*Paleontology is an exact science. It embraces generalizations or laws obtained by induction, which may be deductively applied to the unknown.*

*— Edward D. Cope, 1875*

*We shall never, probably, disentangle the inextricable web of affinities between the members of any one class; but when we have a distinct object in view, …, we may hope to make sure but slow progress.*

*— Charles Darwin, 1859*

*The mosasaurs were the most spectacular of all lizards.*

*— Robert L. Carroll, 1988*

**University of Alberta**

# SYSTEMATICS OF PLIOPLATECARPINAE (SQUAMATA: MOSASAURIDAE)

by

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*To Rie.*

# ABSTRACT

The name, mosasaurs, generally refers to a group of extinct, highly aquatically adapted and large-bodied squamates that lived exclusively during the Late Cretaceous, approximately from 93 to 65 million years ago, in the oceans worldwide. Plioplatecarpines (Plioplatecarpinae) were medium-sized mosasaurs seldom reaching 10 m in total body length, generally exhibiting along their gracile jaws the lowest number of marginal teeth among mosasaurs. Remains of plioplatecarpines are abundantly found particularly from the Western Interior Basin of North America; however, their taxonomy, interrelationships, and biodiversity remained largely unexplored. A large-scale systematic review of this group of mosasaurs was conducted based on examination of nearly 500 specimens of plioplatecarpine mosasaurs collected predominantly from North America and Western Europe. From a synthesis of morphological, biostratigraphic, and biogeographic data, two new genera are erected thus recognizing as valid, 7 genera and 11 species. According to the preferred hypothesis of their interrelationships, *Ectenosaurus clidastoides* is found to be the basal-most member, in part as a result of its high tooth count and unusually elongate jaw morphology. The interrelationships of the remaining plioplatecarpines are resolved as follows: (*Angolasaurus bocagei*, ((*Selmasaurus russelli*, *S. johnsoni*), (*Plesioplatecarpus planifrons*, (*Platecarpus tympaniticus*, ((*Latoplatecarpus willistoni*, *L. nichollsae*), (*Plioplatecarpus primaevus*, (*P. houzeaui*, *P. marshi*))))))). The new genera, *Plesioplatecarpus* and *Latoplatecarpus*, assist in resolving the long-standing problem of paraphyly/polyphyly of the genus

*Platecarpus*, now only recognized from *P. tympaniticus*, the generic type. Such establishment of new genera also reduces the average number of species per genus to a little over 1.5, but this ratio likely will increase as the number of specimens in each genus increases with future discoveries, which will then allow us to better understand intra- and interspecific variations within respective genera. In addition to the new phylogeny, a novel cranial anatomy is identified in these mosasaurs. Namely, the quadrate tilted forward in many plioplatecarpines, rather than being upright, since it was along the distal portion of the elongate suprastapedial process that the quadrate articulated with the suspensorium.

# ACKNOWLEDGMENTS

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I now thank my Canadian host family, the Sorochans. Without their generous offer of letting me stay with them for the very first three years of my education in this country, I strongly wonder if I could come this far. Their warm support like a real family had eventually led me to be part of their family as well, and for this special experience I owe them my deepest sense of gratitude.

As I earlier introduced my best man, now I would like to acknowledge my sweet wife, Rie. The magnitude of her support and understanding towards me and what I do are beyond description, and as such I cannot seem to thank her enough. I hope my dedication of this thesis to her will at least in part represent my infinite gratitude towards her, and by extension, towards my family members in law.

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## Institutional Abbreviations

**ALMNH PV**, Alabama Museum of Natural History, Tuscaloosa, Alabama, USA;

**AMNH (FR)**, American Museum of Natural History, New York, New York, USA;

**ANSP**, The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA;

**BMNH/BMNH R**, Natural History Museum, London, United Kingdom;

**CDM**, Courtenay and District Museum, Courtenay, British Columbia, Canada;

**CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada;

**DMNH**, Museum of Nature and Science, Dallas, Texas, USA;

**FHSM VP**, Fort Hays Sternberg Museum, Hays, Kansas, USA;

**FMNH UC/PR**, Field Museum, Chicago, Illinois, USA;

**GSATC,** Geological Survey of Alabama Type Collection, Tuscaloosa, Alabama, USA;

**IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;

**KU**, The University of Kansas Natural History Museum, Lawrence, Kansas, USA;

**LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA;

**M**, Canadian Fossil Discovery Centre (previously Morden and District Museum), Morden, Manitoba, Canada;

**RMM**, Red Mountain Museum, now housed at McWane Science Center, Birmingham, Alabama, USA;

**RSM P**, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada;

**SDSMT**, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA;

**SMU**, Southern Methodist University, Dallas, Texas, USA;

**TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada;

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

**UNO**, University of New Orleans, New Orleans, Louisiana, USA;
**USNM**, Smithsonian National Museum of Natural History, Washington D. C., USA;
**UW**, University of Wisconsin-Madison Geology Museum, Madison, Wisconsin, USA; **YPM**, Yale University Peabody Museum of Natural History, New Haven, Connecticut, USA.

### Anatomical Abbreviations

It is noted that anatomical abbreviations greatly vary from figure to figure, sometimes the same abbreviation being assigned to more than one anatomical feature. For this reason, readers are referred to respective figure captions where anatomical abbreviations specific to each figure are contained.

