus lemonnieri*. The tibiae of *Plotosaurus* and *Mosasaurus conodon* also show this feature (Russell, 1967; Lindgren et al., 2008), but the flange does not reach the proximal head in either *Tylosaurus* or *Platecarpus* (Russell, 1967). The anterior border of this flange is not emarginated in *E. heterodontus*, similar to *Mosasaurus lemonnieri* and *M. conodon*, but an emargination is present in *Clidastes liodontus* (Fig. 2–9C; Russell, 1967:fig. 60) and possibly *Plotosaurus* (Lindgren et al., 2008:fig. 8a–d, 9). The distal end of the tibia bears two facets, one anterior to the other. The larger anterior facet would have articulated with the first metatarsal, while the smaller posterior facet contacted the astragalus. The anterior facets are concave in *E. heterodontus* and *Mosasaurus* (Fig. 2–9B, D) and convex in *Clidastes* (Fig. 2–9C).

Fibula—The fibula is a bell-shaped element, with the distal end much wider than the proximal end, similar to *Clidastes* (Fig. 2–9B, C; Russell, 1967:fig. 60). In *Plotosaurus* and *Mosasaurus* the distal and proximal ends of the fibula are subequal in width (Russell, 1964; Lindgren et al., 2008). The fibula is about three quarters the length of the tibia. These proportions differ from those of *Tylosaurus* or *Platecarpus*, in each of which the fibula is the same length as the tibia (Russell, 1967).

Tarsals, Metatarsals, Phalanges—Several isolated tarsals, metatarsals and phalanges are scattered about the block containing the other elements of the hind limb (Fig. 2–9A). The largest of the tarsal elements associated with the left hind paddle is interpreted as the astragalus. This element is kidney-shaped, with a pedunculate fibular facet on the dorsal surface. The astragalus formed part of the ventral border of the crural foramen, with a pedestal-like extension for contact with the fibula (Fig. 2–9B). No notch appears to be present along the dorsal border of the astragalus. Other smaller, rounded elements likely represent the calcaneum and the fourth distal tarsal (Fig. 2–9A, B). The isolated phalanges are elongate, spindle-shaped elements with moderately expanded epiphyses (Fig. 2–9A). The proportions of the phalanges are most similar to those of *Prognathodon* (e.g., IRSNB R106) and *Clidastes* (Russell, 1967), and differ from the stout, blocky proportions seen in *Plotosaurus* and *Mosasaurus* (Dollo, 1892; Lindgren et al., 2008).

PHYLOGENETIC ANALYSIS

Dataset Selection

Two phylogenetic analyses were performed to assess the relationships of *E. heterodontus* to other mosasauroid taxa. The need for two analyses stems from disparity among published phylogenies of the Mosasauroidea, their datasets, and the lack of inclusion of more recently described taxa from Europe, the Middle East, and Africa. Concerning the latter point, seminal works of Russell (1967) and Bell (1997) focused almost exclusively on the relationships of North American and some Adriatic mosasauroids. These studies only allow comparison of *E. heterodontus* with mosasaurid taxa that are only known from North America. In order to include additional taxa from Africa and Europe, a standardized character set is required.

Analytical Methods

The data matrix presented in this analysis includes additions to the matrix of Bell and Polcyn (2005) that have been standardized according to the character codings and interpretations of Caldwell and Palci (2007). This was deemed to be the most appropriate way to evaluate the results of the addition of several previously described taxa and *E. heterodontus*, because the topologies generated by Caldwell and Palci (2007) could then be used for meaningful comparisons to the cladograms generated in the present analysis. To that end, the character numbers presented here follow those of Caldwell and Palci (2007), while the character descriptions follow those of Bell (1997) and Bell and Polcyn (2005) (Appendix 1).

Addition of *E. heterodontus* to the Matrix of Caldwell and Palci (2007)

The first analysis involved the addition of *E. heterodontus* into the existing matrix of Caldwell and Palci (2007), which used 135 characters and 31 terminal taxa. *E. heterodontus* was added to this taxon-character matrix and subjected to Parsimony with Heuristic Search algorithm and random addition sequence in PAUP Version 4.0b10 (Swofford, 2002). All characters were unordered and equally weighted.

Results—Three most parsimonious trees were recovered, each having 362 steps (CI = 0.464; RI = 0.728; HI = 0.536). The strict consensus tree (Fig. 2–10A) shows polytomies among *Carsosaurus*, *Komensaurus*, and (*Haasiasaurus* (Halisaurinae + Russellosaurina)) (sensu Bell and Polcyn, 2005), similar to those reported in Caldwell and Palci (2007). Unlike Caldwell and Palci (2007), however, the strict consensus tree provided a monophyletic *Clidastes* that is the sister taxon to the Globidensini (*Globidens*, *Prognathodon* and *Plesiotylosaurus*) and Plotosaurini (*Mosasaurus* and *Plotosaurus* sensu Bell, 1997), both of which were resolved as monophyletic. As reported by other authors (Bell, 1997; Christiansen and Bonde, 2002; Schulp, 2006), the Globidensini are united by having (1) fused infrastapedial and suprastapedial processes of the quadrate, (2) a quadrate posteroventral ascending tympanic rim present as a high, elongate crest, (3) a thick quadrate ala, and (4) coarsely ornamented tooth surfaces. Within the

Globidensini, *Globidens* retains a sister group relationship to a paraphyletic *Prognathodon*, as reported by Bell (1997) and Caldwell and Palci (2007). The clade consisting of *Prognathodon* and *Plesiotylosaurus* is united by four apomorphies: (1) a frontal not invaded by posterior end of the nares, (2) large pterygoid teeth, (3) a laterally compressed splenial-angular joint in posterior view, and (4) a highly domed glenoid condyle. *E. heterodontus* is resolved as the sister taxon to the Plotosaurini sensu Bell (1997). Characters supporting this position include (1) the presence of an internarial bar dorsal keel, (2) a thin quadrate ala, (3) the presence of a quadrate ala groove, (4) a gently domed mandibular condyle of the quadrate and (5) a 90-degree inflection of the retroarticular process. All members of the Plotosaurini sensu Bell (1997) are in turn united by having (1) a short suprastapedial process, (2) no anterior deflection of the quadrate mandibular condyle, (3) laterally elongate synapophyses of the middle dorsal vertebrae, (4) proportionally large cervical vertebrae, (5) a saddle-shaped glenoid condyle of the humerus and (6) blocky, hourglass-shaped phalanges. Unlike Caldwell and Palci (2007), all three most parsimonious trees in this analysis recovered a monophyletic *Mosasaurus*, which is united by the reduction in the persistence of zygosphenes and zygantra along the dorsal vertebral series. *Plotosaurus* is differentiated from *Mosasaurus* based on an increase in the number of maxillary and dentary teeth, the presence of a large anterior dentary projection, a higher number of cervical vertebrae and a confinement of prezygapophyses to the anterior trunk region.

Adding Five Species of *Prognathodon* to the Matrix of Caldwell and Palci (2007) and Revising Character Codings for Three Mosasaurines

Although the topologies generated in Phylogenetic Analysis 1 are comparable with those of Bell (1997) and Caldwell and Palci (2007), several mosasaurine taxa are underrepresented. Specifically, the genus *Prognathodon* is only represented by the two North American species, *P. overtoni* and *P. rapax*, and lacks *P. solvayi*, the type species for the genus. The addition of five species of *Prognathodon* to the present taxon-character matrix was done using character codings made by previous authors, with modifications to the previous character state assignments made where necessary. The following taxa were added to the matrix of Caldwell and Palci (2007):

1) *Prognathodon kianda*—*Prognathodon kianda* is an Angolan taxon described by Schulp et al. (2008), although no phylogenetic analysis was presented in their work. Instead, the conclusions drawn by the authors regarding the relative position of *P. kianda* within the genus *Prognathodon* were derived from a preliminary phylogenetic analysis that was performed by Schulp et al. (2006). That analysis presented 26 out of a possible 90 cranial characters coded for *P. kianda*. The lack of data for this taxon was related to the paucity of available material for this species, for which only the premaxilla, left and right maxillae, a right dentary and a jugal were known at the time (Schulp et al., 2006). Schulp et al. (2008) provided additional material for this taxon, including a quadrate, a partial pterygoid, prefrontals and squamosals. Using the descriptions and figures of this new material, an additional 26 characters were coded for Analysis 2 and the character states for characters 67 and 70 from the original assignments in Schulp et al. (2006) were altered.

2) *Prognathodon solvayi*—Character codings for *P. solvayi* were incorporated from Dortangs et al. (2002). Modifications were made to the original character state assignments following reinterpretations from Schulp (2006) and personal observation of the material in 2010. In addition to these modifications, further changes to the dataset were required, as characters 1, 60 and 61 had to be re-examined. Contrary to Dortangs et al. (2002), Schulp (2006) developed a third character state for character 1, which concerns the absence or presence of any premaxillary rostrum. Schulp (2006:24) developed a third character state to denote the prognathous condition: "(2) predental rostrum reduced by prognate dentition." This character state was deemed to be unnecessary, because it was not only an autapomorphy for *P. solvayi*, but could not be consistently coded in the same manner for all species that exhibit prognate dentition. For the sake of consistency, we have chosen to revert to the original assignments by Dortangs et al. (2002) for this character and characters 60 and 61, as the latter two concern predental rostra of the dentaries.

3) *Prognathodon curii*—The original description of *Prognathodon currii* by Christiansen and Bonde (2002) was used in assigning character states to this taxon. Modifications from Schulp (2006) were required, based on poor preservation of the type specimen of *P. currii* and inconsistent character state assignments designated in Christiansen and Bonde (2002). Nearly all of the character state assignments from Schulp (2006) were retained for the present data matrix. Christiansen and Bonde (2002) did not describe any post-cranial material for *P. currii* that was preserved in sufficient detail to merit the addition of more characters to their original matrix. As such, all post-cranial characters were coded as '?'.

4) *Prognathodon saturator*—The nearly complete skull and cervical series of the holotype specimen (NHMM 1998141) of *Prognathodon saturator* allow for a limited number of character state assignments, particularly of the post-cranium. Initial character codings were derived from Dortangs et al. (2002) and modified according to Schulp (2006). Minor changes to some of the character codings in light of personal observations from photos of the holotype (NHMM 1998141), and revisions to the original character state assignments by Konishi (2008) were made.

5) *Prognathodon waiparaensis* Welles and Gregg, 1971—The disarticulated skull and fragmentary vertebral series from Maastrichtian deposits of New Zealand referred to as *P. waiparaensis* were first used in a phylogenetic analysis by Schulp (2006). Character state assignments are taken directly from that work, because there were no personal observations of the holotype material (C.M. zfr 108). In contrast to Schulp's (2006) character coding, Lindgren and Schulp (2010) suggested that *P. waiparaensis* possessed an internarial bar dorsal keel based on referred material of that taxon from California. This feature is considered absent for *P. waiparaensis* in this analysis, because the assignment of the fragmentary material from California to *P.* cf. *waiparaensis* remains tentative (Lindgren and Schulp, 2010:1634).

Because the base model for the present taxon-character matrix is that of Caldwell and Palci (2007), it was necessary to re-evaluate the character state assignments provided for certain taxa that have not since been changed in the light of more recent discoveries and revisions. As such, the following modifications were made to three mosasaurine taxa that were present in Bell (1997):

1) *Plesiotylosaurus crassidens*—Original character state assignments for *P. crassidens* were done by Bell (1997) based on the holotype specimen described by Camp (1942) (LACM 2759). Poor preservation and extensive reconstruction of the skull and mandibles of LACM 2759 allowed for limited character state assignments. Personal observation of LACM 2759 also confirmed that the reconstruction to the skull and mandibles, incomplete preparation, and poor preservation of the type material make many of the character state assignments from Bell (1997) difficult to verify. Lindgren (2009) described new material referable to *P. crassidens* (UCMP 137249) from the Moreno Formation of central California, which included a well preserved premaxilla, a right maxilla, a nearly complete left mandible, frontal, prefrontals, postorbitofrontals, quadrates and a nearly complete temporal arcade. Based on personal observations of this new material and the description provided by Lindgren (2009), seven additional characters were coded (5, 23, 39, 56, 57, 68 and 80) and seven others were altered (6, 9, 10, 32, 48, 55 and 77) from the original codings in Bell (1997).

2) *Mosasaurus missouriensis*—Personal observation by A. LeBlanc in 2010 of the original snout (MNHN 9587) and skull and postcranial material (RFWUIP 1327) of the holotype specimen of *M. missouriensis* led to a reinterpretation of a small number of the original character state assignments for this taxon carried out in Bell (1997). Characters 11, 34, 36, 48 and 102 were changed in light of these observations.

3) *Plotosaurus bennisoni*—Camp (1942) described both species of *Plotosaurus* from middle Maastrichtian deposits of the Moreno Formation in central California. Lindgren et al. (2008) reviewed the anatomical differences between referred specimens of *P. tuckeri* (including a skull; CIT 2750) and the holotype of *P. bennisoni* and concluded that slight differences in skull proportions and minor anatomical differences were likely the result of taphonomic alteration, intraspecific variation, or quite simply ontogenetic differences. As such, it was concluded that the genus *Plotosaurus* was monotypic, with *P. tuckeri* being the junior synonym of *P. bennisoni* (Lindgren et al., 2008). Because *P. tuckeri* is considered to be conspecific with *P. bennisoni*, the characters coded for the two species in Bell (1997) can be combined into a single taxon. As such, many of the postcranial characters that were considered as '?' for *P. bennisoni* in Bell (1997) can now be coded based on the corresponding characters that were coded for *P. tuckeri*. This has led to the coding of 34 additional characters (81, 88, 93, 94, 96, 100, 104-126, 132 and 133) for *P. bennisoni*. In addition to this, Lindgren et al. (2008) also described the first nearly complete hind limb and associated ilium for *Plotosaurus* (UCMP 126284), which led to the coding of characters 129–131.

Results—Analysis of the new taxon-character matrix, consisting of 135 characters and 36 terminal taxa, yielded 252 most parsimonious trees of 399 steps (CI = 0.421; RI = 0.702; HI = 0.579). The 50% majority rule consensus tree (Fig. 2–10B) yields a similar topology to the previous phylogenetic analysis (Fig. 2–10A). *E. heterodontus* is still recovered as the sister taxon to the Plotosaurini sensu Bell (1997). Three polytomies now occur within the Mosasaurinae. First, there is a polytomy among the three species of *Clidastes*. The second polytomy occurs among the three species of *Mosasaurus*, which still form a clade that is distinct from *Plotosaurus*. The third polytomy occurs among *Prognathodon currii*, *P. overtoni*, *P. saturator*, *P. solvayi* and *P. waiparaensis* (Fig. 2–10B). The genus *Prognathodon* is here considered to be polyphyletic, because *Globidens alabamaensis*, *G. dakotensis* and *Prognathodon kianda* represent successive outgroup taxa to a clade consisting of all the other species of *Prognathodon* and *Plesiotylosaurus*, *Eremiasaurus*, *Mosasaurus* and *Plotosaurus*. Characters supporting the basal position of *P. kianda* include (1) the presence of a premaxilla internarial bar keel (this feature is possibly present in *P. waiparaensis* as well, based on material tentatively referred to that taxon; see Lindgren and Schulp, 2010), (2) the presence of a jugal posteroventral process, and (3) a lack of contact between the ectopterygoid and the maxilla. The basal position of *P. kianda* is also supported by the lack of contact between the medial wing of the coronoid and the angular in medial view. This character coding contradicts the description by Schulp et al. (2008); however, the figured elements do not show any contact between the coronoid and the angular (Schulp et al., 2008:fig. 9b). Unfortunately, this character cannot be evaluated for *Globidens alabamaensis* or *G. dakotensis*, because no specimens of these taxa are sufficiently complete (Bell, 1997; Schulp, 2006).

Plesiotylosurus crassidens, *Prognathodon currii*, *P. overtoni, P. rapax*, *P. saturator*, *P. sovayi* and *P. waiparaensis* form a clade that is the sister group to the clade *Eremiasaurus heterodontus* + Plotosaurini sensu Bell (1997). This '*Prognathodon*' clade is supported by (1) the presence of enlarged pterygoid teeth, (2) a laterally compressed splenial-angular joint and (3) a highly domed glenoid condyle. *Plesiotylosaurus* is excluded from *Prognathodon* (excepting *P. kianda*) by several autapomorphies, including (1) a large predental rostrum on the dentary and premaxilla, (2) a rectangular internarial bar and (3) a relatively short suprastapedial process.

Discussion—The results of these analyses suggest that *E. heterodontus* is the sister taxon of Bell's (1997) Plotosaurini. Despite adding more species of *Prognathodon* to the matrix of Caldwell and Palci (2007), *E. heterodontus* is still recovered as the sister taxon to Bell's (1997) Plotosaurini and is not a member of the globidensine clade (*Prognathodon* + *Plesiotylosaurus* + *Globidens*) (Fig. 2–10B). The presence of fused infrastapedial and suprastapedial processes, flared tooth crown bases, large pterygoid teeth and a low tooth count in *E. heterodontus* are traditionally considered globidensine synapomorphies (Bell, 1997; Christiansen and Bonde, 2002). In contrast, the presence of an internarial bar dorsal keel, a thin and grooved quadrate ala and a straight surangular-articular suture are shared between this specimen and the Plotosaurini (Bell, 1997;

Christiansen and Bonde, 2002). The position of *E. heterodontus* within the Mosasaurinae is puzzling, given that it possesses a supposedly definitive feature of globidensine mosasaurs: the fusion of the infrastapedial and suprastapedial processes of the quadrate (Bell, 1997; Christiansen and Bonde, 2002; Dortangs et al., 2002; Schulp, 2006; Polcyn et al., 2010). This position may be the result of poor resolution of the Globidensini in Analysis 2 (Fig. 2–10B). The inclusion of five additional species of *Prognathodon* led to an increase in the number of most parsimonious topologies from three in Analysis 1 (Fig. 2–10A) to 252 in analysis 2 (Fig. 2–10B). The addition of these taxa also created a paraphyletic Globidensini, with *Globidens* and *Prognathodon kianda* falling outside of the clade consisting of all the other species of *Prognathodon* and *Plesiotylosaurus crassidens* (Fig. 2–10B).

The recovery of *Globidens* and *Prognathodon kianda* as outgroups to the Plotosaurini sensu Bell (1997), and all other globidensines, is in stark contrast to what has been reported by several previous authors (Bell, 1997; Christiansen and Bonde, 2002; Dortangs et al., 2002; Bell and Polcyn, 2005; Caldwell and Palci, 2007). This disparity stems from the paucity of postcranial material available for these taxa (Christiansen and Bonde, 2002; Dortangs et al., 2002; Schulp, 2006), and from a change in the character optimization for several characters that were originally identified as synapomorphies of all globidensine taxa. Five unequivocal character state changes support the globidensine clade in Analysis 1 (Figure 2–9A), three of which represent tooth ornamentation and shape characters (75, 76 and 78), while two others are quadrate characters (48 and 45). In the second phylogenetic analysis (Fig. 2–9B), none of these characters support a monophyletic globidensine clade. Some of these features instead support a more basal position for *Globidens*.

The fusion of infrastapedial and suprastapedial processes (character 45) occurs at the base of the node of *Prognathodon kianda* and the rest of the globidensine and plotosaurine mosasaurs in Analysis 2 (Fig. 2–11A). This makes the fusion of these processes the plesiomorphic state for all members of the Mosasaurinae, to the exclusion of *Clidastes* and *Dallasaurus* (contra Bell, 1997; Christiansen and Bonde, 2002; Schulp, 2006; Polcyn et al., 2010). Furthermore, the lack of fusion of these processes is interpreted as a reversal in *Mosasaurus* and *Plotosaurus* and is thus the derived condition for this character within the Mosasaurinae (Fig. 2–11A). Because *E. heterodontus* possesses fused infrastapedial and suprastapedial processes (traditionally viewed as a globidensine feature) and a quadrate alar groove (a plotosaurine synapomorphy), its anatomy casts doubt on the presence of a stereotypically ‘globidensine’ quadrate in any mosasaurine taxon.

The presence of coarse tooth enamel ornamentation (character 75) and basal tooth crown inflation (character 78) are also variably present across taxa that are traditionally grouped within a monophyletic Globidensini (Fig. 2–11B, C; Bell, 1997; Christiansen and Bonde, 2002; Schulp, 2006). This may arise from scoring of character 75, since the coarse anastomosing ridges on the tooth crowns of *Globidens* occur in only some species of *Prognathodon* (Bell, 1997; Schulp, 2006; Schulp et al., 2008). Coarse enamel ornamentation as defined by Bell

(1997) occurs as pustules, or sharp-crested vermiform and anastomosing ridges, along the tooth crown surface. This is most clearly expressed in *Prognathodon currii* and *P. saturator* (Bardet et al., 2005a; Schulp, 2006), although the original character state assignments by Christansen and Bonde (2002) and Dortangs et al. (2002) identified the teeth of the respective species as being smooth (state '0'). The teeth of *Prognathodon waiparaensis* and the generic type *P. solvayi*, on the other hand, lack coarse enamel ornamentation (Lingham-Soliar and Nolf, 1989) and are coded as such in this analysis, as well as others (Dortangs et al., 2002; Schulp, 2006). Further complicating the subdivisions of enamel ornamentation is a lack of these features in *P. kianda* (Schulp et al., 2006; Schulp et al., 2008). Comparisons of tooth ornamentation and aspect ratios led Schulp et al. (2008) to suggest *Prognathodon* is congeneric with *'Liodon'*, an enigmatic taxon diagnosed by the presence of unusually smooth, unornamented tooth crowns (Gaudry 1892; Schulp et al., 2008). These gradational variations in crown ornamentation make scoring of a binary character ambiguous, and cast doubt on crown ornamentation as a statement of homology. The variability of this feature of the dentition in globidensines provides no phylogenetic support for inclusion of *Globidens* within a larger grouping of mosasaurs sharing a homologous form of tooth ornamentation (Fig. 2–11B).

Tooth crown inflation (character 78) is extreme in *Globidens*, where the posterior marginal teeth are nearly spherical and expanded at the base (Bell, 1997). In other mosasaurs exhibiting this trait, posterior marginal teeth are flared at the base, but may deviate significantly from the durophagous dentition of

Globidens (Bardet and Pereda Suberbiola, 2002; Bardet et al., 2005a; Schulp, 2006). This feature is present in *Eremiasaurus heterodontus* and *Plotosaurus bennisoni* and all species of *Prognathodon*, but is absent in *Mosasaurus* and *Plesiotylosaurus* (Fig. 2–11C; Bell, 1993; Bell, 1997; Schulp, 2006). The presence of carinal serrations in *Prognathodon currii*, *P. overtoni*, *P. rapax*, *P. solvayi*, and *Plesiotylosaurus crassidens* renders use of this feature equivocal (Bell, 1997; Christiansen and Bonde, 2002; Bardet et al., 2005a; Lindgren, 2009). These taxa share this feature with *Eremiasaurus*, *Mosasaurus* and *Plotosaurus*, but not *Globidens* (Bell, 1997). Furthermore, if this can be interpreted as a loss of carinal serrations in *Globidens* due to extreme inflation of the tooth crowns (Bell, 1997), it is more parsimonious to assume that the presence of these dental features in *Prognathodon* and the plotosaurine mosasaurs are homologous characters that unite them to the exclusion of *Globidens* (contra Bell, 1997; Christiansen and Bonde, 2002; Schulp, 2006; Polcyn et al., 2010). Alternatively, the traditional hypothesis of a close relationship between *Globidens* and *Prognathodon* indicates at least two independent acquisitions of serrated carinae within the Mosasaurinae. Tooth shape and ornamentation, and thus prey preference, are likely convergent among several taxa of mosasaurids and cross taxonomic boundaries in many documented cases (Massare, 1987). If this is the case, then the use of tooth characters to support a clade traditionally uniting *Globidens* and *Prognathodon* should be abandoned altogether, because these features pertain more to dietary preference of a given species than to their phylogenetic utility. It should also be noted that the dentition of *Globidens* represents a specialized feeding mechanism adapted for exploiting a niche as a durophagous carnivore (Massare, 1987; Schulp et al., 2006; Polcyn et al., 2010). The dentition of this genus suits a particular function and is convergently developed in other durophagous squamate lineages. This is most apparent in the extant *Dracaena guianensis* and *Varanus niloticus*, where the anastomosing ridges, coarse enamel ornamentation and basal tooth crown inflation in the molariform dentition of these taxa superficially resemble the dentition of *Globidens* (Dalrymple, 1979; Rieppel and Labhardt, 1979:fig. 3b).

Removing character 75 (presence or absence of coarse enamel ornamentation) and character 78 (presence or absence of basal tooth crown inflation) from the dataset used in the second analysis yields 36 most parsimonious trees of length 390 (CI = 0.426, RI = 0.705, HI = 0.574). The topology of the 50% majority rule consensus tree (Fig. 2–12) is nearly identical to that of analysis 2, but resolves the polytomy between *Prognathodon* (excluding *P. kianda*) and *Plesiotylosaurus*. Bell (1997), Bell and Polcyn (2005), and Caldwell and Palci (2007) recovered similar relationships between *Prognathodon* and *Plesiotylosaurus*. In this new phylogeny, the Globidensini still represents a paraphyletic grade of mosasaurines with respect to a monophyletic (*E. heterodontus* (*Plotosaurus* + *Mosasaurus*)).

DISCUSSION

Taxonomy

Previous phylogenetic analyses have resolved two distinct clades of mosasaurines with disparate cranial and postcranial anatomies: the Globidensini and the Plotosaurini (Bell, 1997; Christiansen and Bonde, 2002; Dortangs et al., 2002; Bell and Polcyn, 2005; Caldwell and Palci, 2007). This finding is complicated by the addition of more mosasaurine taxa to existing datasets (Fig. 2–10B), due to the degree of anatomical variation that exists across, and within, supposedly well-supported mosasaurine clades. The anatomy of *E. heterodontus* is consistent with that of both plotosaurine and globidensine mosasaurs (both tribes sensu Bell, 1997), which are known from the same phosphatic deposits in the Oulad Abdoun Basin of Morocco (Bardet et al., 2004; Bardet et al., 2005a). We draw the same conclusion from both phylogenetic analyses presented (Fig. 2–10A, B). In this study, *E. heterodontus* is placed at the base of the radiation of the Plotosaurini (sensu Bell, 1997). In addition, characters that traditionally support Globidensine monophyly (e.g. fused infrastapedial and suprastapedial processes and coarse tooth crown ornamentation) instead support a more inclusive clade within the Mosasaurinae (Fig. 2–11).

On the Problem of the Plotosaurini sensu Bell (1997)—Russell (1967) erected the Plotosaurini to include only *Plotosaurus* as a result of several autapomorphies that he believed excluded it from other members of the Mosasaurinae. Bell (1997) later expanded the ingroup composition of the

Plotosaurini to include *Mosasaurus*, abandoning the use of the name Mosasaurini (Russell, 1967) on the grounds that the genus *Mosasaurus* was paraphyletic (Bell, 1997; Chrisitiansen and Bonde, 2002; Dortangs et al., 2002; Caldwell and Palci, 2007). Bell (1997) listed one equivocal and four unequivocal characters that informally diagnose this taxon. Although this follows the principles of phylogenetic taxonomy (de Queiroz and Gauthier, 1992; Wägele, 2005), this method has not been the convention for the naming of higher-ranked mosasauroid taxa (Russell, 1967). The Mosasauroidea, Mosasauridae and Mosasaurinae are named following the principles of Linnean hierarchy and the principle of seniority, accompanied by formal diagnoses, suggesting that all higher-ranked taxa that include *Mosasaurus hoffmanni*, the type genus of Mosasauroidea, should be named accordingly (Wägele, 2005). We recommend that the name Plotosaurini from Bell (1997) be abandoned and resurrect the name Mosasaurini (Russell, 1967) to denote the group consisting of (*Eremiasaurus* (*Mosasaurus* + *Plotosaurus*)).

The diagnosis of the Plotosaurini and its ingroup composition from Russell (1967) are now outdated. The revised diagnosis presented here permits that the Mosasaurini consist of all species of *Mosasaurus* and *Plotosaurus* and *Eremiasaurus heterodontus* to the exclusion of all other members of the Mosasaurinae based on features recognized by previous authors (Bell, 1997; Christiansen and Bonde, 2002; Bell and Polcyn, 2005; Caldwell and Palci, 2007).

Tribe MOSASAURINI Gervais, 1853

Included Taxa—*Eremiasaurus heterodontus* gen. et sp. nov.; *Mosasaurus hoffmanni* Mantell, 1829; *Mosasaurus conodon* Cope, 1881; *Mosasaurus missouriensis* Harlan, 1834; *Mosasaurus lemonnieri* Dollo, 1889; *Mosasaurus beaugei* Arambourg, 1952; *Plotosaurus bennisoni* Camp, 1942.

Type Genus—*Mosasaurus* Conybeare, 1822.

Type Species—*Mosasaurus hoffmanni* Mantell, 1829.

Revised Diagnosis of Mosasaurini—Apomorphies of taxon: premaxillo-maxillary suture rises at a shallow angle anterior to the first maxillary tooth and terminates at a point even with, or posterior to the fourth maxillary tooth position; internarial bar keel present; large triangular or rectangular posteromedial flanges of frontal dorsally overlap parietal table; mandibular condyle of quadrate convex in any view; quadrate ala thin, with a thickness of approximately 1 mm; quadrate alar groove present; retroarticular process rotated 90 degrees and perpendicular to dorsoventral plane of surangular; tibial facet for first metatarsal concave. Differs from Globidensini (sensu Bell, 1997) in having: predental rostra on premaxilla and dentaries present; dorsal profile of premaxilla convex; anterior premaxillary and dentary teeth significantly smaller than middle marginal teeth; frontal median dorsal keel present and extending along entire length of frontal, or restricted to anterior half of element; pterygoid teeth smaller than middle marginal teeth; dentary with pronounced interdental pitting between anterior teeth; zygosphenes and zygantra reduced both in size and persistence along vertebral column. Differs from *Clidastes* in: functional prezygapophyses do not extend further posteriorly than last pygal vertebra; at least eight pygal vertebrae present; anterior flange of tibia extends from distal to proximal tibial heads.

Eremiasaurus heterodontus **compared to** ***Plesiotylosaurus*** **and** ***Prognathodon*****—**The combination of fused infrastapedial and suprastapedial processes of the quadrate and enlarged pterygoid teeth (both of which are present in *E. heterodontus*) are considered diagnostic for *Prognathodon* (Lingham-Soliar and Nolf, 1989; Christiansen and Bonde, 2002; Dortangs et al., 2002; Schulp, 2006). These features should not overshadow other anatomical differences that may warrant generic distinction (Lindgren, 2009). For UALVP 51744 to be included in the genus *Prognathodon*, the generic diagnosis of the latter taxon would have to include several cranial features in order to accommodate the differences observed in *E. heterodontus* including: (1) the presence of premaxillary and dentary rostra, (2) the presence of narial embayments in the frontal, (3) exclusion of the prefrontal from forming a border of the external nares, (4) fourteen to fifteen dentary teeth, and (5) teeth that are faceted, smooth, striated, or coarsely textured. This would create an extremely high degree of variation in the diagnosis for a single genus. Instead, we elect to retain the generic diagnosis for *Prognathodon* from Lingham-Soliar and Nolf (1989) and suggest that UALVP 51744 is generically distinct from *Prognathodon*, a view supported by the phylogenetic analyses presented here.

E. heterodontus can be differentiated from *Plesiotylosaurus* by the presence of a shorter premaxillary-maxillary suture, a smaller premaxillary rostrum, a keeled triangular internarial bar, the exclusion of the prefrontal from the border of the narial opening, and the presence of a quadrate alar groove and fewer dentary teeth (15 in *E. heterodontus* versus 16 in *Plesiotylosaurus*).

Comments on the '*Liodon*'-like Dentition of *E. heterodontus*

Arambourg (1952) figured several small and slender isolated tooth crowns from the Maastrichtian phosphates of Morocco that he attributed to *Mosasaurus* ('*Liodon*') cf. *anceps* based on the presence of smooth enamel surfaces (Arambourg, 1952:pl. 38) that show remarkable similarity to those of *E. heterodontus*. '*Liodon*' is a problematic taxon due to the fragmentary nature of the type material (Russell, 1967). The holotype of '*L.*' *anceps* is a small jaw fragment with two smooth enameled, symmetrically bicarinate teeth (Russell, 1967:142) that have since been broken and lost (Schulp et al., 2008). Schulp et al. (2008) identified this problem and stated that '*Liodon*' constitutes a nomen dubium. Based primarily on similarities in the patterns of heterodonty and the degree of lateral compression of the teeth in three species of '*Liodon*' known from the most complete material for the genus, Schulp et al. (2008) suggested synonymizing this genus with *Prognathodon*. Indeed, laterally compressed teeth do occur in some species of *Prognathodon*, including *P. kianda*, *P. solvayi*, and, to some extent, *P. giganteus*, but other mosasaurine taxa, including *Clidastes* and closely related forms, exhibit these traits as well (Lingham-Soliar and Nolf, 1989; Nicholls and Meckert, 2002; Schulp et al., 2008). In all likelihood, many of these cases of similarity in tooth form are convergent and echo a concern mentioned previously:

phylogenetic hypotheses based on the proposed homology of tooth form are equally likely to represent convergent dietary preferences (Massare, 1987).

The holotype of '*Liodon*' *mosasauroides* Gaudry, 1892 from the Maastrichtian of France (MNHN 1891–14) is the most complete material of the genus (Lingham-Soliar, 1993). The premaxillary teeth, the anterior three maxillary teeth and the anterior five dentary teeth of MNHN 1891–14 interdigitate tightly (Gaudry, 1892; pers. obs.), and exhibit fairly deep interdental pits between adjacent teeth in the anterior portion of the snout, similar to *Mosasaurus hoffmanni* (e.g. MNHN AC. 9648). The premaxilla of '*L.*' *mosasauroides* is conical with a small bony rostrum anterior to the first premaxillary teeth, which are not prognate (Gaudry, 1892:pl. 2). The dentary extends far enough anterior to the first dentary tooth for an excavation on the dorsal margin of the bone that houses the tip of the first premaxillary tooth when the jaws were closed (Gaudry, 1892:pl. 2). This anterior excavation is also seen in *Mosasaurus hoffmanni* (e.g. MNHN AC. 9648; IRSNB R12), but not described for any species of *Prognathodon*. The premaxillo-maxillary suture is long in '*Liodon*' *mosasauroides*, terminating at a point above the fifth maxillary tooth, similar to *Mosasaurus hoffmanni* (Lingham-Soliar, 1995). Although not figured, Gaudry identified four pterygoid teeth preserved on the holotype of '*Liodon*' *mosasauroides* that were much smaller than those of the marginal dentition, similar to *Mosasaurus* (Gaudry, 1892:9). These features all suggest that '*Liodon*' *mosasauroides* might have closer affinities to the Mosasaurini, more specifically to *Mosasaurus hoffmanni* and not to *Prognathodon* (Gaudry, 1892; Russell, 1967;

Lingham-Soliar, 1993; contra Schulp et al., 2008), although more complete material of '*Liodon*' *mosasauroides* would be required to test this hypothesis from a phylogenetic perspective. As such, it is impossible to say whether *E. heterodontus* is a representative of such a poorly known genus based on superficial similarity in tooth morphology.

Caudal Anatomy of *E. heterodontus*

The most notable features of the caudal region of *E. heterodontus* are the presence of a ventral deflection of the tail, a fanning of the caudal neural spines, and an unusually long series of pygal vertebrae (Fig. 22). A downturned bony support for the dorsal tail fluke is a feature shared by several lineages of mosasaurs and likely arose convergently multiple times within the Mosasauridae (Lindgren et al., 2007; Lindgren et al., 2010). The large number of pygal vertebrae, accompanied by a reduced number of intermediate caudals (Figs. 2–2B, 2–8C), is unique to *E. heterodontus*. This is opposite to the trend in most mosasaurs (Russell, 1967) and would suggest that there was a posterior migration of the first haemapophysis-bearing vertebra in the tail region, a trait also seen in *Plotosaurus* (Camp, 1942; Lindgren et al., 2007). Lindgren et al. (2007) hypothesized that these proportions of the posterior trunk and caudal region in *Plotosaurus* were indicative of increased rigidity in the pelvic region and at the base of the tail, resulting in restriction of the main propulsive motions of the tail further posteriorly. Using these proportions of the tail, coupled with the presence of an incipient dorsal caudal fin supported by a broad, sweeping fan of tall neural spines in the terminal caudal region, *Plotosaurus* was reconstructed as a high-speed pursuit predator capable of sustaining higher speeds in an open water environment (Lindgren et al., 2007). Extreme reduction in the number of functional prezygapophyses and the loss of zygosphenes and zygantra may have also contributed to a more rigid vertebral column in *Plotosaurus* (Camp, 1942; Lindgren et al., 2007; Lindgren et al., 2008). The presence of a ventral deflection of the tail (Figs. 2–2, 2–8), similar to what is seen in *Plotosaurus*, and a sweeping fan of neural spines in the same region of the caudal vertebral series suggests similar development of an incipient dorsal fin lobe in *E. heterodontus*, albeit developed to a lesser extent. Unfortunately, the persistence of accessory intervertebral articulations along the vertebral column of *E. heterodontus* cannot be determined due to the state of preservation of the holotype. Nevertheless, such a regionalization of the pygal and caudal regions is a feature shared between *Plotosaurus* and *E. heterodontus*, suggesting some similarity in swimming styles. These features are likely not homologous with those of *Plotosaurus*, given that *E. heterodontus* does not share a derived paddle anatomy (e.g. shortened humeri and spindle-shaped phalanges) with *P. bennisoni* or *Mosasaurus* (Russell, 1967; Lindgren et al., 2008). It is also unlikely that the caudal anatomy of *E. heterodontus* represents an early transition in the development of the *Plotosaurus*-like tail, because *Mosasaurus conodon*, a member of the Plotosaurini as defined by Bell (1997), possesses only eight pygal vertebrae and at least 21 intermediate caudals (Russell, 1967) and yet possesses stout, blocky humeri and phalanges, much like *Plotosaurus* (Camp, 1942). This suggests that the development of the stout paddle elements of *Plotosaurus* and *Mosasaurus* preceded the elongation of the pygal series and restriction of the haemapophyses that supported the posteriorly-situated caudal fin typical of *Plotosaurus*.

CONCLUSIONS

We add to the growing list of mosasaur taxa from the Maastrichtian of Morocco with the description of *Eremiasaurus heterodontus*, a new genus and species of mosasaur, and a basal member of the Mosasaurini, exhibiting an unusually high degree of heterodonty and regionalization of the caudal vertebrae. Heterodonty has been recorded for many members of the Mosasaurinae (Schulp, 2006; Schulp et al., 2008), but in *E. heterodontus* heterodonty is extreme. While the particular diet of this new mosasaur is uncertain, its divergence from other robust-toothed inhabitants of the Maastrichtian seas of Morocco would suggest it fed on food sources not exploited by its larger mosasaurine contemporaries. Changes in body proportions, such as an increase in the number of pygal vertebrae are suggestive of pursuit predation, convergent with the vertebral proportions of *Plotosaurus* from the Maastrichtian of California (Lindgren et al., 2007). Although many features of *E. heterodontus* are comparable to those of *Prognathodon*, incorporating *E. heterodontus* and additional globidensine taxa into the phylogeny of Caldwell and Palci (2007) produces a tree wherein synapomorphies that traditionally supported globidensine monophyly become characters supporting a much more inclusive clade within the Mosasaurinae.

According to this hypothesis, the ‘globidensine’ quadrate (i.e. fusion of infrastapedial and suprastapedial processes) is the primitive condition with respect to a clade consisting of the Globidensini and Mosasaurini. Furthermore, the similarities in quadrate form between *Clidastes* and *Mosasaurus* are a reversal in members of the Mosasaurini to the plesiomorphic condition within the subfamily Mosasaurinae. These findings highlight a need to re-evaluate globidensine monophyly and develop phylogenetic hypotheses that take into account convergence in quadrate and tooth morphology.

FIGURE 2–1. Map and stratigraphic column of the Oulad Abdoun Basin, Morocco (modified from Bardet et al., 2008:Fig. 2–1). **A**, map of northwestern region of Morocco with three main phosphatic basins of the region highlighted in dark grey; **B**, map of the Oulad Abdoun Basin, star indicates probable location from which *Eremiasaurus heterodontus*, UALVP 51744, was recovered; **C**, stratigraphic column of the Late Cretaceous and Early Paleocene (Danian) deposits of the Oulad Abdoun Basin with a list of mosasaurid taxa described from Upper Couche III. **Abbreviations**: **BBB**, basal bonebed; **LCIII**, Lower Couche III; **Li**, limestones; **Ma**, marls; **Ph**, phosphates; **UCIII**, Upper Couche III.

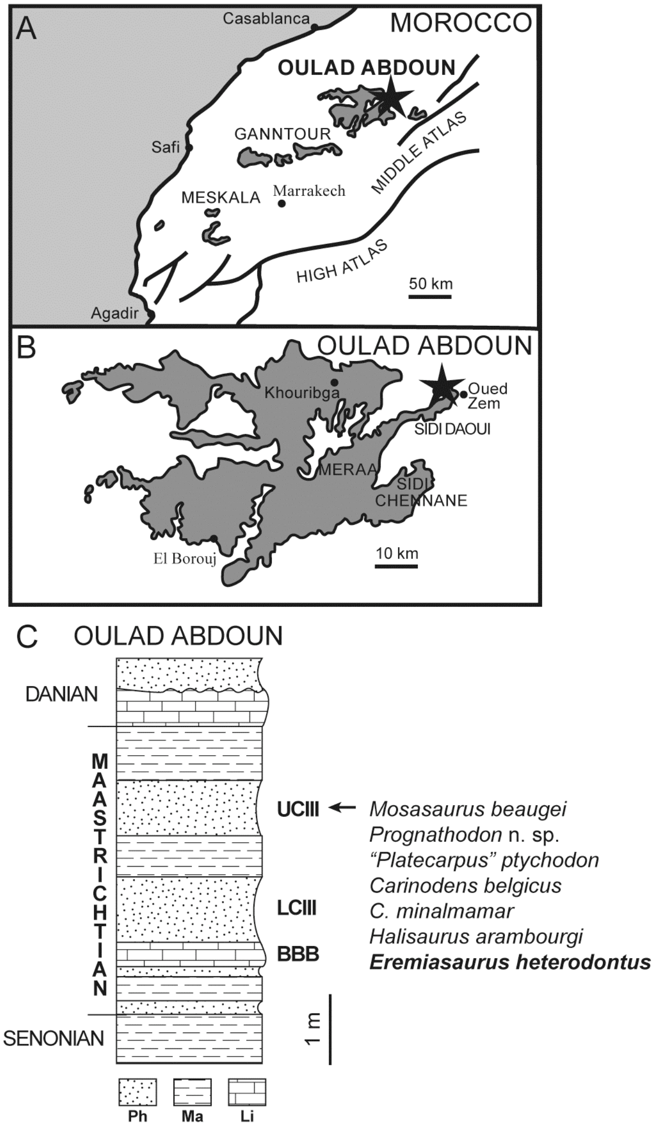

A
MOROCCO
Casablanca
OULAD ABDOUN
GANNTOUR
Safi
MESKALA
Marrakech
MIDDLE ATLAS
HIGH ATLAS
50 km
Agadir
B
OULAD ABDOUN
Khouribga
Oued Zem
SIDI DAOUI
MERAA
SIDI CHENNANE
10 km
El Borouj
C
OULAD ABDOUN
DANIAN
MAASTRICHTIAN
SENONIAN
UCIII
LCIII
BBB
Mosasaurus beaugei
Prognathodon n. sp.
“Platecarpus” ptychodon
Carinodens belgicus
C. minalmamar
Halisaurus arambourgi
Eremiasaurus heterodontus
1 m
Ph
Ma
Li

FIGURE 2–2. Entire preserved skeleton of *Eremiasaurus heterodontus*, UALVP 51744. **A**, composite photo of skull and preserved post-crania. Scale bar equals 50 cm. **B**, diagram of *E. heterodontus*, UALVP 51744, with posterior trunk and caudal vertebral regions labeled. **Abbreviations**: **as**, astragalus; **c**, coracoid; **c7**, seventh cervical vertebra; **f**, femur; **fi**, fibula; **h**, humerus; **lil**, left ilium; **lis**, left ischium; **ph**, phalanx; **pyg1**, first pygal vertebra; **ril**, right ilium; **ris**, right ischium; **sc**, scapula; **t**, tibia. [planned for page width]

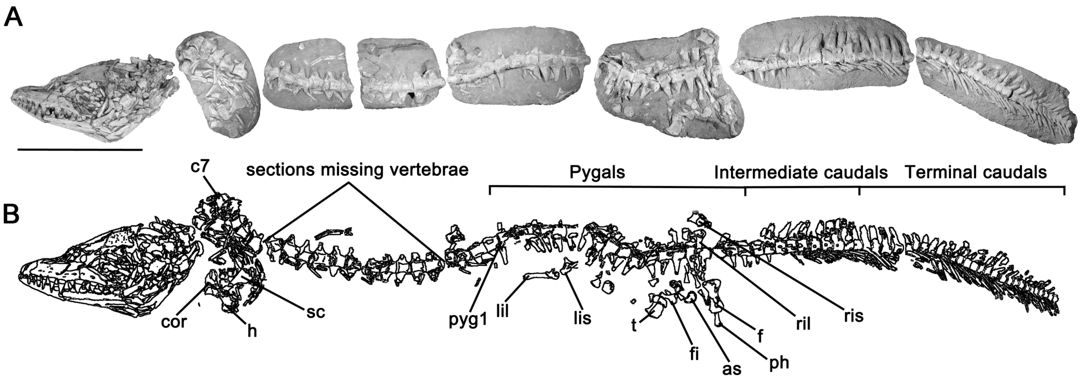
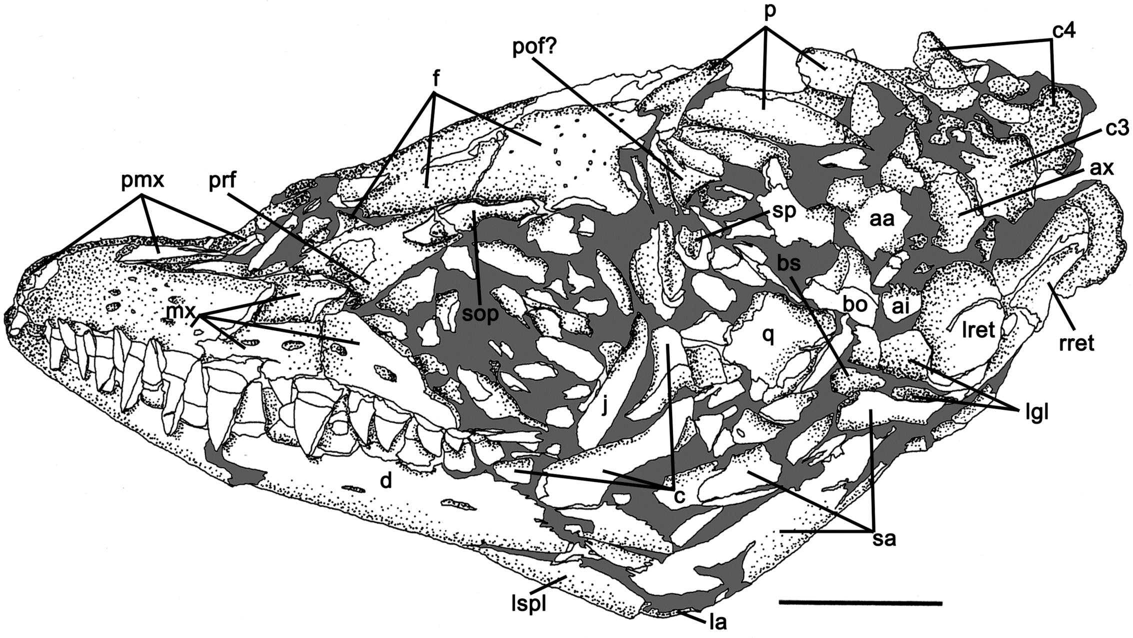

A
B
c7
sections missing vertebrae
Pygals
Intermediate caudals
Terminal caudals
cor
h
sc
pyg1
lil
lis
t
fi
as
ph
f
ril
ris

FIGURE 2–3. Skull of *Eremiasaurus heterodontus*, UALVP 51744, in left lateral view. **A**, diagram; **B**, photo. **Abbreviations**: **aa**, atlas neural arch; **ai**, atlas intercentrum; **ax**, axis; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **c3**, third cervical vertebra; **c4**, fourth cervical vertebra; **f**, frontal; **hy**, hyoid; **j**, jugal; **la**, left angular; **lgl**, left glenoid fossa; **lret**, left retroarticular process; **lspl**, left splenial; **mcd**, mandibular condyle; **mx**, maxilla; **p**, parietal; **pof**, postorbitofrontal; **pmx**, premaxilla; **prf**, prefrontal; **q**, quadrate; **rret**, right retroarticular process; **sa**, surangular; **sop**, supraorbital process; **sp**, suprastapedial process. Scale bars equal 10 cm. [planned for page width]

A


p
c4
pof?
f
c3
ax
pmx
prf
sp
aa
bs
mx
sop
bo
ai
lret
rret
q
lgl
j
d
c
sa
lspl
la

B

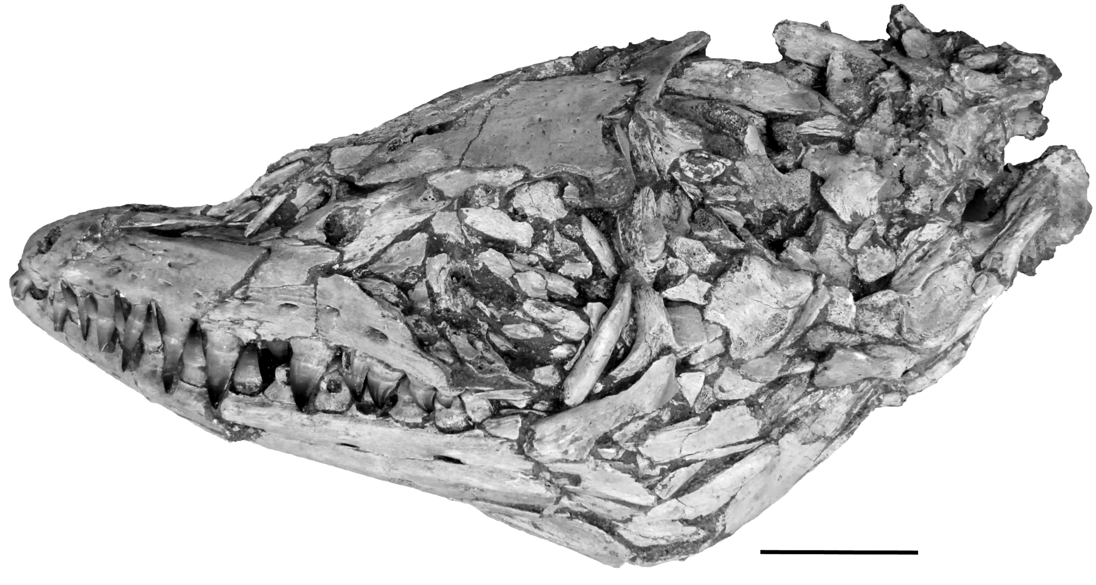


FIGURE 2–4. Skull of *Eremiasaurus heterodontus*, UALVP 51744, in right lateral view. **A**, diagram; **B**, photo; **C**, closeup of preserved pterygoid tooth row. **Abbreviations**: **c**, coronoid; **c3**, third cervical vertebra; **c4**, fourth cervical vertebra; **f**, frontal; **gl**, glenoid fossa; **hy**, hyoid; **j**, jugal; **la**, left angular; **ld**, left dentary; **lspl**, left splenial; **mcd**, quadrate mandibular condyle; **mx**, maxilla; **p**, parietal; **pof**, postorbitofrontal; **pmx**, premaxilla; **prf**, prefrontal; **ptt1**, first pterygoid tooth; **ptt2**, second pterygoid tooth; **ptt3**, third pterygoid tooth; **ptt4**, fourth pterygoid tooth; **ptt5**, fifth pterygoid tooth; **ptt?**, isolated pterygoid tooth of unknown position; **q**, quadrate; **qa**, quadrate ala; **ra**, right angular; **rd**, right dentary; **rspl**, right splenial; **sa**, surangular; **sop**, supraorbital process; **sp**, suprastapedial process; **sq**, squamosal. Scale bars equal 10 cm.

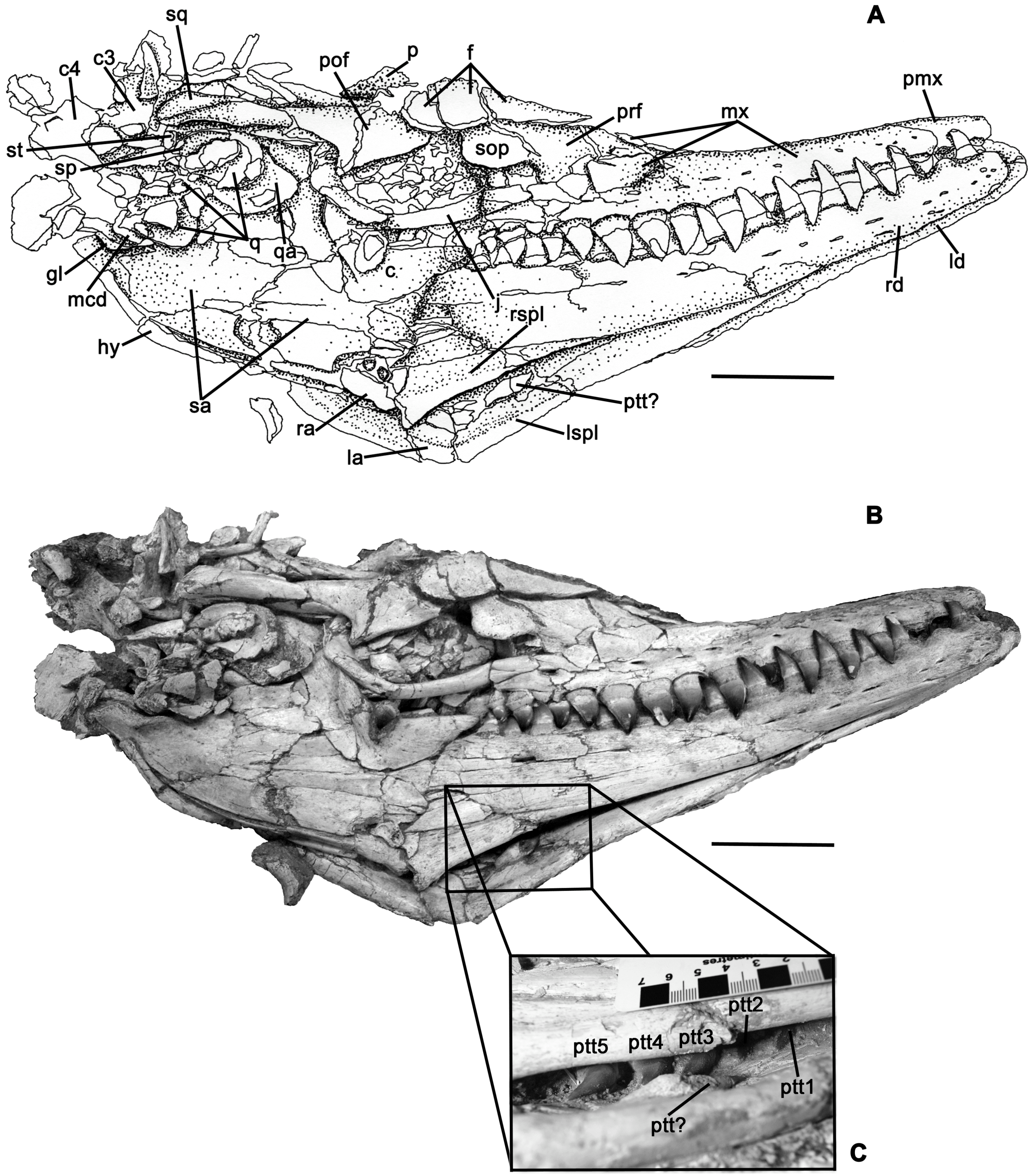

A
sq
c4
c3
pof
p
f
pmx
prf
mx
st
sp
sop
q
qa
c
j
gl
mcd
rd
ld
hy
rspl
sa
ptt?
ra
lspl
la
B
ptt2
ptt5
ptt4
ptt3
ptt1
ptt?
C

FIGURE 2–5. Reconstruction of the skull of *Eremiasaurus heterodontus* in lateral view. **Abbreviations: a**, angular; **c**, coronoid; **d**, dentary; **f**, frontal; **ip**, infrastapedial process; **j**, jugal; **mx**, maxilla; **p**, parietal; **pmx**, premaxilla; **pof**, postorbitofrontal; **prf**, prefrontal; **q**, quadrate; **qag**, quadrate alar groove; **ret**, retroarticular process; **sa**, surangular; **sp**, suprastapedial process; **spl**, splenial; **sq**, squamosal; **st**, supratemporal.

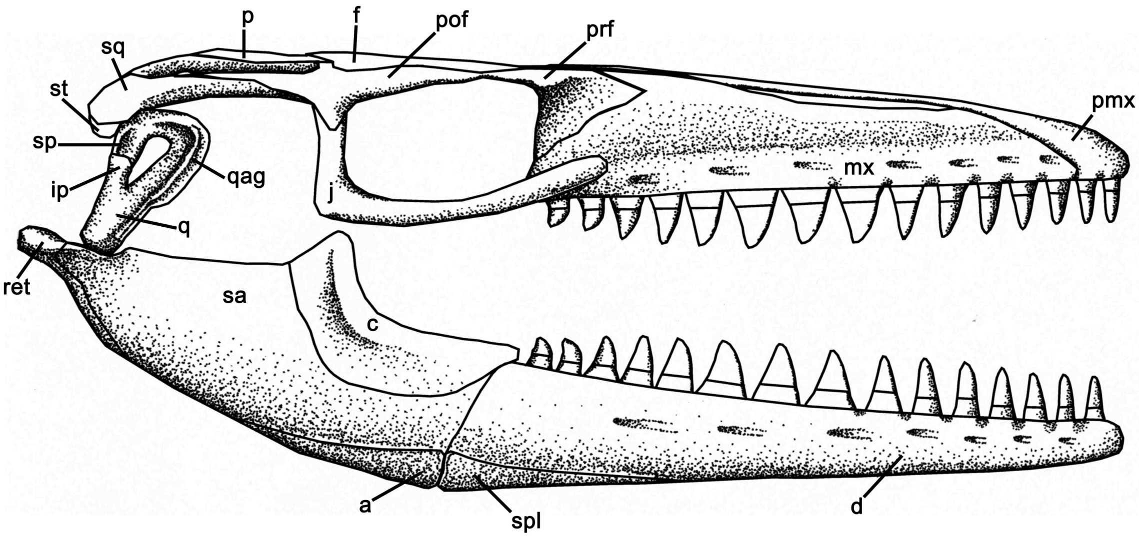

p
f
pof
prf
sq
st
pmx
sp
qag
ip
mx
j
q
ret
sa
c
a
spl
d

FIGURE 2–6. Preserved portions of right quadrate of *Eremiasaurus heterodontus*, UALVP 51744. **A**, diagram of right quadrate, dashed line indicates former position of quadrate ala, grey areas indicate missing regions or portions covered by matrix, thick lines indicate the outline of the main body of the quadrate. **B**, photo of right quadrate. **C**, image of the lateral border of the quadrate ala showing the alar groove. **Abbreviations**: **dm**, point of origin of *M. depressor mandibulae*; **ip**, infrastapedial process; **mcd**, mandibular condyle; **qa**, quadrate ala; **qag**, quadrate ala groove; **qm**, quadrate meatus; **sp**, suprastapedial pocess. Scale bars equal 2 cm.

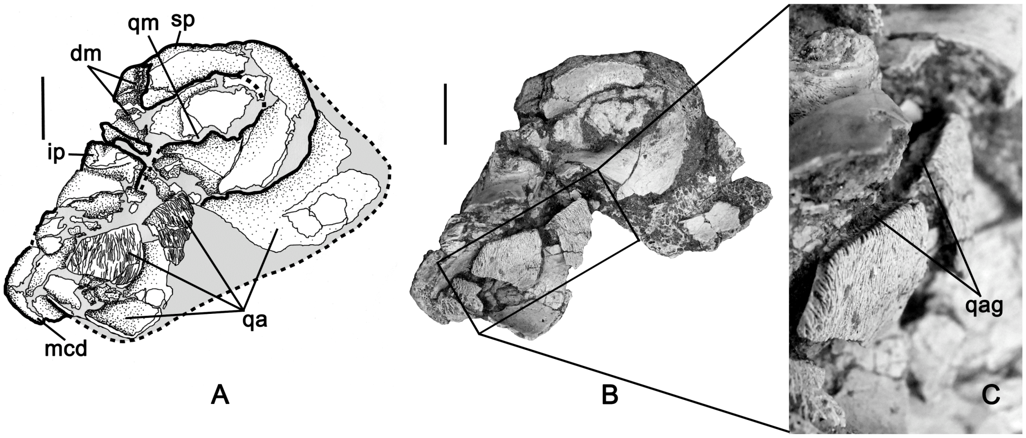

qm
sp
dm
ip
qa
mcd
qag
A
B
C

FIGURE 2–7. Posterior cervical and anterior dorsal vertebral series, pectoral girdle elements and humerus from the second block of *Eremiasaurus heterodontus* (UALVP 51744). **A**, diagram, grey shaded areas represent matrix infilling or heavily damaged portions. **B**, photo. **Abbreviations**: **c7**, seventh cervical vertebra; **cg**, glenoid condyle of humerus; **cor**, coracoid; **d1**, first dorsal vertebra; **h**, humerus; **hyp**, hypapophysis; **pgp**, postglenoid process; **prez**, prezygapophysis; **sc**, scapula; **syn**, synapophysis. Scale bar equals 10 cm.

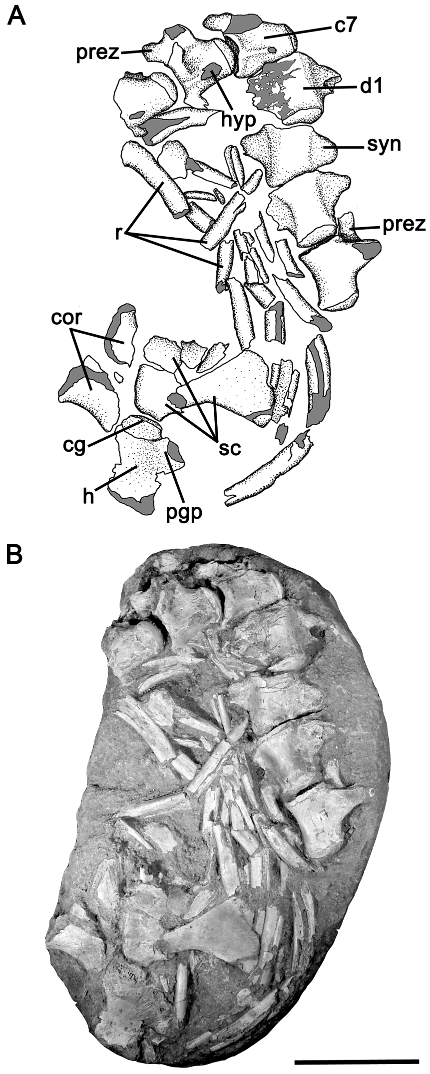

A
c7
prez
d1
hyp
syn
r
prez
cor
cg
sc
h
pgp
B

FIGURE 2–8. Caudal anatomy and restoration of the tail of *Eremiasaurus heterodontus*. **A**, photographs of the posterior two blocks containing the intermediate and terminal caudal vertebrae. **B**, diagram of the intermediate and terminal caudal segments. **C**, restoration of the tail, incorporating the pygal vertebral region. The presence and position of the incipient dorsal fin lobe is inferred following Lindgren et al. (2007:fig. 3b) and Lindgren et al. (2010:fig. 8b). **Abbreviations**: **pyg**, pygal vertebra; **ic**, intermediate caudal vertebra; **tc**, terminal caudal vertebra. Scale bars equal 10 cm.

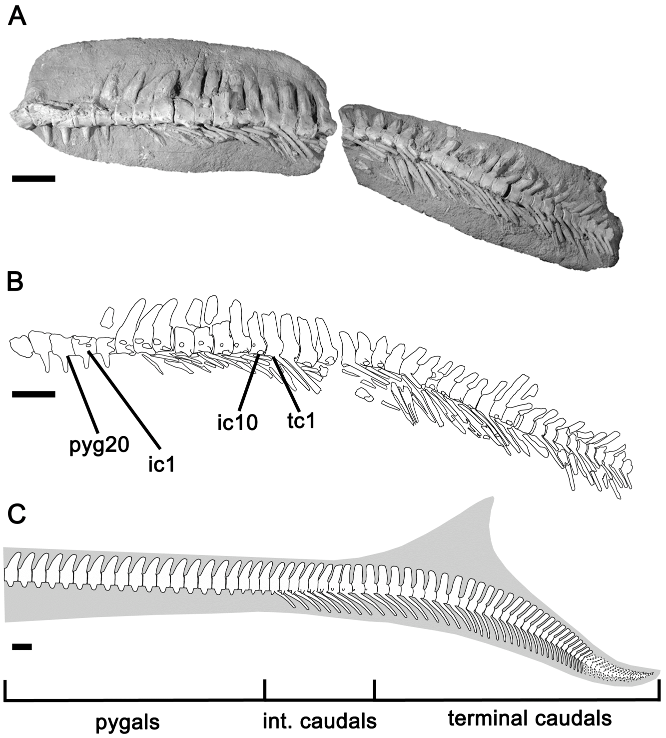

A
B
pyg20
ic1
ic10
tc1
C
pygals
int. caudals
terminal caudals

FIGURE 2–9. Comparison of hind limb elements between *Eremiasaurus*, UALVP 51744, *Clidastes* and *Mosasaurus*. All hind limbs reconstructed as the medial aspects of the left hind limb. **A**, closeup of sixth block of UALVP 51744 showing positions of isolated hind limb elements as they were preserved. Scale bar equals 10 cm. **B**, reconstruction of preserved portions of the hind limb of *Eremiasaurus*. Scale bar equals 5 cm. **C**, reconstruction of a partial hind limb of *Clidastes* (modified from Russell, 1967:fig. 60). **D**, reconstruction of a partial hind limb of *Mosasaurus* (modified from Dollo, 1892:Fig. 2–1). **Abbreviations**: **4**, fourth distal tarsal; **aft**, anterior flange of the tibia; **as**, astragalus; **cf**, crural foramen; **cm**, calcaneum; **dfhe**, distal fibular head expansion; **fe**, femur; **fi**, fibula; **fmt1**, facet for the first metatarsal; **t**, tibia.

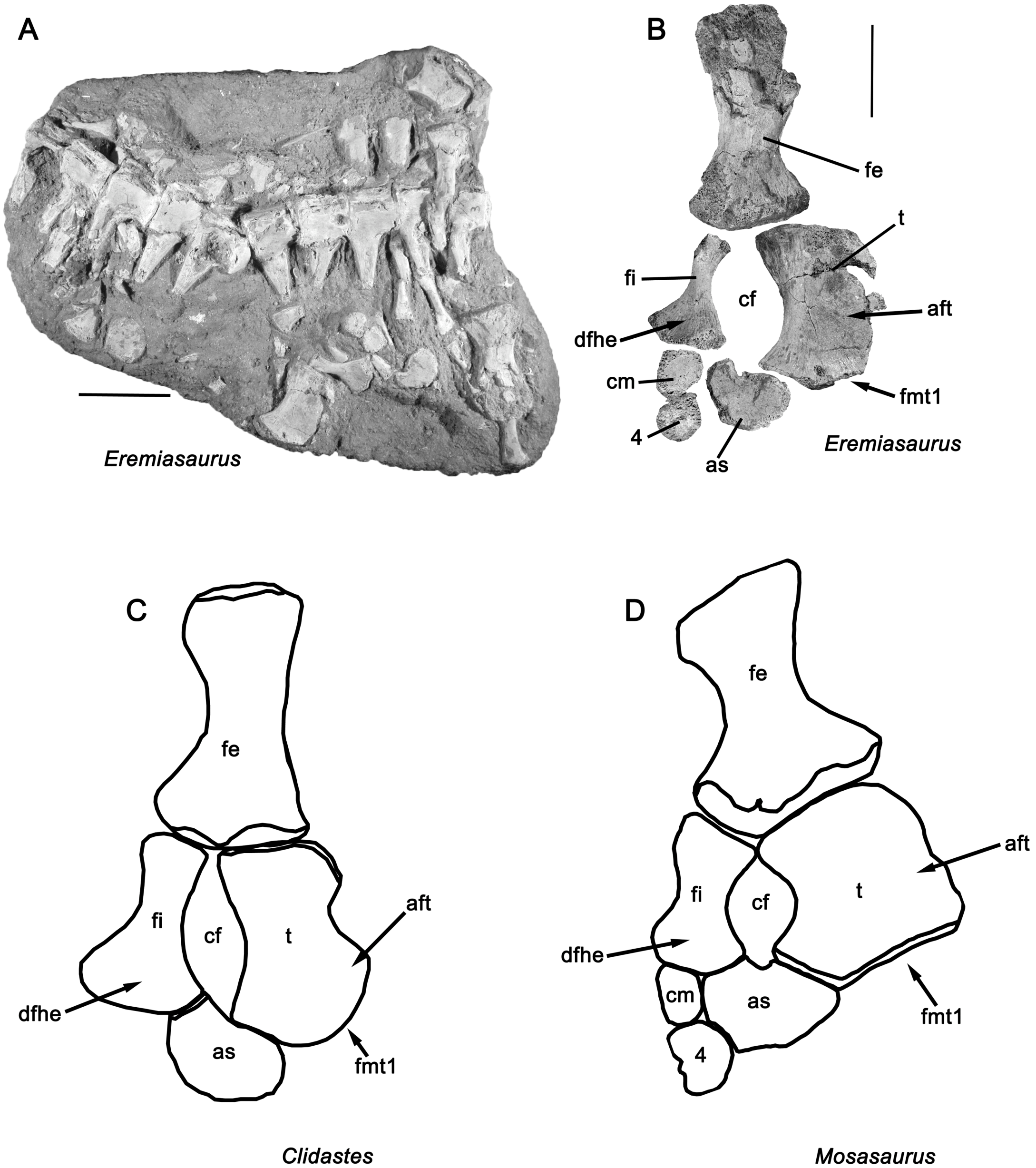

A
Eremiasaurus
B
fe
t
fi
cf
aft
dfhe
cm
fmt1
4
as
Eremiasaurus
C
fe
fi
cf
t
aft
dfhe
as
fmt1
Clidastes
D
fe
aft
fi
cf
t
dfhe
cm
as
fmt1
4
Mosasaurus

FIGURE 2–10. 50% majority rule consensus trees from phylogenetic analyses 1 and 2. **A**, 50% majority rule consensus tree of 3 most parsimonious trees of length 362, showing relationships within the Mosasauroidea. **B**, 50% majority rule consensus tree of 252 most parsimonious trees of length 399. Lighter shaded boxes indicate taxa normally grouped within the Mosasaurini (Plotosaurini sensu Bell, 1997). Darker shaded boxes indicate taxa normally grouped in the Globidensini.

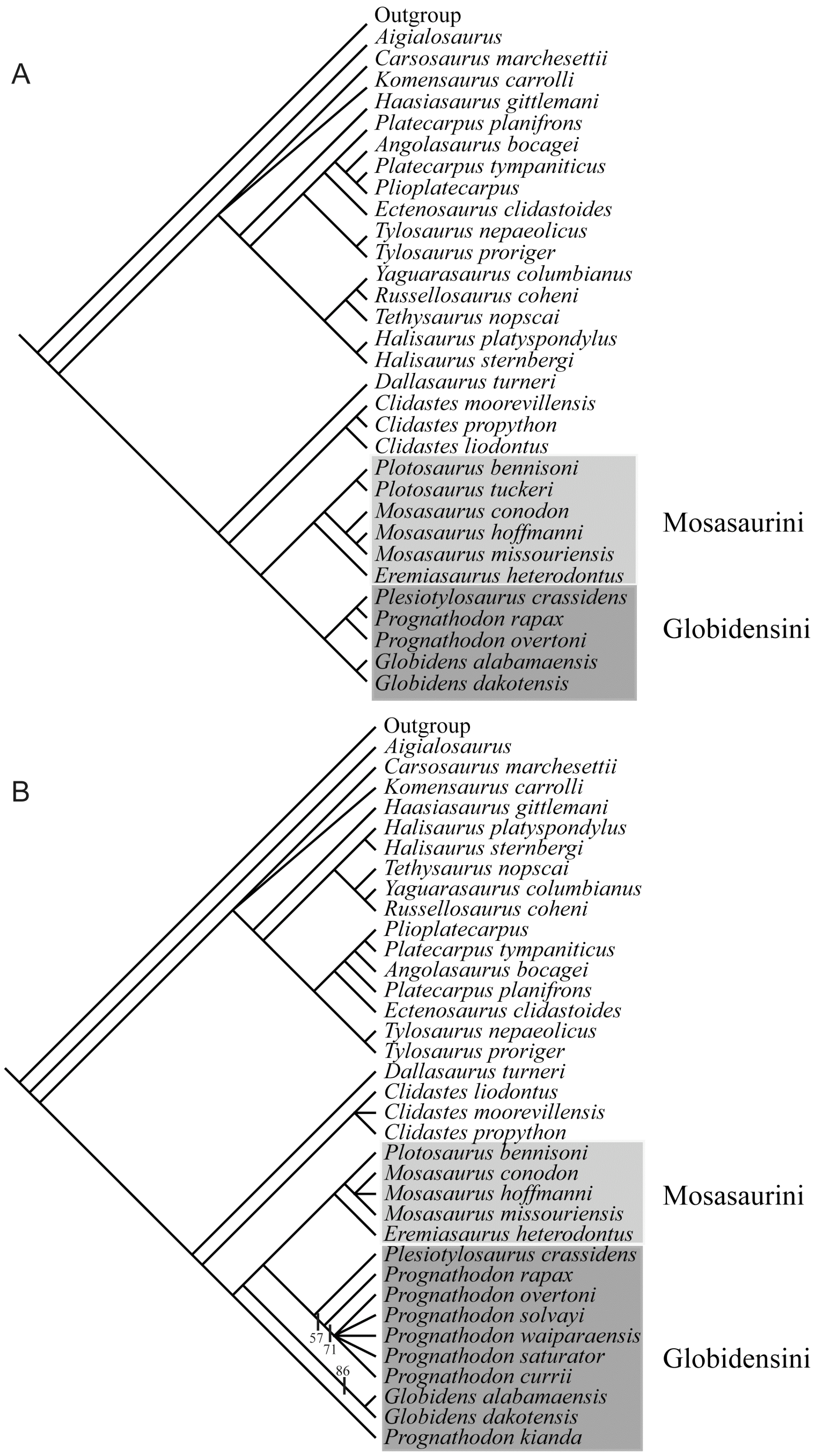

A
Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Platecarpus planifrons
Angolasaurus bocagei
Platecarpus tympaniticus
Plioplatecarpus
Ectenosaurus clidastoides
Tylosaurus nepaeolicus
Tylosaurus proriger
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopscai
Halisaurus platyspondylus
Halisaurus sternbergi
Dallasaurus turneri
Clidastes moorevillensis
Clidastes propython
Clidastes liodontus
Plotosaurus bennisoni
Plotosaurus tuckeri
Mosasaurus conodon
Mosasaurus hoffmanni
Mosasaurus missouriensis
Eremiasaurus heterodontus
Mosasaurini
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Globidens alabamaensis
Globidens dakotensis
Globidensini
B
Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Halisaurus platyspondylus
Halisaurus sternbergi
Tethysaurus nopscai
Yaguarasaurus columbianus
Russellosaurus coheni
Plioplatecarpus
Platecarpus tympaniticus
Angolasaurus bocagei
Platecarpus planifrons
Ectenosaurus clidastoides
Tylosaurus nepaeolicus
Tylosaurus proriger
Dallasaurus turneri
Clidastes liodontus
Clidastes moorevillensis
Clidastes propython
Plotosaurus bennisoni
Mosasaurus conodon
Mosasaurus hoffmanni
Mosasaurus missouriensis
Eremiasaurus heterodontus
Mosasaurini
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Prognathodon solvayi
Prognathodon waiparaensis
Prognathodon saturator
Prognathodon currii
Globidens alabamaensis
Globidens dakotensis
Prognathodon kianda
Globidensini
57
71
86

FIGURE 2–11. Character reconstruction of 3 characters that were traditionally considered globidensine synapomorphies prior to this analysis. All trees represent the 50% majority rule consensus tree from analysis 2. **A**, reconstruction of character 45 (presence/absence of quadrate process fusion), bold lines indicate taxa possessing state 1: processes fused. **B**, reconstruction of character 75 (presence/absence of coarse enamel ornamentation), bold lines indicate taxa possessing state 1: presence of very coarsely ornamented teeth. **C**, reconstruction of character 78 (tooth crown inflation), bold lines indicate taxa possessing state 1: crowns swollen at base or near tip.


A
Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Halisaurus platyspondylus
Halisaurus sternbergi
Tethysaurus nopscai
Yaguarasaurus columbianus
Russellosaurus coheni
Plioplatecarpus
Platecarpus tympaniticus
Angolosaurus bocagei
Platecarpus planifrons
Ectenosaurus clidastoides
Tylosaurus nepaeolicus
Tylosaurus proriger
Dallasaurus turneri
Clidastes liodontus
Clidastes moorevillensis
Clidastes propython
Plotosaurus bennisoni
Mosasaurus conodon
Mosasaurus hoffmanni
Mosasaurus missouriensis
Eremiasaurus heterodontus
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Prognathodon solvayi
Prognathodon waiparaensis
Prognathodon saturator
Prognathodon currii
Globidens alabamaensis
Globidens dakotensis
Prognathodon kianda
B
Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Halisaurus platyspondylus
Halisaurus sternbergi
Tethysaurus nopscai
Yaguarasaurus columbianus
Russellosaurus coheni
Plioplatecarpus
Platecarpus tympaniticus
Angolosaurus bocagei
Platecarpus planifrons
Ectenosaurus clidastoides
Tylosaurus nepaeolicus
Tylosaurus proriger
Dallasaurus turneri
Clidastes liodontus
Clidastes moorevillensis
Clidastes propython
Plotosaurus bennisoni
Mosasaurus conodon
Mosasaurus hoffmanni
Mosasaurus missouriensis
Eremiasaurus heterodontus
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Prognathodon solvayi
Prognathodon waiparaensis
Prognathodon saturator
Prognathodon currii
Globidens alabamaensis
Globidens dakotensis
Prognathodon kianda
C
Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Halisaurus platyspondylus
Halisaurus sternbergi
Tethysaurus nopscai
Yaguarasaurus columbianus
Russellosaurus coheni
Plioplatecarpus
Platecarpus tympaniticus
Angolosaurus bocagei
Platecarpus planifrons
Ectenosaurus clidastoides
Tylosaurus nepaeolicus
Tylosaurus proriger
Dallasaurus turneri
Clidastes liodontus
Clidastes moorevillensis
Clidastes propython
Plotosaurus bennisoni
Mosasaurus conodon
Mosasaurus hoffmanni
Mosasaurus missouriensis
Eremiasaurus heterodontus
Plesiotylosaurus crassidens
Prognathodon rapax
Prognathodon overtoni
Prognathodon solvayi
Prognathodon waiparaensis
Prognathodon saturator
Prognathodon currii
Globidens alabamaensis
Globidens dakotensis
Prognathodon kianda

FIGURE 2–12. 50% majority rule of 36 most parsimonious trees after deletion of character 75 (presence or absence of coarse enamel ornamentation) and character 78 (presence or absence of basal tooth crown inflation) from the dataset used in the second analysis. TL = 390, CI = 0.426, RI = 0.705, HI = 0.574.


Outgroup
Aigialosaurus
Carsosaurus marchesettii
Komensaurus carrolli
Haasiasaurus gittlemani
Halisaurus platyspondylus
Halisaurus sternbergi
Tethysaurus nopscai
Yaguarasaurus columbianus
Russellosaurus coheni
Plioplatecarpus
Platecarpus tympaniticus
Angolasaurus bocagei
Platecarpus planifrons
Ectenosaurus clidastoides
Tylosaurus nepaeolicus
Tylosaurus proriger
Dallasaurus turneri
Clidastes liodontus
Clidastes moorevillensis
Clidastes propython
Plotosaurus bennisoni
Mosasaurus conodon
Mosasaurus hoffmanni
Mosasaurus missouriensis
Eremiasaurus heterodontus
Mosasaurini
Prognathodon rapax
Plesiotylosaurus crassidens
Prognathodon overtoni
Prognathodon saturator
Prognathodon waiparaensis
Prognathodon solvayi
Prognathodon currii
Globidens alabamaensis
Globidens dakotensis
Prognathodon kianda
Globidensini

LITERATURE CITED

Arambourg, C. 1935. Note préliminaire sur les vertébrés fossiles des phosphates du Maroc. Bulletin de la Société géologique de France 10:127–47.