# CHAPTER ONE

# GENERAL INTRODUCTION

# INTRODUCTION TO MOSASAURS

The mosasaurs (Squamata: Mosasauridae) were a group of secondarily aquatic tetrapods that inhabited the world oceans and epicontinental seas during the Late Cretaceous, approximately from 93 to 65 million years ago (e.g., Bardet et al., 2003; Polcyn and Bell, 2005; Jagt et al., 2008). Over this geologically brief span of their existence, mosasaurs became gigantic, some exceeding 10 m in total body length, and attained a high degree of both taxonomic diversification and aquatic adaptation. The last major reptile lineage to have become fully aquatic during the Mesozoic era, mosasaurs continued to be at the pinnacle of the marine ecosystems until their evolutionary and ecological success came to an abrupt halt, brought about by the end-Cretaceous mass extinction event (Jagt et al., 2008 and references therein).

Mosasaurs are currently known from over 60 nominal species within 30 or more genera, most of which can be assigned to one of the three higher taxa, Mosasaurinae, Halisauromorpha/Halisaurinae, and Russellosaurina (e.g., Bardet et al., 2005; Bell and Polcyn, 2005; Fig. 1-1). This high taxonomic diversity reflects the high morphological disparities among known mosasaurs, particularly in their cranial features (e.g., Russell, 1967; Bell, 1997).

The quadrate morphology, for instance, has long been used to distinguish mosasaurs at the specific or generic level, often in combination with the dermal skull roof morphology involving a frontal and a parietal (e.g., Russell, 1967; Bell, 1997; Konishi and Caldwell, 2007; Konishi, 2008; but see Konishi and Caldwell, 2009). Both general and specific jaw morphology can also characterize different mosasaur taxa. At least three types of rostral projection are known in the upper jaw of mosasaurs, while some mosasaurs lack such a projection altogether (e.g., Bell, 1997:fig. 5). The size of the jaws in proportion to the skull also varies in mosasaurs: some possess a blunt muzzle (e.g., *Prognathodon*), some exhibit a highly slender and elongate one (e.g., *Ectenosaurus*), and yet many others show an intermediate condition (e.g., *Mosasaurus*). The preceeding character also seems to correlate well with the marginal tooth count in mosasaurs. Using the same genera, *Prognathodon* had 12–13 maxillary teeth, *Ectenosaurus* possessed 17, and *Mosasaurus* exhibited 13–15 such teeth (Russell, 1967; Schulp, 2006a; Schulp et al., 2008). As a notable exception to this normal range of tooth count in mosasaurs, *Pluridens walkeri* from western Africa possessed at least 28 dentary teeth, "at least one and a half times the number of (dentary) teeth" of any other mosasaur taxon known to date (Lingham-Soliar, 1998:709).

In addition to the tooth count, various dental morphologies occurred in mosasaurs as well. In certain taxa, the teeth were highly bulbous, implying durophagous food habits (e.g., *Globidens*, *Carinodens*, and *Igdamanosaurus*), some had conical teeth for opportunistic food habits including piscivory (e.g., plioplatecarpines and tylosaurines), and yet others exhibited a marginal dentition somewhat intermediate in morphology between those two types (e.g., *Prognathodon*) (e.g., Russell, 1967; Lingham-Soliar, 1991; Schulp, 2006a, c).

At least one direct piece of evidence of tooth type and prey item association can be derived from a large specimen of *Tylosaurus*, found in the early Campanian strata of South Dakota. The specimen was preserved with its gastric contents that contained remains of a small plioplatecarpine mosasaur, a large bony fish (*Bananogmius evolutus*), a shark (cf. *Cretolamna* or *Lamna*), and a diving bird (*Hesperornis* sp.) (Martin and Bjork, 1987). The wide range of ingested prey items by this individual mosasaur implies that *Tylosaurus* was an opportunistic predator, and its dentition was capable of effectively handling prey items of various hardnesses and sizes. As all of these prey vertebrates must have been agile swimmers, one can infer that *Tylosaurus* was an active hunter despite its enormous size.

In stark contrast to the cranial morphology, the postcrania in mosasaurs exhibited a much smaller degree of morphological variation, most probably as a result of the common, stringent evolutionary and physical constraints they continuously experienced as large, fully aquatic organisms (e.g., Motani, 2005; Lindgren et al., 2007). In Williston's (1898:pl. LXXII) skeletal recostruction of the three most common mosasaur genera found in the Niobrara Chalk in western Kansas, it is evident that their postcrania closely resemble one another, exhibiting an elongate torso and a tail with four paddles. Cranially, on the other hand, they each exhibit one of the three jaw types mentioned earlier (Fig. 1-2). The three genera also differ in their body size as well as represent different subfamilies, illustrating that a similar selective pressure was being applied to different groups of mosasaurs so as to converge on a similar overall postcranial body form. A prime example of this may be seen in the genus *Prognathodon*. While possessing a heavily-constructed skull and lower jaws (e.g., Christiansen and Bonde, 2002; Schulp, 2006a), their postcranium was not robust in any noticeable respect and probably resembled that of *Clidastes* in overall proportions (Schulp, 2006b; pers. observ.; cf. Fig. 1-1).