Arambourg, C. 1952. Les vertébrés fossils des gisements de phosphates (Maroc–Algérie–Tunisie). Notes et Mémoires du service géologique du Maroc 92: 1–372.

Bardet, N., X. Pereda Suberbiola. 2002. Marine reptiles from the Late Cretaceous Phosphates of Jordan: palaeobiogeographical implications. Geodiversitas 24:831–839.

Bardet, N., X. Pereda Suberbiola, M. Iarochène, F. Bouyahyaoui, B. Bouya, and M. Amaghzaz. 2004. *Mosasaurus beaugei* Arambourg, 1952 (Squamata, Mosasauridae) from the Late Cretaceous phosphates of Morocco. Geobios 37:315–324.

Bardet, N., X. Pereda Suberbiola, M. Iarochène, M. Amalik, and B. Bouya. 2005a. Durophagous Mosasauridae (Squamata) from the Upper Cretaceous phosphates of Morocco, with description of a new species of *Globidens*. Netherlands Journal of Geosciences 84:167–175.

Bardet, N., X. Pereda Suberbiola, M. Iarochène, B. Bouya, and M. Amaghzaz. 2005b. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the

Halisaurinae (Squamata: Mosasauridae). Zoological Journal of the Linnean Society 143:447–472.

Bardet, N., X. Pereda Suberbiola, A. S. Schulp, and B. Bouya. 2008. New material of *Carinodens* (Squamata, Mosasauridae) from the Maastrichtian (Late Cretaceous) phosphates of Morocco in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:29–36.

Bardet, N., X. Pereda Suberbiola, S. Jouve, E. Bourdon, P. Vincent, A. Houssaye, J.–C. Rage, N.–E. Jalil, B. Bouya, and M. Amaghzaz. 2010. Reptilian assemblages from the latest Cretaceous – Palaeogene phosphates of Morocco: from Arambourg to present time. Historical Biology 22:186–199.

Bell, G. L., Jr. 1993. A phylogenetic revision of North American and Adriatic Mosasauroidea (Squamata). Unpublished Ph.D thesis, University of Texas at Austin, 293 pp.

Bell, G. L., Jr. 1997. Chapter 11. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293–332 in J. M. Callaway, and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bell, G. L., Jr., and M. J. Polcyn. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). Netherlands Journal of Geosciences 84:177–194.

Caldwell, M. W., and A. Palci. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. Journal of Vertebrate Paleontology 27:863–880.

Caldwell, M. W., and Bell, G. L., Jr. 2005. Of German princes and North American rivers: Harlan's lost mosasaur snout rediscovered. Netherlands Journal of Geosciences 84:207–211.

Camp, C. L. 1942. California Mosasaurs. Memoirs of the University of California 13:1–68.

Camp, C. L. 1951. *Plotosaurus*, a new generic name for *Kolposaurus* Camp, preoccupied. Journal of Paleontology 25:822.

Cappetta, H. 1987. Mesozoic and Cenozoic Elasmobranchii, Chondrichthyes II. In: Schultze, H.-P. (Ed.), Handbook of Paleoichthyology. Gustav Fischer Verlag, Stuttgart and NewYork, vol. 3B, 193 p.

Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22:629–644.

Conybeare, W. D. 1822. Fossil crocodiles and other saurian animals; pp. 284–304 in J. Parkinson, outlines of Oryctology. An Introduction to the Study of Fossil Organic Remains; Especially of Those Found in the British Strata: Intended to Aid the Student in his Enquiries Respecting the Nature of Fossils, and Their Connection with the Formation of the Earth vii.

Cope, E. D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. Boston Society of Natural History Proceedings 12:250–266.

Cope, E. D. 1871. On some species of Pythonomorpha from the Cretaceous beds of Kansas and New Mexico. Proceedings of the American Philosophical Society of 11:574–584.

Cope, E. D. 1868. On new species of extinct reptiles. Proceedings of the Academy of Natural Sciences of Philadelphia 20:181.

Dalrymple, G. H. 1979. The jaw mechanism of the snail-crushing lizards, *Dracaena* Daudin 1802 (Reptilia, Lacertilia, Teiidae). Journal of Herpetology 13:303–311.

Dames, W. 1881. Frischzahne aus der obersenonen Tuffkreide von Maastricht (Rhombodus, g.n.). Neues Jahrbuch für Mineralogie, Geologie und Palaontologie 1:115–117.

De Queiroz, K., and J. Gauthier. 1992. Phylogenetic Taxonomy. Annual Review of Ecology and Systematics 23:449–480.

Dollo, L. 1889. Note sur les vertébrés fossiles récemment offerts au Musée de Bruxelles par M. Alfred Lemonnier. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 3:181–182.

Dollo, L. 1892. L'ostéologie des mosasauriens. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie 4:218–259.

Dollo, L. 1904. Les mosasauriens de la Belgique. Bulletin de la Société Belge de Géologie, de Paléontologie et Hydrologie 19:125–131.

Dortangs, R. W., A. S. Schulp, E. W. A. Mulder, J. W. M. Jagt, H. H. G. Peeters, and D. Th. de Graaf. 2002. A large new mosasaur from the Upper

Cretaceous of the Netherlands. Netherlands Journal of Geosciences 81:1–8.

Dutchak, A. R., and M. W. Caldwell. 2006. Redescription of *Aigialosaurus dalmaticus* Kramberger, 1892, a Cenomanian mosasauroid lizard from Hvar Island, Croatia. Canadian Journal of Earth Sciences 43:1821–1834.

Dutchak, A. R., and M. W. Caldwell. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. Journal of Vertebrate Paleontology 29:437–452.

Gaudry, A. 1892. Les pythonomorphes de France. Mémoires de la Société Géologique de France (Paléontologie) 10: 13 + iv pp.

Gervais, P. 1853. Observations relatives aux reptiles fossiles de France. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 36:374–377, 470–474.

Gheerbrant, E., J. Sudre, H. Cappetta, C. Mourer–Chauviré, E. Bourdon, M. Iarochène, M. Amaghzaz, and B. Bouya. 2003. Les localités à mammifères des carrières de Grand Daoui, basin des Oulad Abdoun, Maroc, Yprésien: premier état des lieux. Bulletin de la Société Géologique de France 174:279–293.

Harlan, R. 1834. Notice of the discovery of the remains of the *Ichthyosaurus* in Missouri, N. A. Transactions of the American Philosophical Society 4:405–409.

Konishi, T. 2008. A new specimen of *Selmasaurus* sp., cf. *S. russelli* (Mosasauridae: Plioplatecarpini) from Greene County, Western Alabama, USA in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:95–105.

Konishi, T., and M. W. Caldwell. 2007. New specimens of *Platecarpus planifrons* (Cope, 1874) (Squamata: Mosasauridae) and a revised taxonomy of the genus. Journal of Vertebrate Paleontology 27:59–72.

Lindgren, J., J. W. M. Jagt, and M. W. Caldwell. 2007. A fishy mosasaur—the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. Lethaia 40:153–160.

Lindgren, J., M. W. Caldwell, and J. W. M. Jagt. 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). Journal of Vertebrate Paleontology 28:1043–1054.

Lindgren, J. 2009. Cranial osteology of the giant mosasaur *Plesiotylosaurus* (Squamata, Mosasauridae). Journal of Paleontology 83:448–456.

Lindgren, J., M. W. Caldwell, T. Konishi, and L. M. Chiappe. 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. PLoS ONE 5:e11998. Doi:10.1371/journal.pone.0011998.

Lingham-Soliar, T. 1991. Mosasaurs from the Upper Cretaceous of Niger. Palaeontology 34:653–670.

Lingham-Soliar, T. 1993. The mosasaur *Leiodon* bares its teeth: pp. 443–458 in W. A. S. Sarjeant (ed.), Fossil vertebrates: faunas and concepts (Special issue, Halstead Memorial Volume). Modern Geology 18.

Lingham-Soliar, T. 1994. The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 64:177–211.

Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, upper Maastrichtian of the Netherlands. Philosophical Transactions of the Royal Society of London B347:155–180.

Lingham-Soliar, T., and D. Nolf. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 59:137–190.

Linneus, C. 1758. Systema Naturae, Edition X, vol. 1 (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.) Holmiae Salvii, 824 pp.

Machalski, M., J. W. M. Jagt, R. W. Dortangs, E. W. A. Mulder, and A. Radwanski. 2003. Campanian and Maastrichtian mosasaurid reptiles from central Poland. Acta Palaeontologica Polonica 48:397–408.

Mantell, G. A. 1829. A tabular arrangement of the organic remains of the county of Sussex. Geological Society of London Transactions 3:201–216.

Marsh, O. C. 1872. Note on *Rhinosaurus*. American Journal of Science 3rd series 4:147.

Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7:121–137.

Merriam, J. C. 1894. Ueber die Pythonomorphen der Kansas-Kreide. Palaeontolographica 41:1–39, pls. 1–4.

Mulder, E. W. A. 1999. Transatlantic latest Cretaceous mosasaurs (Reptilia, Lacertilia) from the Maastrichtian type area and New Jersey. Geologie en Mijnbouw 78:281–300.

Nicholls, E. L., and Meckert, D. 2002. Marine reptiles from the Nanaimo Group (Upper Cretaceous) of Vancouver Island. Canadian Journal of Earth Sciences 39:1591–1603.

Noubhani, A. 2010. The selachians' faunas of the Moroccan phosphate deposits and the KT mass-extinctions. Historical Biology 22:71–77.

Office Chérifien des Phosphates. 1989. The phosphate basins of Morocco; pp. 301–311 in Northolt, A. J. G., Sheldon, R. P., and Davidson, D. F. (eds.): Phosphates deposits of the world, Vol. 2 – Phosphate rock resources. Cambridge University Press, Cambridge.

Oppel, M. 1811. Die Ordungen Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, München, 86 pp.

Owen, R. 1840–1845. Odontography; or, a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure in the vertebrate animals. London: Hippolyte Bailliere. Vol. 1 (text) xix + lxxiv + 655 pp; Vol. 2 (atlas)37 pp. + 168 pls.

Polcyn, M. J., L. L. Jacobs, A. S. Schulp, and O. Mateus. The North African mosasaur *Globidens phosphaticus* from the Maastrichtian of Angola. Historical Biology 22: 175–185.

Rieppel, O., and L. Labhardt. 1979. Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). Herpetologica 35:158–163.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs (Reptilia, Sauria). Peabody Museum of Natural History, Yale University, Bulletin 23:1–241.

Schulp, A. S. 2006. A comparative description of *Prognathodon saturator* (Mosasauridae, Squamata), with notes on its phylogeny; pp. 19–56 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. L. Jacobs, M. L. Morais, and T. da S. Tavares. 2006. New mosasaur material from the Maastrichtian of Angola, with notes on the phylogeny, distribution and palaeoecology of the genus *Prognathodon*: pp. 57–67 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. J. Jacobs, and M. L. Morais. 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon* in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:1–12.

Schulp, A. S., N. Bardet, and B. Bouya. 2009. A new species of the durophagous mosasaur *Carinodens* (Squamata, Mosasauridae) and additional material of *Carinodens belgicus* from the Maastrichtian phosphates of Morocco. Netherlands Journal of Geosciences 88:161–167.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Wägele, J.-W. (ed.). 2005. Foundations of phylogenetic systematics. Verlag Dr. Friedrich Pfeil, München, 365 pp.

Weiler, W. 1930. Frischreste aus dem nubischen Sandstein von Mohamid und Edfu und aus den Phosphaten Oberagyptens und der Oase Bahariga, Agypten, in Ergebnisse der Forschungsreisen Prof. E. Stromer's *in* den Wusten Agyptens: Abhandlungen Bayerische Akademie der Wissenschaft, Math.-Naturk. Abteilung N. F., 7, 12–42.

Welles, S. P., and D. R. Gregg. 1971. Late Cretaceous marine reptiles of New Zealand. Records of the Canterbury Museum 9:1–111.

Wright, K. R., and S. W. Shannon. 1988. *Selmasaurus russelli*, a new plioplatecarpine mosasaur (Squamata, Mosasauridae) from Alabama. Journal of Vertebrate Paleontology 8:102–107.

APPENDIX 1. Description of characters used in phylogenetic analysis (modified from Bell, 1997).

1. Premaxilla predental rostrum I: total lack of a bony rostrum (0); or presence of any predental rostrum (1). In lateral profile, the anterior end of the premaxilla either exhibits some bony anterior projection above the dental margin, or the bone recedes posterodorsally from the dental margin. State 1 produces a relatively taller lateral profile with an obvious “bow” or “prow”.
2. Premaxilla predental rostrum II: rostrum very short and obtuse (0); or distinctly protruding (1); or very large and inflated (2). In *Clidastes* a short, acute, protruding rostrum (state 1) produces a “V-shaped” dorsal profile and, as far as is known, is peculiar to that genus. An alternative condition, described as “U-shaped”, includes those taxa whose rostral conditions span the whole range of states of characters 1 and 2. Hence, the descriptive character is abandoned in favor of a more informative structure-based series.
3. Premaxilla shape: bone broadly arcuate anteriorly (0); or relatively narrowly arcuate or acute anteriorly (1). In virtually all lizards the premaxilla is a very widely arcuate and lightly constructed element, and the base of the internarial process is quite narrow as in *Opetiosaurus*. All other mosasaurids have a very narrowed premaxilla with the teeth forming a tight curve and the internarial process being proportionally wider (state 1).

4. Premaxilla internarial bar width: narrow, distinctly less than half of the maximum width of the rostrum in dorsal view (0); or wide, being barely narrower than the rostrum (1).

5. Premaxilla internarial bar base shape: triangular (0); or rectangular (1). A vertical cross section through the junction of the internarial bar and the dentigerous rostrum produces an inverted triangle in most taxa. But in state 1, this cross section is transversely rectangular because the broad ventral surface of the bar is planar.

6. Premaxilla internarial bar dorsal keel: absent (0); or present (1). In state 1 a ridge rises above the level of a normally smoothly continuous transverse arch formed by the bones of the anterior muzzle. Because of the distinct difference of form, these structures may not be homologous in *Tylosaurus* and *Mosasaurus*-*Plotosaurus*.

7. Premaxilla internarial bar venter: with entrance for the fifth cranial (facial) nerve close to rostrum (0); or far removed from rostrum (1). The conduit that marks the path of the fifth cranial nerve from the maxilla into the premaxilla is expressed as a ventrolateral foramen within the premaxillo-pmaxillary sutural surface at the junction of the internarial bar and the dentigerous rostrum. State 1 includes a long shallow groove on the ventral surface of the bar. Anteriorly, this groove becomes a tunnel entering the bone at an extremely shallow angle, but disappearing below the surface at least 1 cm behind the rostrum.

8. Frontal shape: sides sinusoidal (0); or bone nearly triangular and sides relatively straight (1). In state 1, the area above the orbits is expanded and an

isosceles triangle is formed by the rectilinear sides. In certain taxa, a slight concavity is seen above the orbits, but anterior and posterior to this, there is no indication of a sinusoidal or recurved edge.

9. Frontal width: element broad and short (0); intermediate dimensions (1); or long and narrow (2). Mosasauroid frontals can be separated into a group that generally has a maximum length to maximum width ratio greater than 2:1 (state 2), between 1.5:1 and 2:1 (state 1), or equal to or less than 1.5:1 (state 0).

10. Frontal narial emargination: frontal not invaded by posterior end of nares (0); or distinct embayment present (1). In some mosasauroids, the posterior ends of the nares are concomitant with the anterior terminus of the frontal-prefrontal suture and, therefore, there is no marginal invasion of the frontal by the opening. However, in other mosasauroids this suture begins anterior and lateral to the posterior ends of the nares, causing a short emargination into the frontal.

11. Frontal midline dorsal keel: absent (0); or low, fairly inconspicuous (1); or high, thin, and well developed (2).

12. Frontal ala shape: sharply acuminate (0); or more broadly pointed or rounded (1). In state 0, the anterolateral edge of the ala is smoothly concave, thus helping to form the sharply pointed or rounded and laterally oriented posterior corners. In some Natantia, the anterolateral edge of the ala may be concave, but the tip is not sharp and directed laterally.

13. Frontal olfactory canal embrasure: canal not embraced ventrally by descending processes (0); or canal almost or completely enclosed below (1). In

state 1, very short descending processes from sides of the olfactory canal surround and almost, or totally enclose the olfactory nerve.

14. Frontal posteroventral midline: tabular boss immediately anterior to the frontal-parietal suture absent (0); or present (1). A triangular boss with a flattened ventral surface at the posterior end of the olfactory canal is represented by state 1.

15. Frontal-parietal suture: apposing surfaces with low interlocking ridges (0); or with overlapping flanges (1). In state 0, an oblique ridge on the anterior sutural surface of the parietal intercalates between a single median posterior and a single lateral posterior ridge from the frontal. In state 1, these ridges are protracted into strongly overlapping flanges. The dorsal trace of the suture can be quite complex with a portion of the parietal embraced by the posterior extension of these frontal flanges.

16. Frontal-parietal suture overlap orientation: suture with oblique median frontal and parietal ridges contributing to overlap (0); or with all three ridges almost horizontal (1). In state 0, the median ridge from the frontal and the single parietal ridge are oriented at a distinct angle to the upper skull surface while the outer, or lateral, frontal ridge appears to be nearly horizontal. In *Tylosaurus nepaeolicus* and *T. proriger* (state 1), the obliquity of the intercalating ridges is reclined almost to the horizontal, greatly extending the amount of lateral overlap.

17. Frontal invasion of parietal I: lateral sutural flange of frontal posteriorly extended (0); or median frontal sutural flange posteriorly extended (1); or both extended (2). In all mosasaurines the oblique median frontal sutural ridge extends onto the dorsal surface of the parietal table and embraces a portion of the anterior

table within a tightly crescentic midline embayment. In *Plioplatecarpus*, and *Platecarpus*, the lateral oblique sutural ridge from the frontal is greatly protracted posteriorly to cause a large, anteriorly convex embayment in the dorsal frontal-parietal suture. In this case the entire posterolateral corner of the frontal is extended backwards to embrace the anterolateral portion of the parietal table on both sides. Consequently, the parietal foramen is very widely embraced laterally and the oblique anterior sutural ridge of the parietal occupies a position inside the embayment within the frontal.

18. Frontal medial invasion of parietal II: if present, posteriorly extended median sutural ridge short (0); or long (1). The median oblique sutural ridge is either short, not reaching back to the parietal foramen (state 0), or tightly embraces the foramen while extending backwards to a position even with or beyond its posterior edge (state 1).

19. Parietal length: dorsal surface relatively short with epaxial musculature insertion posterior, between suspensorial rami only (0); or dorsal surface elongate, with epaxial musculature insertion dorsal as well as posterior (1).

20. Parietal table shape: generally rectangular to trapezoidal, with sides converging, but not meeting (0); or triangular, with sides contacting in front of suspensorial rami (1); or triangular table with posterior portion forming parasagittal crest or ridge (2).

21. Parietal foramen size: relatively small (0); or large (1). If the foramen is smaller than or equal to the area of the stapedial pit, it is considered small. If the foramen is significantly larger or if the distance across the foramen is more than

half the distance between it and the nearest edge of the parietal table, the derived state is achieved.

22. Parietal foramen position I: foramen generally nearer to center of parietal table, well away from frontal-parietal suture (0); or close to or barely touching suture (1); or huge foramen straddling suture and deeply invading frontal (2). Generally in state 1, the distance from the foramen to the suture is about equal to or less than one foramen's length.

23. Parietal foramen ventral opening: opening is level with main ventral surface (0); or opening surrounded by a rounded, elongate ridge (1).

24. Parietal posterior shelf: presence of a distinct horizontal shelf projecting posteriorly from between the suspensorial rami (0); or shelf absent (1). In some mosasauroids, a somewhat crescent-shaped shelf (in dorsal view) lies at the posterior end of the bone medial to, and below, the origination of the suspensorial rami.

25. Parietal suspensorial ramus compression: greatest width vertical or oblique (0); or greatest width horizontal (1). In *Tylosaurus*, the anterior edge of the ramus begins very low on the lateral wall of the descending process, leading to formation of a proximoventral sulcus, but the straps are horizontal distally.

26. Parietal union with supratemoral: suspensorial ramus from parietal overlaps supratemporal without interdigitation (0); or forked distal ramus sandwiches proximal end of supratemporal (1).

27. Prefrontal supraorbital process: process absent, or present as a very small rounded knob (0); or a distinct, to large, triangular or rounded overhanging wing (1).

28. Prefrontal contact with postorbitofrontal: no contact at edge of frontal (0); of elements in contact there (1). State 1 is usually described as the frontal being emarginated above the orbits. Often this character can be evaluated by examining the ventral surface of the frontal where depressions outline the limits of the sutures for the two ventral elements.

29. Prefrontal-postorbitofrontal overlap: prefrontal overlapped ventrally by portorbitofrontal (0); or prefrontal overlapped laterally (1). Postorbitofrontal ventral overlap of the prefrontal is extreme in *Platecarpus tympaniticus*, and *Plioplatecarpus*, such that there is even a thin flange of the frontal interjected between the prefrontal above and the postorbitofrontal below. In *T. proriger*, the postorbitofrontal sends a long narrow process forward to fit into a lateral groove on the prefrontal. In *Plesiotylosaurus*, the overlap is relatively short and more oblique, and there is no groove on the prefrontal.

30. Postorbitofrontal shape: narrow (0); or wide (1). In *Clidastes* and the Globidensini, the lateral extent of the element is almost equal to half of the width of the frontal and the outline of the bone is basically squared, while in all the other ingroup and outgroup taxa, it is a fairly narrow hourglass shape.

31. Postorbitofrontal transverse dorsal ridge: absent (0); or present (1). In state 1, an inconspicuous, low and narrowly rounded ridge traces from the

anterolateral corner of the parietal suture across the of the element to disappear behind the origin of the jugal process.

32. Postorbitofrontal squamosal ramus: does (0); or does not (1), reach end of temporal fenestra.

33. Maxilla tooth number: 20-24 (0); or 17-19 (1); or 15-16 (2); or 14 (3); or 13 (4); or 12 (5).

34. Maxillo-premaxillary suture posterior terminus: suture ends above a point that is anterior to or even with the midline of the fourth maxillary tooth (0); or between the fourth and ninth teeth (1); or even with or posterior to the ninth tooth (2). These somewhat arbitrary divisions of the character states are meant to describe in more concrete terms those sutures that terminate far anteriorly, those that terminate less anteriorly, and those that terminate near the midlength of the maxilla, respectively.

35. Maxilla posterodorsal process: recurved wing of maxilla dorsolaterally overlaps a portion of the anterior end of the prefrontal (0); or process absent (1).

36. Maxilla posterodorsal extent: recurved wing of maxilla prevents emargination of prefrontal on dorsolateral edge of external naris (0); or does not (1).

37. Jugal posteroventral angle: angle very obtuse or curvilinear (0); or slightly obtuse, near 120 degrees (1); or 90 degrees (2).

38. Jugal posteroventral process: absent (0); or present (1).

39. Ectopterygoid contact with maxilla: present (0); or absent (1).

40. Pterygoid tooth row elevation: teeth arise from robust, transversely flattened, main shaft of pterygoid (0); or teeth arise from thin pronounced vertical ridge (1). In state 0, the teeth emanate from the relatively planar surface of the thick, slightly dorsoventrally compressed main shaft of the pterygoid. In state 1, a tall, thin dentigerous ridge emanates ventrally from a horizontal flange that forms the base of the quatratic ramus and the ectopterygoid process, thus causing the main shaft to be trough-shaped.

41. Pterygoid tooth size: anterior teeth significantly smaller than marginal teeth (0); or anterior teeth large, approaching size of marginal teeth (1).

42. Quadrate suprastapedial process length: process short, ends at a level well above midheight (0); or of moderate length, ending very near midheight (1); or long, distinctly below midheight (2).

43. Quadrate suprastapedial process constriction: distinct dorsal constriction (0); or virtually no dorsal constriction (1). Lack of constriction results in an essentially parallel-sided process in posterodorsal view, but can also include the tapering form characteristic of some *Tylosaurus*.

44. Quadrate suprastapedial ridge: if present, ridge on ventromedial edge of suprastapedial process indistinct, straight and/or narrow (0); or ridge wide, broadly rounded, and curving downward, especially above stapedial pit (1).

45. Quadrate suprastapedial process fusion: no fusion present (0); or process fused to elaborated process from below (1). A posterior rugose area may be inflated and broadened mediolaterally to partially enclose the ventral end of a broad and elongate suprastapedial process as in *Halisaurus*. In *Globidens*,

Prognathodon and *Plesiotylosaurus*, the process is fused ventrally to a narrow pedunculate medial extension of the tympanic rim. A similar condition is present in *Ectenosaurus*, except that the tympanic rim is not medially extended and has a short projection that overlaps a portion of the suprastapedial process posteriorly.

46. Quadrate stapedial pit shape: pit broadly oval to almost circular (0); or relatively narrowly oval (1); or extremely elongate with a constricted middle (2). In state 0, the length to width ratio is less than 1.8:1; in state 1 it ranges from 1.8:1 to 2.4:1; and in state 2, it is greater than 2.4:1.

47. Quadrate infrastapedial process: absent (0); or present (1). The infrastapedial process can be expressed as an elaborated or swollen rugose area on the posteroventral face of the main quadrate shaft, as an extension of the ascending posteroventral portion of the tympanic rim, or as a small protuberance emanating from the ventral end of the anterior meatal wall. These various structures are probably not homologous.

48. Quadrate posteroventral ascending tympanic rim condition: small, low ridge present (0); or a high, elongate crest (1); or a crest extremely produced laterally (2). In state 1, this extended rim causes a fairly deep sulcus in the ventral portion of the intratympanic cavity. In *Plioplatecarpus*, the entire lower tympanic rim and ala are expanded into a large conch (state 2), which tremendously increases the depth of the intratympanic cavity.

49. Quadrate ala thickness: ala thin (0); or thick (1). In state 0, the bone in the central area of the ala is only about 1 mm thick in medium-sized specimens and that area is usually badly crushed or completely destroyed. Alternatively, the ala

extends from the main shaft with only minor thinning, providing a great deal of strength to the entire bone.

50. Quadrate conch: ala and main shaft encompassing a deeply bowled area (0); or alar concavity shallow (1). A relatively deeper sulcus in the anterior part of the intratympanic cavity and more definition to the ala and the main shaft are features of state 0.

51. Basisphenoid pterygoid process shape: process relatively narrow with articular surface facing mostly anterolaterally (0); or somewhat thinner, more fan-shaped with a posterior extension of the articular surface causing a more lateral orientation (1).

52. Quadrate ala groove: absent (0); or long, distinct, and deep groove present in anterolateral edge of ala (1).

53. Quadrate median ridge: single thin, high ridge, dorsal to ventral (0); or ridge low and rounded with divergent ventral ridges (1).

54. Quadrate anterior ventral condyle modification: no upward deflection of anterior edge of condyle (0); or distinct deflection present (1). A relatively narrow bump in the otherwise horizontal trace of the anterior articular edge is also supertended by a sulcus on the anteroventral face of the bone.

55. Quadrate ventral condyle: condyle saddle-shaped, concave in anteroposterior view (0); or gently domed, convex in any view (1).

56. Basioccipital tubera size: short (0); or long (1). Long tubera are typically parallel-sided in posterior profile and protrude ventrolaterally at exactly 45

degrees from horizontal. Short tubera have relatively large bases that taper distally, and emanate more horizontally.

57. Basioccipital tubera shape: tubera not anteroposteriorly elongate (0); or anteroposteriorly elongate with rugose ventrolateral surfaces (1).

58. Basioccipital canal: absent (0); or present as a small pair separated by a median septum (1); or present as a large pair separated by a median septum (2); or present as a single bilobate canal (3).

59. Dentary tooth number: 20-24 (0); or 17-19 (1); or 15-16 (2); or 14 (3); or 13 (4); or 12 (5). It is easy to assume this character is correlated with the number of maxillary teeth, except that is not the case in *Ectenosaurus clidastoides*, which has 16 or 17 maxillary teeth and only 13 dentary teeth.

60. Dentary anterior projection: projection of bone anterior to first tooth present (0); or absent (1).

61. Dentary anterior projection length: short (0); or long (1). In state 1, the projection of bone anterior to the first tooth is at least the length of a complete tooth space.

62. Dentary medial parapet: parapet positioned at base of tooth roots (0); or elevated and strap-like, enclosing about half of height of tooth attachment in shallow channel (1), or strap equal in height to lateral wall of bone (2). States 1 and 2 are possible sequential stages of modification from a classically pleurodont dentition to the typical mosasaur "subthecodont" dentition.

63. Splenial-angular articulation shape: splenial articulation in posterior view almost circular (0); or laterally compressed (1); or intermediate (2).

64. Splenial-angular articular surface: essentially smooth cancavo-convex surfaces (0); or distinct horizontal tongues and grooves present (1).

65. Coronoid shape: coronoid with slight dorsal curvature, posterior wing not widely fan-shaped (0); or very concave above, posterior wing greatly expanded (1).

66. Coronoid posteromedial process: small but present (0); or absent (1).

67. Coronoid medial wing: does not reach angular (0); or contacts angular (1).

68. Coronoid posterior wing: without medial crescentic pit (0); or with distinct excavation (1). In state 1, there is a posteriorly open, C-shaped exavation in the medial side of the posterior wing of this element.

69. Surangular coronoid buttress: low, thick, about parallel to lower edge of mandible (0); or high, thin, rapidly rising anteriorly (1). A rounded dorsal edge of the surangular remains almost parallel to the ventral edge as it approaches the posterior end of the coronoid, meeting the latter element near its posteroventral edge in state 0. In state 1, the dorsal edge rises and thins anteriorly until meeting the posterior edge of the coronoid near its apex, producing a triangular posterior mandible in lateral aspect.

70. Surangular-articular suture position: behind the condyle in lateral view (0); or at middle of glenoid on lateral edge (1). In state 1, there is usually an interdigitation in the dorsal part of the suture.

71. Surangular-articular lateral suture trace: suture descends and angles or curves anteriorly (0); or is virtually straight throughout its length (1). In state 1, the suture trails from the glenoid posteriorly about halfway along the dorsolateral

margin of the retroarticular process, then abruptly turns anteriorly off the edge and strikes in a straight line for the posterior end of the angular.

72. Articular retroarticular process inflection: moderate inflection, less than 60 degrees (0); or extreme inflection, almost 90 degrees (1). In *Mosasaurus*, *Plotosaurus*, and *Prognathodon overtoni*, the posterior terminus of the lower jaw lies almost horizontal, probably allowing for more muscle attachment.

73. Articular retroarticular process innervation foramina: no large foramina on lateral face of retroarticular process (0); or one to three large foramina present (1).

74. Tooth surface I: teeth finely striate medially (0); or not medially striate (1). In "Russellosaurinae", medial tooth striations are very fine and groups of tightly spaced striae are usually set apart by facets, leading to a fasciculate appearance.

75. Tooth surface II: teeth not coarsely textured (0); or very coarsely ornamented with bumps and ridges (1). In both species of *Globidens* and in *Prognathodon overtoni*, the coarse surface texture is extreme, consisting of thick pustules, and vermiform or anastomosing ridges. Teeth in *P. rapax* are smooth over the majority of their surface, but usually a few widely scattered, large, very long, sharp-crested vermiform ridges are present.

76. Tooth facets: absent (0); or present (1). *Halisaurus* teeth are smoothly rounded except for the inconspicuous carinae. *Clidastes* is described in numerous places as having smooth unfaceted teeth, but many immature individuals and some larger specimens have teeth with three distinct facets on the medial faces.

Adult *Tylosaurus proriger* has indistinct facets. *Mosasaurus* has taken this characteristic to the extreme.

77. Tooth fluting: absent (0); or present (1). In *Ectenosaurus*, and some *Platecarpus planifrons*, several broadly rounded vertical ridges alternate with shallow, round-bottomed grooves completely around the teeth.

78. Tooth inflation: crowns of posterior marginal teeth conical, tapering throughout (0); or crowns of posterior marginal teeth swollen near the tip or above the base (1). The rear teeth of *Globidens* and *Prognathodon overtoni* are distinctly fatter than other mosasauroid teeth, but those of *P. rapax* are also swollen immediately distal to the base.

79. Tooth carinae I: absent (0); or present but extremely weak (1); or strong and elevated (2). *Halisaurus* exhibits the minimal expression of this character (state 1) in that its marginal teeth are almost perfectly round in cross section; the carinae are extremely thin and barely stand above the surface of the teeth. *Globidens* is convergent in the strict sense of the character, but this is probably a result of obliteration of the carinae by the extreme inflation.

80. Tooth carinae serration: absent (0); or present (1).

81. Tooth replacement mode: replacement teeth form in shallow excavations (0); or in subdental crypts (1). All mosasauroids that can be evaluated have an “anguimorph” type of tooth replacement, which is to have interdental positioning of replacement teeth and resorption pits associated with each.

82. Atlas neural arch: notch in anterior border (0); or no notch in anterior border (1).

83. Atlas synapophysis: extremely reduced (0); or large and elongate (1). In state 1, a robust synapophysis extends well posteroventral to the medial articular surface for the atlas centrum, and it may be pedunculate (*Clidastes*) or with a ventral “skirt” that gives it a triangular shape (*Mosasaurus*). A very small triangular synapophysis barely, if at all, extends posterior to the medial articular edge in state 0.

84. Zygosphenes and zygantra: absent (0); or present (1). This character assesses only the presence of zygosphenes and zygantra, not their relative development. Nonfunctional and functional are considered as present.

85. Zygosphene and zygantra number: present on may vertebrae (0); or present on only a few (1).

86. Hypapophyses: last hypapophysis occurs on or anterior to seventh vertebra (0); or on ninth or tenth vertebra (1).

87. Synapophysis height: facets for rib articulations tall and narrow on posterior cervicals and anterior trunk vertebrae (0); or facets ovoid, shorter than the centrum height on those vertebrae (1).

88. Synapophysis length: synapophyses of middle trunk vertebrae not laterally elongate (0); or distinctly laterally elongate (1). The lateral extension of the synapophyses from the middle of the trunk is as much as 70-80% of the length of the same vertebra is represented by state 1.

89. Synapophysis ventral extension: synapophyses extend barely or not at all below ventral margin of cervical centra (0); or some extend far below ventral margin of centrum (1). In state 1, two or more anterior cervical vertebrae have rib

articulations that dip well below the centrum, causing a very deeply concave ventral margin in anterior profile.

90. Zygapophysis development: zygapophyses present far posteriorly on trunk vertebrae (0); or zygapophyses confined to anterior trunk series (1). In state 0, zygapophyses extend at least to the sacral area.

91. Vertebral condyle inclination: condyles of trunk vertebrae inclined (0); or condyles vertical (1).

92. Vertebral condyle shape I: condyles of anteriormost trunk vertebrae extremely dorsoventrally depressed (0); or slightly depressed (1); or essentially equidimensional (2). In state 0, posterior height: width ratios of anterior trunk vertebrae are close to 2:1. In state 1, they are close to 4:3, but posterior to this, the ratio decreases as the vertebrae become proportionally higher.

93. Vertebral condyle shape II: condyles of posterior trunk vertebrae not higher than wide (0); or slightly compressed (1). In state 1, the posterior condylar aspect reveals outlines that appear to be higher than wide and even perhaps slightly subrectangular, due to the slight emargination for the dorsal nerve cord.

94. Vertebral synapophysis dorsal ridge: sharp ridge absent on posterior trunk synapophyses (0); or with a sharp-edged and anteriorly precipitous ridge connecting distal synapophysis with prezygapophysis (1). In state 0, the ridge in question, if present, may be incomplete or it may be rounded across the crest with the anterior and posterior sides about equally sloping.

95. Vertebral length proportions: cervical vertebrae distinctly shorter than longest vertebrae (0); or almost equal or are the longest (1).

96. Presacral vertebrae number I: relatively few, 32 or less (0); or numerous, 39 or more (1). Here, presacral vertebrae are considered to be all those anterior to the first bearing an elongate transverse process.

97. Presacral vertebrae number II: if few, then 28 or 29 (0); or 30 or 31 (1).

98. Sacral vertebrae number: two (0); or less than two (1). Numerous well-preserved specimens of derived mosasauroids have failed to show any direct contact of the pelvic girdle with vertebrae in the sacral area. Certainly, no transverse processes bear any type of concave facet for the ilium, and so it is generally assumed that a ligamentous contact was established with only one transverse process. Depending on one's perspective, it could be said that derived mosasauroids have either no or one sacral vertebra.

99. Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0); or several spines dorsally elongated behind middle of tail (1).

100. Hemal arch length: hemal arches about equal in length to neural arch of same vertebra (0); or length about 1.5 times greater than neural arch length (1). This ratio may be as great as 1.2:1 in state 0. Comparison is most accurate in the middle of the tail and is consistent even on those vertebrae in which the neural spines are also elongated.

101. Hemal arch articulation: arches articulating (0); or arches fused to centra (1). Among the outgroups, the hemal arches fuse to the centra generally only in the latest life stages. These are considered to have state 0 for this character. All mosasaurines have fused hemals and all "russellosaurines" have articulating hemals. No mosasaurian is known to change this condition in any ontogenetic

stage represented by fossil material, but the possibility that some very old "russellosaurines" fused the hemals awaits discovery.

102. Tail curvature: no structural downturn of tail (0); or tail with decurved posterior portion (1).

103. Body proportions: head and trunk shorter than or about equal to tail length (0); or head and trunk longer than tail (1).

104. Scapula/coracoid size: both bones about equal (0); or scapula about half the size of coracoid (1).

105. Scapula width: no anteroposterior widening (0); or distinct fan-shaped widening (1); or extreme widening (2). In state 0, the anterior and posterior edges of the scapula encompass less than one quarter of the arc of a circle, but in state 1, the arc is increased to approximately one third. In state 2, the distal margin encompasses almost a half-circle and the anterior and posterior borders are of almost equal length.

106. Scapula dorsal convexity: if scapula widened, dorsal margin very convex (0); or broadly convex (1). In state 0, the anteroposterior dimension is almost the same as the proximodistal dimension. In state 1, the anteroposterior dimension is much larger.

107. Scapula posterior emargination: posterior border of bone gently concave (0); or deeply concave (1). In state 1, there is a deeply arcuate emargination on the posterior scapular border, just dorsal to the glenoid. It is immediately bounded dorsally by a corner, which begins a straight-edged segment that continues to the dorsal margin.

108. Scapula-coracoid fusion: ontogenetic fusion occurs (0); or no fusion at any life stage (1). Fully grown representatives of the outgroups and the only known specimen of *Opetiosaurus* have fused the scapula and coracoid. This occurs in no other mosasauroid specimen, regardless of size.

109. Scapula-coracoid suture: unfused scapula-coracoid contact has interdigitate suture anteriorly (0); or apposing surfaces without interdigitation (1).

110. Coracoid neck elongation: neck rapidly tapering from medial corners to a relatively broad base (0); or neck gradually tapering to a relatively narrow base (1). In state 1, this character describes an outline of the bone, which is nearly symmetrical and gracefully fan-shaped, with gently concave, nearly equidistant sides.

111. Coracoid anterior emargination: present (0); or absent (1).

112. Humerus length: humerus distinctly elongate, about three or more times longer than distal width (0); or greatly shortened, about 1.5 to 2 times longer than distal width (1); or length and distal width virtually equal (2); or distal width slightly greater than length (3).

113. Humerus postglenoid process: absent or very small (0); or distinctly enlarged (1).

114. Humerus glenoid condyle: if present, condyle gently domed and elongate, ovoid in proximal view (0); or condyle saddle-shaped, subtriangular in proximal view and depressed (1); or condyle highly domed or protuberant and short ovoid to almost round in proximal view (2). In some taxa, the condylar surfaces of the limbs were finished in thick cartilage and there was no bony surface of the

condyle to be preserved. This condition is scored as not represented. In some taxa, the glenoid condyle extends more proximally than does the postglenoid process (state 2), and it is not ovoid as state 0.

115. Humerus deltopectoral crest: crest undivided (0); or split into two separate insertional areas (1). In state 1, the deltoid crest occupies an anterolateral or anterior position confluent with the glenoid condyle, while the pectoral crest occupies a medial or anteromedial area that may or may not be confluent with the glenoid condyle. The deltoid crest is often quite short, broad, and indistinct, being easily erased by degradational taphonomic processes.

116. Humerus pectoral crest: located anteriorly (0); or medially (1). In state 1, the pectoral crest is located near the middle of the flexor (or medial) side on the proximal end of the bone.