Nevertheless, it has been suggested recently that postcranial modifications toward a fish-like body form had occurred in at least one lineage of mosasaurs. According to Lindgren et al. (2007), the derived mosasaurine mosasaur *Plotosaurus* from middle Maastrichtian strata of California exhibited a deep, piscine body form in contrast to an elongate, lizard-like body-plan that was retained in most other members of mosasaurs. Lindgren et al. (2007) linked this novel postcranial morphology in *Plotosaurus* to adaptations toward pelagic environments, suggesting that *Plotosaurus* was a tail-propelled swimmer and was likely capable of sustained cruising as in modern cetaceans. Although Motani (2005) pointed out that experiments had yet to establish the notion that a stiffer body yields more efficient cruising in aquatic animals, Lindgren et al. (2007) used shortened vertebrae, less-curved and enlarged central articulation surfaces, and steeply inclined zygapophyseal facets (in the anterior trunk region) to support the stiffening of the vertebral column in *Plotosaurus*. Lindgren et al. (2007) then combined these precaudal features with the semilunate tail, which they also identified in *Plotosaurus*, to conclude that the mosasaur employed an oscillatory (= tail-propelling), rather than anguilliform or carangiform (= body-undulating), swimming style closely comparable to that of extant, pelagic vertebrates exemplified by whales and dolphins.

While Lindgren et al.'s (2007) reconstruction of a fish-like body form in *Plotosaurus* was significant, as they identified a new major adaptive change in the axial skeleton of a mosasaur, mosasaurs in a traditional/pre-cladistic sense (e.g., Williston, 1898; Camp, 1923; Russell, 1967) were all considered to have possessed well-developed paddles that indicated their high degree of aquatic adaptation in the appendicular skeleton. However, most of the recent phylogenetic analyses of mosasauroids that included both ‘traditional’ (i.e., paddled) mosasaurs and semiaquatic ‘aigialosaurs’ have repeatedly suggested that mosasaurs are either paraphyletic (Bell, 1993, 1997) or polyphyletic (e.g., Bell and Polcyn, 2005; Polcyn and Bell, 2005; Dutchak and Caldwell, 2006; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009), unless some or all known non-paddled mosasauroids (i.e., ‘aigialosaurs’) were included (Fig. 1-1). In particular, these phylogenetic hypotheses indicated that paddle-like appendages evolved on multiple occasions within mosasauroids; thus, such a feature could no longer be deemed a synapomorphy uniting mosasaurs or the Mosasauridae (Dutchak, 2005).

Whereas Caldwell and Palci (2007) criticized Bell and Polcyn (2005) for failing to re-diagnose the family Mosasauridae sensu Williston (1898), who had diagnosed the family to possess paddles, Dutchak and Caldwell (2009) suggested that “the lack of consensus among the numerous analyses in the recent literature” on mosasauroid interrelationships, and “the plasticity of the systematic results” of their own study would make such a large-scale taxonomic revision premature (p. 447). As an example, according to one of Dutchak and Caldwell’s (2009) analyses, *Halisaurus*—a mosasauroid that clearly possesses paddles and thus has been considered to be a ‘mosasaur’—was grouped with two limbed mosasauroids *Komensaurus* and *Haasiasaurus*, together forming a sister clade to all the other mosasauroids, including limbed *Aigialosaurus* (Fig. 1-1). According to Bell and Polcyn (2005) on the other hand, *Aigialosaurus bucchichi* and *A. dalmaticus* were successive sister taxa to the other mosasauroids, in part of which *Haasisaurus* was sister to the clade ((*Komensaurus* (*Halisaurus*)) (Russellosaurina)).

Because of this high instability in mosasauroid ingroup relationships among different studies within the last five years, and concurring with Dutchak and Caldwell's (2009) suggestions, throughout this volme the terms Mosasauridae, mosasaurid(s), and mosasaur(s) will be used synonymously to mean (a) paddled mosasauroids following Williston (1898) and Camp's (1923) diagnoses provided for the family Mosasauridae.

## INTRODUCTION TO THE THESIS

In order for the aforementioned ingroup relationships of mosasauroids to be resolved, it is of paramount importance that ingroup relationships for each of the constituent taxonomic units be rigorously examined and resolved as well. Ever since the first most comprehensive cladistic analysis on mosasauroids was performed by Bell (1993), the tribe Plioplatecarpini Russell, 1967, has been a problematic taxon for the following two main reasons: (1) *Platecarpus* has been consistently recovered as paraphyletic/polyphyletic; and (2) the phylogenetic position of *Ectenosaurus* had been unstable by becoming basal to different groups of mosasaurs (e.g., Caldwell, 2000; Dutchak and Caldwell, 2009). In addition, the genus *Plioplatecarpus* was never fully incorporated into any testable phylogenetic analyses, lacking the European species including the generic type *P. marshi* (e.g., Bell, 1997; Cuthbertson et al., 2007).

In order to resolve these phylogenetic uncertainties concerning plioplatecarpine mosasaurs, I have undertaken a global systematic survey of the group by examining over 400 specimens of known plioplatecarpine taxa collected in North America and Western Europe. The following sections provide brief introductions to the four chapters that follow (Note: although the first-person singular form is not used in those four chapters, each chapter constitutes my original work).

## Introduction to Chapter Two

*Platecarpus* Cope, 1869, had long been in a state of major taxonomic flux. In particular, *Platecarpus planifrons* (Cope, 1874) was considered invalid by Russell (1967), and although Bell (1993) recognized its validity, only three diagnostic characters were provided without redescription of either the holotype or any other referable specimen of this species. In this chapter, *P. planifrons* is formally re-established, supported by the new diagnosis based on descriptions and comparisons of three specimens, one of which also represents one of the best-preserved mosasaur skulls ever collected. According to the newly revised diagnosis of the species, the alpha-level taxonomy of the genus *Platecarpus* Cope, 1869 is also reviewed.