117. Humerus ectepicondylar groove: groove or foramen present on distolateral edge (0); or absent (1).

118. Humerus ectepicondyle: absent (0); or present as a prominence (1). A radial tuberosity is reduced in size in *Prognathodon*, but very elongated in *Plesiotylosaurus*.

119. Humerus entepicondyle: absent (0); or present as a prominence (1). The ulnar tuberosity protrudes posteriorly and medially from the posterodistal corner of the bone immediately proximal to the ulnar facet, causing a substantial dilation of the posterodistal corner of the humerus.

120. Radius shape: radius not expanded anterodistally (0); or slightly expanded (1); or broadly expanded (2).

121. Ulna contact with centrale: broad ulnare prevents contact (0); or ulna contacts centrale (1). In state 1, the ulnare is omitted from the border of the antebrachial foramen. There is usually a well-developed faceted articulation between the ulna and the centrale (or intermedium, as used by Russell, 1967).

122. Radiale size: large and broad (0); or small to absent (1).

123. Carpal reduction: carpals number six or more (0); or five or less (1).

124. Pisiform: present (0); or absent (1).

125. Metacarpal I expansion: spindle-shaped, elongate (0); or broadly expanded (1). The broad expansion is also associated with an anteroproximal overhanging crest in every case observed.

126. Phalanx shape: phalanges elongate, spindle-shaped (0); or blocky, hourglass-shaped (1). All the basic taxa of *Mosasaurus* and *Plotosaurus* have phalanges that are slightly compressed and anteroposteriorly expanded on both ends.

127. Ilium crest: crest blade-like, points posterodorsally (0); or elongate, cylindrical (1).

128. Ilium acetabular area: arcuate ridge supertending acetabulum (0); or acetabulum set into broad, short V-shaped notch (1). The primitive ilium has the acetabulum impressed on the lateral wall of the bone, with a long narrow crest anterodorsally as the only surrounding topographic feature. In state 1, the acetabular area is set into a short, broadly V-shaped depression that tapers dorsally. The lateral walls of the ilium are therefore distinctly higher than the rim of the acetabulum.

129. Pubic tubercle condition: tubercle an elongate protuberance located closer to the midlength of the shaft (0); or a thin semicircular crest-like blade located close to the acetabulum (1).

130. Ischiadic tubercle size: elongate (0); or short (1). In state 0, the tubercle is as long as the shaft of the ischium is wide, but it is only a short narrow spur in state 1.

131. Astragalus: notched emargination for the crural foramen, without pedunculate fibular articulation (0); or without notch, pedunculate fibular articulation present (1). For state 0, the tibia and fibula are of equal length about the crural foramen and the astragalus contacts both to about the same degree. The form of the latter element is symmetrical and subcircular with a sharp proximal notch. In state 1, the outline of the element is basically reniform and the tibial articulation is on the same line as the crural emargination. The fibula is also shortened and its contact with the astragalus is narrow.

132. Appendicular epiphyses: formed from ossified cartilage (0); or from thick unossified cartilage (1); or epiphyses missing or extremely thin (2). Ends of the limb bones show distinct vascularization and rugose surfaces indicating an apparently thick nonvascularized, unossified cartilage cap. Extremely smooth articular surfaces suggest the epiphyses were excessively thin or perhaps even lost.

133. Hyperphalangy: absent (0); or present (1).

134. Exit for basilar artery from basioccipital: absent (0); or through two ventral foramina (1); or through a single ventral foramen (2); or through two foramina on anterodorsal basisphenoid (3).

135. Posterior thoracic vertebra: not markedly longer than anterior thoracic vertebrae (0); or are markedly longer (1).

APPENDIX 2. Character matrix used for phylogenetic analysis (modified from Caldwell and Palci, 2007). Note: (-), Not Applicable; for taxa coded for polymorphic states, A = (0, 1); B = (1, 2).

	5	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**50**
Outgroup	0?000	000?0	0??00	???00	000??	000?0	00?0?	00?00	0???0	???00
Carsosaurus marchesettii	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Aigialosaurus	0?00?	0?021	00??0	???10	10?10	?00?0	00???	000??	?1??0	???1?
Haasiasaurus gittlemani	?????	?????	?????	?????	?????	?????	?????	?????	?11?0	20?00
Komensaurus carrolli	?????	?????	?????	?????	?????	?????	?????	?????	?20?0	?1000
Halisaurus platyspondylus	10100	00021	10000	0??10	101?0	?00??	???11	????1	?2001	01000
Halisaurus sternbergi	0?100	?0021	00000	0??00	10100	000??	??021	0???0	020?1	??000
Dallasaurus turneri	?????	??0??	0???1	?10??	?????	?????	?????	????0	?????	?????
Clidastes liodontus	11100	0?020	010?1	01010	01111	?10?1	00210	02??1	010?0	00000
Clidastes moorevillensis	11100	00020	01001	01010	01111	?10?1	0021?	020?1	010?0	01010
Clidastes propython	11100	0?120	01001	01010	0111?	?10?1	0021?	0???1	010?0	01010
Ectenosaurus clidastoides	11100	01020	01111	02011	10001	?00?0	11110	11100	01001	21101
Globidens alabamaensis	?????	??10?	11101	01???	?????	?10?1	0??1?	????1	010?1	111?0
Globidens dakotensis	1110?	0?101	11??1	01010	01?11	?11?1	01410	020?1	010?1	01110
Mosasaurus conodon	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Mosasaurus hoffmanni	11100	1?000	11??1	01110	02111	?1100	0131?	?21?1	000?0	01101
Mosasaurus missouriensis	11100	1?100	11??1	01110	01?11	?11?0	0?300	1???1	000?0	01100
Platecarpus planifrons	10100	00001	011?1	00?11	10?11	?00??	11500	0?100	02100	11000
Platecarpus tympaniticus	00100	00001	11111	00?11	11011	?0100	11500	011?0	02110	11100
Plesiotylosaurus crassidens	11101	??10?	11??1	01110	01111	?1110	0041?	1??01	100?1	01110
Plioplatecarpus	?????	??001	11001	00?11	13011	?0100	01?0?	?1100	02110	01200
Plotosaurus bennisoni	10100	1?101	01??1	01110	11?11	111?0	00110	02001	000?0	01100
Prognathodon overtoni	10100	0?100	11001	01010	01?11	111?0	01500	?20?1	110?1	01110
Prognathodon rapax	10100	0?100	01001	01110	01111	?11??	?041?	020?1	110?1	01110
Tylosaurus nepaeolicus	12111	1?001	01011	1??10	00?11	101?0	0140?	??110	011?0	21011
Tylosaurus proriger	12111	11001	11?11	1??10	01?11	10110	?1410	11100	000?0	21000
Yaguarasaurus columbianus	0010?	0?020	00???	02012	00?11	000?0	?1300	1111?	?1100	21001
Russellosaurus coheni	101??	00020	00111	02012	00011	000?0	1120?	11110	01100	21001
Angolasaurus bocagei	101??	0?01?	11???	0??11	00?1?	?00?0	??50?	???1?	?2100	01100
Tethysaurus nopcsai	1010?	0?021	10??1	02012	00?11	000—0	?100?	?11??	00100	21011
Eremiasaurus heterodontus	10100	1?101	11??1	01?10	?1?11	?11?0	10400	020?1	?1??1	?1?0?
Prognathodon solvayi	0—000	00100	01001	01010	11111	110?0	0050?	110?1	11001	01100
Prognathodon currii	1000?	???01	11???	???10	???11	?11?0	0?50?	120??	1????	?1??0
Prognathodon kianda	10100	1??00	?1??1	?1?10	?1?11	??0??	?040?	?2111	?10?1	01110
Prognathodon saturator	???00	??10?	11001	01110	111??	?1000	00???	?20?1	11?01	01110
Prognathodon waiparaensis	10100	00???	?????	?????	?????	?????	?????	?21?1	11??1	01110

APPENDIX 2. (Continued)

	55	60	65	70	75	80	85	90	95	100
Outgroup	?0000	000?0	00??0	00000	0?0?0	000?0	00?00	0?000	0?00?	0?00?
Carsosaurus marchesettii	?????	?????	?????	?????	?????	?????	?????	0000?	0????	0?0??
Aigialosaurus	?0???	00???	?1??0	00?01	00?00	00020	0?010	?0000	0???0	00000
Haasiasaurus gittlemani	?????	???00	00101	00000	00000	0001?	0??10	00000	01000	000?0
Komensaurus carrolli	?0???	?????	?????	???00	00???	?????	???1?	??0?0	01??0	0?0?0
Halisaurus platyspondylus	?0001	?????	??201	?0001	00010	00010	1??0?	?????	00???	?????
Halisaurus sternbergi	?0?01	??0?1	?1201	?0?01	00010	?0010	0?10?	?0010	00??0	01110
Dallasaurus turneri	?????	????0	0020?	?001?	???10	0002?	0011?	?0010	11110	???0?
Clidastes liodontus	00010	100B0	022?1	00010	00?10	10020	10110	00000	12010	1?111
Clidastes moorevillensis	00010	10020	02201	00010	00010	10020	10110	00000	12?10	1?111
Clidastes propython	00010	10010	02201	?1010	00010	10020	10110	00000	12?10	???1?
Ectenosaurus clidastoides	110??	00330	02001	?0000	00100	11020	10010	01000	1???0	?????
Globidens alabamaensis	??010	?????	??201	0?110	00011	00110	1011?	?0?0?	12??0	?????
Globidens dakotensis	?0A10	100??	?????	?????	???11	00110	1011?	00?0?	12?10	?????
Mosasaurus conodon	?????	???1?	?2201	????0	00010	10021	10111	0010?	12011	?????
Mosasaurus hoffmanni	?1101	10030	02201	0?110	11010	10021	10111	01100	120?1	??111
Mosasaurus missouriensis	?1A01	10?30	02?01	01110	11010	1002?	1011?	0000?	12011	1?1??
Platecarpus planifrons	?0A11	00250	02200	10000	00100	11020	11010	0000?	11??0	?????
Platecarpus tympaniticus	10A11	00351	?2210	10000	00100	10020	11001	00000	11000	00100
Plesiotylosaurus crassidens	?0?10	11?20	02111	01110	0??10	10021	1????	?0000	12?10	?????
Plioplatecarpus	?0A11	00351	?2210	10000	00100	10020	1??0?	?0000	11000	0????
Plotosaurus bennisoni	01101	10?10	1?2?1	???10	11000	0012?	?010?	10?01	12??1	1???1
Prognathodon overtoni	??010	10030	02101	01110	01011	00121	1????	??0??	12???	?????
Prognathodon rapax	00011	100?1	?2101	0???0	00011	00121	10110	?0000	12110	?????
Tylosaurus nepaeolicus	10010	01?40	12200	00000	00000	10021	10001	0000?	1100?	?????
Tylosaurus proriger	10010	01040	12200	01000	00000	10021	1100?	00000	11000	01100
Yaguarasaurus columbianus	10000	00131	?????	?????	???00	?0010	0??1?	?????	?????	?????
Russellosaurus coheni	10000	00121	?1100	10001	00100	?0010	0????	?????	?????	?????
Angolasaurus bocagei	10001	00251	?22?0	10001	00100	?002?	0??1?	?????	?????	?????
Tethysaurus nopcsai	1?000	00111	–1100	10001	00000	?000–	0??10	?1110	000??	?????
Eremiasaurus heterodontus	?1?11	1??20	02201	0??10	11?10	00121	101??	0100?	120?0	??111
Prognathodon solvayi	?0011	1?141	–2?01	0101?	00000	?0121	10?10	00100	12?10	?????
Prognathodon currii	????1	??51	–????	????0	00??1	00?20	?????	?????	?????	?????
Prognathodon kianda	00010	1??20	021?1	00010	00010	00120	1????	?????	?????	?????
Prognathodon saturator	00010	1??3?	?2101	??010	01011	00121	10?10	?0100	12110	????0
Prognathodon waiparaensis	?0010	???3?	??101	?????	???00	?0121	1????	?????	?????	?????

APPENDIX 2. (Continued)

	105	**110**	**115**	**120**	**125**	**130**	**135**
Outgroup	00000	??000	00000	00000	00000	00000	?0000
Carsosaurus marchesettii	?????	?0110	00000	00000	00000	0001?	?00?0
Aigialosaurus	00000	?00?0	0000?	00000	00000	0001?	?0000
Haasiasaurus gittlemani	???11	101?1	00?00	00000	01110	000??	?00??
Komensaurus carrolli	0????	?????	?????	??000	0?000	?0011	?0000
Halisaurus platyspondylus	1????	?????	?????	?????	?????	??1??	???00
Halisaurus sternbergi	10111	11110	01001	00001	01110	01111	?0000
Dallasaurus turneri	1??00	?010?	?01?0	0000?	?????	000??	?0?01
Clidastes liodontus	10101	10100	02101	01112	10001	01000	12001
Clidastes moorevillensis	1??01	10100	02101	01112	10001	01000	12001
Clidastes propython	1????	???00	02101	01112	10?0?	?????	?2?01
Ectenosaurus clidastoides	???01	01110	021??	?0012	01010	0????	?1031
Globidens alabamaensis	?????	??10?	?2101	0111?	?????	?????	?2?01
Globidens dakotensis	?????	?????	?????	?????	?????	?????	???01
Mosasaurus conodon	1???1	?0101	03111	0111?	1????	?????	?2?01
Mosasaurus hoffmanni	11?02	10101	13111	01112	10001	11000	12101
Mosasaurus missouriensis	11?01	??100	?????	????2	100?1	1????	?2?01
Platecarpus planifrons	???01	01110	020?1	100?2	01110	0????	?1?20
Platecarpus tympaniticus	01001	01110	020??	1?012	01110	01011	01030
Plesiotylosaurus crassidens	???01	10101	13121	01112	10001	0????	?2?0?
Plioplatecarpus	0??01	01110	020?1	10012	01110	0????	?1?30
Plotosaurus bennisoni	?1?02	10101	13111	01112	10001	1??1?	?2101
Prognathodon overtoni	1????	?????	?2121	01?1?	?????	?????	???01
Prognathodon rapax	1??01	?0101	12121	01112	10001	0????	?2?01
Tylosaurus nepaeolicus	?????	?????	?10?1	?0001	?1110	0????	???00
Tylosaurus proriger	01011	01110	110?1	10001	?1110	010?0	01100
Yaguarasaurus columbianus	?????	?????	?????	?????	?????	?????	???20
Russellosaurus coheni	?????	?????	?????	?????	?????	?????	???1?
Angolasaurus bocagei	?????	?????	?????	?????	?????	?????	???30
Tethysaurus nopcsai	0??11	10100	0????	?011?	?????	?0?0?	?????
Eremiasaurus heterodontus	11001	?011?	??10?	?????	?????	01??0	1???1
Prognathodon solvayi	???01	?011?	?????	?????	?????	?????	?????
Prognathodon currii	?????	?????	?????	?????	?????	?????	?????
Prognathodon kianda	?????	?????	?????	?????	?????	?????	?????
Prognathodon saturator	1??0?	??1??	?????	????2	?????	?????	?????
Prognathodon waiparaensis	?????	?????	?????	?????	?????	?????	?????

CHAPTER THREE

CRANIAL ANATOMY OF *PLOTOSAURUS BENNISONI* CAMP, 1942 (SQUAMATA: MOSASAURIDAE) FROM THE MAASTRICHTIAN OF CALIFORNIA

INTRODUCTION

Mosasaur remains have been reported from the Maastrichtian portions of the Moreno Formation of central California since as early as 1918 (Camp, 1942). However, it was not until 1936, when Allan Bennison, then a high school student, discovered isolated mosasaur vertebrae while prospecting in the Mount Diablo Range that the search for mosasaur remains in central California became more active (Camp, 1942). Diligent work in the years following this discovery led to the recovery of the remains of several more mosasaurs, particularly from the Penoche Hills of the San Jaoquin Valley (Lindgren et al., 2008). Fieldwork in the late 1930s yielded an apparently endemic mosasaur fauna that was represented by two genera and three species, all described by Camp (1942). The most striking of these finds was the discovery in 1937, again by Bennison, of a complete and pristinely preserved skull of a small mosasaur (UCMP 32778) from the Garzas Sand Member that was later designated as the holotype for *Kolposaurus* (= *Plotosaurus*, Camp, 1951) *bennisoni* Camp, 1942. Camp (1942) described a second larger mosasaur from a locality approximately 65 kilometers southeast of the *P. bennisoni* locality, the remains of which consist of a string of 54 articulated vertebrae, including posterior dorsals, pygals and caudals (Camp, 1942) that he deemed to be found in stratigraphically older deposits of the Tierra Loma Shale. This served as the holotype for a second species of *Kolposaurus* (= *Plotosaurus*), *P. tuckeri* (UCMP 33913), diagnosed as a member of this genus based on the small number of anterior vertebrae that bore functional zygapophyses (Camp,

1942) and differentiated from *P. bennisoni* based on its larger size and presumed older stratigraphic occurence. Unfortunately, no direct anatomical comparisons were possible between the skull and anterior 18 vertebrae of the holotype of *P. bennisoni* and the posterior vertebral series of the *P. tuckeri* holotype. Camp (1942) also identified a series of 39 vertebrae and a complete skull (CIT 2750) as well as two preserved series of caudal (CIT 2751) and caudal and pygal vertebrae (CIT 2755) as referred specimens of *P. tuckeri*. This assignment was based on the fact that (1) CIT 2755 possessed an identical number (29) of pygal vertebrae to the holotype of *P. tuckeri*; (2) CIT 2751 and CIT 2755 possessed identical tail shapes and could be considered to have come from the same species, and (3) the skull of CIT 2750 was much larger than that of *P. bennisoni* and the latter came from the same horizon as the other larger specimens referred to *P. tuckeri* (Camp, 1942:11–12).

Camp's (1942) restoration of *Plotosaurus* was necessarily composite, incorporating regions of overlap of the vertebral columns of these holotypes and referred specimens of *P. tuckeri* and *P. bennisoni* in order to reconstruct what is still considered today the most aquatically adapted member of the Mosasaurinae known (Camp, 1942; Lindgren et al., 2007; Lindgren et al., 2009). A subsequent re-description of the postcranial anatomy of *Plotosaurus* by Lindgren et al. (2008) provided insight into the validity of these restorations and also provided new material that bridged the preservational gap between the two holotypes. This redescription provided a more accurate depiction of the axial and appendicular anatomy of *Plotosaurus*, supplementing the diagnosis of this taxon from Camp

(1942) with additional autapomorphies, and also provided sufficient merit to synonymize *P. tuckeri* with *P. bennisoni* (Lindgren et al., 2008). *Plotosaurus* is now recognized to be monotypic, suggesting that all available postcranial material for this taxon in CIT and UCMP collections belongs to the same species as the ichthyosaur-like skull of the holotype, UCMP 32778 (Lindgren et al., 2008). As such, *P. bennisoni* is effectively known from more than 16 specimens that preserve an extensive amount of material pertaining to the vertebral and appendicular anatomies, and also from a number of skulls in various states of preservation, from fragmentary (UCMP 131809) to exquisite (UCMP 32778). Most importantly, the suite of characters of the postcranium of *Plotosaurus* that pertain to a shift in mosasaur predatory tactics, from elongate, slender ambush predators to streamlined pelagic cruisers (Lindgren et al., 2007; Lindgren et al., 2009) can now be tied to the morphology of the skull. Following the example set by Lindgren et al. (2008), a redescription of the cranial anatomy of *Plotosaurus bennisoni* is undertaken here to (1) supplement the detailed description of UCMP 32778 by Camp (1942); (2) highlight, reinterpret and figure important features of this taxon, based on the holotype and several referred specimens, and (3) provide comparative statements that pertain to new observations of the anatomies of other mosasaurids and how this relates to the evolution of mosasaurine mosasaurs within the frame of the most recent phylogenies of the Mosasauridae. This redescription also provides the foundation for a more detailed review of the functional morphology of the skull of *Plotosaurus* discussed in Chapter 4.

MATERIALS AND METHODS

The material illustrated herein is from the holotype specimen of *Plotosaurus bennisoni* (UCMP 32778). Photographs were taken by J. Lindgren and M. Caldwell and the illustrations were done by tracing the images in Adobe Photoshop version 11.0 or in Adobe Illustrator version 14.0.0 for MacIntosh/Windows. Some of the illustrations were hand-stippled and then scanned back into either program. All referred material described herein pertains to personal observation of the specimens, save for CIT 2750, which was not available during the author's collections visit to the Natural History Museum of Los Angeles County in the spring of 2009. Observations of this specimen were made from photographs taken by T. Konishi.

SYSTEMATIC PALEONTOLOGY

SQAMATA Oppel, 1811

MOSASAURIDAE Gervais, 1853

MOSASAURINAE Gervais, 1853

PLOTOSAURUS Camp, 1951

Type species—*Kolposaurus bennisoni* Camp, 1942

Revised diagnosis (cf., Camp, 1942; Russell, 1967; Lindgren et al., 2008)—Premaxillary teeth prognate, smaller than maxillary teeth; internarial bar constricted at a point between seventh and tenth maxillary teeth; maxilla with 18 teeth; septomaxillae elongate and fused posteriorly; orbits and nares exceptionally large compared to all other mosasaurines; prefrontals excluded from posterolateral margins of nares in dorsal view; prefrontals and postorbitofrontals broadly contacting lateral to frontal; embayments in anterior margin of frontal; frontal widely expanded with lateral borders nearly parallel; dorsal surface of frontal convex dorsal to orbits; frontal excluded from orbit margin in dorsal view; postorbitofrontal overlapping vertical ramus of jugal; angle between horizontal and vertical rami of jugal obtuse; pineal foramen large and oval; parietal table anteroposteriorly short, with parietal rami diverging anterior to the midpoint of the temporal fenestra in dorsal view; rectangular processus descensus parietalis overlaps parietal ramus of prootic and reaches dorsal margin of trigeminal notch; quadrate suprastapedial process short, but nearly contacting a dome-shaped infrastapedial process above the midheight of the quadrate shaft; quadrate suprastapedial process braced posteriorly and posteromedially by squamosal, supratemporal and paroccipital process; basioccipital canals absent; pterygoids with 13–14 teeth each; pterygoid teeth ventrolaterally directed at widest point of interpterygoid vacuity; ectopterygoid long, excluding jugal from ventrolateral margin of orbit and inserting into notch on palatine anteriorly; dorsal surface of ectopterygoid concave; epipterygoid, spiraling and bowing laterally; epipterygoid inserts into notch between descending process of parietal and parietal ramus of prootic; vomerine processes of palatines in contact posterior to their overlap of the vomers; vomers contacting one another along their entire lengths; anterior tips of dentaries elongated, extending more anteriorly than the premaxillary rostrum; contact between dentaries extends posteriorly to approximately sixth dentary tooth position; dentaries with 17–18 teeth; dorsal margins of dentaries gently convex; intramandibular joint inclined less than 45 degrees from the horizontal; vertebral centra proportionally robust, shorter than in other mosasaurs; 8–10 cervicals; 28–37 pygals; lengths of caudal centra less than condyle width; scapula equal in size or somewhat larger than coracoid; femur stout, broad and heavy; hyperphalangy, up to 16 phalanges in each digit.

PLOTOSAURUS BENNISONI (Camp, 1942)

Kolposaurus bennisoni Camp, 1942: 2–8; figs. 1–3, 13 (right), 14, 15 (right), 17, pl. 1 (originial description).

Kolposaurus tuckeri Camp, 1942: 8–10; figs. 4–10, 13 (second from right), pls. 2, 3 (original description).

Figs. 3–1–6

Holotype—UCMP 32778 (Camp, 1942:figs. 1–3, pl. 1) complete skull, 18 anterior vertebrae, interclavicle and rib fragments.

Type Locality—Merced County, central California (UCMP locality no. V3718).

Horizon—Upper lower to lower upper Maastrichtian Garzas Sand Member of the Moreno Formation,

Diagnosis—As for genus.

Referred Material—CIT 2750, skull, cervical and dorsal vertebrae, shoulder girdle, partial forelimbs; CIT 2945, incomplete skull, pectoral girdle, pubis, partial vertebral column, forepaddle elements; UCMP 45303, incomplete skull, shoulder girdle, articulated series of cervical and dorsal vertebrae, pygals, rib fragments; UCMP 57582, nearly complete skull; UCMP 131809, isolated right dentary fragment; UCMP 137247, skull and nearly complete vertebral column; UCMP 152554, fragmentary skull and postcranial skeleton.

GEOLOGICAL SETTING

Marine deposits of the Moreno Formation (Great Valley Group) crop out in the Tumey and Panoche Hills of Fresno and Merced counties along the western slopes of the San Joaquin Valley (Camp, 1942; Squires and Saul, 2003; Lindgren et al., 2008; Lindgren, 2009; Lindgren and Schulp, 2010). The two shallow-marine horizons from which mosasaur remains have been recovered have been dated as late early to early late Maastrichtian, based on benthic foraminifers and gastropods (Squires and Saul, 2003). Mosasaur remains have predominantly been recovered from a single horizon within the Moreno Formation, the Tierra Loma Shale, exposures of which are found in Fresno County. Most of the mosasaur material from these shallow-marine silts and shales are flattened and heavily impregnated with gypsum (Lindgren et al., 2008; Lindgren, 2009; Lindgren and Schulp, 2010). The informally named Garzas Sand member to the North in Merced County yielded UCMP 32778, where the potential for three-dimensionally preserved mosasaur specimens is apparently higher. Both of these 'members' of the Moreno Formation are of the same age, based on invertebrate biostratigraphic markers (Squires and Saul, 2003), although local lateral facies changes produce exposures that are thought to be lower Paleocene as well (Squires and Saul, 2003; Lindgren et al., 2008).

DESCRIPTION AND COMPARISONS

UCMP 32778 consists of a complete skull, cervical series and anterior dorsal vertebrae of *Plotosaurus bennisoni*. The skull is well preserved with no evidence of distortion or crushing, although the surface is abraded in some areas, making sutures difficult to identify. The total length of the skull is approximately 46 cm from the anterior tip of the premaxilla to the posterior end of the squamosals (measured along the midline) and 16 cm wide at its widest point (Camp, 1942). UCMP 32778 is likely the juvenile or subadult form of *P. bennisoni*, given that UCMP 57582 is a skull referable to this taxon, and measures approximately one meter in length (pers. obs.). As noted by Camp (1942) all of the marginal teeth of UCMP 32778 interdigitate, indicating that the lower and upper jaws are preserved in their natural positions. The temporal arcade is complete and undistorted. Posteriorly, the quadrate suspensoria, quadrates and quadrate rami of the pterygoids are preserved in bisymmetrical positions, indicating that these elements have not been crushed.

Skull

Premaxilla—The anterior border of the premaxillary rostrum forms an obtuse angle in lateral view and barely extends further anterior to the first pair of premaxillary teeth (Fig. 3–1). Both pairs of premaxillary teeth are slightly prognate, such that their occlusal tips are roughly even with the anterior borders of their respective tooth bases. This condition is similar to the slight anterior inclination of the premaxillary teeth as described by Lingham-Soliar (1995) for *Mosasaurus hoffmanni*. The premaxillary tooth crowns are conical and expanded at their bases. These tooth crowns are smaller than those of the anterior and middle maxillary and dentary teeth (Fig. 3–1). The premaxillary-maxillary suture rises dorsally from the alveolar margin and then is inclined posterodorsally at a shallower angle before being concealed from lateral view. This suture continues in dorsal view in a sinuous pattern posteromedially before terminating at a point dorsal to the fourth maxillary tooth. The sinuous nature of the premaxillary-maxillary suture along the anterodorsal surface of the skull is the result of an overlapping of the maxilla dorsally on the premaxilla anterior to the narial openings. A lack of displacement of any of the elements of the snout and the symmetrical nature of this suture indicates that this is a genuine feature. In dorsal view, there is a rounded mid-sagittal prominence that disappears posterior to the premaxillary-maxillary sutural terminus (Fig. 3–2). Two sulci flank this median prominence along the dentigerous portion of the premaxilla. In the middle of each sulcus are two foramina. Posteriorly, the dorsal surface of the internarial bar is convex. The internarial bar becomes laterally compressed at the point dorsal to the seventh and eighth maxillary teeth and then re-expands posteriorly. At the premaxilla-frontal junction, the internarial bar overlaps the premaxillary process of the frontal.

Maxilla—In lateral view, the ventral margin of the maxilla is concave and becomes wider posteriorly. There is a nearly 90-degree angle at the junction of the lateral and dorsal surfaces of the maxilla, similar to *Mosasaurus missouriensis* (pers. obs.). Anterior to the premaxillary-maxillary suture terminus, the anterodorsal expansion of the maxilla is wrinkled where it overlaps the dorsal surface of the premaxilla. The emargination for the external narial opening is widest at approximately the point dorsal to the eighth maxillary tooth position, coinciding with the thinnest point of the internarial bar (Fig. 3–2). A posterodorsal wing of the maxilla contacts the frontal in dorsal view and excludes the prefrontal from forming the posterolateral corners of the external narial openings. Posteriorly, the maxilla extends posterior to the contact of the jugal. This posterior extension persists for over a quarter of the length of the horizontal ramus of the jugal. The foramina along the lateral surface of the maxillae become progressively smaller anteriorly. A ventromedian wall of the maxilla forms the ventrolateral border of the nasal vestibule. Posteriorly, there is a broad contact between the palatines and the posteromedial surfaces of the maxillae.

There are 18 maxillary tooth spaces, with the posterior two concealed by the overlapping jugal in lateral view (Fig. 3–1). The anterior four maxillary teeth are inclined anteriorly, based on the inclination of the exposures of the roots (Fig. 3–1A, B). The anterior six tooth crowns resemble those of the premaxilla in that they are straight and conical, expanded at their bases and striated. The seventh to ninth tooth crowns are the largest in the tooth row. The teeth become progressively smaller posterior to this point and become more prominently striated. The 14th to 18th maxillary teeth are the smallest, with flared bases, and convex anterior surfaces in lateral view. The anterior twelve to thirteen maxillary teeth interdigitate with the adjacent teeth from the dentary for most of the length of the marginal tooth row. In this region, a lateral flaring of the dentition accompanies the interdigitation of the tooth crowns, such that the tooth crowns do not produce interdental pits in the opposing tooth bearing element as in other mosasaurs (Lingham-Soliar, 2002). Posterior to this point, the teeth are oriented more dorsoventrally and do not reach the dental border of the dentary. At least the posterior four maxillary teeth laterally overlap the posterior dentary teeth when the jaws are closed (Fig. 3–1).

Septomaxilla—Camp (1942) reported the presence of posteriorly fused septomaxillae in UCMP 32778. The presence of these elements can only be confirmed from the left side, as the right narial opening has not been fully prepared (Fig. 2A). Camp (1942) also provided serial cross sections through the nasal region in UCMP 32778, noting the positions of these elements along the length of the snout, which was undertaken while the snout and the remainder of the skull were separated, as evidenced by the crack that encircles the posterior snout region. Personal observation confirms that the left septomaxilla fuses with its right counterpart at a point that must be anterior to the junction of the premaxilla and the frontal. This is confirmed by a groove that extends along the dorsal surface of the fused septomaxillae that housed the descending keel of the internarial bar. Posterior to the site of fusion of the left and right septomaxillae, a pair of posterodorsally-inclined hook-shaped processes extend from separate left and right septomaxillae at a point posterior to the junction of the premaxilla and the frontal. These processes do not contact any elements dorsally or posteriorly. The posterior terminus of the septomaxillae is obscured by matrix, but these elements persist as separate dorsoventral splints of bone posterior to the posterior margins of the choanae, where they are flanked laterally by dorsoventral walls of the palatines, as illustrated by Camp (1942). The septomaxillae diverge anteriorly at roughly the point of the vomeropalatine suture in dorsal view. The left septomaxilla abuts against the ventrolateral surface of the descending internarial bar keel anteriorly and a portion of the element curves laterally to contact the vomer (prevomer sensu Camp, 1942), but neither element contacts the maxilla laterally to enclose the floor of the nasal vestibule.

Septomaxillae have also been reported for *Plioplatecarpus primaevus* and *Platecarpus planifrons* (Holmes, 1996; Konishi and Caldwell, 2007). The septomaxillae in these taxa differ from the same element in *Plotosaurus*. In *Plioplatecarpus primaevus*, the septomaxilla is described as a broad shield-shaped element that appears to be restricted to the anterior half of the opening for the external naris (Holmes, 1996). This element contacts the premaxilla medially and the maxilla laterally and formed the anteroventral border of the nasal vestibule (Holmes, 1996). The relative dimensions of this element and its topological relationships to the premaxilla and maxilla in *P. primaevus* are more reminiscent of the condition in *Varanus* and other terrestrial squamates in that the septomaxilla retains a broad contact with both of these elements (Estes and Pregill, 1988; Caldwell et al., 1995; Lee, 1997). The septomaxillae of *Plotosaurus* do not contact the anteromedial surfaces of the maxillae as they do in *Varanus* and *P. primaevus* (Holmes, 1996). Konishi and Caldwell (2007) describe a second condition for plioplatecarpine mosasaurs in which the septomaxillae of *Platecarpus planifrons* extend posteriorly to an anterior notch of the palatine posterior to the anterior process of the frontal, which is more reminiscient of the thin and extremely elongate septomaxilla in *Plotosaurus*. The posterior termination of the septomaxillae of *Plotosaurus* differs from *Platecarpus* in that the paired septomaxillae do not contact the palatines posteriorly, but extend along the cranial midline, medial to the palatines.

Nasal—Camp (1942) described a left nasal in UCMP 32778. This element is a prong of bone that is situated at a point anterior to the premaxillary-frontal suture. The premaxilla and the nasal respectively form the dorsal and ventral portions of an embracing contact with the premaxillary process of the frontal (Camp, 1942:fig. 14). Anteriorly, the nasal is nested in a depression ventral to the overhanging dorsal surface of the internarial bar. The nasal terminates posterior to the point of the greatest constriction of the internarial bar in dorsal view. The right nasal is absent, although Camp (1942:28) described a depression on the right side of the internarial bar that marks its in vivo position.

Frontal—The frontal is a rectangular element that possesses two anterolateral processes bilateral to the premaxillary process that mark the posterior extent of the external narial opening in dorsal view (Fig. 3–2A, B). The premaxillary process of the frontal extends further anteriorly than the anterolateral processes that border the external narial opening. These narial embayments in the frontal are also present in *Plioplatecarpus* (Lingham-Soliar, 1994; Holmes, 1996; Konishi and Caldwell, 2009), *Prognathodon currii* (see Christiansen and Bonde, 2002), and *Tylosaurus* (Bullard and Caldwell, 2010), but are lacking in all members of the sister taxon *Mosasaurus* (Russell, 1967; Lingham-Soliar, 1995). There is a rounded sagittal prominence on the dorsal surface of the frontal that extends from the premaxillary process to nearly halfway across the midline of the element. This prominence is flanked bilaterally by a convex surface dorsal to the midpoint of the orbit (Fig. 3–2B). This supraorbital bulging in the dorsal surface of the frontal has also been reported in *Plioplatecarpus* (Konishi and Caldwell, 2009). In *Mosasaurus*, the dorsal surface of the frontal is flat except for a well-developed midline dorsal keel that extends nearly the entire length of the element (e.g., BMNH 42929; IRSNB 3154; Lingham-Soliar, 1995:fig. 6e). The lateral margins of the frontal in *Plotosaurus* are sub- parallel and are excluded from forming the dorsal borders of the orbits by a contact between the prefrontals and postorbitofrontals laterally. Two pointed posterolateral extensions of the frontal overlap the parietal posteriorly. These extensions of the frontal are more sharply pointed than those of *Mosasaurus* (Russell, 1967; Lingham-Soliar, 1995). A pair of rectangular median flanges of the frontal extend posteriorly and surround the pineal foramen along the dorsal surface of the parietal in *Plotosaurus*. These flanges are proportionally broader than those of *Mosasaurus* (Lingham-Soliar, 1995; Lindgren et al., 2008) and extend posteriorly to the anterior borders of the supratemporal fenestrae. Camp (1942) suggested that shorter, more triangular posteromedian flanges of the frontal in CIT 2750 were among a list of features that distinguished the skull of *P. tuckeri* (CIT 2750) from *P. bennisoni* (UCMP 32778). Lindgren et al. (2008) re-examined this material and deemed this variation in the shape and length of these structures to be the result of taphonomic distortion. Other skulls referable to *Plotosaurus* (e.g., UCMP 45303; UCMP 57582) have rectangular posteromedial flanges of the frontal (Lindgren et al., 2008). The posterolateral and posteromedial flanges of the frontal contribute to a sinusoidal overlapping contact at the frontoparietal junction. The posteromedial flanges of the frontal extend on either side of the pineal foramen, but do not form the borders of the foramen, which is entirely within the parietal on the dorsal surface of the skull.

Prefrontal—Both prefrontals are complete. Anteriorly, the prefrontal is excluded from the posterolateral border of the external narial opening by an overlapping recurved wing of the maxilla, similar to *Ectenosaurus* and *Tylosaurus* (Fig. 3–2A, B; Russell, 1967). The supraorbital processes in *Plotosaurus* are sheaths of bone that overhang the dorsal margin of the orbit. These processes are smaller than those of *Clidastes*, *Prognathodon* and *Plesiotylosaurus* (Camp, 1942;

Russell, 1967; Lingham-Soliar and Nolf, 1989; Lindgren, 2009). Instead of forming a triangular anterodorsal prominence dorsal to the orbit as in other mosasaurs, the dorsal sheath of the prefrontal in *Plotosaurus* contacts the anterior border of the postorbitofrontal in an almost continuous supraorbital margin that excludes the frontal (Fig. 3–2). The posterior margin of the prefrontal forms an interdigitating suture with the anterior surface of the postorbitofrontal in dorsal view. This contact between the prefrontal and postorbitofrontal is also seen in *Plesiotylosaurus*, where the frontal is also excluded from forming the supraorbital margin in dorsal view (Lindgren, 2009). It is also present in *Mosasaurus* and *Prognathodon* (Russell, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995), but it is less laterally extensive in these taxa. There is no contact between the prefrontal and postorbitofrontal in *Clidastes* and the frontal forms a large portion of the dorsolateral margin of the orbit in that genus (Russell, 1967). In ventral view, the prefrontal of *Plotosaurus* is associated with the postorbitofrontal and the ventrolateral surface of the frontal. The vertical lamina of the prefrontal in UCMP 32778, which forms the anterior border of the orbit, is fairly concave. There is an acute angle formed by the descending vertical lamina and supraorbital process of the prefrontal in lateral view (Fig. 3–1). Ventrally, the vertical lamina of the prefrontal overlaps the posterodorsal process of the palatine. The prefrontal forms approximately the dorsal half of the anterior wall of the orbit, whereas the ventral half is formed by the palatine. Camp (1942) suggested that the lacrimal formed the ventrolateral margin of the orbit; however, it is difficult to identify the contact between either the maxilla and the lacrimal, or the palatine and the lacrimal in UCMP 32778. Isolated lacrimals have been reported for *Platecarpus* and *Prognathodon*; however, these identifications are based on isolated elements from fragmentary specimens (Russell, 1967; Lingham-Soliar and Nolf, 1989) and are here only tentatively considered as lacrimals.

Lacrimal—Mosasaur lacrimals are seldom recovered or described. The element is present in *Aigialosaurus bucchichi* (Durchak and Caldwell, 2009) as a small triangular element that forms a contact with the jugal laterally and the maxilla medially. Russell (1967) also illustrated a left lacrimal for *Clidastes liodontus*, which extends from the anterior terminus of the jugal to the posterior surface of the maxilla. Camp (1942) illustrated the lacrimal of *Plotosaurus* as being situated between the jugal and maxilla along the anteroventral border of the orbit, but did not illustrate its contact with these elements anteriorly (Camp, 1942). Surface abrasion makes the identification of the anterior and posterior borders of the lacrimal difficult, but the element does at least form the border of a small foramen between the lacrimal and prefrontal that is situated dorsal to the contact between the jugal and maxilla. The suture between the maxilla and the lacrimal is situated farther anteriorly than in Camp’s (1942) interpretation (Fig. 3–1A), suggesting that the lacrimal was more anteroposteriorly extensive than what was predicted by Camp (1942) and is similar to the condition in *Clidastes* (Russell, 1967).