## Introduction to Chapter Three

A critical review of initial characterizations of *Plioplatecarpus nichollsae* Cuthbertson et al., 2007, is provided in this chapter, based mainly on a particularly well-preserved specimen referable to the taxon, and a species-level taxonomy of *Plioplatecarpus* is discussed including the new species. Re-characterization of *P. nichollsae* permits some reliable comparisons with both *Platecarpus* and the other, formerly known species of *Plioplatecarpus*. Such comparisons reinforce the basic notion of Cuthbertson et al. (2007) that the taxon exhibits a suite of characters that either diagnose *Platecarpus*, *Plioplatecarpus*, or this taxon exclusively (= autapomorphies). While many of Cuthbertson et al.'s (2007) characterizations of *Platecarpus* and *Plioplatecarpus* are revised in this chapter, the current study also identifies new synapomorphies uniting all the members of *Plioplatecarpus* including *P. nichollsae* amongst plioplatecarpines. It is concluded that *P. nichollsae* shares more derived characters with *Plioplatecarpus* than does *Platecarpus*, yet its 'morphological intermediacy' between those two taxa is also pointed out. Along with its stratigraphic position between *Platecarpus* and the other *Plioplatecarpus* species, it is consequently proposed that *Plioplatecarpus nichollsae* likely represents an evolutionary link between *Platecarpus* and the other members of *Plioplatecarpus*, regardless of its current generic identity. No further systematic revisions are proposed in this chapter however, as this constitutes the main focus of the following chapter along with the novel global phylogenetic analyses of plioplatecarpine mosasaurs, incorporating the new morphological data obtained in the last and current chapters.

## Introduction to Chapter Four

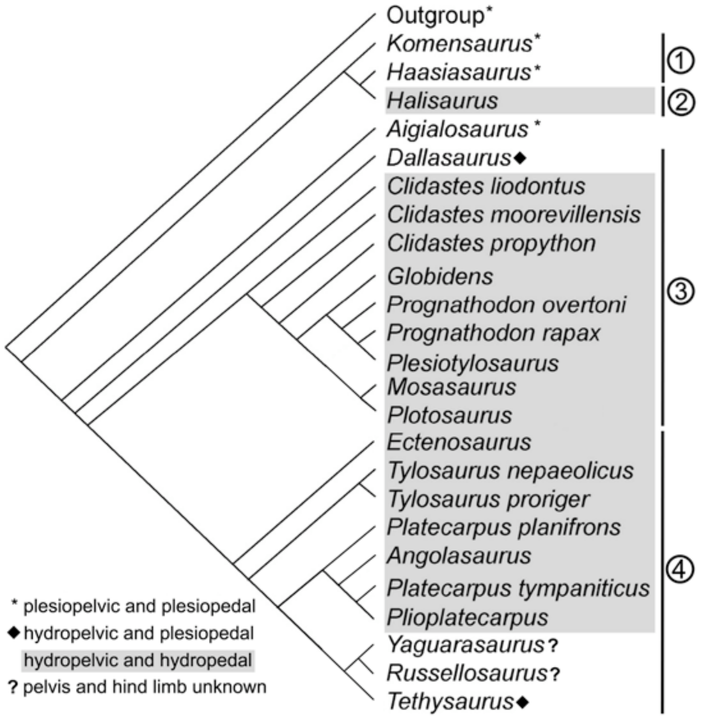
This chapter revisits the taxonomic issue raised in Chapter Two, where it is proposed that the type and only specimen of *Platecarpus tympaniticus* Cope, 1869, a generic type, may not be diagnosable enough to be considered as a senior synonym of any other congener. Through re-examination and detailed redescription of the fragmentary holotype material, however, it is here concluded that the specimen shares a few key diagnostic features with *Platecarpus ictericus* Cope, 1870, to the exclusion of all the other known plioplatecarpine species, and it is consequently proposed that *P. tympaniticus* is a senior synonym of *P. ictericus*. As *Platecarpus planifrons* is now recognized under a different genus, *Platecarpus* becomes a monotypic taxon. However, some specimens referred to *P. tympaniticus* in this chapter may in future prove to belong to (a) separate species of this common mosasaur genus.

## Introduction to Chapter Five

This chapter first describes a new form of plioplatecarpine mosasaur from lower middle Campanian strata of the Western Interior Basin, North America, and refers it to a new genus *Latoplatecarpus*. A series of global phylogenetic analyses of plioplatecarpines is then undertaken to examine their ingroup relationships, by scoring 97 characters against 19 taxa, which includes 11 nominal and one referred plioplatecarpine species. Based on the resultant tree topologies, character distribution, and geographic and temporal distribution among the plioplatecarpines, the following taxonomic revisions are suggested: (1)