Postorbitofrontal—The postorbitfrontal in *Plotosaurus* is a four-pronged element that borders the posterodorsal margin of the orbit and extends posteriorly onto the dorsal surface of the squamosal. Anteriorly, the postorbitofrontal contacts the prefrontal and the ventrolateral margin of the frontal at approximately the mid-point of the dorsal orbital margin. Camp (1942:4–5) suggested that a faint trace of a suture between the postorbital and postfrontal persisted in UCMP 32778; however, the state of surface preservation of these elements makes it too difficult to identify such a faint outline. Medially, the nature of the contact between the parietal process of the postorbitofrontal and the parietal cannot be defined due to surface abrasion and cracking. It is assumed that the parietal-postorbitofrontal contact is similar to other mosasaurines, where a convex lateral wing of the parietal overlaps the postorbitofrontal (Fig. 3–2B; Russell, 1967). Laterally, the descending jugal process curves ventrally and is oriented dorsoventrally at the point where it overlaps the jugal (Fig. 3–1). There is a sulcus on the dorsal surface of the descending process that opens posterolaterally. The orbital rim of the postorbitofrontal is thickened where it borders the posterodorsal margin of the orbit. Posteriorly, the squamosal process extends along the dorsal surface of the squamosal to the posterolateral corner of the supratemporal fenestra (Fig. 3–2).

Jugal—Both jugals are preserved in contact with the maxillae anteriorly, the postorbitofrontals posterodorsally, and the lacrimals (sensu Camp, 1942) and ectopterygoids medially. The jugal is a curved L-shaped bone with a horizontal ramus that is at least 2.5 times longer than the vertical ramus (Fig. 3–1). This ratio is comparable to the dimensions of the jugals of *Mosasaurus* (Lingham-Soliar, 1995) and *Prognathodon* (Schulp, 2006; Schulp et al., 2008). The angle between the horizontal and vertical rami is obtuse. This angle is wider than that of

Mosasaurus (Russell, 1967; Bell, 1997; Lingham-Soliar, 1995), but is comparable to *Prognathodon solvayi*, where the vertical ramus is dorsally and slightly posteriorly directed (Lingham-Soliar and Nolf, 1989). Anteriorly, the jugal contacts the posterolateral surface of the maxilla. The horizontal ramus of the jugal terminates anteriorly in an interdigitiating suture with the maxilla on the right side (Fig. 3–1D) and in an overlapping contact on the left (Fig. 3–1B). In ventral view, the horizontal ramus thins anteriorly into a flange of bone that overlaps the posterior end of the maxilla laterally (Fig. 3–4). The posterior two maxillary tooth spaces are concealed from lateral view by the overlapping horizontal ramus of the jugal. A posterior extension of the maxilla persists along approximately one quarter of the length of the medial side of the horizontal ramus. The jugal contacts the lacrimal along the anterolateral margin of the orbit (Camp, 1942), but the true extent of the lacrimal is not identifiable. Posterior to this contact, the horizontal ramus of the jugal contacts the ectopterygoid to a point even with the junction between the horizontal and vertical rami of the jugal posteriorly. In *Plotosaurus*, the ectopterygoid excludes the jugal from forming the ventrolateral border of the orbit. At the junction of the two rami (Fig. 3–4) a pointed posteroventral process projects from the jugal (contra Russell, 1967). The dorsal surface of the vertical ramus is overlapped by a triangular jugal process of the postorbitofrontal. There is a V-shaped notch in the dorsal tip of the jugal that marks the extent of the overlap by the postorbitofrontal.

Parietal—The posteromedial and posterolateral extensions of the frontal overlap the anterior surface of the parietal table (Fig. 3–2). The pineal foramen is an oval opening that is entirely bounded by the parietal. Two converging anterior processes of the parietal with raised dorsal margins form the anterior border of the pineal foramen. There is a line separating these two processes anterior to the pineal foramen. Although the pineal foramen in *Plotosaurus* is proportionally larger than in most other mosasaurines (Camp, 1924; Russell, 1964), it is surrounded by posteromedial flanges of the frontal that extend posteriorly at least another half of the length of the pineal foramen (Fig. 3–2). The parietal table is relatively short in *Plotosaurus* compared to other mosasaurines (Camp, 1942). The dorsolateral ridges of the parietal table diverge posterior to the pineal foramen, at a point anterior to the mid-length of the supratemporal fenestra (Fig. 3–2). At no point are the dorsolateral ridges of the parietal table parallel, and the lateral margins of the parietal table are concave throughout their lengths. This is different from the rectangular parietal tables and the presence of parallel or sub-parallel dorsolateral ridges in*Clidastes* (Russell, 1967; Shannon, 1975:pl. 1), *Mosasaurus* (Goldfuss, 1845:pl. 6; Russell, 1967; Lingham-Soliar, 1995), and *Prognathodon* (Christiansen and Bonde, 2002; Schulp, 2006:fig 6d; Schulp et al., 2008:fig 6a). Laterally, a rectangular descencus processes parietalis extends ventrally over the parietal process of the prootic (Fig. 3–1B, D). This descending process is the longest reported for any known mosasaur (Camp, 1942; Russell, 1967). The descencus processus parietalis overlaps the prootic laterally and terminates along the dorsal border of the trigeminal notch, where it also overlapped the epipterygoid (Camp, 1942). A similarly elongate descending process of the parietal has been reported for *Mosasaurus missouriensis*, however, Camp (1942) suggested that it was shorter than that of *Plotosaurus*. Personal observation of the holotype of *M. missouriensis* confirms Camp's (1942) observation that RFWUIP 1327 possesses a similar configuration of this structure and that its precise length is difficult to equate to that of *Plotosaurus*, given its state of preservation (Goldfuss 1845). This descending process does at least approach the dorsal border of the trigeminal notch and thus extensively overlaps the prootic as it does in *Plotosaurus* and has not been reported in any other species of *Mosasaurus*.

In *Plotosaurus*, the supratemporal rami of the parietal diverge at approximately the mid-length of the supratemporal fenestra (Fig. 3–2). These rami curve posterolaterally and terminate in an overlapping contact with the squamosals posteriorly, excluding the supratemporals from view dorsally. Throughout their length, the supratemporal rami are dorsoventrally compressed and have elliptical cross-sections. As noted by Russell (1967), there are dorsal and ventral extensions of the supratemporal rami of the parietal that embrace the supratemporal dorsoventrally (Fig. 3–3B; 3–4A). This tight association of the parietal and anterior portion of the supratemporal is also seen in *Prognathodon* (Russell, 1967; Bell, 1997; IRSNB R 33), *Mosasaurus lemonnieri* (IRSNB 3109; AL pers. obs.) and the tylosaurine *Tylosaurus* (Russell, 1967), but is absent or weakly expressed in *Clidastes* (Camp, 1942; Russell, 1967). Amongst non-mosasaurine mosasaurs, for example *Halisaurus*, *Platecarpus* and *Plioplatecarpus*, the typical configuration of the supratemporal and parietal is a loose attachment, whereby the parietal only overlaps the supratemporal dorsally

(Holmes, 1996; Holmes and Sues, 2000; Konishi and Caldwell, 2007; Konishi and Caldwell, 2009). Posteroventrally, the parietal of *Plotosaurus* is united to the dorsal surface of the supraoccipital. The tight association of these two elements is similar to *Halisaurus*, where there was no room for the cartilaginous processus ascendens tecti synotici to fill the gap between the parietal and supraoccipital dorsally (Frazzetta, 1962; Callison, 1967; Holmes and Sues, 2000).

Squamosal—The anterior ramus of the squamosal is cylindrical and extends from the triangular body of the element at the posterolateral corner of the supratemporal fenestra to the ventral surface of the postorbitofrontal (Figs.3–1, 3–2). The anterior terminus of the squamosal is at a point even with the jugal process of the postorbitofrontal. Posterior to this point, the squamosal ramus of the postorbitofrontal overlaps the squamosal and is housed in a groove along the dorsal surface of the element. At the posterolateral corner of the supratemporal fenestra, the squamosal is expanded into a triangular body that contacts the parietal rami, concealing the supratemporal from dorsal view (Fig. 3–2). Contact between the squamosal and the supratemporal ramus of the parietal is also seen in *Mosasaurus* (Lingham-Soliar, 1995), *Prognathodon* (Russell, 1967; Schulp, 2006) *Taniwhasaurus* (Fernandez and Martin, 2009) and *Tylosaurus* (Russell, 1967; Bullard and Caldwell, 2010), but not in *Clidastes liodontus*, as figured by Russell (1967:fig.72) and Bell (1997:fig. 6a). Posteriorly, the squamosal curves ventrally at an angle of 90 degrees and forms the posterolateral portion of the quadrate suspensorium (Figs. 3–1, 3–3). In lateral view (Figs. 3–3C, D), the posterior portion of the squamosal tightly embraces the posterior surface of the suprastapedial process of the quadrate, similar to the condition in *Taniwhasaurus* (Martin and Fernandez, 2009). In posterior view (Fig. 3–3A, B) the squamosal terminates dorsal to the point of the scar for the *M. depressor mandibulae* on the suprastapedial process and forms a curving suture with the lateral surface of the supratemporal.

Supratemporal—The supratemporal is partially obscured by a contact with the supratemporal ramus of the parietal anteriorly and the squamosal laterally (Fig. 3–1). The wedge-shaped anterior end of the supratemporal is united to a dorsal and ventral extension of the parietal ramus. At the posteromedial corner of the temporal arcade, the supratemporal persists as a dorsoventral slip of bone in dorsal view (Fig. 3–2) that descends 90 degrees from the horizontal to embrace the quadrate posteriorly (Fig. 3–3A, B). In posterior view (Figs. 3–3A, B; 3–4A, B), the supratemporal is ventromedially-directed and extends over the posterior surface of the suprastapedial process, medial to the scar for the *M. depressor mandibulae*. The supratemporal extends further ventrally over the suprastapedial process than does the posterior end of the squamosal, the former element nearly reaching the posteromedial tip of the suprastapedial process. Medially, the supratemporal contacts the lateral surface of the paroccipital process (Fig. 3–3A, B).

Quadrate—Both quadrates are well preserved and contact the associated suspensorial elements of the skull (Fig. 3–1). The quadrate shaft is held in a dorsoventral orientation by the quadrate suspensorium. The hook-shaped suprastapedial process extends posteriorly from the main shaft of the quadrate and then curves ventrally at a 90-degree angle, reflecting a similar angle between the horizontal and vertical components of the squamosal and supratemporal. The suprastapedial process also curves medially and encloses the stapedial notch, nearly contacting an infrastapedial process along the posteromedial surface of the quadrate shaft. Along the posterior surface of the suprastapedial process, there is a rounded fossa that is interpreted as the scar for the profound slip of the *M. depressor mandibulae* (digastric muscle sensu Camp, 1942) (Russell 1967; Konishi, 2008). This fossa is surrounded by the squamosal dorsally and by the supratemporal medially (fig. 3–3A). Fernandez and Martin (2009) and Konishi and Caldwell (in press) have reported similar arrangements of the squamosal and supratemporal along the posterior surface of the quadrate suprastapedial process in *Taniwhasaurus* and the Plioplatecarpinae respectively. A curved ventrolateral corner of the paroccipital process encircles the posteromedial corner of the suprastapedial process. The quadrate ala extends laterally from the surface of the quadrate and has a groove along its lateral border, similar to *Mosasaurus* (Russell, 1967; Bell, 1997). An ascending crest of the quadrate ala extends from the posterolateral corner of the quadrate shaft dorsal to the mandibular condyle and nearly reaches the infrastapedial process along the medial side at approximately the mid-height of the element. In posterior view, the ascending crest of the left quadrate is continuous with the infrastapedial process (Figs. 3–3A, B); however, this is the result of the state of surface preservation in UCMP 32778. The separation between these two features is present in other isolated quadrates attributed to *Plotosaurus* (CIT 2945, UCMP 152554). The infrastapedial process is a rounded protuberance along the mid-height of the posteromedial surface of the quadrate shaft. The stapedial pit is concealed from view, but isolated quadrates of other specimens of *Plotosaurus* (e.g., UCMP 152554) show that it is a circular depression along the medial surface of the quadrate shaft. In *Mosasaurus*, the stapedial pit is proportionally larger and oval-shaped, nearly matching the height of the stapedial notch in medial view (Lingham-Soliar, 1995). The mandibular condyle is convex and widest mediolaterallly with no anterior extension of the articular surface (Figs. 3–3C, D). The quadrate ramus of the pterygoid is situated near, but does not contact, the quadrate dorsal to the mandibular condyle on the medial surface.

Prootic—The prootic is a triradiate bone that contacts the ventral surface of the parietal anterodorsally, the basisphendoid ventrally, the supraoccipital posterodorsally and the paroccipital process and supratemporal posteriorly (Russell, 1967). The parietal process of the prootic extends anterodorsally from the body of the element at approximately 45 degrees in UCMP 32778. The lateral surface of the parietal process of the prootic is concealed by the descencus processus parietalis, which extends ventrally to the anterodorsal corner of the trigeminal notch (Figs. 3–1B, C). At the junction of the parietal process and the descending ramus of the prootic is the trigeminal notch. Unlike *Clidastes* (Russell, 1967:fig. 12) and *Mosasaurus* (Lingham-Soliar, 1995:fig. 13a), the trigeminal notch in *Plotosaurus* opens anterodorsally and is more deeply excavated into the anterior surface of the prootic than in these genera. The anterodorsal opening of the trigeminal notch is bilaterally symmetrical and its orientation is the result of a dorsal expansion of the alar process of the basisphenoid along the anteroventral corner of the trigeminal notch (Camp, 1942). The posterior ramus of the prootic extends posterolaterally along the posterior surface of the paroccipital process. A dorsoventrally oriented suture separates the supraoccipital and paroccipital processes from the posterior surface of the prootic.

Opisthotic-Exoccipital—The opisthotic and exoccipital are fused into a single paroccipital process, as in other mosasaurs (Russell, 1967). Medially, the paroccipital process contacts the ventrolateral portion of the supraoccipital. The paroccipital process extends posterolaterally, forming the proximal contact with the supraoccipital at a 45 degree angle (Fig. 3–4). At the distal terminus, the process is dorsoventrally expanded and contacts the medial surface of the supratemporal. There is a well-developed ventral extension of the paroccipital process that extends further ventrally than the supratemporal and curves laterally at its ventral terminus to encircle the posteromedial corner of the suprastapedial process of the quadrate (Figs. 3–3A, B; 3–4). This ventral process has been reported in *Plioplatecarpus nichollsae*, although the articulation with the quadrate was not preserved (Konishi and Caldwell, 2009).

Supraoccipital—The supraoccipital is a dorsoventral wall of bone in *Plotosaurus* that forms the posterior surface of the braincase (Fig. 3–4). The supraoccipital contacts the paroccipital processes laterally and forms the dorsal margin of the foramen magnum. The posterior wall of the supraoccipital is ornamented with three parallel crests that extend the length of the element. The sagittal crest is the highest of the three and extends from the dorsal margin of the foramen magnum to the posteroventral surface of the parietal. Here, the supraoccipital contacts the parietal (Fig. 3–4; Camp, 1942). Two smaller crests extend lateral to the sagittal crest but not as far dorsally, creating a triangular dorsal termination of the supraoccipital in posterior view. The lateral crests diverge ventrally, cross the supraoccipital-parocccipital suture and are oriented sub- horizontally along the posterior surfaces of the paroccipital processes. These crests are interpreted as the points of insertion for the *M. rectus capitis posterior* (sensu Russell, 1967). Unlike other squamates, there is no gap between the posterodorsal surface of the braincase and the skull roof at the supraoccipital-parietal junction (contra Callison, 1967). The absence of the processus ascendens tecti synotici (nodule of cartilage between the parietal and supraoccipital) is shared with *Plotosaurus* and other mosasaurine taxa, including *Clidastes* (Russell, 1967), *Mosasaurus* (Lingham-Soliar, 1995; IRSNB 3109, RFWUIP 1327), and the halisauromorph, *Halisaurus* (Holmes and Sues, 2000). There is almost no posterior overhanging of the parietal over the supraoccipital in *Plotosaurus*. In *Mosasaurus lemonnieri* (e.g., IRSNB 3109) and *M. missouriensis* (RFWUIP 1327), there is a posterior extension of the parietal that overhangs the posterior wall of the braincase.

Basioccipital—The dorsal and anterior surfaces of the basioccipital are concealed by the surrounding elements of the braincase. Two basal tubera extend ventrolaterally from the body of the basioccipital at approximately 45 degrees. These tubera are partially covered ventrally by ventroposterior extensions of the basisphenoid (Figs. 3–4; 3–5). The exact shape of the occipital condyle is not clear, because the atlas is preserved in articulation at the back of the skull.

Basisiphenoid—The ventral floor of the basisphenoid is exposed posterior to the pterygoids. Two disc-shaped basipterygoid processes extend ventrolaterally and nearly contact the pterygoids. These processes extend over the dorsal surfaces of the pterygoids anterior to the notch between the quadrate rami and basisphenoid processes of the pterygoids. The floor of the basisphenoid is sulcate between the ventroposterior tongues that cover the ventral surfaces of the basioccipital tubera (Fig. 3–5). In lateral view, the alar processes of the basisphenoid extend dorsally and form the anteroventral border of the trigeminal notch, which opens anterodorsally. A parasphenoid rostrum extends anteriorly between the orbits. The posterodorsal surface of the parasphenoid rostrum is sulcate.

Orbitosphenoid—Preservation of the ossified orbitosphenoid is rare in mosasaurs, and has only been documented conclusively, due to its preservation in situ, in UCMP 32778 (Camp, 1942; Russell, 1967). The orbitosphenoid is an ‘L’-shaped element with an expanded, fan-shaped anterior end. The orbitosphenoid in UCMP 32778 is inclined mediolaterally from the sagittal plane of the skull and is located dorsolateral to the basisphenoid and the base of the parasphenoid rostrum (Fig. 3–6A). Anteriorly, the orbitosphenoid is suspended by a band of cartilage (preserved as brownish granules in the matrix filling the orbit), known as the planum supraseptale. The planum supraseptale extends from the anterodorsal surface of the orbitosphenoid to the ventral surface of the frontal, similar to other squamates (Tarazona et al., 2008). The ventral border of the orbitosphenoid forms an arc that encloses the posterior half of the optic chiasm (Camp, 1942; Tarazona et al., 2008). The ventral arm of the orbitosphenoid is straight and directed ventrally and would have provided the origin for several of the eye muscles, including the *M. inferior rectus* (Camp, 1942; Tarazona et al., 2008). There is a rod-like extension of the orbitosphenoid projecting from the anteroventral corner of the element. Anterior to this, a congregation of granules that Camp (1942) inferred to be calcified cartilage extends anteroventrally along what would have been the medial wall of the orbit. Due to its position along the midline of the skull, this band of calcified cartilage likely represents the remains of the interorbital septum (Tarazona, 2008). Camp (1942) also described an ossification along the midline of the skull dorsal to the parasphenoid rostrum that represents remains of an ossified interorbital septum. The dark coloration of the granules extending from the anteroventral corner of the orbitosphenoid supports the presence of a well-developed interorbital septum (Fig. 3–6A), although the presence of any ossification cannot be determined conclusively.

Pterygoid—Both pterygoids are well-preserved, but are obscured dorsally by matrix (Figs. 3–5; 3–6B). Camp (1942) identified 15 pterygoid tooth spaces in UCMP 32778, although Lindgren et al. (2008) and personal observation of the material have determined a pterygoid tooth count of 13 or 14. Unfortunately, the anterior portions of both pterygoid tooth rows are obscured by matrix, making the exact number of pterygoid teeth unclear. In *Clidastes*, these pterygoid teeth are directed ventrally and arranged in straight lines along the pterygoids (Russell, 1967). In *Mosasaurus*, these teeth are arranged in a curve, where the middle pterygoid teeth are situated furthest from the midline of the skull (Russell, 1967; Lingham-Soliar, 1995), whereas in *Plotosaurus*, the dentigerous ramus of the pterygoid flares out laterally in such a way that the posterior 6–7 teeth are sub-horizontal (Fig. 3–5). Although taphonomic distortion may have exaggerated this feature in UCMP 32778, this is unlikely to be the sole explanation for the orientation of the posterior pterygoid dentition. The state of preservation of the skull implies that the pterygoids are no more damaged or displaced than any of the adjacent elements of the skull roof, mandibles, or palatal complex (Figs. 3–4; 3–5). Moreover, both sets of pterygoid teeth are flared out bisymmetrically, suggesting this orientation of the teeth is genuine. Posterior to the pterygoid tooth row, the quadrate rami are also preserved in bilateral contacts with the quadrates (Fig. 3–5), indicating there is little if any distortion of these elements. Anteriorly, the pterygoids terminate in an anteromedially-oriented suture with the ventral surfaces of the palatines posterior to the margins of the choanae. The interpterygoid vacuity is widest at a point adjacent to the middle teeth of the pterygoid and narrowest at the anterior ends of the dentigerous rami. The space between the pterygoids is narrower than in most other mosasaurs. Posterior to the last pterygoid tooth, a tongue-shaped basisphenoid process extends posterolaterally. The quadrate rami diverge at a shallower angle from the main body of the pterygoid than in *Platecarpus* or *Plioplatecarpus* (Russell, 1967; Konishi and Caldwell, 2009) and form the lateral border of a notch between the basisphenoid process and the base of the quadrate ramus. The quadrate rami of the pterygoids become wider posteriorly where they nearly meet the ventromedial surfaces of the quadrates. At this point, the medial surfaces of the quadrate rami are sulcate, opening medially towards the basisphenoid and basioccipital. The basipterygoid processes of the basisphenoid extend along the anterior margin of this notch dorsally.

Epipterygoid—In most squamates, the epipterygoid is a cylindrical element that is expanded at the distal tips to contact the pterygoid ventrally and the ascending wing of the prootic and parietal dorsally (Frazzetta, 1962; Russell, 1967; Payne et al., 2011; pers. obs.). In *Plioplatecarpus nichollsae*, the epipterygoid is a bowed element with a grooved dorsal extremity, which was likely capped with cartilage in life (Konishi and Caldwell, 2009). Russell (1967:fig. 23b) figures an isolated epipterygoid of *Platecarpus ictericus* that appears to be bowed at approximately mid-shaft, with a cup-shaped ventral end for articulation with the pterygoid and a smaller tapering dorsal end for articulation with the parietal ramus of the prootic. In *Plotosaurus*, only the left epipterygoid is visible ventral to the ventral margin of the descensus processus parietalis and directly posterior to the orbitosphenoid (Fig. 3–6B). The epipterygoid contacts the pterygoid ventrally, anterior to the notch at the base of the basipshenoid process. The ventral extremity of the element is convex, although the ventral tip of the element is concealed due to its contact with the dorsal surface of the pterygoid. Dorsal to the contact with the pterygoid, the epipterygoid curves posterolaterally and spirals, such that the anterior surface of the element faces medially a quarter of the length dorsally up the shaft. Dorsal to this point, the epipterygoid curves medially. The shaft of the epipterygoid is compressed dorsal to the point of the spiraling, and tapers to a mediolaterally-compressed blade at its dorsal extremity. The dorsal tip has likely been dislodged because it rests medial to the parietal ramus of the prootic. In life, as noted by Camp (1942), the dorsal end was housed within a recess between the anterior margin of the parietal ramus of the prootic and the anteroventral corner of the descensus processus parietalis (Fig. 3–6).

Ectopterygoid—The ectopterygoid contacts the ectopterygoid process of the pterygoid posteromedially and the posteromedial end of the jugal laterally. The ectopterygoid has been displaced on either side; however, the ectopterygoid extended anteriorly to contact the palatine, based on the length of the element. The ectopterygoid tapers anteriorly to a point, which was housed in a shallow depression in the orbital border of the palatine. This element is longer than in most other mosasaurids (Camp, 1942). In *Platecarpus*, this element does not exclude the jugal from forming the ventrolateral border of the orbit as it does in *Plotosaurus* (Russell, 1967; Konishi and Caldwell, 2007). The dorsal surface of the ectopterygoid is concave, reflecting a similar curvature of the jugal and posterodorsal process of the palatine.

Palatine—Both palatines are preserved in their natural postions and are undistorted. The posterodorsal process of the palatine forms the ventral corner of the anterior wall of the orbit. The posterior borders of the palatines contact the anterior ends of the pterygoids in a suture that trends posterolaterally from the posteromedial corner of the main palatine body (Fig. 3–5). The palatines contact the medial walls of the maxillae and form the posterior and posterolateral borders of the internal narial openings. A palatine process, which is only composed of the palatine, forms the medial border of the internal narial opening for most of its length. In ventral view, the palatine processes converge medially and contact at a point just posterior to the vomeropalatine suture. In *Mosasaurus missouriensis*, *M. hoffmanni* and *M. beaugei*, these processes are separated throughout their length posterior to the vomeropalatine suture (Goldfuss, 1845; Lingham-Soliar, 1995; Mulder, 1999; Bardet et al., 2004). Anterior to this point, the palatines of *Plotosaurus* diverge anterolaterally and form the ventromedial borders of the internal narial openings where they also obliquely overlap the vomers. Along the posteromedial corner of the internal narial opening, the palatine is dorsoventrally oriented, being highest at a point even with the posterior terminus of the septomaxilla in dorsal view. In dorsal view, the palatine becomes a horizontal sheath of bone that overlaps the vomer anteriorly. The vomeropalatine suture is situated at a point even with the eighth maxillary tooth position in dorsal view (Fig. 3–2). The vomeropalatine suture terminates further anteriorly on the dorsal surface than it does on the ventral (Figs. 3–2; 3–5), indicating that there is a region of overlap between these two elements, where the palatine overlaps the vomer (Camp, 1942:fig. 14).

Vomer—Vomeropalatine sutures are rarely preserved in mosasaurs (Russell, 1967), save for in a few specimens of *Platecarpus*, *Plioplatecarpus*, *Prognathodon* and *Mosasaurus* (Goldfuss, 1845:pl. 8; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Holmes, 1996; Konishi and Cadwell, 2007; 2009).

Konishi and Caldwell (2007) described a contact between the vomer and the anteromedial corner of the pterygoid in *Platecarpus planifrons*. Contact between these two elements is not observed in *Plotosaurus*. In *Plotosaurus*, the vomers terminate posteriorly at a point that is anterior to the anteromedial corners of the pterygoids and are separated from the pterygoids by the converging anterior processes of the palatines. There is a similar relationship between the palatines and vomers in *Mosasaurus missouriensis*, where there is an elongate anterior process of the palatine that contacts the vomer anteriorly, separating the vomer from the anterior surface of the pterygoid (Goldfuss, 1845). The vomers in *Plotosaurus* form the floor of the internarial septum anterior to the vomeropalatine suture and are in contact along the midline of the skull throughout their length. In *Platecarpus*, *Plioplatecarpus* and *Prognathodon* the vomers are separated (Lingham-Soliar and Nolf, 1989; Holmes, 1996; Konishi and Cadwell, 2007; 2009), whereas in *Mosasaurus*, they are more closely associated along the midline, however, they are not in direct contact as they are in *Plotosaurus* (Goldfuss, 1845; Lingham-Soliar, 1995). The ventral surfaces of the vomers are smooth and flat. The dorsal surfaces are overlapped by the septomaxillae anteriorly, leaving little room for the Jacobson's organ between the vomers and septomaxillae anteriorly (Camp, 1942; Lingham-Soliar, 1995). The anterior ends of the vomers are concealed by matrix.

Mandibles

Dentary—The dentary of *Plotosaurus* is slender and has a diagnostically convex dorsal margin. This curvature of the dentary follows that of the maxilla, and creates a ventral snout bend in UCMP 32778 (Fig. 3–1). There is an edentulous anterior extension of the dentary that extends anterior to the first dentary tooth by more than the length of a single tooth space. This rostrum of the dentary extends further anteriorly than the premaxilla, a feature that is unique to *Plotosaurus* (Camp, 1942; Russell, 1967) and is present in several specimens (e.g., CIT 2750; 2945; UCMP 57582; 137247; 131809). In ventral view, the dentaries contact each other along the midline of the skull for approximately the anterior quarter of their lengths, to a point lingual to the sixth dentary tooth (Fig. 3–5). Camp (1942) identified 17 dentary teeth in UCMP 32778, however, this count was attributed to alveoli that were visible in lateral view. Considering that 17 teeth or alveoli are visible, there is space posteriorly for an additional tooth between the last visible alveolus and the anterior tip of the coronoid; however, due to the preservation of UCMP 32778 with its jaws closed, the overlapping maxillary teeth conceal the posterodorsal portion of the dentary on either side. A larger specimen of *Plotosaurus* (CIT 2750), assigned to *P. tuckeri* by Camp (1942), exhibits a dentary tooth count of 17, whereas an even larger specimen (UCMP 57582) possesses 18 dentary teeth. This implies that ontogenetic or intraspecific variation exists in the number of dentary teeth in *Plotosaurus*. This is the highest dentary tooth count known for a mosasaurine (Lingham-Soliar, 1995). By comparison, most globidensine mosasaurs possess 14–15 dentary teeth

(Lingham-Soliar and Nolf, 1989; Schulp, 2006; Schulp et al., 2008), whereas the maximum dentary tooth count for *Mosasaurus* is 16 (Lingham-Soliar, 1995). *Pluridens walkeri* Lingham-Soliar, 1998, from the Maastrichtian of Niger has a higher tooth count than *Plotosaurus* (> 28, versus 17–18 in *Plotosaurus*), but the affinities of this enigmatic taxon are uncertain due to the fragmentary nature of the holotype (Lingham-Soliar, 1998).

The dentition of UCMP 32778 mirrors that of the upper jaw, where the anterior nine or ten dentary teeth are conical and flare laterally from the dental margin, interdigitating with the opposing teeth when the jaws are closed. The posterior teeth are oriented more dorsoventrally and become progressively shorter and more curved posteriorly. The maxillary teeth also overlap the posterior dentary teeth.

Coronoid—The coronoid is a saddle-shaped element that straddles an ascending coronoid buttress of the surangular posteriorly and nearly contacts the dentary anteriorly (Fig. 3–1). The anterior portion of the coronoid tapers to a point that does not overlap the posterodorsal corner of the dentary. Posteriorly, a large dorsoventral posterior process of the coronoid ends at approximately half of the height of the orbit in UCMP 32778. A large posterior process of the coronoid is also seen in *Mosasaurus* and *Prognathodon* (Russell, 1967; Lingham-Soliar, 1995; Christiansen and Bonde, 2002; Dortangs et al., 2002). Other specimens of *Plotosaurus*, which preserve the medial view of the coronoid show that the medial wing of the coronoid contacted the anterodorsal surface of the angular.

Splenial—The splenials of UCMP 32778 are concealed by the dentaries in lateral view (Fig. 3–1). In ventral view, the lateral surfaces of the splenials are visible along almost half of the posteroventral margins of the dentaries (Fig. 3–5). The posterior ends of the splenials are preserved in contact with the angulars in their natural position. As such, the intramandibular joint is oriented sub-horizontally, compared to the traditional reconstruction of a dorsoventrally oriented intramandibular joint in other mosasaurs (Russell, 1964; Callison, 1967; Russell, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995). The splenio-angular joint is more laterally compressed than in *Mosasaurus* (Lingham-Soliar, 1995) and is elliptical in cross section, similar to *Prognathodon* (Lingham-Soliar and Nolf, 1989; Schulp, 2006; Schulp et al., 2008).

Angular—Similar to the splenial, the angular is oriented more horizontally than what has been reported for other mosasaurs. The anterior surface of the angular is convex and elliptical and is in articulation with the posterior surface of the splenial. Lateral to the contact with the splenial, a region of the surface of the surangular marks the extent of movement at the splenial-angular joint. Ridges along the anterolateral surface of the angular indicate that the only possible range of motion at this joint was perpendicular to the long axis of the splenial-angular articulation. There is an embayment in the anteroventral surface of the surangular where the lateral surface of the angular is most exposed in ventral view. Posteriorly, the angular-surangular suture is difficult to distinguish from the surface cracks along the posterior portion of the mandible and the contribution of the angular to the posteroventral portion of the lower jaw is unclear (Fig. 3–5B). Due to the state of preservation of UCMP 32778, the medial surface of the angular is concealed. Other specimens of *Plotosaurus* (CIT 2750; CIT 2945) preserve the medial surface of the angular, the anteromedial portion of which extends dorsally to contact the descending medial wing of the coronoid, forming a wall of bone that medially overlaps the prearticular.

Surangular—The surangular forms nearly the entire lateral wall of the post-dentary complex. Similar to *Mosasaurus* and *Prognathodon*, there is a long and thin wall of the surangular that steeply ascends from the anterior border of the glenoid fossa to the posterior border of the coronoid, creating a triangular shape to the post-dentary complex in lateral view (Fig. 3–1; Russell, 1967; Lingham-Soliar, 1995). The lateral surface of the surangular is convex and overlaps the angular ventrally. Posteriorly, the surangular forms roughly the anterior half of the glenoid fossa and extends posteriorly to form a portion of the ventrolateral surface of the retroarticular process, as in *Mosasaurus* (Figs. 3–1; 3–3; Russell, 1967; Lingham-Soliar, 1995:fig. 14b).

Articular-Prearticular—Only the articular contribution to the glenoid fossa and the retroarticular process are visible in UCMP 32778. Unlike other mosasaurs, the dorsal surface of the retroarticular process is rotated such that it is horizontal in lateral view (Fig. 3–2; 3–3) and in ventral view, the retroarticular process is also curved medially (Fig. 3–5). The retroarticular process is rectangular in dorsal and ventral views, and its dorsal surface is concave. The fused articular and prearticular form the posteromedial half of the glenoid fossa and form a raised posterior border of the cotylus, in which sits the quadrate (Fig.

3–3C, D). In other specimens of *Plotosaurus* (CIT 2750; CIT 2945), the prearticular forms a tongue of bone that is surrounded ventrally and medially by the angular, and laterally by the surangular. The anterior extension of the prearticular continues anteriorly into the groove between the dentary and the splenial, as it does in other mosasaurs (Russell, 1967).

CONCLUSIONS

Camp's (1942) description of *Plotosaurus bennisoni* was originally based on a single well-preserved specimen, which provided a weatlth of anatomical details for this taxon. The redescription of the now monotypic genus, *Plotosaurus*, was undertaken to provide additional anatomical information and figures that compliment Camp's (1942) description and diagnosis of this taxon. Moreover, revisiting the cranial anatomy of *Plotosaurus* has revealed new details that can be examined in an undistorted three-dimensional perspective, due to the exquisite preservation of the holotype. These features include (1) the dorsoventral orientations of the squamosal, supratemporal and suprastapedial process of the quadrate, (2) the ventrolateral orientation of the pterygoid teeth, (3) the unique orientation of the intramandibular joint and (4) the elongated region of contact between the dentaries. While these features are considered autapomorphies of *Plotosaurus*, this redescription provides an anatomical framework around which a discussion of the aquatic adaptations and functional morphology of the cranial anatomy of *Plotosaurus* is undertaken in the proceeding chapter.

FIGURE 3–1. Skull of *Plotosaurus bennisoni* (UCMP 32778) in lateral view. **A**, photograph of UCMP 32778 in left lateral view; **B**, diagram; **C**, photograph of UCMP 32778 in right lateral view; **D**, diagram. Grey areas indicate the presence of matrix or absence of bone. **Abbreviations: a**, angular; **c**, coronoid; **cb**, coronoid buttress of surangular; **d**, dentary; **dpp**, descencus processus parietalis; **ed**, edentulous extension of dentary; **f**, frontal; **l**, lacrimal; **j**, jugal; **mcd**, mandibular condyle; **mx**, maxilla; **os**, orbitosphenoid; **p**, parietal; **pal**, palatine; **pf**, pineal foramen; **pmx**, premaxilla; **pof**, postorbitofrontal; **popr**, paroccipital process; **prf**, prefrontal; **q**, quadrate; **qag**, quadrate alar groove; **qr**, quadrate ramus of pterygoid; **ret**, retroarticular process; **sa**, surangular; **soc**, supraoccipital; **sop**, supraorbital process of prefrontal; **spl**, splenial; **sq**, squamosal; **st**, supratemporal. Scale bar equals 10 cm.

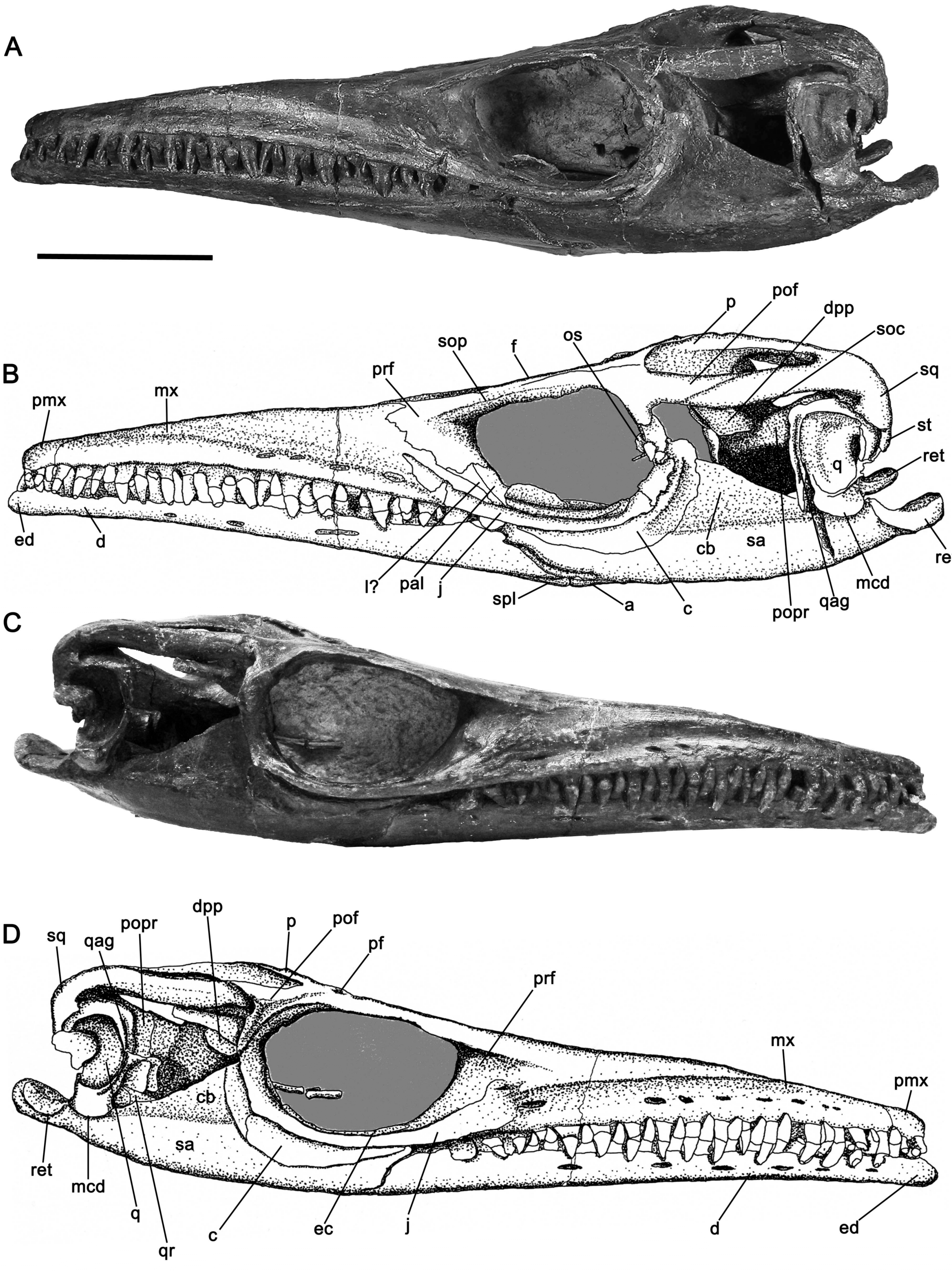

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FIGURE 3–2. Skull of *Plotosaurus bennisoni* (UCMP 32778) in dorsal view. **A**, photograph; **B**, diagram. Dotted lines indicate probable position of suture between parietal and postorbitofrontal. Grey areas indicate the presence of matrix or absence of bone. **Abbreviations: aa**, atlas neural arch; **dmr**, dorsomedial ridge of premaxilla; **dpp**, descencus processus parietalis; **ex**, exoccipitals; **f**, frontal; **j**, jugal; **int**, internarial bar of premaxilla; **mx**, maxilla; **p**, parietal; **pal**, palatine; **pf**, pineal foramen; **pmx**, premaxilla; **pof**, postorbitofrontal; **popr**, paroccipital process; **prf**, prefrontal; **q**, quadrate; **ret**, retroarticular process; **sob**, supraorbital bulge **soc**, supraoccupital; **sq**, squamosal; **st**, supratemporal; **sx**, septomaxilla; **v**, vomer. Scale bar equals 10 cm.

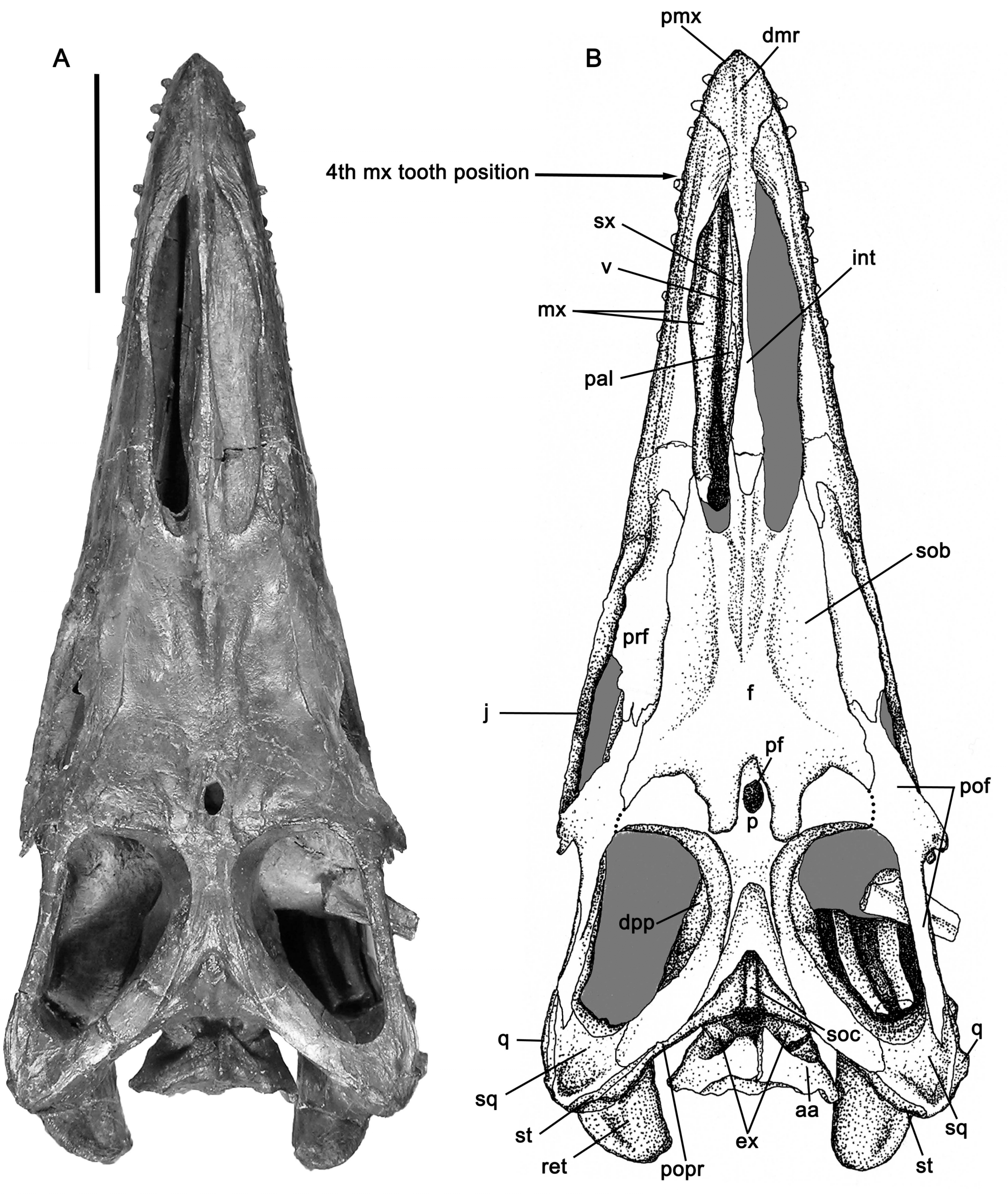
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FIGURE 3–3. Right quadrate and elements of the quadrate suspensorium of *Plotosaurus bennisoni* (UCMP 32778). **A**, diagram of quadrate and suspensorium in posterior view, anterior to the right. Dotted line indicates approximate position of suture between supratemporal and parietal; **B**, photo; **C**, diagram of quadrate and suspensorium in lateral view, anterior to the left; **D**, photo. **Abbreviations**: **atc**, ascending tympanic crest of quadrate; **dm**, scar for *M. depressor mandibulae*; **ip**, infrastapedial process; **mcd**, mandibular condyle; **p**, parietal; **popr**, paroccipital process; **q**, quadrate; **qa**, quadrate ala; **qag**, quadrate alar groove; **qr**, quadrate ramus of pterygoid; **ret**, retroarticular process; **sa**, surangular; **sp**, suprastapedial process; **sq**, squamosal; **st**, supratemporal. Scale bars equal 5 cm.

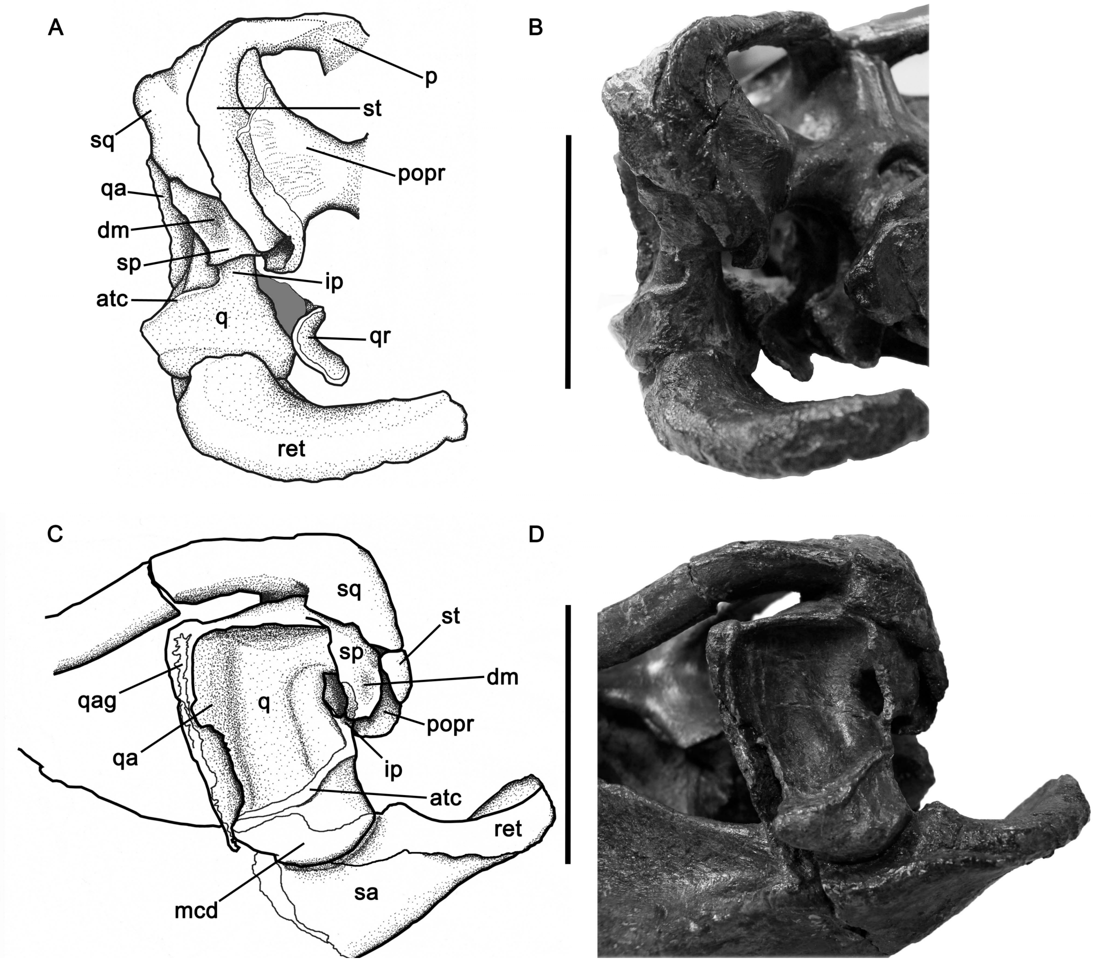
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FIGURE 3–4. Skull of *Plotosaurus bennisoni* (UCMP 32778) in posterior view, dorsal is up. **A**, photo; **B**, diagram. Grey areas indicate the presence of matrix or absence of bone. **Abbreviations: aa**, atlas neural arch; **ai**, atlas intercentrum; **bt**, basioccipital tuber; **dpp**, descencus processus parietalis; **msc**, midsagittal crest of supraoccipital; **p**, parietal; **popr**, paroccipital process; **pr**; supratemporal ramus of parietal; **q**, quadrate; **qr**, quadrate ramus of pterygoid; **ret**, retroarticular process; **soc**, supraoccipital; **sp**, suprastapedial process; **sq**, squamosal; **st**, supratemporal. Scale bar equals 10 cm.

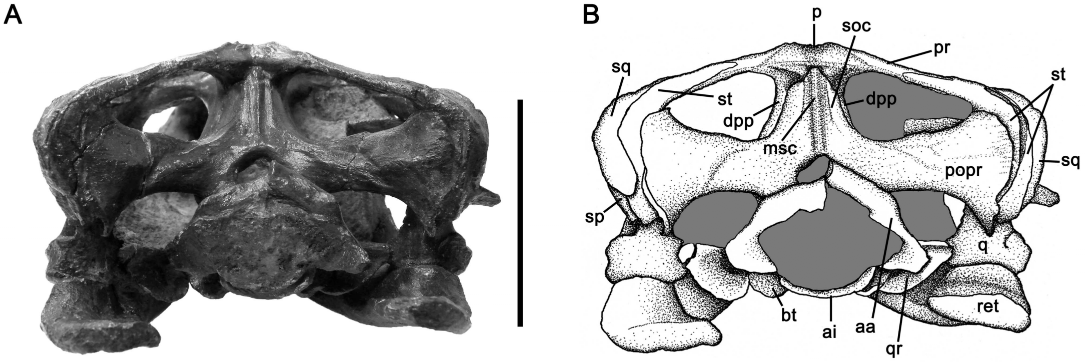
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FIGURE 3–5. Images of the left orbital region and epipterygoid of *Plotosaurus bennisoni* (UCMP 32778). **A**, photo of left orbit, anterior to the left; **B**, photo of epipterygoid and anterolateral region of braincase. **Abbreviations: bs**, basisphenoid; **dpp**, descencus processus parietalis; **ep**, epipterygoid; **ios**, interorbital septum; **os**, orbitosphenoid; **plsp**, planum supraseptale; **po**, prootic; **ps**, parasphenoid rostrum; **pt**, pterygoid. Scale bars equal 5 cm.

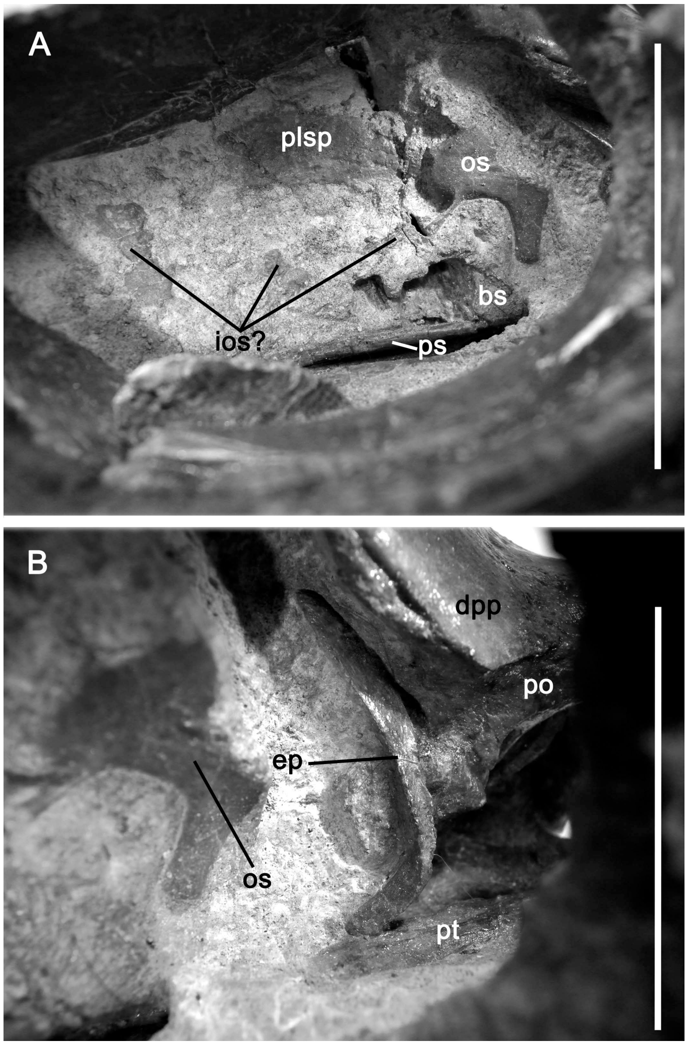
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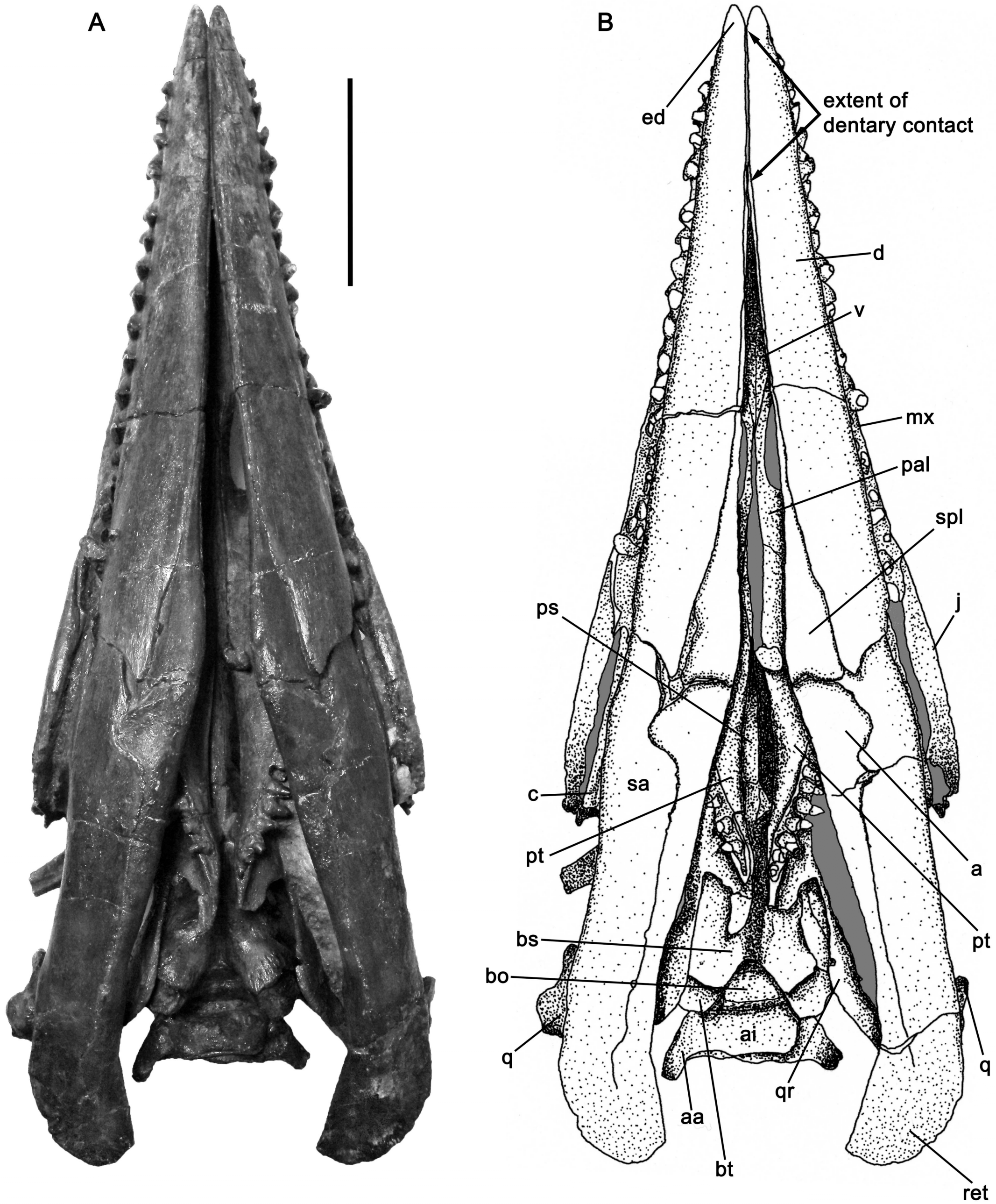
FIGURE 3–6. Skull of *Plotosaurus bennisoni* (UCMP 32778) in ventral view. **A**, photo; **B**, diagram. Grey areas indicate the presence of matrix or absence of bone. **Abbreviations: a**, angular; **aa**, atlas neural arch; **ai**, atlas intercentrum; **bo**, basioccipital; **bs**, basisphenoid; **bt**, basioccipital tuber; **d**, dentary; **c**, coronoid; **ed**, edentulous extension of dentary; **j**, jugal; **mx**, maxilla; **pal**, palatine; **ps**, parasphenoid rostrum; **pt**, pterygoid **q**, quadrate; **qr**, quadrate ramus of pterygoid; **ret**, retroarticular process; **sa**, surangular; **spl**, splenial; **v**, vomer. Scale bar equals 10 cm.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LITERATURE CITED

Bardet, N., X. Pereda Suberbiola, M. Iarochène, F. Bouyahyaoui, B. Bouya, and M. Amaghzaz. 2004. *Mosasaurus beaugei* Arambourg, 1952 (Squamata, Mosasauridae) from the Late Cretaceous phosphates of Morocco. Geobios 37:315–324.

Bell, G. L., Jr. 1997. Chapter 11. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293–332 in J. M. Callaway, and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bullard, T. S., and M. W. Caldwell. 2010. Redescription and rediagnosis of the tylosaurine mosasaur *Hainosaurus pembinensis* Nicholls, 1988, as *Tylosaurus pembinensis* (Nicholls, 1988). Journal of Vertebrate Paleontology 30:416–426.

Caldwell, M.W., R. L. Carroll, and H. Kaiser. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroides and varanoids. Journal of Vertebrate Paleontology 15:516–531.

Callison, G. 1967. Intracranial mobility in Kansas mosasaurs. The University of Kansas Paleontological Contributions 26:1–15.

Camp, C. L. 1942. California Mosasaurs. Memoirs of the University of California 13:1–68.

Camp, C. L. 1951. *Plotosaurus*, a new generic name for *Kolposaurus* Camp, preoccupied. Journal of Paleontology 25:822.

Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22:629–644.

Conybeare, W. D. 1822. Fossil crocodiles and other saurian animals; pp. 284–304 in J. Parkinson, Outlines of Oryctology. An Introduction to the Study of Fossil Organic Remains; Especially of Those Found in the British Strata: Intended to Aid the Student in his Enquiries Respecting the Nature of Fossils, and Their Connection with the Formation of the Earth vii.

Dortangs, R. W., A. S. Schulp, E. W. A. Mulder, J. W. M. Jagt, H. H. G. Peeters, and D. Th. de Graaf. 2002. A large new mosasaur from the Upper Cretaceous of the Netherlands. Netherlands Journal of Geosciences 81:1–8.

Dutchak, A. R., and M. W. Caldwell. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. Journal of Vertebrate Paleontology 29:437–452.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. Journal of Morphology 111:287–319.

Fernandez, M. S., and J. E. Martin. 2009. Description and phylogenetic relationships of *Taniwhasaurus antarcticus* (Mosasauridae, Tylosaurinae) from the upper Campanian (Cretaceous) of Antarctica. Cretaceous Research 30:717–726.

Gervais, P. 1853. Observations relatives aux reptiles fossiles de France. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 36:374–377, 470–474.

Goldfuss, A. 1845. Der Schädelbau des *Mosasaurus*, durch Beschreibung einer neuen Art dieser Gattung erläutert. Nova Acta Academiae Caesar Leopoldino-Carolinae Germanicae Natura Curiosorum 21:173–200.

Holmes, R. 1996. *Plioplatecarpus primaevus* (Mosasauridae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of the North American Western Interior Seaway. Journal of Vertebrate Paleontology 16:673–687.

Holmes, R. B., and H. -D. Sues. 2000. A partial skeleton of the basal mosasaur *Halisaurus platyspondylus* from the Severn Formation (Upper Cretaceous: Maastrichtian) of Maryland. Journal of Paleontology 74:309–316.

Konishi, T., and M. W. Caldwell. 2007. New specimens of *Platecarpus planifrons* (Cope, 1874) (Squamata: Mosasauridae) and a revised taxonomy of the genus. Journal of Vertebrate Paleontology 27:59–72.

Konishi, T., and M. W. Caldwell. 2009. New material of the mosasaur *Plioplatecarpus nichollsae* Cuthbertson et al., 2007, clarifies problematic features of the holotype specimen. Journal of Vertebrate Paleontology 29:417–436.

Konishi, T., and M. W. Caldwell. A new plioplatecarpine mosasaur from the lower middle Campanian of North America, and an analysis of plioplatecarpine phylogeny. Journal of Vertebrate Paleontology:in press.

Lee, M. S. Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. Philosophical Transactions of the Royal Society of London: Biological Sciences: 352:53–91.

Lindgren, J., J. W. M. Jagt, and M. W. Caldwell. 2007. A fishy mosasaur—the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. Lethaia 40:153–160.

Lindgren, J., M. W. Caldwell, and J. W. M. Jagt. 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). Journal of Vertebrate Paleontology 28:1043–1054.

Lindgren, J. 2009. Cranial osteology of the giant mosasaur *Plesiotylosaurus* (Squamata, Mosasauridae). Journal of Paleontology 83:448–456.

Lindgren, J., C. Alwmark, M. W. Caldwell, and A. R. Fiorillo. 2009. Skin of the Cretaceous mosasaur *Plotosaurus*: implications for the aquatic adaptations in giant marine reptiles. Biology Letters 5:528–531.

Lingham-Soliar, T. 1994. The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. Bulletin de l’Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 64:177–211.

Lingham-Soliar, T. 1998. A new mosasaur *Pluridens walkeri* from the Upper Cretaceous, Maastrichtian of the Iullemmeden Basin, Southwest Niger. Journal of Vertebrate Paleontology 18:709–717.

Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, upper Maastrichtian of the Netherlands. Philosophical Transactions of the Royal Society of London B347:155–180.

Lingham-Soliar, T. 2002. First occurrence of premaxillary caniniform teeth in the Varanoidea: presence in the extinct mosasaur *Goronyosaurus* (Squamata: Mosasauridae) and its functional and paleoecological implications. Lethaia 35:187–190.

Lingham-Soliar, T., and D. Nolf. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 59:137–190.

Mulder, E. W. A. 1999. Transatlantic latest Cretaceous mosasaurs (Reptilia, Lacertilia) from the Maastrichtian type area and New Jersey. Geologie en Mijnbouw 78:281–300.

Oppel, M. 1811. Die Ordungen Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, München, 86 pp.

Russell, D. A. 1964. Intracranial mobility in mosasaurs. Peabody Museum of Natural History, Yale University, Postilla 86:1–19.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs (Reptilia, Sauria). Peabody Museum of Natural History, Yale University, Bulletin 23:1–241.

Schulp, A. S. 2006. A comparative description of *Prognathodon saturator* (Mosasauridae, Squamata), with notes on its phylogeny; pp. 19–56 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. J. Jacobs, and M. L. Morais. 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon* in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:1–12.

Shannon, S. W. 1975. Selected Alabama mosasaurs. University of Alabama, Tuscaloosa; unpublished Masters Thesis: 86 pp.

Squires, R. L., and L. R. Saul. 2003. New Late Cretaceous (Campanian and Maastrichtian) marine gastropods from California. Journal of Paleontology 77:50–63.

Tarazona, O. A., and M. P. Ramirez–Pinilla. 2008. The unusual orbitosphenoid of the snakelike lizard, *Bachia bicolor*. Journal of Anatomy 213:120–130.

CHAPTER FOUR

INSIGHTS INTO THE AQUATIC ADAPTATIONS OF DERIVED MOSASAURINES BASED ON A REASSESSMENT OF THE SKULL OF *PLOTOSAURUS BENNISONI* CAMP, 1942 (SQUAMATA: MOSASAURIDAE)

INTRODUCTION

The postcranial anatomy of *Plotosaurus* has been of particular interest in recent studies of aquatic adaptations of derived mosasaurs (Lindgren et al., 2007; Lindgren et al., 2008; Lindgren et al., 2009). Most of the previous research has centered on swimming abilities of this derived mosasaurine, with a focus on the evolution of a more efficient thunniform or sub-carangiform style of swimming, the development of an incipient dorsal fin lobe and a drag resistant dermal covering (Lindgren et al., 2007; Lindgren et al., 2008; Lindgren et al., 2009). These works have been important in reshaping reconstructions of mosasaurs as highly agile pelagic predators with fusiform body outlines (Lindgren et al., 2007; Lindgren et al., 2010), as opposed to the serpentine ambush predators of earlier restorations (Russell, 1967). The cranial anatomy of *Plotosaurus* by comparison has received little attention subsequent to Camp's (1942) original description of *P. bennisoni* and *P. tuckeri* from the Maastrichtian Moreno Formation of central California. As with the studies of the postcranial anatomy of *Plotosaurus*, previous statements regarding its cranial anatomy have focused on the degree to which it was adapted to life as an aquatic predator (Camp, 1942; Ligham-Soliar, 1995). These statements often refer to general anatomical features (e.g., long snouts, large orbits) and ambiguously refer to morphological similarity to other aquatic tetrapods, most notably the ichthyosaurs, as a proxy for the degree of aquatic specialization that the most derived mosasaurs were able to achieve prior to their extinction at the end of the Cretaceous (Camp, 1942; Lingham-Soliar, 1995). Many of the anatomical features associated with such changes to the cranial anatomy of more aquatically adapted mosasaurines are not thoroughly explored before attributing a functional significance to such traits. These osteological features should be described first, but more importantly, ascribing functional hypotheses regarding aquatic adaptations of the skull of derived mosasaurs should address primarily how the skull functioned in acquiring and processing food items (Taylor, 1987).

A re-evaluation of the skull of the holotype of *Plotosaurus bennisoni* (UCMP 32778) is crucial for understanding how this derived mosasaurine was able to feed in an aquatic medium, which is essential to understanding aquatic adaptation as it pertains to the evolution of particular features of the mosasaur skull (Taylor, 1987; Lingham-Soliar, 1989; Lingham-Soliar, 1995). Moreover, the skull of UCMP 32778 is three-dimensionally preserved, with nearly all of the elements oriented in their natural positions with the animal's mouth closed, thus proving to be an excellent candidate for evaluating simple biomechanical and functional hypotheses that Camp (1942) originally made regarding the feeding behavior of *Plotosaurus*. Comparisons are made here with other closely related mosasaurines and more distantly related plioplatecarpine mosasaurs for which similar features have been described to examine the degree of development of features of the skull of *Plotosaurus* compared to other mosasaurs. Some features, such as enlarged orbits and long and narrow snouts were convergently developed in other aquatic tetrapods and can be examined together, because they represent morphotypes that all result from common environmental constraints imposed by living in an aquatic medium (Taylor, 1987; Rieppel, 2002; Bloodworth and Marshall, 2005; Young et al., 2010). Others are morphological features that can only be examined and compared within the Mosasauroidea. These include the loss of intracranial kinesis, the retention of intramandibular kinesis and, most importantly, the retention of mobile quadrates (Russell, 1964; Callison, 1967; Lingham-Soliar, 1995). Many authors argue that intracranial kinesis, the ability to move portions of the dermal skull roof relative to the rigid braincase, was present in early mosasaurids, but was lost in later forms, while streptostyly and intramandibular kinesis were retained in even the most derived mosasaurids (Camp, 1942; Russell, 1964; Callison, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995). While there is a consensus amongst previous authors that this statement holds true for *Plotosaurus*, the particular features that would denote such a restriction in intracranial kinesis have not been explored in significant detail and should be compared to kinetic models of terrestrial squamates (Frazzetta, 1962; Herrel et al., 1999, 2000) and earlier mosasaurines (Russell, 1964; Callison, 1967) to garner meaningful comparisons. Most importantly, the loss of these kinetic mechanisms should be placed in a functional context to understand how this pertains to aquatic adaptation in mosasaurs.

DISCUSSION

On the Evolution of the Palatal Complex and Snout of *Plotosaurus*

Plotosaurus most closely resembles *Mosasaurus* in many features of the skull, including snout proportions; however, many of the features that unite these taxa within the Mosasaurini vary in the degree of their expression between the two genera (Camp, 1942). Lingham-Soliar (1995) diagnosed *Mosasaurus hoffmanni* as having closely united palatal elements, likely as a result of having a long and narrow snout. Most other blunt-snouted mosasaurs retain a fairly wide interpterygoid vacuity, although this opening is still much more narrow than in terrestrial squamates (Russell, 1967; Lingham-Soliar and Nolf, 1989; Konishi and Caldwell, 2007). While it is true that *M. hoffmanni* possesses a long and narrow snout (Lingham-Soliar, 1995), without a more concrete definition of 'closely united palatal elements', *M. hoffmanni* shares this feature with *M. missouriensis*, *M. beaugei* and *Plotosaurus bennisoni* based on superficial similarity (Goldfuss, 1945:pl. 8; Lingham-Soliar, 1995; Bardet et al., 2004) and it is therefore not diagnostic for *M. hoffmanni*. There are, however, minor differences in the topological arrangements of the vomers, palatines and pterygoids among these taxa. These differences highlight a trend towards concentration of the palatal elements towards the midline of the skull in later forms, while the external dimensions of the snout may have remained relatively constant. In *Mosasaurus missouriensis*, the palatines contact the anterolateral surfaces of the pterygoids and the medial surfaces of the maxillae posterolaterally (Fig. 4–1A; Goldfuss, 1845; RFWUIP 1327). Anterior to these contacts, the long and slender vomerine processes of the palatines are oriented parallel to the sagittal plane of the skull and form a significant portion of the medial walls of the choanae. Goldfuss (1845) did not figure the vomeropalatine contact in RFWUIP 1327, but the holotype reveals that the vomerine processes overlap the vomers anteriorly at approximately the tenth maxillary tooth. At no point do the vomerine processes of the palatines converge and contact each other along the midline of the skull (Fig. 4–1A). The vomers are poorly preserved anterior to the vomeropalatine suture in RFWUIP 1327, but it is clear that they were slightly separated, leaving a gap between them along the midline. Vomeropalatine contacts have never been reported for *M. hoffmanni*, although this contact is preserved in IRSNB R12 (contra Lingham-Soliar, 1995; Mulder, 1999). The vomerine processes are clearly anterior extensions of the palatines and not separate structures as depicted by Lingham-Soliar (1995) and Mulder (1999). In *M. hoffmanni*, the vomerine processes are oriented sub-parallel to the sagittal plane and are dorsoventrally taller than they are wide where they form the posteromedial borders of the choanae (Fig. 4–1B). These processes diverge anterolaterally along the vomeropalatine suture and contact the posterolateral corners of the vomers at a point extending from the tenth to ninth maxillary teeth. While the left and right vomers appear to be closely associated in ventral view, they are distinctly separated posteriorly according to Lingham-Soliar (1995). The arrangement of the palatal complex in *M. beaugei* cannot be determined, based on the state of preservation of the referred material for this taxon (Bardet et al., 2004). The condition in *Plotosaurus* more closely resembles that of *M. hoffmanni* than *M. missouriensis*, where there are anterolateral extensions of the vomerine processes of the palatines anterior to the vomeropalatine suture that obliquely overlap the vomers. Tooth positions cannot be used for comparing the position of the vomeropalatine sutures along the snout between *Plotosaurus* and *Mosasaurs*, due to a large discrepancy in maxillary tooth numbers (18 in *Plotosaurus* versus 14 in *M. hoffmanni*), but they are in similar positions along the palate in both taxa. There are three distinct differences in the construction of the palate between *Plotosaurus* and *M. hoffmanni*: (1) The vomerine processes of *Plotosaurus* converge and contact along the midline of the skull posterior to their contact with the vomers; (2) in ventral view, the vomers terminate posteriorly in a V-shaped contact with the palatines and (3) the vomers are in contact along the midline of the skull throughout their lengths (Fig. 4–1C). Contact of the palatines along the midline of the skull has never been reported for mosasaurs (Russell, 1967) and represents an unusually tight association of the elements of the palatal complex about the sagittal plane in *Plotosaurus*, even more so than in *Mosasaurus*. Moreover, the identification of the anterior extent of the palatines in *M. hoffmanni* and *M. missouriensis* also suggests that the plesiomorphic condition for the Mosasaurini is for the vomers to be posteriorly separated from the pterygoids by the vomerine processes of the palatines, a very different condition from that inferred by Konishi and Caldwell (2007) for the russellosaurine (sensu Bell and Polcyn, 2005) *Platecarpus planifrons*.

Other elements of the snout region of *Plotosaurus* also reflect a trend towards narrowing of the elements associated with the midline of the snout. In

UCMP 32778 the septomaxillae consist of a pair of gently curving plates of bone that are attached to the lateral walls of the descending keel of the anterior portion of the internarial bar (Fig. 4–2). Posteriorly, these elements are fused at a point ventral to the nasal and form a dorsoventral strap of bone underneath the internarial bar, thus contributing to the bony internarial septum. Posterior to this point, these elements are again separate, but are still tall and slender straps of bone that run along the midline of the snout posterior to the contact of the frontal and premaxilla. While fusion of these elements is here considered to be unique to *Plotosaurus*, their topological relationships to adjacent elements of the snout are equally unusual. The anterior termination of the septomaxillae is obscured by matrix in UCMP 32778, but it is clear that at least to a point between the third and fourth maxillary teeth, the septomaxillae do not contact the medial surfaces of the maxillae (Fig. 4–2). At this point along the snout, the septomaxillae still predominantly form a dorsoventral wall that abuts the ventrolateral surface of the internarial bar. The only horizontal component of the left septomaxilla is a small laterally projecting plate of bone that overlaps the vomer anteriorly; however, the vomer still extends further laterally along the floor of the narial chamber than does the septomaxilla (Fig. 4–2). In terrestrial squamates and in *Plioplatecarpus primaevus*, the anterior portions of the septomaxillae broadly contact the maxillae and the premaxilla, forming the floor of the nasal vestibule (Caldwell et al., 1995; Holmes, 1996; Konishi and Caldwell, 2007). The first report of septomaxillae in *Platecarpus* by Konishi and Caldwell (2007) suggests that these elements are elongate and strap-like in other distantly related mosasaurids. These elements in

Platecarpus are indeed more elongate than in *Plioplatecarpus primaevus*, but they remain two distinct elements throughout their lengths, unlike the condition in *Plotosaurus* (Konishi and Caldwell, 2007). Posteriorly, the septomaxillae of *Platecarpus planifrons* insert into anterior notches of the palatines (Konishi and Caldwell, 2007:66), while in *Plotosaurus*, they pass medial to the palatines and terminate even with, or posterior to, the posterior borders of the internal narial openings.

The dentaries of *Plotosaurus* are also long and slender compared to other mosasaurs (Camp, 1942). The depth of the dentaries measured in lateral view is 15 mm below the first dentary tooth and only 45 mm below the last tooth (total length of each dentary = 311 mm) (Camp, 1942). These slender proportions are further accentuated by the fact that the ventral margins of the dentaries are slightly rotated medially, as opposed to being completely oriented in the vertical plane as they are in restorations of other mosasaurids (Russell, 1967:fig. 90, 95). The dentaries also converge along the sagittal plane of the skull further posteriorly in *Plotosaurus* compared to other mosasaurs, reminiscent of the elongate mandibular symphyses of other aquatic tetrapods, although not as elongated as in the slender-snouted ichthyosaurs and mesosaurs (McGowan and Motani, 2003:fig. 43; Modesto, 2006:fig. 11). Both upper and lower jaws are also filled with an unusually large number of teeth by comparison to other mosasaurs, rivaled only by *Pluridens* from the Maastrichtian of Niger (Lingham-Soliar, 1998).

Functional Significance of a Long and Narrow Snout to Underwater Feeding Behavior in *Plotosaurus*

The functional significance of a shift in the configuration of the palatal complex and the septomaxillae in *Plotosaurus* is still unclear; however, the constituent elements of the snout are clearly more elongate and narrow than in most other mosasaurs (Camp, 1942). The external snout proportions of *Plotosaurus* are consistent with a trend towards snout elongation in members of the Mosasaurini, as the snout of UCMP 32778 represents nearly 60% of the length of the skull (measured as the ratio between the length of the upper left tooth row and the total skull length), compared to 40% in the blunt-snouted *Plioplatecarpus primaevus* and 50% in *Platecarpus* (Holmes, 1996). Long and narrow snouts are convergently developed in many aquatic tetrapods including extant gavials (Thorbjarnarson, 1990) and odontocetes (Taylor, 1987; Fordyce and Muizon in Mazin and Buffrénil, 1996; Bloodworth and Marshall, 2005) and the extinct ichthyosaurs (Taylor, 1987; McGowan and Motani, 2003), sauropterygians (Rieppel, 2002), mesosaurs (Modesto, 2006) and metriorhynchoid crocodiles (Young et al., 2010). Common to all of these taxa are the environmental constraints imposed upon an organism when feeding in a viscous medium (Gans, 1969; Taylor, 1987; Rieppel, 2002). Elongate and narrow snouts act as a pair of forceps that require a degree of precision in order to capture individual prey items and remove them from the water column. Prey items of such predators are proportionally much smaller than the predator and are therefore easily deflected away from the jaws by the pressure wave created during jaw closure (Taylor, 1987; Bloodworth and Marshall, 2005; Modesto, 2006). Selective pressures on the snouts of aquatic tetrapods favor long and slender forms that simultaneously reduce drag and the forward displacement of water, as the jaws swing closed (Taylor, 1987; Rieppel, 2002; Bloodworth and Marshall, 2005). In order to further reduce the chance of deflecting prey items away from the snout, many aquatic tetrapods use quick lateral strikes to capture small soft-scaled fish, cephalopods or small crustaceans, capturing them primarily with laterally directed piercing tooth crowns (Massare, 1987; Taylor, 1987; Thorbjarnarson, 1990; Rieppel, 2002; Modesto, 2006; Young et al., 2010). Prey items are quickly subdued by penetration of the long and conical tooth crowns and need not be forcibly held in place by robust teeth to cope with their struggles to break free (Taylor, 1987). In *Plotosaurus*, the longest teeth occupy the middle portion of the jaws (Camp, 1942), while the anterior three-quarters of the marginal dentition consists of interdigitating tooth crowns that leave little space between adjacent teeth when the jaws are closed. The high number of marginal teeth and the precision with which they appear to have interdigitated would have created an efficient fish-trap, reminiscent of the dentition of sauropterygians, mesosaurs, gavials and many long-snouted ichthyosaurs (Taylor, 1987; Rieppel, 2002; McGowan and Motani, 2003; Modesto, 2006).

Plotosaurus is unusual among mosasaurs in its possession of a ventral curve to the snout. Snout bends have been reported for long-snouted ichthyosaurs as well (Romer, 1968:figs. 2, 3; McGowan and Motani, 2003:fig. 89); however, it is unclear whether or not these represent preservational artifacts (McGowan and

Motani, 2003:89). In *Plotosaurus*, the feature is genuine, given the pristine state of preservation of UCMP 32778. It is the concave ventral border of the maxilla and the convex curvature of the dorsal border of the dentary that creates the ventrally directed snout bend in UCMP 32778 (Camp, 1942; pers. obs.). Gently concave ventral borders of the maxillae are not uncommon amongst mosasaurines and appear to be present in the closely related *Mosasaurus missouriensis*, but it is the convexity of the dorsal surface of the dentary that is unique to *Plotosaurus* (Camp, 1942). The convex curvature of the dentaries in *Plotosaurus* likely contributed to the slender profile of the snout, which may have aided in reducing drag when the jaws were closed (Taylor, 1987; Rieppel, 2002, Young et al., 2010), but may have served primarily to increase the precision of tooth interdigitation during prey capture, particularly in the middle region of the marginal dentition, where the teeth are longest. In *Prognathodon* and *Mosasaurus hoffmanni* in particular, the dorsal borders of the dentaries are usually concave, possibly to aid in resisting the higher compressive forces associated with increased bite force (Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Christiansen and Bonde, 2002; Dortangs et al., 2002). Precise tooth interdigitation may only occur in these taxa between the anterior-most upper and lower teeth, where the tooth bearing elements would be in closest proximity when the jaws were closed, similar to extant squamates that exhibit similar dentary curvature (Lingham-Soliar and Nolf, 1989; Dalrymple, 1979). *Plotosaurus* represents a marked departure from the imprecise pattern of tooth interdigitation seen in other mosasaurs and terrestrial squamates (Dalrymple, 1979), where such an arrangement is usually attributed to a macrophagous or durophagous diet. Instead, a convex dorsal border of the dentary in *Plotosaurus* effectively brings the lower dentition closer together with the maxillary teeth, creating a tighter meshwork of the tooth crowns to capture small fish and minimize the chances of the prey escaping.