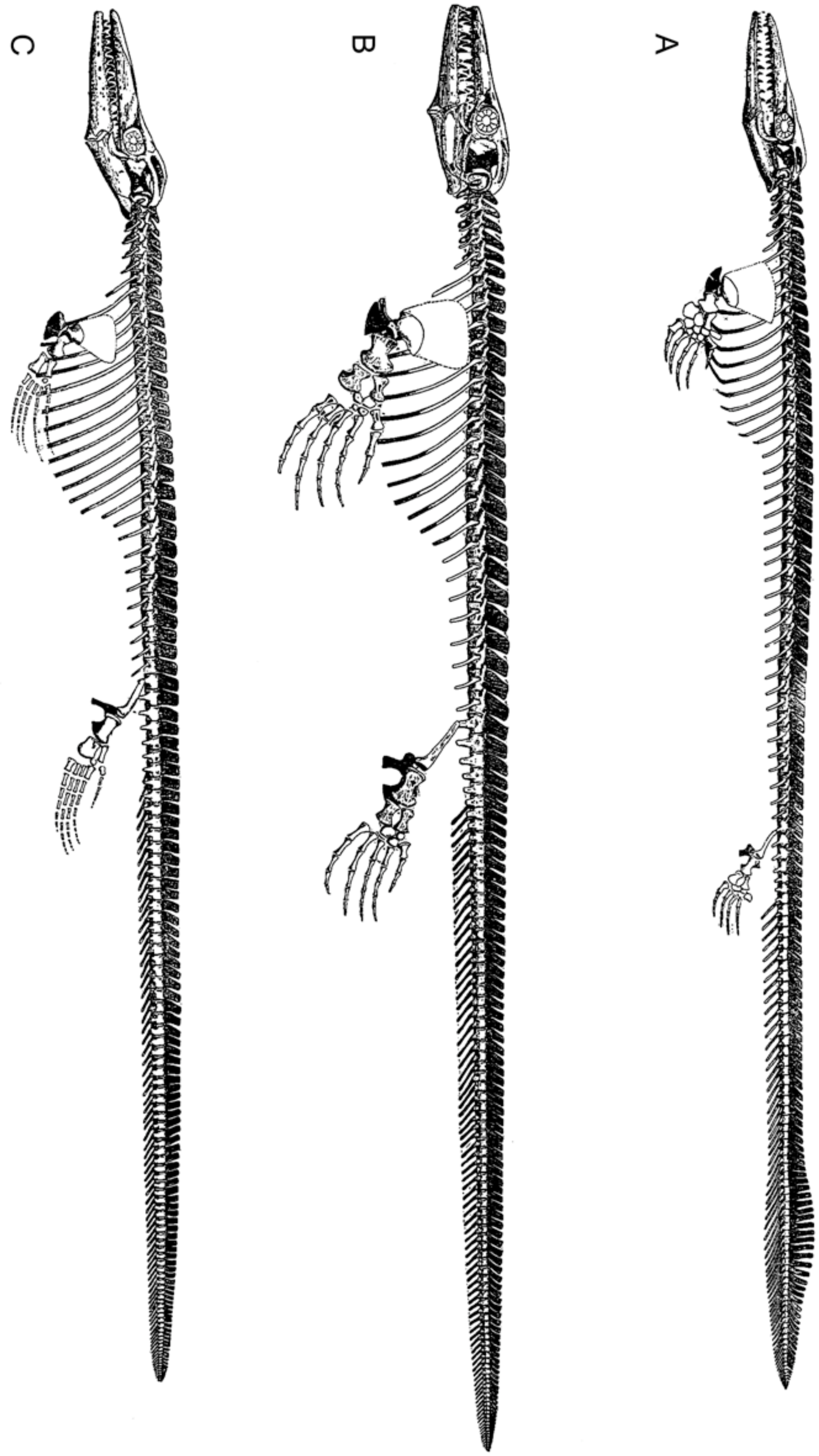
establishment of *Plesioplatecarpus* gen. nov. and *Plesioplatecarpus planifrons* (Cope, 1874) (new combination); (2) assignment of the North American specimens thus far referred to as *Platecarpus* sp., cf. *P. somenensis* to *Plioplatecarpus nichollsae* Cuthbertson et al., 2007; and (3) re-assignment of *Plioplatecarpus nichollsae* Cuthbertson et al., 2007 to *Latoplatecarpus* gen. nov. as *Latoplatecarpus nichollsae* (Cuthbertson et al., 2007) (new combination). These systematic revisions result in generation of four monotypic plioplatecarpine genera, but further investigations are expected to recognize increased alpha-level diversity within each of these genera, as Bell (1993, 1997) had suggested for the genus *Ectenosaurus*. Based on the preferred interrelationships among these mosasaurs, the clade Plioplatecarpinae is defined and re-diagnosed.

FIGURE 1-1. Large-scale interrelationships among mosasauroids after Dutchak and Caldwell (2009), with distribution of three types of pelvic and hind limb anatomy sensu Caldwell and Palci (2007) among constituent taxa. Here, the Mosasauridae sensu Bell and Polcyn (2005) are polyphyletic. In addition, if plesiopedal condition in *Tethysaurus* was retained from its last common ancestor with *Dallasaurus*, a paddle-like limb (hydropedal as well as hydropelvic condition, shaded grey) among mosasaurids evolved at least five times. If *Tethysaurus* regained the plesiopedality from its hydropedal ancestor, paddle-like limbs evolved twice, once in *Halisaurus* and once in the last common ancester between Mosasaurinae and Russellosaurina.



① + ② Halisauromorpha + ③ Mosasaurinae + ④ Russellosaurina = Mosasauridae (sensu Bell and Polcyn, 2005)

FIGURE 1-2. Skeletal restorations of three mosasaur genera commonly found in the Niobrara Chalk of west-central Kansas, USA, modified from Williston (1898:pl. VXXII). **A**, *Clidastes liodontus*; **B**, *Platecarpus tympaniticus*; **C**, *Tylosaurus proriger*. Their respective total body lengths are approximately 3.5 m, 6.5 m, and 9–10 m (Russell, 1967; pers. observ.).


A
B
C

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# CHAPTER TWO

# NEW SPECIMENS OF *PLATECARPUS PLANIFRONS* (COPE, 1874) (SQUAMATA: MOSASAURIDAE) AND A REVISED TAXONOMY OF THE GENUS

A nearly identical version of this chapter was published as: 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.

# INTRODUCTION

The mosasaur genus *Platecarpus* is very well known from the Late Cretaceous Western Interior Seaway in North America. In terms of paleobiogeography, the various species range from the southern extent of the seaway (e.g., Alabama and Mississippi) to the most northern part in the North West Territories, Canada (Nicholls and Russell, 1990). However, the greatest concentration, literally thousands of specimens, is found in the Smoky Hill Chalk Member of the Niobrara Chalk Formation in Kansas (e.g., Williston, 1914; Russell, 1967; Everhart, 2001). The Smoky Hill Chalk Member ranges in age from the upper Coniacian to the lower Campanian, is the upper most member of the Niobrara Chalk Formation and conformably overlies the lower member, the Fort Hays Limestone (Hattin, 1982).

Williston (1897) proposed the first biostratigraphic subdivisions for the Smoky Hill Chalk Member when he divided the unit into the lower *Rudistes* Beds and the upper *Hesperornis* Beds. Russell (1967) used these same concepts when he divided the Niobrara mosasaurs into lower and upper groups within the Smoky Hill Chalk Member. Most recently, Everhart (2001) used Hattin's (1982) 23 marker units as stratigraphic reference points to revise and improve the accuracy of the taxon range zones for three Kansas mosasaur genera: *Clidastes, Tylosaurus*, and *Platecarpus*. Although Russell (1967) placed *Platecarpus coryphaeus* in the 'lower' and *P. ictericus* in the 'upper' group within the member, not all subsequent workers (Nicholls, 1988; Bell, 1993; 1997; Schumacher, 1993; Sheldon, 1996; Everhart, 2001; Bell and Polcyn, 2005; Polcyn and Bell, 2005a) recognized the validity of these two species, and synonymized them with the type species, *P. tympaniticus* (Eutaw Formation, Mississippi). Thus the stratigraphic range for this species was extended from the bottom to the top of the Smoky Hill Chalk Member (Schumacher, 1993; Everhart, 2001). In addition to *P. tympaniticus*, these later workers added *P. planifrons* (Cope, 1874) to their biostratigraphic columns even though Russell (1967) considered it to be nomen vanum. According to Everhart (2001), *P. planifrons* ranges from the bottom of the Member up to Marker Unit 7 of Hattin (1982). The age of this range zone is upper Coniacian to lower Santonian.

In 1973 and 1976 the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) collected a substantial number of Niobrara Chalk vertebrate specimens on the south side of the Smoky Hill River along Sand Creek in southeastern Gove County, Kansas (Fig. 2-1). Among the vertebrate fossils of significance to this study are two well-preserved *Platecarpus* specimens, UALVP 24240 and 40402. UALVP 24240, collected in 1976, is a superbly preserved skull, while UALVP 40402, collected in 1973, is a less complete and slightly disarticulated skull and four anterior cervical vertebrae.

In this study, we re-diagnose *Platecarpus planifrons* as a valid species of mosasaur (see Cope, 1874 vs. Russell, 1967). We recharacterize the holotype specimen (AMNH 1491), and describe and assign UALVP 24240, 40402, and YPM 40508 to the species. Finally, we discuss the implications of this new diagnosis in terms of the current species taxonomy of *Platecarpus*.

**Institutional Abbreviations**—**AMNH**, American Museum of Natural History, New York, New York; **ANSP**, The Academy of Natural Sciences, Philadelphia, Pennsylvania; **CMN**, Canadian Museum of Nature, Ottawa, Ontario; **FHSM**, Fort Hays Sternberg Museum, Hays, Kansas; **KU**, The University of Kansas Natural History Museum, Lawrence, Kansas; **RSM P**, Royal Saskatchewan Museum, Regina, Saskatchewan; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta; **YPM**, Yale University Peabody Museum of Natural History, New Haven, Connecticut.

## MATERIALS AND METHODS

The two specimens, UALVP 24240 and 40402 were photographed using a Nikon D-100 digital camera, while YPM 40508 was photographed using a Nikon COOLPIX 4500. Photographs were traced using Adobe Photoshop 7.0 for Macintosh/Windows to create line drawings, some of which were then hand-stippled and then scanned back into Adobe Photoshop.

## SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Linnaeus, 1758

Order SQUAMATA Oppel, 1811

Family MOSASAURIDAE Gervais, 1852

Parafamily RUSSELLOSAURINA Bell and Polcyn, 2005

Genus *PLATECARPUS* Cope, 1869

**Generic Type**—*PLATECARPUS TYMPANITICUS* Cope, 1869.

**Holotype**—ANSP 8484, 8487–88, 8491, 8558–59, 8562, all from one individual, includes a partial left surangular, right quadrate, partial right pterygoid, anterior dorsal vertebra, two cervical vertebrae, and partial basioccipital-basisphenoid complex. ANSP 8491, the partial right pterygoid, is currently missing.

**Type Locality and Horizon**—From "a greenish sandstone" (Leidy, 1865:35) of the Eutaw Formation, near Columbus, Mississippi, USA. The stratigraphic range is upper Santonian or lower Campanian (Kiernan, 2002).