Enlarged orbits in *Plotosaurus*

Observed feeding behavior of extant gavials suggests that they primarily use visual cues to identify prey items before using vertical or lateral strikes to capture them (Thorbjarnarson, 1990). Although feeding behavior in extinct groups cannot be directly observed, the presence of enlarged orbits in many ichthyosaurs, mesosaurs and metriorhynchoids suggests that many of the extinct long-snouted aquatic tetrapods were visual hunters as well (Fernandez et al., 2005; Modesto, 2006; Young et al., 2010). Camp (1942) noted that *Plotosaurus* possessed one of the largest orbits of any mosasaur and correlated this with increased marine habits. Sclerotic rings are rarely preserved in mosasaurs, but provide better insight into the absolute eyeball size than do measurements of the orbit (Fernandez et al., 2005; Motani et al., 1999). Sclerotic rings have been reported for *Platecarpus* (Lindgren et al., 2010), *Mosasaurus* (Lingham-Soliar, 1995) and *Prognathodon* (Lingham-Soliar and Nolf, 1989), but Camp (1942) reported that sclerotic rings were absent in UCMP 32778. For this reason, all statements made here related to the size of the eye in UCMP 32778 are based on osteological markers that indicate an accommodation for a larger orbit. A flattened sclerotic ring is present in the right orbit of a large specimen of *Plotosaurus*, UCMP 57582, which suggests that the reason for the absence of this structure in the holotype specimen is likely preservational or ontogenetic. Unfortunately, this structure is crushed and distorted and would not provide an accurate proxy for the diameter of the eye.

Comparisons with non-mosasaurine mosasaurs would suggest that relative orbit size might have been larger in *Plioplatecarpus primaevus* based on the fact that the snout in this taxon is much shorter than that of *Plotosaurus* (Holmes, 1996). Nevertheless, there are similarities in the way the elements forming the orbital rim are modified to accommodate a larger space for the eye in *Plioplatecarpus* and *Plotosaurus*. In *Plioplatecarpus*, the enlarged orbital rim is formed dorsally by the convexity of the frontal above the orbit (Holmes, 1996; Konishi and Caldwell, 2009). The supraorbital bulging of the frontals is also seen in *Plotosaurus* and is associated with a sagittal keel along the dorsal surface of the frontal, similar to *Plioplatecarpus* (Konishi and Caldwell, 2009). This bulging of the frontal is absent in *Mosasaurus hoffmanni* and *M. missouriensis* and the dorsal surface of the frontal in these two species is flat, save for the sagittal keel that extends the length of the element (Lingham-Soliar, 1995). The anteriorly sloping frontal and supraorbital process of the prefrontal in *Plotosaurus* may have also contributed to the enlarged orbit, although these features would require further investigation in *Plioplatecarpus* to determine if this occurred in the latter taxon as well. The floor of the orbit in *Plotosaurus* is formed mostly by a concave ectopterygoid and horizontal ramus of the jugal, features that would have created additional space for the eye ventrally. Lastly, the vertical and horizontal rami of the jugal form an angle greater than 90 degrees, possibly as a means of increasing the circumference of the orbital rim.

Loss of Intracranial Mobility in *Plotosaurus*

There is substantial disagreement as to the degree of cranial kinesis that persisted in mosasaurs relative to the kinetic skulls of other squamates (Frazzeta, 1972; Russell, 1964, 1967; Calliston, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Herrel et al., 1999; Herrel et al., 2000). Cranial kinesis refers to the general condition where elements of the dermal skull roof and palate move relative to a rigid braincase (Frazzetta, 1962; Russell, 1964; Lingham-Soliar, 1995; Herrel et al., 2000). The kinetic mechanisms of extant squamates have been divided into particular movements or rotations at junctions of two or more associations of bones of the skull termed 'units' (Frazzetta, 1962; Russell, 1964; Lingham-Soliar, 1995; Herrel et al., 2000). Following Frazzetta (1962) and Russell (1964, 1967), mosasaur skulls can be divided into five distinct units, the constituent elements of which are not mobile with respect to each other, but are moveable at junctions between adjacent units at specific joints following specific axes of rotation (Fig. 4–3A). Anteriorly, the muzzle unit consists of the premaxilla, nasals, septomaxillae, vomers, maxillae, prefrontals, frontal, palatines and possibly the postorbitofrontals (Frazetta, 1962,1964; Callison, 1967). This unit meets the basal unit (consisting of the pterygoid, ectopterygoid and occasionally the jugal) at the pterygopalatine suture and, when present, at a ligamentous connection of the jugal to the postorbitofrontal, or along the ectopterygoid-jugal contact when there is a solid jugal-postorbitfrontal contact (Russell, 1964). Posterodorsally, the muzzle unit articulates with the parietal unit (consisting of the parietal, supratemporals, postorbitofrontals and squamosals) along a transversely oriented axis known as the mesokinetic axis (Fig. 4–3A; Frazetta, 1962; Russell, 1964, 1967; Callison, 1967). The parietal unit overlaps the braincase laterally where the descensus processus parietalis overlaps the prootic and posterodorsally at the parietal-supraoccipital suture (the metakinetic joint). The parietal unit also contacts the braincase posterolaterally along the suture between the supratemporal and paroccipital process (the metakinetic axis) and contacts the quadrate posteroventrally along the 'cephalic condyle' of the quadrate (Fig. 4–3A; Russell, 1964, 1967; Callison, 1967; Lingham-Soliar, 1995). Most authors agree that the quadrate and the epipterygoid behave independently of the other units during intracranial kinesis, and therefore represent their own distinct units (Frazzeta, 1962; Russell, 1964; 1967; Calliston, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Herrel et al., 1999; Herrel et al., 2000).

Intracranial kinesis was likely lost in more derived mosasaurs (Camp, 1942; Russell, 1964; 1967; Callison, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Rieppel and Zaher, 2001); however, the particular osteological features that would indicate such a restriction in mobility of the cranial elements occurred have not been explored in significant detail. To that end, most studies have suggested that a loss of mesokinesis (movement along the frontoparietal suture) and metakinesis (movement of the dermal skull roof along the paroccipital processes and the parietal-supraoccipital suture) can be attributed to the high compressive forces associated with a strong bite in mosasaurines (Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995). While stabilization of the dermal skull roof may be a plausible explanation for larger mosasaurines specializing on harder prey items (e.g., *Mosasaurus hoffmanni*, *Prognathodon*), this explanation falls short of identifying the functional significance of an akinetic skull in piscivorous mosasaurs, such as *Plotosaurus*. Here, the particular regions of the skull of *Plotosaurus* (UCMP 32778) that are modified from the kinetic squamate (sensu Frazetta, 1962; Herrel et al., 1999; Herrel et al., 2000) and mosasaur (sensu Russell, 1964; 1967; Callison, 1967) skull conditions, and that contributed to a completely akinetic skull, are described. It is argued that the akinetic skull of *Plotosaurus* imparted a distinct advantage that is directly related to preying on small fish.

Loss of metakinesis—Metakinesis has been inferred to be present in some mosasaurs and lost in later forms (Russell, 1964; 1967; Callison, 1967; Lingham-Soliar, 1995). When the kinetic condition is present, the anterior portion of the parietal is depressed or raised relative to the frontal, while the posterior portions of the parietal, supratemporal and squamosal are displaced dorsoventrally relative to the fixed paroccipital processes (the metakinetic axis) (Fig. 4–3A, C, E). In modern lizards displacement of the posterior portion of the parietal is thought to occur at the contact between the parietal and the supraoccipital (the metakinetic joint), where the processus ascendens tecti synotici, a small granule of cartilage, fills the gap between the two elements and would have permitted limited dorsoventral movements (Frazzeta, 1972; Russell, 1964; 1967; Calliston, 1967; Herrel et al., 1999; Herrel et al., 2000). This motion is best depicted in *Varanus*, where the supratemporal rami of the parietal and the supratemporals are oriented dorsoventrally and could have slid dorsally and ventrally along the lateral surfaces of the paroccipital processes **(**Frazetta, 1962:fig. 1c). While some mosasaurs (e.g., *Clidastes* and *Halisaurus*) retain an elongate and somewhat vertically inclined supratemporal ramus (Callison, 1967:fig. 9; Russell, 1967:fig. 32; Holmes and Sues, 2000), most have short horizontally oriented supratemporal rami of the parietal that dorsally overlap the supratemporals (Russell, 1967; Bell, 1997; Holmes and Sues, 2000). Russell (1967) suggested that vertical adjustments of the parietal above the paroccipital processes in mosasaurs must have occurred along the loose overlap of the supratemporal ramus of the parietal and the supratemporal (Fig. 4–3A). A loose overlapping contact is present in some plioplatecarpines (Russell, 1967; Holmes, 1996; Konishi and Caldwell, 2007; 2008) and possibly in *Clidastes* (Camp, 1942), but the parietal-supratemporal contact is more elaborate in more derived mosasaurines. *Plotosaurus* shares with *Mosasaurus* and *Prognathodon* a second ventral extension of the supratemporal ramus of the parietal that underlies the supratemporal and clasps the thin anterior portion of the latter element dorsally and ventrally (Camp, 1942; Bell, 1997; Christiansen and Bonde, 2002), thereby restricting movement between the parietal and the supratemporal (Fig. 4–3B). The dorsal portion of the supratemporal ramus of the parietal in *Plotosaurus* also contacts the squamosal posterolaterally, further overlapping the dorsal surface of the underlying supratemporal. Similar to

Halisaurus (Holmes and Sues, 2000), *Plotosaurus* also possesses a strong union of the supraoccipital and the parietal. In posterior view, there is no gap between the two elements in UCMP 32778, suggesting that the metakinetic joint is lost in *Plotosaurus* and replaced by a strong union of the braincase to the dermal skull roof. In addition, the unusually long descending processes of the parietal that laterally overlap the prootic further impede motion between the parietal and the braincase, effectively unifying the parietal unit and the occipital segment (braincase) (Fig. 4–3B, D, E). All of these features confirm previous authors' claims that the metakinetic capacities of the skull of *Plotosaurus* were lost (Camp, 1942; Russell, 1964, 1967 Lingham-Soliar, 1989; Lingham-Soliar, 1995; Rieppel and Zaher, 2001).

Loss of mesokinesis—Previous authors have identified the secondary axis of intracranial kinesis to be a dorsoventral movement of the muzzle relative to the parietal unit along the mesokinetic axis (Frazzeta, 1972; Russell, 1964; 1967; Calliston, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Herrel et al., 1999; Herrel et al., 2000), which runs transversely across the skull roof at the fronto-parietal suture (Fig. 4–4A). In kinetic squamate skulls, flexion at the frontoparietal suture (the mesokinetic joint sensu Frazetta, 1962) occurs as a result of the muzzle unit being elevated and the parietal unit being depressed anteriorly (Fig. 4–3A; Frazetta, 1962:fig. 2b), or the muzzle unit depressed relative to the parietal unit while the quadrate is retracted (Fig. 4–3E; Frazetta, 1962:fig. 2c). Only a few mosasauroids retain a straight frontoparietal suture and in many cases, such a feature is considered the plesiomorphic condition (Lingham-Soliar and

Nolf, 1989; Lingham-Soliar, 1995; Bell, 1997), with some instances of reversal (Lingham-Soliar and Nolf, 1989). *Plotosaurus* is similar to *Mosasaurus* in that two posteriorly directed median flanges of the frontal overlap the parietal posteriorly in dorsal view (Camp, 1942:fig. 13; Lingham-Soliar, 1995) and would have likely impeded the dorsoventral movements of the frontal relative to the parietal (Fig. 4–4D, E). Moreover, the large rectangular median flanges in *Plotosaurus* are proportionally larger and longer than those of other mosasaurines (Camp, 1942; Bell, 1997:fig 6g; Lindgren et al., 2008), extending to the anterior borders of the supratemporal fenestrae. Lateral to this overlap, the posterolateral corners of the frontal terminate sharply along the dorsal surface of the postorbitofrontals. Together, these features create a highly sinuous overlapping contact of the frontal over the parietal and the postorbitofrontal, much more so than in the other mosasaurines like *Clidastes*, *Mosasaurus* and *Prognathodon* (Fig. 4–4; Callison, 1967; Russell, 1967:fig. 72, 89; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Schulp, 2006:fig. 7).

Becaues the postorbitofrontal in most squamates (and in *Varanus* specifically) is only slightly overlapped anterodorsally by the frontal, it is believed that the postorbitofrontal moves along with parietal as the muzzle unit is elevated or depressed in extant squamates that exhibit mesokinesis (Fig. 4–4A; Frazetta, 1962; Callison, 1967). Russell (1964; 1967) stated that the strong contact between the postorbitofrontals and the frontal is a key difference in understanding cranial kinesis in mosasaurs as compared to the kinetic mechanisms of extant squamates, as this effectively extends the muzzle unit posteriorly along the temporal arcades (Fig. 4–4C, D, E). In contrast, Callison (1967:13) suggested that, while the postorbitfrontal was overlapped primarily by the frontal in *Clidastes*, the lack of contact of this element with the prefrontal anteriorly indicates that the postorbitfrontal moved as a part of the parietal unit during mesokinesis. *Clidastes* would thus represent an intermediate stage in the loss of mesokinesis in mosasaurines, given Callison's (1967:13) interpretation, because the postorbitofrontal still remained separated from the muzzle unit anteriorly, and the frontoparietal suture was not as complex as it in other mosasaurines. While the mesokinetic capacities of the skull of *Clidastes* should be explored further in the future, it is beyond the scope of the current study. The interpretations of Russell (1964) and Callison (1967) are provided here for *Clidastes* in Fig. 4–4B, C, but it is clear that the contact of the postorbitfrontal and prefrontal in later mosasaurines (Fig. 4–4D, E) would have prevented movement of the postorbitofrontal with the parietal unit. This is particularly true for *Plotosaurus* (Fig. 4–4E), where the frontal overlaps a significant portion of the postorbitofrontal (Camp, 1942). The frontal of *Plotosaurus* is also excluded from the dorsolateral orbit margin by an extensive contact between the prefrontal and the postorbitofrontal. While contact between the prefrontals and postorbitofrontals exist in other mosasaurines (Camp, 1942; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Bell, 1997; Schulp, 2006; Lindgren, 2009), it is much more laterally extensive in *Plotosaurus* (Fig. 4–4E). Not only do these two elements contact along the ventrolateral surface of the frontal, but there is also an extensive interdigitating suture that persists lateral to the frontals and above the orbit in dorsal view. This extensive contact, along with the extensive overlap of the frontal over the parietal, would have completely repressed intracranial movements along the mesokinetic axis in *Plotosaurus* (Fig. 4–3B, D, F).

Loss of mobility of the pterygoid and epipterygoid—In *Varanus* and some gekkonids, a strong ligamentous connection of the quadrate ramus of the pterygoid to the quadrate and, more importantly, the combined actions of the *M. levator pterygoidei* and *M. protractor pterygoidei* act to move the pterygoids dorsally and anteriorly respectively during protraction of the muzzle unit. Conversely, the *M. pterygoideus* pulls the pterygoids posteriorly during the retraction phase (Frazetta, 1962; Herrel et al., 1999; Herrel et al., 2000). By extension, it has been postulated by some authors that mosasaurs had the ability to move the pterygoids anteroposteriorly, because their pterygoids retain a loose contact with the quadrate (streptostyly), a movable joint with the palatine, and together with the ectopterygoid can slide against the medial surface of the jugal (Callison, 1967; Rieppel and Zaher, 2001). The ability to move the pterygoids anteroposteriorly is thought to have allowed mosasaurs to use the pterygoid dentition, mandible and muzzle protraction and retraction to actively pull prey items towards the back of the throat in a process known as ratchet feeding (Fig. 4–3A, C, E; Callison, 1967; Taylor, 1987; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Rieppel and Zaher, 2001). While movement of the pterygoids is clearly displayed in some extant squamates (Frazetta, 1962; Herrel et al., 1999; Herrel et al., 2000), and some mosasaurs indeed possessed large pterygoid dentition (Lingham-Soliar and Nolf, 1989; Christiansen and Bonde, 2002; Schulp, 2006), there are fundamental differences in the kinetic capacities of mosasaur skulls and, more specifically, the skull of *Plotosaurus* (Russell, 1964; 1967). The kinetic condition in extant squamates involves an anterior and medial movement of both pterygoids simultaneously as a result of the coordinated actions of the *M. levator pterygoidei* and *M. protractor pterygoidei* (Frazetta, 1962; Herrel et al., 2000). The lateral flaring of the posterior portions of the pterygoids cause them to be drawn closer together medially as they are pulled anteriorly with respect to the basisphenoid (Frazetta, 1962:295). Such an anterodorsal displacement of the pterygoids requires some flexibility at the pterygopalatine contact and sufficient space between the pterygoids anteriorly to allow them to converge slightly during protraction of the muzzle. Anterior displacement of the pterygoids is impeded in *Plotosaurus* by a close association of the pterygoids to each other medially as well as to the palatines anteriorly. Anteriorly, there is a tight interdigitating suture between the pterygoids and palatines in UCMP 32778 that would have limited any movement of the elements relative to each other (Camp, 1942:fig. 14). This suture is straight in *Mosasaurus hoffmanni* (IRSNB R12; Lingham-Soliar, 1995:fig. 3b). Furthermore, the large ectopterygoids of *Plotosaurus* contact the medial surfaces of the jugals laterally and the palatines anteriorly, both of which are in turn firmly attached to the maxillae further anteriorly (Fig. 4–4A). In kinetic models, sliding of the ectopterygoid along the medial face of the jugal occurs as the pterygoids are protracted (Frazetta, 1962). In *Plotosaurus*, the ectopterygoid reaches the orbital lamina of the palatine and rests in a notch in this element even when the jaws were closed (Camp, 1942).

These contacts create a solid union of the basal unit (consisting of the pterygoids, ectopterygoids and possibly the jugals) to the muzzle unit anterolaterally that did not permit any forward sliding motions during the protraction phase (Fig. 4–3B, D, F).

The close association of the epipterygoid to the parietal and prootic also suggests that the pterygoids of *Plotosaurus* were immoveable. In extant squamates, the epipterygoid is ligamentously connected to the ventrolateral surface of the parietal, the lateral face of the parietal ramus of the prootic, or both (Frazetta, 1962; Callison, 1967). As the ventral end of the epipterygoid is displaced anterodorsally along with the pterygoids, the basal unit and parietal units are drawn closer together (Fig. 4–3A; Frazetta, 1962:303). During muzzle and basal unit protraction, the dorsal extremity of the epipterygoid is displaced dorsally along the lateral walls of the prootic and the parietal, placing tension on the ligaments attaching the epipterygoid to these elements. It is the tensile resistence of this ligamentous connection that determines the extent of the anterodorsal movement of the pterygoids (Frazetta, 1962). In *Plotosaurus*, the epipterygoid was not ligamentously bound to the lateral walls of the parietal and prootic, but was instead situated within a small groove between the anteroventral end of the processus descensus parietalis of the parietal and the anterior border of the prootic, a condition that has not been seen in any other mosasaur (Fig. 4–4A; Camp, 1942). Being overlapped by the descending process of the parietal, there would have been no capacity for the epipterygoid to be displaced dorsally relative to the parietal or the braincase as in Frazetta's (1962), Callison's (1967) and

Russell's (1967) models (Fig. 4–4B, D, F). Lastly, the spiraled and bowed shape of the epipterygoid in *Plotosaurus* suggests less of a capacity for the element to resist the dorsoventral compressive forces during pterygoid protraction, compared to the straight cylindrical shape of the element in most other squamates.

Loss of streptostyly and mandible protraction—Several authors have noted that cranial kinesis may have been lost in later mosasaurs, however all mosasauroids apparently retained streptostylic quadrates (Camp, 1942; Russell, 1964; 1967; Callison, 1967; Lingham-Soliar and Nolf, 1989; Carroll and DeBraga, 1992; Lingham-Soliar, 1995; Holmes and Sues, 2000; Rieppel and Zaher, 2001). Streptostyly can only occur if there is a loose attachment of the quadrate rami of the pterygoids to the ventromedial surfaces of the quadrates so that the quadrates can move independently of the rest of the skull (Frazzetta, Rusell, 1964; 1967; Rieppel, 1978; Smith, 1980; Herrel et al., 1999). In kinetic models of extant squamates, the quadrate pivots at the quadrate-squamosal-paroccipital joint as the lower jaws are depressed and protracted relative to the skull (Frazzetta, 1962; Smith, 1980; Herrel et al., 1999; Herrel et al., 2000). This pivoting motion can occur in extant lizards, because the quadrate is suspended dorsally by these suspensorial elements and the quadrate is not tightly embraced posterodorsally (see Frazzetta, 1962:fig. 5; Callison, 1967:fig. 2; Rieppel, 1978; Smith, 1980:fig. 2a, b). Protraction of the quadrate may be brought about directly by the action of the *M. depressor mandibulae*, which originates on the dorsal surface of the retroarticular process and inserts on to the posterodorsal surface of the quadrate (Russell, 1964; 1967) pulling the dorsum of the quadrate and the retroarticular process closer together (Callison, 1967; Herrel et al., 1999). Alternatively, the quadrate may be protracted via contraction of the *M. pterygoideus*, which serves to pull the mandibles anteriorly (Smith, 1980). Contraction of either or both of these muscles may cause the quadrate to rotate forward in lizards and it is clear that protraction of the pterygoids, which are only ligamentously bound to the quadrates posteriorly, is mechanically independent of quadrate rotation (Frazzetta, 1962; Russell, 1964; Rieppel, 1978; Smith, 1980). Streptostyly can therefore occur even when mesokinesis and metakinesis are lost (Frazzetta, 1962). This forms the principle argument for streptostyly being conserved in even the most derived mosasaurids (Camp, 1942, Russell, 1964; 1967; Callison, 1967; Lingham-Soliar, 1995).

Compared to most other squamates, mosasaur quadrates possess an unusually long suprastapedial process, which extends posteroventrally from the dorsal quadrate shaft and creates a circular outline of the element in lateral view (Russell, 1967; Bell, 1997). For forward rotation of the mandibular condyle to occur in mosasaurs, the suprastapedial process would have to rotate an equal amount posteriorly (Callison, 1967). This posterior rotation of the suprastapedial process has been interpreted by some to be caused by contraction of the *M. depressor mandibulae*, which appears to have had an extensive origination on the distal tip of the suprastapedial process (Callison, 1967; Russell, 1967). Many authors have restored the quadrate and susprensorium of mosasaurs as a sliding or pivoting contact, where the distal tip of the suprastapedial process is completely free and visible in posterior view and capable of rotating or pivoting posteroventrally along its loose contact with the squamosal and supratemporal dorsally (Fig. 4–5A, B; see also Callison, 1967:fig. 1, 9, 10; Russell, 1967:fig. 20, 32, 83, 90, 92, 95; Lingham-Soliar and Nolf, 1989:fig. 6a, 38a; Carroll and DeBraga, 1992:fig. 7a, b; Lingham-Soliar, 1995:fig. 4a; Holmes, 1996:fig. 2c; Holmes and Sues, 2000:fig. 1). While the pterygoids of *Plotosaurus* must have only been ligamentously attached to the quadrates, allowing the quadrates to move independently of the skull (Camp, 1942), there are fundamentally different topological relationships of the elements of the quadrate suspensorium to the dorsal surface of the quadrate in UCMP 32778 that would have prevented streptostylic movements in *Plotosaurus* (Fig. 4–5C). Unlike current restorations of the suspensorium of other mosasaurs, the quadrate of *Plotosaurus* is not only suspended from the skull by the squamosal, supratemporal and paroccipital process, but it is also braced by these elements posteriorly and medially (Figs. 4–5C; 4–6A). In posterior view, the squamosal, supratemporal and paroccipital process form a diagonal line of contact that runs along the posterior face of the vertically oriented distal tip of the suprastapedial process, concealing most of the posterodorsal surface of the quadrate from view, except for the scar for the *M. depressor mandibulae*. This feature has also been reported for *Taniwhasaurus antarcticus* (Fernandez and Martin, 2009), although the posterior bracing mechanism in this taxon likely involved a greater posterior and medial contribution of the supratemporal than that of *Plotosaurus*.

There is some contention over which particular kinetic mechanisms and muscular contractions affect the orientation of the quadrates in streptostylic squamate skulls (Frazetta, 1962; Russell, 1964; Callison, 1967; Smith, 1980; Herrel et al., 1999; Herrel et al., 2000). In gekkonids, protraction of the entire muzzle unit, and subsequent quadrate rotation, can be initialized solely by the contraction of the *M. depressor mandibulae* (Herrel et al., 1999; Herrel et al., 2000). In *Varanus*, jaw abduction is mechanically independent of quadrate rotation, and therefore the quadrate is more passively rotated as the pterygoids are protracted by the *M. levator pterygoidei* and *M. protractor pterygoidei* and the lower jaws are pulled anteriorly by contraction of the *M. pterygoideus* (Frazzetta, 1962; Russell, 1964; 1967; Rieppel, 1978; Smith, 1980). Neither scenario is likely to have contributed to rotation of the quadrate in *Plotosaurus*, based on the inability of the suprastapedial process to be displaced posteriorly (contra Camp, 1942; Russell, 1964). Assuming that the pterygoids remained immobile in *Plotosaurus* (as mentioned above), contraction of the *M. levator pterygoidei* and the *M. protractor pterygoidei* would not have pulled the pterygoids anterodorsally, and their ligamentous attachment to the quadrate would not have pulled the mandibular condyle anteriorly. The tight association of the suspensorium to the posterodorsal portion of the quadrate would have eliminated any possible posterior rotation of the suprastapedial process during contraction of the *M. pterygoideus* and thus would have prevented forward rotation of the mandibular condyle of the quadrate (contra Camp, 1942; Callison, 1967). Furthermore, the 90-degree angle formed by the suprastapedial process, the squamosal and supratemporal in UCMP 32778 creates a vertically oriented point of contact between the suprastapedial process and the suspensorium, a feature not seen in other mosasaurs (Figs. 4–5C; 4–6A, B). Upon contraction of the *M. depressor mandibulae*, the position of the suprastapedial process would remain fixed to the articulation with the suspensorium posteriorly, but the contraction of this muscle would still function to depress the lower jaws, since this muscle inserted on to a completely horizontal retroarticular process (Fig. 4–6B). Lateral movement of the ventral portion of the quadrate must have been impeded as well in *Plotosaurus*. The suprastapedial process is not only braced posteriorly, but also medially by the fan-like expansion of the paroccipital process and a portion of the supratemporal. As such, the dorsal portion of the quadrate was unable to pivot medially in order to accommodate for lateral movements of the mandibular condyle.

Intramandibular kinesis in *Plotosaurus*—The mandibles of mosasaurs are divided into an anterior dentigerous unit (consisting of the dentaries and splenials) and a posterior articular unit (consisting of the articular, prearticular, surangular, angular and coronoid), which are joined along the splenio-angular articulation (Fig. 4–5; Russell, 1964; Callison, 1967). The well-developed articulation between the splenial and angular at the intramandibular joint permitted either passive ventrally-directed movements of the dentaries relative to the posterior mandibles during prey capture, or dorsally-directed movements by contraction of the *M. adductor mandibulae externus superficialis* during retraction of the muzzle (Fig. 4–3A, E; Russell, 1964; Callison, 1967). Two alternative scenarios for the direction of movement of the two mandibular units at the intramandibular joint persist in the literature. Serving as an effective shock absorber, the dentaries may have passively swung ventrally, parallel to the long axis of the intramandibular joint, during the initial grasping or biting of a prey item and would have been returned to the normal resting position by tensile ligaments along the dorsal surface of the dentaries and the coronoids (Russell, 1964; 1967). Alternatively, it has been postulated that the long anterior extension of the prearticular across the intramandibular joint and into the medial surface of the dentigerous unit would not have permitted movement along the long axis of this joint, but would have instead allowed for limited lateral flexion or 'buckling' at the intramandibular joint (Lingham-Soliar, 1995; Lee et al., 1999). This lateral bulging of the mandibles, coupled with lateral flaring of the quadrates in the streptostylic condition, would have served to increase gape size as the prey item was being processed or captured (Lingham-Soliar, 1995; Lee et al., 1999; Rieppel and Zaher, 2001).

As mentioned previously, lateral movement of the mandibular condyles in *Plotosaurus* was likely prevented by the posteromedial contact of the paroccipital process with the suprastapedial process of the quadrate. Any movement at the intramandibular joint would have been independent of the movements of the quadrates. The intramandibular joint of UCMP 32778 is barely visible in lateral view (Fig. 4–6), but the lateral surface of this joint is completely visible in ventral view. This is due to the fact that the intramandibular joint, along with the posterior portions of the dentaries, are inclined less than 45 degrees from the horizontal plane, differing markedly from the nearly vertical orientation of the same elements in restorations of other mosasaurs (e.g., Russell, 1964:fig. 7).

Furthermore, the dentaries of *Plotosaurus* could not have moved in the same plane as the long axis of the intramandibular joint, due to an unusual relationship of the dentaries anteriorly. *Plotosaurus* differs markedly from other mosasaurs in that there is an elongated line of contact between the left and right dentaries anteriorly as opposed to a short and presumably loose mandibular symphysis seen in other mosasaurs (Lee et al., 1999). Traditional restorations of the intramandibular joint of mosasaurs concern only a single side of the skull and only in two-dimensions (Fig. 4–3, C, E; see Russell, 1964; 1967). In *Plotosaurus* it is clear that displacement of the dentaries at the intramandibular joint is inhibited, because of the contact of the dentaries that, when taken into account from a three-dimensional perspective, would have permitted the dentaries to act as a single unit when the jaws were opened or closed (Figs. 4–3B, F; 4–6B). This feature is considered here as unique to *Plotosaurus*, pending recovery of three-dimensional material of other mosasaurs. Small striations along the anterolateral surfaces of the angulars indicate that if any motion were to occur at the intramandibular joint, it would be in a plane perpendicular to the long axis of the splenio-angular articulation. This ventrolateral 'buckling' of the mandibles was likely very limited in *Plotosaurus*, given the prevalence of these striations only on the anterior-most portions of the angulars in UCMP 32778 and the shallow articular surfaces of the angular in another specimen (CIT 2945).

Functional Significance of an Akinetic Mosasaur Skull

The loss of intracranial mobility likely occurred in several derived mosasaurine taxa and has been considered to be a feature of more aquatically adapted forms (Camp, 1942; Russell, 1964; 1967; Callison, 1967; Lingham-Soliar, 1995; Rieppel and Zaher, 2001). Previous functional explanations for the evolution of an akinetic mosasaur skull have addressed adaptation to marine life and the difficulties associated with feeding in a viscous medium (Camp, 1942; Callison, 1967; Russell, 1967) or the development of compensatory mechanisms to cope with increased bite force (Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995). While some mosasaurine taxa were generalists, macrophagous or even durophagous, requiring robust teeth and strong jaw adductor musculature (Massare, 1987; Lingham-Soliar and Nolf, 1989 Lingham-Soliar, 1995; Schulp, 2005; Bardet et al., 2008), *Plotosaurus* was selectively preying on smaller, softer bodied prey items as determined by the small gape, tooth morphology and presence of the remains of small fish in the visceral regions of some specimens (Camp, 1942; Massare, 1987; Taylor, 1987). As such, a functional hypothesis for the loss of the kinetic capacities of the skull of *Plotosaurus* need not take into account a bracing mechanism for resisting the forces exerted during hard biting or intraoral processing of harder prey items as in *Globidens*, *Mosasaurus* or *Prognathodon* (Taylor, 1987; Smith, 1980; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995).

Taylor (1987), Rieppel (2002) and Young et al. (2010) highlighted that relative prey size plays a key role not only in the feeding behavior of aquatic tetrapods, but also in how prey items are manipulated by the jaws during feeding. Ratchet feeding has been attributed to the kinetic and streptostylic skulls of other mosasaurs as a means of forcing larger prey items towards the back of the throat (Fig. 4–5A, B; Callison, 1967; Taylor, 1987; Lingham-Soliar, 1995; Lingham-Soliar and Nolf, 1989; Rieppel and Zaher, 2001). The protraction and retraction of the pterygoid and dentary teeth through simultaneous movements of the quadrates and pterygoids (Figs. 4–3; 4–5) would drag prey items backwards into the throat (Callison, 1967; Taylor, 1987). For *Plotosaurus*, the loss of movement of the quadrates and pterygoids coupled with a piscivorous diet would suggest that elaborate intraoral processing of food items was probably not required, because prey were small enough to be swallowed whole and without much difficulty (Taylor, 1987). This behavior persists even in extant odontocetes and has been noted for extinct marine tetrapods as well (Taylor, 1987; Bloodworth and Marshall, 2005). Lingham-Soliar and Nolf (1989) and Lingham-Soliar (1995) used relative size of the pterygoid dentition in mosasaurs as a proxy for the involvement of the pterygoids in feeding. In *Plesiotylosaurus* and *Prognathodon*, large and recurved pterygoid teeth may have helped to hold struggling prey in the oral cavity as it was forced to the back of the throat (Callison, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995; Lindgren, 2009). Conversely, Lingham-Soliar (1995) attributed smaller pterygoid teeth to the decreased importance of ratchet feeding in certain taxa. While *Plotosaurus* possesses a high number of pterygoid teeth, comparable to *Clidastes* (Camp, 1942; Russell, 1967), their small size and orientation suggest an alternative function of the pterygoid dentition in the former genus. The pterygoid tooth crowns in *Plotosaurus*, although numerous, are not large, nor are they noticeably recurved, save for the posterior three or four. More importantly, these small tooth crowns are more ventrolaterally directed in the middle of the pterygoid tooth row and may have instead served primarily to passively funnel small prey items towards the throat, using the inertia of the prey itself to move it posteriorly. Underwater inertial feeding as defined by Gans (1969) would account for this posterior movement of prey in aquatic tetrapods that specialize on small prey items (contra Russell, 1964), and must have been used by other lineages (e.g., ichthyosaurs and mesosaurs), since similar skull forms to *Plotosaurus* were probably not kinetic either and were clearly successful (McGowan and Motani, 2003; Modesto, 2006). It is also unlikely that *Plotosaurus* would have come to the surface in order to inertial feed or use the force of gravity to draw prey inwards, because these behaviors usually only persist in aquatic tetrapods that feed on proportionally larger prey items (Russell, 1964; Gans, 1969; Taylor, 1987; Lingham-Soliar, 1995).

Functional explanations for a loss of streptostyly in *Plotosaurus* are also probably related to the way in which small prey items were captured and processed. *Plotosaurus* probably did not use its marginal dentition for tearing, shearing and breaking apart prey into smaller pieces, but for capturing them, easily subduing soft-scaled fishes with long conical piercing teeth (Massare, 1987; Taylor, 1987). Rotation of the quadrates would not be required, nor favored, since jaw protraction and retraction (Fig. 4–5A, B) has been hypothesized to function in breaking apart large prey items and actively dragging them further into the oral cavity (Camp, 1942; Russell, 1964; 1967; Callison, 1967; Taylor, 1987; Lingham-Soliar, 1995). These motions in *Plotosaurus* would not be possible, given the tight interdigitation of the long conical teeth and the lack of movement at the quadrate-squamosal, splenio-angular, fronto-parietal joints and along the elongated mandibular symphyses. Simple dorsoventral movements of the mandibles, which would have acted in unison, relative to the skull would have been sufficient for capturing fish (Figs. 4–3B, D; 4–6B; Taylor, 1987; Thorbjarnarson, 1990).

While Camp (1942) suggested that streptostyly and intramandibular kinesis may have aided in simultaneously increasing gape and allowing for mandibular protraction and retraction in *Plotosaurus*, a reinterpretation of the cranial anatomy of UCMP 32778 would suggest otherwise. Restriction of the posterior movement of the suprastapedial process of the quadrate, the inclined angle of the intramandibular joint and the slender and elongate snout suggest that *Plotosaurus* possessed a small gape by mosasaur standards (Fig. 4–6B). Given the slightly procumbent anterior marginal dentition and the unusually small gape angle in the akinetic model of the skull of *Plotosaurus* presented here (Fig. 4–6), this piscivorous mosasaur probably adopted a more simplistic feeding behavior analogous to the ram-based feeding of some slender-snouted odontocetes (Bloodworth and Marshall, 2005). Bottlenose dolphins (*Tursiops truncatus*) chase down small fish and other prey using a clap-trap jaw to capture prey items from close range. Direct contact of the anterior teeth with the prey item is the primary mode of capture as opposed to using suction (Bloodworth and Marshall, 2005).

Bloodworth and Marshall (2005) noted that the ram-based behavior in *Tursiops truncatus* is reflected in a smaller maximum gape angle as compared to odontocetes that may rely more heavily on a suction-based feeding mechanism. Smaller maximum gape angles are thus more advantageous for capturing small prey items and limiting the chance of deflecting them away from the mouth during rapid jaw closure.

CONCLUSIONS

Plotosaurus bennisoni is an excellent candidate for the study of the evolutionary patterns associated with an increasingly pelagic lifestyle in mosasaurs. As a derived mosasaurine, *Plotosaurus* was well suited for life as a high-speed pursuit predator of the open seas (Lindgren et al., 2007), but this hypothesized lifestyle is derived mainly from anatomical and functional analyses of the postcranial skeleton. While most of the adaptations of the postcranial skeleton of *Plotosaurus* are easily correlated with the development of a more efficient swimming style (Lindgren et al., 2007), identification of features deemed ‘aquatic adaptations’ in the skulls of mosasaurids are more ambiguous (Camp, 1942; Russell, 1964; Callison, 1967; Lingham-Soliar, 1995). Cranial anatomy of aquatic tetrapods is likely to have evolved, as with the postcranium, in conjuction with a dramatic change in predatory tactics following the transition from land to sea. More specifically, aquatic tetrapods face the challenge of feeding in a viscous medium, which was likely a driving factor in the morphological evolution of the crania of many lineages of aquatic reptiles and mammals that specialized on smaller prey (Gans, 1969; Taylor, 1987; Lingham-Soliar and Nolf, 1989; Massare, 1990; Lingham-Soliar, 1995 Fordyce and Muizon in Mazin and Buffrénil, 2001; Rieppel, 2002; Bloodworth and Marshall, 2005; Young et al., 2010). Long snouts and conical grasping teeth evolved independently in many lineages of aquatic tetrapods that specialized on small slippery prey items, such as soft-scaled fish and cephalopods (Massare, 1987), to which *Plotosaurus* was clearly no exception. Unique to mosasaurs is the identification of the loss of cranial kinesis as a feature of more aquatically adapted forms (Russell, 1964; Callison, 1967). While cranial kinesis may have been lost in some mosasauroids, previous authors argue that streptostyly was apparently retained as a means of either increasing gape size or actively pulling prey in by protraction and retraction of the lower jaws and toothed pterygoids (Callison, 1967; Taylor, 1987; Lingham-Soliar, 1995). Camp's (1942) functional analysis of the cranial anatomy of *Plotosaurus* falls victim to the historical convention that mosasaurs retained some degree of streptostyly, which they inherited from their presumed terrestrial squamate ancestors (Camp, 1942; Russell, 1964; Callison, 1967; Rieppel and Zaher, 2001).

The present anatomical review of *Plotosaurus* was done as part of an investigation of the particular features in a derived mosasaurine that would have restricted mesokinesis, metakinesis, and most importantly, streptostyly (contra Camp, 1942; Russell, 1964; Callison, 1967). Here a novel function for the evolution of an akinetic skull was proposed that does not imply that the bracing mechanisms that restricted movement at the numerous intracranial joints evolved to cope with an increase in bite force (Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995). Similar to the conclusions drawn based on the postcranial anatomy of *Plotosaurus* (Lindgren et al., 2007; Lindgren et al., 2008), the loss of cranial kinesis and streptostyly signifies a dramatic shift in predatory behavior of this derived mosasaurine, with an emphasis on small prey capture in an aquatic environment rather than on the intraoral processing of larger prey. As pointed out by Lingham-Soliar (1995), the success of derived mosasaurines was likely the result of a dietary shift from the generalist behavior of earlier forms to specialists like *Plotosaurus*. *Plotosaurus* was probably unique in its dietary habits and occupied a specific predatory niche among mosasaurs of the eastern Pacific during the Maastrichtian. Niche partitioning likely contributed to the success of *Plotosaurus*, as it coexisted with a rich fauna of other large mosasaurs, including *Plesiotylosaurus*, *Mosasaurus* and *Prognathodon* (Camp, 1942; Lindgren, 2009; Lindgren and Schulp, 2010).