**Revised Diagnosis**—Small predental rostrum of premaxilla may or may not be present; up to 12 maxillary teeth; posterior termination of maxillary-premaxillary suture between second and third maxillary tooth; prefrontal forms posterior one third of lateral border of external naris; incipient supraorbital process on prefrontal; lateral margin of frontal gently curved in preorbital region; lateral borders of frontal converge anterior to orbits; frontal forms median notch to receive anterior portion of parietal table; lateral margins of parietal table form narrow parietal crest anterior to divergence of suspensorial rami; 10 or more pterygoid teeth; ectopterygoid process projects anterolaterally from dentigerous body of pterygoid; posteroventral process of jugal present; suprastapedial process of quadrate elongate (more than two-thirds total quadrate height); supra- and infrastapedial processes unfused; large, vertically elongate stapedial pit; elongate, parallel-sided stapedial notch; mandibular condyle gently convex, transversally wide; small ventral opening for basilar artery between basioccipital and basisphenoid; 11 to 12 teeth in dentary; retroarticular process rounded with large foramina on ventral surface; marginal teeth recurved, and possess anterior and posterior carinae, lingual striations and labial facets; 29 presacral vertebrae, 5 pygals, 91–96 caudals; three ossified tarsals.

### *PLATECARPUS PLANIFRONS* (Cope, 1874)

(Figs. 2-2–2-6)

*Clidastes planifrons* Cope, 1874:31.

*Platecarpus planifrons* Williston, 1898:188.

**Holotype**—AMNH 1491, incomplete cranial and postcranial elements, consisting of frontal, right pterygoid, quadrates, parietal, left postorbitofrontal, left squamosal, left splenial, left angular, left surangular, left coronoid, basisphenoid-basioccipital, fifteen anterior vertebrae including atlas-axis, and other miscellaneous bone fragments.

**Type Locality and Horizon**—Seven miles southeast (“southwest” according to the AMNH specimen label, which is likely mistaken: Everhart, pers. comm.) of Castle Rock, Trego County, Kansas, USA, from the lower part of the Smoky Hill Chalk Member, Niobrara Chalk Formation, upper Coniacian or lower Santonian (Everhart, 2001).

**Referred Material, Locality and Horizon**—UALVP 24240 (Figs. 2-2, 2-3), articulated skull, lower jaws, atlas and axis; UALVP 40402 (Fig. 2-4), disarticulated skull and lower jaw bones with four anterior cervical vertebrae; YPM 40508 (Figs. 2-5, 2-6), disarticulated and fragmentary cranial and postcranial material including premaxilla, left maxilla, nearly complete frontal, right jugal, ectopterygoid(?), pterygoids, left squamosal, left quadrate, lower jaw fragments, several vertebrae, and phalanges. UALVP 24240 and 40402 collected from the southeast corner of Gove County (coordinates: T15S R26W), on the west side of Sand Creek, Smoky Hill River, west-central Kansas, USA (Fig. 2-1A, C). The horizon is either upper Coniacian or lower Santonian (Everhart, 2001). YPM 40508 comes from Trego County (coordinates: T11, R21), Kansas, USA (Fig. 2-1B), horizon is upper Coniacian or lower Santonian (Everhart, 2001).

**Revised diagnosis**—Thin, elongate septomaxillae forming floor of posterior half of narial chamber; prefrontal and postorbitofrontal not contacting above orbit; dorsal surface of frontal planar, no supraorbital bulge; dorsal median keel of frontal absent; frontal preorbital width greater than interorbital width; frontal with paired posteromedian flanges; parietal foramen enclosed within parietal table; parietal table short; 10 to 15 pterygoid teeth; anterodorsal border of quadrate with distinct posterior notch; distal end of suprastapedial process tapering medially; stapedial pit narrow, keyhole shaped; thin, well-defined vertical crest on medial face of quadrate shaft; retroarticular process drawn out posteromedially.

## DESCRIPTION: UALVP 24240

UALVP 24240 is an exceptionally well-preserved skull. Each cranial element is well preserved and has undergone little or no plastic deformation. Despite its large size, most of the cranial sutures are not co-ossified, thus allowing for more accurate identification and description of each bone element.

### Skull

**Premaxilla**—The premaxilla is anteriorly rounded in dorsal view (Fig. 2-2). The profile of the dentigerous portion of the premaxilla is comparable to that of Bell (1997:fig. 5A), in which the anterior surface of the bone ascends vertically from the dental margin for a short distance and then gradually recedes posterodorsally. Two premaxillary teeth are present on each side. There is no rostrum anterior to the tooth margin (Fig. 2-3). Dorsally, there are two parallel rows of foramina that are not mirror images of each other. The posterior termination of the premaxillo-maxillary suture is at a point above the third maxillary tooth.

The frontal process of the premaxilla, or internarial bar, resembles an elongate hourglass-shape in dorsal view. The bar thins at its midpoint where it forms the medial borders of the external nares and is widest at the contacts with the frontal and maxillae. In cross section, internarial portion of the bar forms an inverted triangle (see Bell [1997]).

**Maxilla**—The maxilla is deepest above the third maxillary tooth (Fig. 2-2). The portion of the maxilla that is dorsally bound by the premaxilla is wedge-shaped, with a slightly convex dorsal border and a straight, horizontal dental margin. At the anterior extremity, however, the posterior border of this wedge descends almost vertically, thereby making the profile slightly rectangular. Posteriorly, the maxilla contacts the prefrontal along a sigmoidal suture; two thirds of the lateral margin of the external naris is bordered by the maxilla. The maxilla thickens medioventrally where it forms the lateral wall and floor of the narial chamber and contacts the septomaxilla and palatine (Figs. 2-2, 2-3). The exits for the fifth cranial nerve run parallel to the dental margin and are not symmetrical right to left. There are 12 marginal teeth on the maxilla, with the last two being slightly smaller. A number of posterolingually positioned replacement teeth are also preserved along the dental groove. Posterior to the last marginal tooth the maxilla ends in an edentulous, acute triangular process equal to the length of the last alveolus.