FIGURE 4–1. Comparisons of the palatal complexes of two species of *Mosasaurus* and *Plotosaurus bennisoni* (UCMP 32778). **A**, palatines and vomers of the holotype of *Mosasaurus missouriensis* (RFWUIP 1327). Dashed lines indicate the position of the vomeropalatine suture, the exact shape of which is difficult to discern based on the preservation of this region in the holotype. Anterior ends of vomers are truncated due to the absence of the premaxilla; **B**, palatines and vomers of *Mosasaurus hoffmanni*, based on a relatively complete and uncrushed specimen (IRSN R12); **C**, palatines and vomers of the holotype of *Plotosaurus bennisoni* (UCMP 32778) modified from Camp (1942:fig. 14). Anterior ends of vomers are concealed by matrix in the holotype. **Abbreviations: pal**, palatine; **v**, vomer; **vop**, vomerine process of the palatine. Palatal complexes are not to scale with respect to each other.

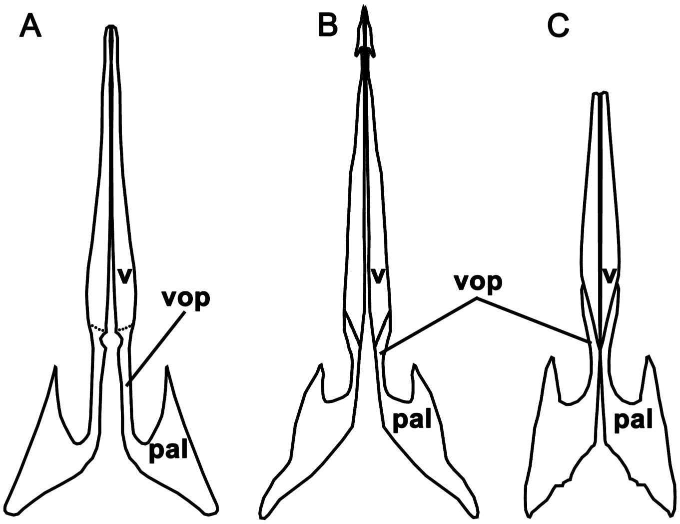
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FIGURE 4–2. Illustration of the snout of *Plotosaurus bennisoni* (UCMP 32778) in dorsolateral view. Grey areas indicate portions concealed by matrix. **Abbreviations: dgr**, dorsal groove of fused septomaxillae; **f**, frontal; **fsx**, fused septomaxillae; **int**, internarial bar of premaxilla; **j**, jugal; **lsx**, left septomaxilla; **mx**, maxilla; **n**, nasal; **pal**, palatine; **pmx**, premaxilla; **prf**, prefrontal; **rsx**, right septomaxilla; **v**, vomer. Scale bar equals 5 cm.

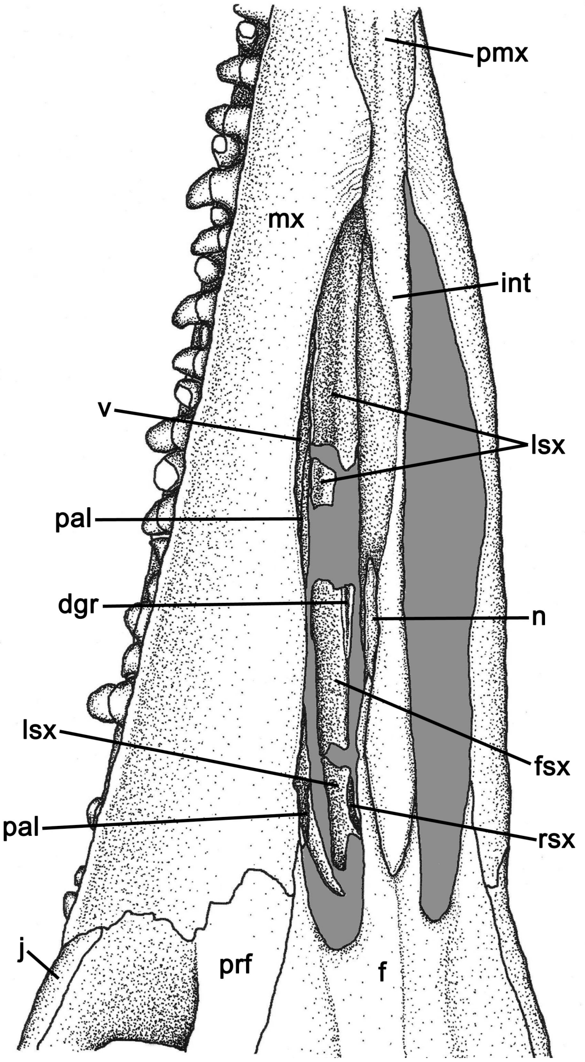
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FIGURE 4–3. Intracranial kinesis in a generalized mosasaur compared to *Plotosaurus*. **A**, muzzle unit protracted, parietal unit depressed anteriorly, pterygoids protracted and anterior mandibular unit depressed in a generalized kinetic mosasaur skull. Modified from Russell (1964:fig. 5a); **B**, elevation of the muzzle unit in *Plotosaurus* as a result of rotation of the entire skull at the quadrate-mandibular joint; **C**, 'resting' positions of intracranial units in a generalized mosasaur (modified from Russell, 1964:fig. 5b); **D**, 'resting' positions of intracranial units in *Plotosaurus*; **E**, muzzle unit retracted, parietal unit raised anteriorly, pterygoids retracted and anterior mandibular unit raised in a generalized kinetic mosasaur skull (modified from Russell, 1964:fig. 5c); **F**, anterior mandibular unit raised in *Plotosaurus*. **Abbreviations: am**, anterior mandibular unit; **ba**, basal articulation; **dpp**, descensus processus parietalis; **ep**, epipterygoid; **eppt**, epipterygoid-pterygoid joint; **imj**, intramandibular joint; **max**, mesokinetic axis; **mj**, mandibular joint; **mtj**, metakinetic joint; **mtx**, metakinetic axis; **oc**, occipital segment (braincase); **pm**, posterior mandibular unit; **pt**, pterygoid; **pu**, parietal unit; **q**, quadrate; **qj**, quadratosquamosal joint. Grey areas indicate changes to the skull of *Plotosaurus* compared to the kinetic condition in Russell's (1964) generalized mosasaur model. Grey circles indicate the presence of intracranial joints.

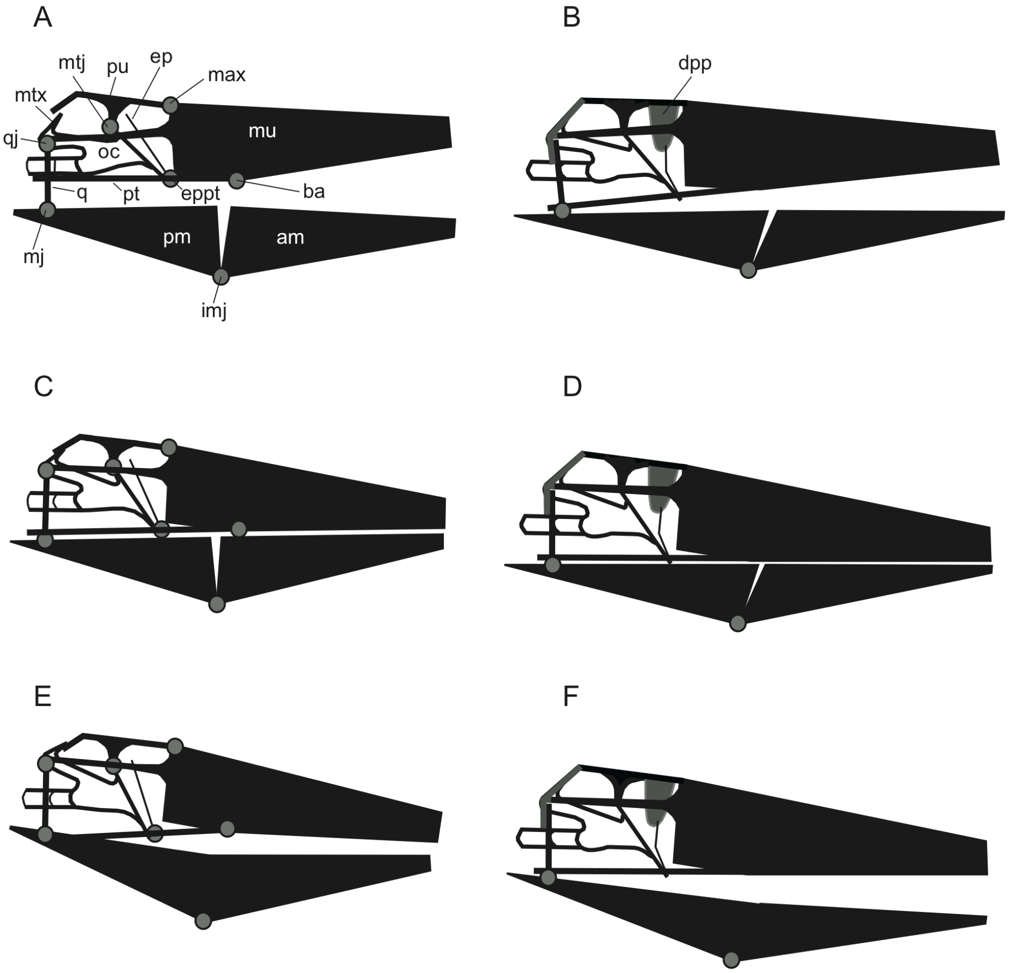
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FIGURE 4–4. Comparisons of the muzzle units (composed of the elements shaded in grey) of three mosasaurines compared to *Varanus* in dorsal view. **A**, outline of the skull of *Varanus indicus* (modified from Frazzetta, 1962:fig. 1a); **B**, outline of the skull of *Clidastes liodontus* (modified from Russell, 1967:fig. 72) showing the extent of the muzzle unit as interpreted by Callison (1967); **C**, skull of *Clidastes liodontus* showing the extent of the muzzle unit as interpreted by Russell (1964); **D**, outline of the skull of *Mosasaurus sp.* modified from Williston (1895:pl. 15). Sutural positions added based on the description of *M. hoffmanni* by Lingham-Soliar (1995); **E**, outline of the skull of *Plotosaurus bennisoni* (UCMP 32778). **Abbreviations: f**, frontal; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **pmx**, premaxilla; **pof**, postorbitofrontal; **prf**, prefrontal; **sq**, squamosal. Skulls are not to scale.

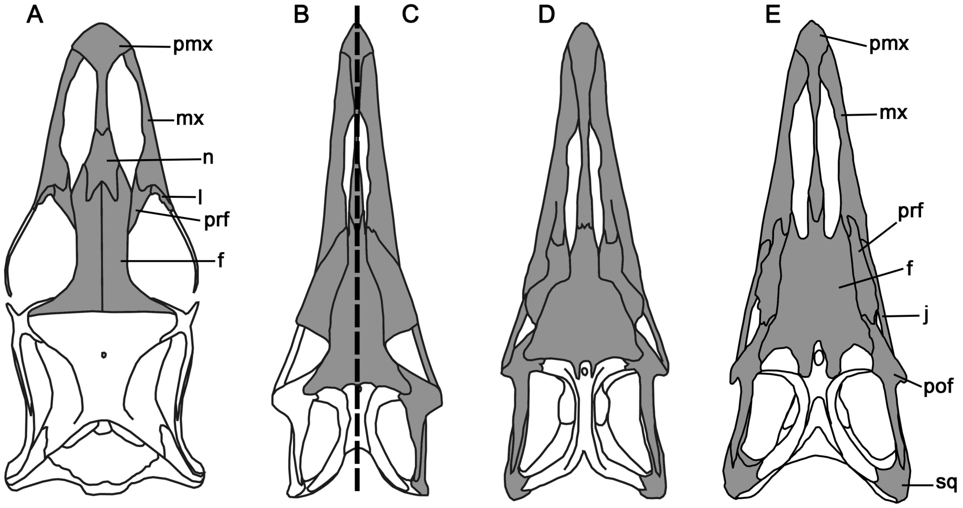
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FIGURE 4–5. Streptostyly and ratchet feeding in a generalized mosasaur skull compared to the condition in *Plotosaurus*. **A**, protraction of the quadrate and mandible in a kinetic mosasaur skull (modified from Russell, 1964:fig. 6a); **B**, retraction of the quadrate and mandible in a kinetic mosasaur skull (modified from Russell, 1964:fig. 6b); **C**, non-streptostylic condition in *Plotosaurus*, which prevents anteroposterior movement of the quadrate and mandible. **Abbreviations:** **am**, anterior mandibular unit; **dpp**, descencus processus parietalis; **ep**, epipterygoid; **imj**, intramandibular joint; **max**, mesokinetic axis; **mj**, mandibular joint; **mtj**, metakinetic joint; **oc**, occipital segment (braincase); **pm**, posterior mandibular unit; **pt**, pterygoid; **pu**, parietal unit; **q**, quadrate; **qj**, quadratosquamosal joint. Grey areas indicate changes to the skull of *Plotosaurus* compared to the kinetic condition in Russell's (1964) generalized mosasaur model. Grey circles indicate the presence of intracranial joints.

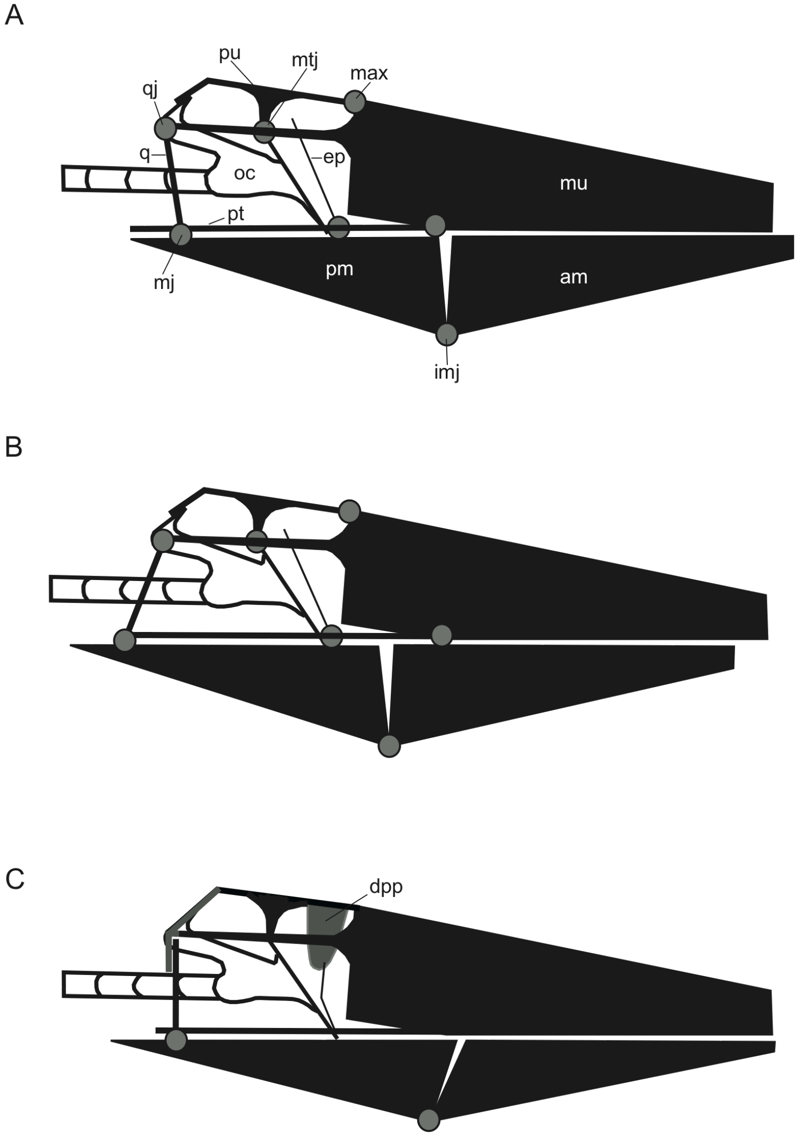
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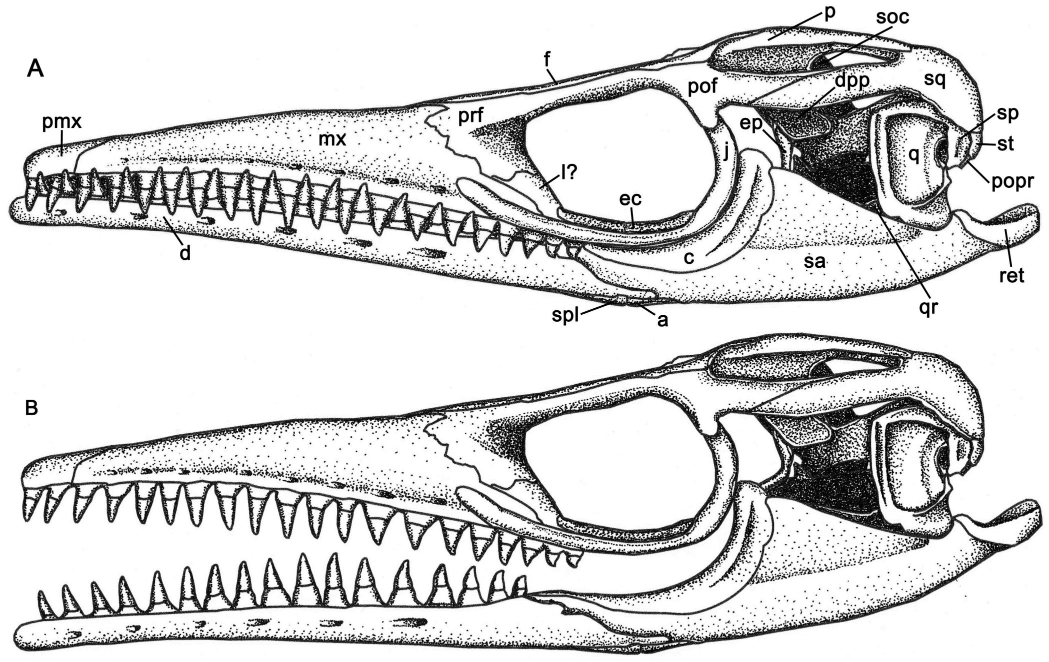
FIGURE 4–6. Restoration of the skull of *Plotosaurus bennisoni* (UCMP 32778) to illustrate the lack of metakinetic, mesokinetic, intramandibular and streptostylic movements of the skull as the jaws are opened. **A**, illustration of UCMP 32778 with jaws closed. Only the teeth, vertical ramus of the jugal and the ventrolateral portion of the quadrate ala were restored. **B**, illustration of UCMP 32778 with jaws opened. The mandible was rotated to the point where the posterior rim of the glenoid fossa abutted against the posterior border of the quadrate mandibular condyle. **Abbreviations: a**, angular; **c**, coronoid; **d**, dentary; **dpp**, descensus processus parietalis; **ec**, ectopterygoid; **ep**, epipterygoid; **f**, frontal; **j**, jugal; **mx**, maxilla; **p**, parietal; **pal**, palatine; **pmx**, premaxilla; **pof**, postorbitofrontal; **popr**, paroccipital process; **prf**, prefrontal; **q**, quadrate; **qr**, quadrate ramus of the pterygoid; **ret**, retroarticular process; **sa**, surangular; **soc**, supraoccipital; **sp**, suprastapedial process; **spl**, splenial; **sq**, squamosal; **st**, supratemporal.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LITERATURE CITED

Bardet, N., X. Pereda Suberbiola, M. Iarochène, F. Bouyahyaoui, B. Bouya, and M. Amaghzaz. 2004. *Mosasaurus beaugei* Arambourg, 1952 (Squamata, Mosasauridae) from the Late Cretaceous phosphates of Morocco. Geobios 37:315–324.

Bardet, N., X. Pereda Suberbiola, A. S. Schulp, and B. Bouya. 2008. New material of *Carinodens* (Squamata, Mosasauridae) from the Maastrichtian (Late Cretaceous) phosphates of Morocco in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:29–36.

Bell, G. L., Jr. 1997. Chapter 11. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293–332 in J. M. Callaway, and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bloodworth, B., and C. D. Marshall. 2005. Feeding kinematics of *Kogia* and *Tursiops* (Odontoceti: Cetacea): characterization of suction and ram feeding. The Journal of Experimental Biology 208:3721–3730.

Caldwell, M.W., R. L. Carroll, and H. Kaiser. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroides and varanoids. Journal of Vertebrate Paleontology 15:516–531.

Caldwell, M. W., and Bell, G. L., Jr. 2005. Of German princes and North American rivers: Harlan's lost mosasaur snout rediscovered. Netherlands Journal of Geosciences 84:207–211.

Callison, G. 1967. Intracranial mobility in Kansas mosasaurs. The University of Kansas Paleontological Contributions 26:1–15.

Camp, C. L. 1942. California Mosasaurs. Memoirs of the University of California 13:1–68.

Camp, C. L. 1951. *Plotosaurus*, a new generic name for *Kolposaurus* Camp, preoccupied. Journal of Paleontology 25:822.

Carroll, R. L., and M. DeBraga. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. Journal of Vertebrate Paleontology 12:66–86.

Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22:629–644.

Conybeare, W. D. 1822. Fossil crocodiles and other saurian animals; pp. 284–304 in J. Parkinson, outlines of Oryctology. An Introduction to the Study of Fossil Organic Remains; Especially of Those Found in the British Strata: Intended to Aid the Student in his Enquiries Respecting the Nature of Fossils, and Their Connection with the Formation of the Earth vii.

Cope, E. D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. Boston Society of Natural History Proceedings 12:250–266.

Cope, E. D. 1871. On some species of Pythonomorpha from the Cretaceous beds of Kansas and New Mexico. Proceedings of the American Philosophical Society of 11:574–584.

Cope, E. D. 1868. On new species of extinct reptiles. Proceedings of the Academy of Natural Sciences of Philadelphia 20:181.

Dalrymple, G. H. 1979. The jaw mechanism of the snail-crushing lizards, *Dracaena* Daudin 1802 (Reptilia, Lacertilia, Teiidae). Journal of Herpetology 13:303–311.

Dollo, L. 1889. Note sur les vertébrés fossiles récemment offerts au Musée de Bruxelles par M. Alfred Lemonnier. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 3:181–182.

Dollo, L. 1892. L'ostéologie des mosasauriens. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie 4:218–259.

Dollo, L. 1904. Les mosasauriens de la Belgique. Bulletin de la Société Belge de Géologie, de Paléontologie et Hydrologie 19:125–131.

Dortangs, R. W., A. S. Schulp, E. W. A. Mulder, J. W. M. Jagt, Peeters, H. H. G., de Graaf, D. Th. 2002. A large new mosasaur from the Upper Cretaceous of the Netherlands. Netherlands Journal of Geosciences 81:1–8.

Dutchak, A. R., and M. W. Caldwell. 2006. Redescription of *Aigialosaurus dalmaticus* Kramberger, 1892, a Cenomanian mosasauroid lizard from Hvar Island, Croatia. Canadian Journal of Earth Sciences 43:1821–1834.

Dutchak, A. R., and M. W. Caldwell. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. Journal of Vertebrate Paleontology 29:437–452.

Endo, H, R. Aoki, H. Taru, J. Kimura, M. Sasaki, M. Yamamoto, K. Arishima, and Y. Hayashi. 2002. Comparative functional morphology of the masticatory apparatus in the long-snouted crocodiles. Anatomical and Histological Embryology 31:206–213.

Fernandez, M. S., and J. E. Martin. 2009. Description and phylogenetic relationships of *Taniwhasaurus antarcticus* (Mosasauridae, Tylosaurinae) from the upper Campanian (Cretaceous) of Antarctica. Cretaceous Research 30:717–726.

Fernandez, M. S., F. Archuby, M. Talevi, and R. Ebner. 2005. Ichthyosaurian eyes: paleobiological information content in the sclerotic ring of *Caypullisaurus* (Ichthyosauria, ophthalmosauria). Journal of Vertebrate Paleontology 25:330–337.

Fordyce, E., and C. de Muizon. 2001. Evolutionary history of cetaceans: a review; pp. 169–233 in J. –M. Mazin, and V. de Buffrénil (eds.), Secondary Adaptations of Tetrapods to Life in Water. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. Journal of Morphology 111:287–319.

Gans, C. 1969. Comments on inertial feeding. Copeia 4:855–857.

Gervais, P. 1853. Observations relatives aux reptiles fossiles de France. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 36:374–377, 470–474.

Goldfuss, A. 1845. Der Schädelbau des *Mosasaurus*, durch Beschreibung einer neuen Art dieser Gattung erläutert. Nova Acta Academiae Caesar Leopoldino-Carolinae Germanicae Natura Curiosorum 21:173–200.

Herrel, A., F. De Vree, and C. Gans. 1999. Cranial kinesis in Gekkonid lizards. The Journal of Experimental Biology 202:3687–3698.

Herrel, A., P. Aerts, and F. De Vree. 2000. Cranial kinesis in geckoes: functional implications. Journal of Experimental Biology 203:1415–1423.

Holmes, R. 1996. *Plioplatecarpus primaevus* (Mosasauridae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of the North American Western Interior Seaway. Journal of Vertebrate Paleontology 16:673–687.

Holmes, R. B., and H. -D. Sues. 2000. A partial skeleton of the basal mosasaur *Halisaurus platyspondylus* from the Severn Formation (Upper Cretaceous: Maastrichtian) of Maryland. Journal of Paleontology 74:309–316.

Konishi, T., and M. W. Caldwell. 2007. New specimens of *Platecarpus planifrons* (Cope, 1874) (Squamata: Mosasauridae) and a revised taxonomy of the genus. Journal of Vertebrate Paleontology 27:59–72.

Konishi, T., and M. W. Caldwell. 2009. New material of the mosasaur *Plioplatecarpus nichollsae* Cuthbertson et al., 2007, clarifies problematic features of the holotype specimen. Journal of Vertebrate Paleontology 29:417–436.

Lee, M. S. Y., G. L. Jr. Bell, and M. W. Caldwell. 1999. The origin of snake feeding. Nature 400:655–659.

Lindgren, J., J. W. M. Jagt, and M. W. Caldwell. 2007. A fishy mosasaur—the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. Lethaia 40:153–160.

Lindgren, J., M. W. Caldwell, and J. W. M. Jagt. 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). Journal of Vertebrate Paleontology 28:1043–1054.

Lindgren, J. 2009. Cranial osteology of the giant mosasaur *Plesiotylosaurus* (Squamata, Mosasauridae). Journal of Paleontology 83:448–456.

Lindgren, J., C. Alwmark, M. W. Caldwell, and A. R. Fiorillo. 2009. Skin of the Cretaceous mosasaur *Plotosaurus*: implications for the aquatic adaptations in giant marine reptiles. Biology Letters 5:528–531.

Lindgren, J., M. W. Caldwell, T. Konishi, and L. M. Chiappe. 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. PLoS ONE 5:e11998. Doi:10.1371/journal.pone.0011998.

Lindgren, J., and A. S. Schulp. 2010. New material of *Prognathodon* (Squamata: Mosasauridae), and the mosasaur assemblage of the Maastrichtian of California, U.S.A. Journal of Vertebrate Paleontology 30:1632–1636.

Lingham-Soliar, T., and D. Nolf. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 59:137–190.

Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, upper Maastrichtian of the Netherlands. Philosophical Transactions of the Royal Society of London B347:155–180.

Lingham-Soliar, T. 1998. A new mosasaur *Pluridens walkeri* from the Upper Cretaceous, Maastrichtian of the Iullemmeden Basin, Southwest Niger. Journal of Vertebrate Paleontology 18:709–717.

Linneus, C. 1758. Systema Naturae, Edition X, vol. 1 (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.) Holmiae Salvii, 824 pp.

Mantell, G. A. 1829. A tabular arrangement of the organic remains of the county of Sussex. Geological Society of London Transactions 3:201–216.

Marsh, O. C. 1872. Note on *Rhinosaurus*. American Journal of Science 3rd series 4:147.

Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7:121–137.

Massare, J. A., and J. M. Callaway. 1990. The affinities and ecology of Triassic ichthyosaurs. Geological Society of America Bulletin 102:409–416.

McGowan, C., and R. Motani. 2003. Ichthyopterygia. In: Suess, H. –D., ed. Handbook of Paleoherpetology. Munich:. Verlag Dr. Friedrich Pfeil. Pp. I–VIII, 1–175.

Merriam, J. C. 1894. Ueber die Pythonomorphen der Kansas-Kreide. Palaeontolographica 41:1–39, pls. 1–4.

Modesto, S. P. 2006. The cranial skeleton of the Early Permian aquatic reptile *Mesosaurus tenuidens*: implications for relationships and palaeobiology. Zoological Journal of the Linnean Society 146:345–368.

Mulder, E. W. A. 1999. Transatlantic latest Cretaceous mosasaurs (Reptilia, Lacertilia) from the Maastrichtian type area and New Jersey. Geologie en Mijnbouw 78:281–300.

Oppel, M. 1811. Die Ordungen Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, München, 86 pp.

Owen, R. 1840–1845. Odontography; or, a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure in the vertebrate animals. London: Hippolyte Bailliere. Vol. 1 (text) xix + lxxiv + 655 pp; Vol. 2 (atlas)37 pp. + 168 pls.

Rieppel, O. 1978. Streptostyly and muscle function in lizards. Cellular and molecular life sciences 34:776–777.

Rieppel, O., and L. Labhardt. 1979. Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). Herpetologica 35:158–163.

Rieppel, O., and H. Zaher. 2001. Re-building the bridge between mosasaurs and snakes. Neues Jahrbuch fur Geologie und Paläontologie-Abhandlunge 221:111–132.

Rieppel, O. 2002. Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. Zoological Journal of the Linnean Society 135:33–63.

Romer, A. S. 1968. An ichthyosaur skull from the Cretaceous of Wyoming. Contributions to Geology, University of Wyoming 7:27–41.

Russell, D. A. 1964. Intracranial mobility in mosasaurs. Peabody Museum of Natural History, Yale University, Postilla 86:1–19.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs (Reptilia, Sauria). Peabody Museum of Natural History, Yale University, Bulletin 23:1–241.

Schulp, A. S. 2005. Feeding the mechanical mosasaur: what did *Carinodens* eat? Netherlands Journal of Geosciences 84:345–357.

Schulp, A. S. 2006. A comparative description of *Prognathodon saturator* (Mosasauridae, Squamata), with notes on its phylogeny; pp. 19–56 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. J. Jacobs, and M. L. Morais. 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the

Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon* in M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3:1–12.

Smith, K. K. 1980. Mechanical significance of streptostyly in lizards. Nature 283:778–779.

Taylor, M.A. 1987. How tetrapods feed in water: a functional analysis by paradigm. Zoological Journal of the Linnean Society 91:171–195.

Thorbjarnarson, J. B. 1990. Notes on the feeding behavior of the gharial (*Gavialis gangeticus*) under semi-natural conditions. Journal of Herpetology 24:99–100.

Young, M. T., S. L. Brusatte, M. Ruta, and M. B. De Andrade. 2010. The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. Zoological Journal of the Linnean Society 158:801–859.

CHAPTER FIVE

GENERAL CONCLUSIONS

In this thesis, a new genus and species of mosasaur from the Maastrichtian phosphates of Morocco is described, increasing the taxonomic diversity of the Mosasaurinae. *Eremiasaurus heterodontus* was recovered as a basal member of the Mosasaurini. An assessment of the monophyly of two major mosasaurine clades was undertaken as part of an investigation of the phylogenetic utility of tooth and quadrate characters to diagnose globidensine and mosasaurin taxa. *E. heterodontus* possesses a 'globidensine' arrangement of the infrastapedial and suprastapedial processes of the quadrate, but a mosasaurin-like premaxilla and grooved quadrate alar rim. Phylogenetic analyses were performed using the most recently published dataset (Caldwell and Palci, 2007), modified from Bell (1997), so that comparisons could be made between this new phylogeny of the Mosasaurinae and those of other authors (e.g., Christiansen and Bonde, 2002; Dortangs et al., 2002; Schulp, 2006; Schulp et al., 2006a). Five species of *Prognathodon* were added to a second analysis based on personal observation of the holotype and referred specimens of *Prognathodon solvayi* and from character state assignments and descriptions for *Prognathodon currii*, *P. saturator*, *P. waiparaensis* and *P. kianda* from the literature (Christiansen and Bonde, 2002; Dortangs et al., 2002; Schulp, 2006; Schulp et al., 2008). Character state assignments for several taxa already present in the taxon-character matrix of Caldwell and Palci (2007) were revised based on personal observations of the holotypes of *Plotosaurus bennisoni*, *Mosasaurus missouriensis* and *Plesiotylosaurus crassidens* and new anatomical observations from Caldwell and Bell (2005), Lindgren et al. (2008) and Lindgren (2009).

The second phylogeny of the Mosasaurinae highlights three major findings: (1) the difficulty in coding for finer-scale tooth enamel ornamentation and tooth shape characters for globidensine taxa (all members of which are thought to possess crenulated apices and flared tooth crown bases); (2) the addition of several *Prognathodon* species from previous works creates poorly defined ingroup relationships of most of the globidensines and (3) the addition of *Eremiasaurus heterodontus* to the dataset from Caldwell and Palci (2007) creates a new topology of the Mosasaurinae in which characters thought to represent synapomorphies of the Globidensini become synapomorphies of a more inclusive clade (Mosasaurini + Globidensini). This challenges the conventional dichotomy between the globidensines and mosasaurins by recovering a paraphyletic globidensine grade of mosasaurs that share many features of the quadrate and dentition with a morphologically transitional form, *E. heterodontus*, which was recovered as the basal member of the Mosasaurini. The slender blade-like dentition of *E. heterodontus* is a testament to the variability in the dentition of mosasaurines, suggesting that evolutionary hypotheses that are based on tooth form (e.g. Lindgren, 2005; Schulp et al., 2006b) are susceptible to homoplasy, because tooth characters are better correlated to diet than to assessing evolutionary relatedness (Massare, 1987). Additionally, this new phylogenetic hypothesis suggests that the open tympanic notch in *Mosasaurus* and *Plotosaurus* represents a secondary loss of quadrate process fusion; a reversal to the condition seen in more basal mosasaurines, like *Clidastes*. The fact that *Mosasaurus* and *Plotosaurus* share a lack of quadrate process fusion with *Clidastes* should thus not be considered a feature that unites *Clidastes* with the two former genera. This hypothesis lends itself well to the phylogenies of Bell (1997) and subsequent authors (e.g., Christiansen and Bonde, 2002; Dortangs et al., 2002; Caldwell and Palci, 2007) who dramatically altered Russell's (1967) original definition of the Mosasaurini (= Plotosaurini sensu Bell, 1997) to include *Plotosaurus* and *Mosasaurus* to the exclusion of *Clidastes*.

Monophyly of the clade consisting of *Mosasaurus* and *Plotosaurus* is well supported in the literature (Bell, 1997; Christiansen and Bonde, 2002; Dortangs et al., 2002; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009), but resolving the relationships of *Plotosaurus* to species of *Mosasaurus* has proven to be difficult using the dataset from Bell (1997). Most phylogenetic analyses of the Mosasaurinae have recovered a paraphyletic *Mosasaurus* (e.g., Bell, 1997; Bell and Polcyn, 2005; Caldwell and Palci, 2007), due to the discrepancy in the number of characters that unite species of *Mosasaurus* to the exclusion of *Plotosaurus*. Bell (1997) hypothesized that *Plotosaurus* is derived from a common ancestor within the genus *Mosasaurus*, which would suggest that their generic distinction should be abandoned, pending the discovery of additional anatomical features that would separate *Plotosaurus* from *Mosasaurus*. As Camp (1942) noted, *Plotosaurus* shares many anatomical features with *Mosasaurus*, but many of these vary in the degree of their expression or proportions in the ichthyosaur-like skull and postcranium of *Plotosaurus*. The redescription of the cranial anatomy of the monotypic *Plotosaurus*, based primarily on the three-dimensionally preserved holotype specimen, will hopefully provide anatomical details that may be used to distinguish *Plotosaurus* from *Mosasaurus missouriensis*, *M. hoffmanni*, *M. conodon* and *M. beaugei* in future phylogenetic analyses. For its present uses, however, this description provides a framework for examining cranial features that can be correlated with the unusually high degree of aquatic specialization exhibited in the postcranium of *Plotosaurus* (Lindgren et al., 2007; Lindgren et al., 2008).

In Chapter 4, the cranial features of *Plotosaurus* were examined and placed in a functional context, being related primarily to underwater feeding (Taylor, 1987). As a pelagic thunniform or sub-carangiform swimmer, the feeding habits of *Plotosaurus* were unique compared to other mosasaurs. The long and narrow snout and enlarged orbits of this peculiar mosasaur are features that it shares with other unrelated marine tetrapods, and have been correlated with its high degree of aquatic adaptation (Camp, 1942; Lingham-Soliar, 1995). One evolutionary trend of the mosasaurs that can be best scrutinized by redescribing the holotype of *Plotosaurus* is the loss of intracranial kinesis and its adaptive significance. While many authors have argued that mesokinesis and metakinesis were lost in later forms (Russell, 1964; Callison, 1967; Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995), the anatomical features that would have restricted these motions have not been explored in detail. It was discovered that mesokinesis and metakinesis were indeed repressed in *Plotosaurus*, but in addition, rotation of the quadrates (streptostyly) and flexion at the intramandibular joint were repressed or even lost (contra Russell, 1964; Callison, 1967). As a psicivorous mosasaur, the loss of these kinetic mechanisms were linked to the precise pattern of tooth interdigitation in *Plotosaurus* and the dietary habits of extant odontocetes, gavials and extinct aquatic tetrapods. It was argued that an akinetic mosasaur skull could have arisen as an adaptation for piscivory or preying on small prey items and not hard-biting (contra Lingham-Soliar and Nolf, 1989; Lingham-Soliar, 1995). This sets precedence for future work to examine if such a departure from the kinetic skulls of extant squamates (Frazzetta, 1962; Smith et al., 1980; Herrel et al., 1999) occurred in earlier mosasaurs as well (Russell, 1964; contra Callison, 1967) and may be a feature that characterizes the aquatic lifestyles of the Mosasaurinae, Mosasauridae, or the Mosasauroidea.

LITERATURE CITED

Bell, G. L., Jr. 1997. Chapter 11. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293–332 in J. M. Callaway, and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bell, G. L., Jr., and M. J. Polcyn. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). Netherlands Journal of Geosciences 84:177–194.

Caldwell, M. W., and A. Palci. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. Journal of Vertebrate Paleontology 27:863–880.

Camp, C. L. 1942. California Mosasaurs. Memoirs of the University of California 13:1–68.

Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22:629–644.

Dortangs, R. W., A. S. Schulp, E. W. A. Mulder, J. W. M. Jagt, H. H. G. Peeters, and D. Th. de Graaf. 2002. A large new mosasaur from the Upper Cretaceous of the Netherlands. Netherlands Journal of Geosciences 81:1–8.

Dutchak, A. R., and M. W. Caldwell. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. Journal of Vertebrate Paleontology 29:437–452.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. Journal of Morphology 111:287–319.

Lindgren, J. 2005. Dental and vertebral morphology of the enigmatic mosasaur *Dollosaurus* (Reptilia, Mosasauridae) from the lower Campanian (Upper Cretaceous) of southern Sweden. Bulletin of the Geological Society of Denmark 52:17–25.

Lindgren, J., J. W. M. Jagt, and M. W. Caldwell. 2007. A fishy mosasaur—the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. Lethaia 40:153–160.

Lindgren, J., M. W. Caldwell, and J. W. M. Jagt. 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). Journal of Vertebrate Paleontology 28:1043–1054.

Lingham-Soliar, T., and D. Nolf. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre 59:137–190.

Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, upper Maastrichtian of the Netherlands. Philosophical Transactions of the Royal Society of London B347:155–180.

Russell, D. A. 1964. Intracranial mobility in mosasaurs. Peabody Museum of Natural History, Yale University, Postilla 86:1–19.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs (Reptilia, Sauria). Peabody Museum of Natural History, Yale University, Bulletin 23:1–241.

Schulp, A. S. 2006. A comparative description of *Prognathodon saturator* (Mosasauridae, Squamata), with notes on its phylogeny; pp. 19–56 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., M. J. Polcyn, O. Mateus, L. L. Jacobs, M. L. Morais, and T. da S. Tavares. 2006a. New mosasaur material from the Maastrichtian of Angola, with notes on the phylogeny, distribution and palaeoecology of the genus *Prognathodon*: pp. 57–67 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Schulp, A. S., J. W. M. Jagt, and F. Fonken. 2006b. New material of the mosasaur *Carinodens belgicus* from the Upper Cretaceous of The Netherlands: pp.

69–72 in A. S. Schulp (ed.), On Maastricht Mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg 45(1).

Taylor, M.A. 1987. How tetrapods feed in water: a functional analysis by paradigm. Zoological Journal of the Linnean Society 91:171–195.