**Frontal**—The frontal bone is well preserved (Fig. 2-2). Anteriorly, the premaxillary processes form a narrow, 'V-shaped notch' (Russell, 1967:19); posteriorly the frontal expands into an hour-glass shaped element, the constriction of which results from deep supraorbital embayments. The frontal is widest posteriorly forming gently-rounded right and left alae at the posterolateral corners.

In UALVP 24240, the median dorsal ridge of the frontal is weakly expressed as a gentle mid-sagittal bulge. In addition, the frontal table is uniformly planar, exhibiting no bulging above the orbital region as seen in many *Platecarpus* specimens that also possess a well-developed median dorsal ridge (e.g., AMNH 1820). The dorsal surface of the frontal table bears numerous small foramina as well as short straight radiating grooves. The ventral surface of the frontal is largely obscured by the parasphenoid and pterygoids, although the crest that contacts the posterior border of the prefrontal is visible (Fig. 2-3).

**Prefrontal**—Both right and left prefrontals are complete (Fig. 2-2). The lateral surface is slightly concave, gradually flattening anteriorly toward the sutural line with the maxilla. Anteromedially, the flattened lamina forms approximately the posterior one third of the lateral margin of the external naris. A small, rounded supraorbital process is present and exposed on the left side.

**Parietal**—The parietal is well preserved although it is broken into two pieces (Fig. 2-2). The parietal foramen, located within the parietal, is relatively large and nearly circular in outline. The divergent suspensorial rami create a 90-degree angle. They are both incomplete distally but the right is slightly better preserved. Along the mid-sagittal line and between the suspensorial rami, the dorsal surface of the parietal is shallowly sulcate. The articulations for the postorbitofrontals (postorbital processes) are complete on both sides and project laterally from the parietal table but do not reach the posterolateral corners of the frontal.

**Postorbitofrontal**—The postorbitofrontals are both displaced and overturned (Figs. 2-2, 2-3). On the right side, the anterior portion of the ventral surface is relatively smooth and planar. The short, ventrally directed jugal process bears a medially-facing articulating facet for the jugal. The posteriorly-directed squamosal ramus bears a grooved articular facet for the squamosal along its ventral surface. Dorsally, the main body of the left element possesses a large semicircular articulating facet for the left frontal ala.

**Jugal**—Both right and left jugals are well preserved, although portions of the anterior-most part of the horizontal rami are missing (Figs. 2-2, 2-3). Even so, the horizontal ramus is nearly 2.5 times longer than the vertical ramus. The posteroventral process on the jugal forms a strong posterior ‘keel’ (cf. Russell, 1967:figs. 37 and 38). Immediately anterior to the posteroventral process, on the medial surface of the right jugal, is the articular facet for the ectopterygoid. The jugal exhibits a sulcate, elongated articular facet for the maxilla; this facet runs anteriorly about half the length of the horizontal ramus. On the left jugal, the postorbitofrontal process is hook-shaped and possesses an anterolaterally-facing facet for the postorbitofrontal.

**Ectopterygoid**—Both right and left ectopterygoids are preserved on UALVP 24240 (Figs. 2-2, 2-3). The bone is small and L-shaped. According to Russell (1967), the medial ramus articulates with the ectopterygoid process of the pterygoid, and the slender anterior ramus articulates with the ventromedial surface of the jugal. The left ectopterygoid is in contact with the left jugal though displaced from its proper articulation. The element appears undistorted, and a longitudinal groove separates two smooth surfaced ‘wings’; the outer surfaces are highly rugose.

**Pterygoid**—Both the pterygoids are nearly perfectly preserved (Figs. 2-2, 2-3); on the right, there are 10 recurved teeth/tooth positions, each of which is half of the size of a maxillary tooth. The teeth are larger toward the middle of the row, gradually decreasing in diameter toward the extremities. In contrast to the maxillary teeth, the replacement teeth erupt from the posterolateral (labial) corner of each alveolus. Posteriorly, the pterygoid extends a long wing-like process to the quadrate. Medial to the quadrate process of the pterygoid there is a tongue-like, shorter basisphenoid process cupping the ventral portion of basipterygoid process of the basisphenoid. The anteriormost extension of the pterygoid is well defined by a broad, oblique sutural contact with both the palatine and vomer. At about the middle of the bone, the ectopterygoid process, abruptly projects laterally and slightly anteriorly. Laterally, the facets for the ectopterygoid are oriented somewhat ventrally. The body of the pterygoid is transversally widest where it shows the most lateral curvature. The medial border is nearly straight. At the midline, the two pterygoids are at least 2 cm apart, forming the incisura piriformis.

**Epipterygoid**—Only the left epipterygoid is visible and is located near the anterolateral side of the left descending ramus of the parietal (Fig. 2-2). The bone is a thin, rod-like element, the proximal end of which is rounded and finely grooved. These grooves suggest the presence in life of a proximal cartilaginous cap. The flattened distal end is slightly expanded.

**Palatine and Vomer**—The well-preserved right palatine is still in articulation with the pterygoid, maxilla, and vomer (Fig. 2-3). Russell (1967) stated that the pterygoid-palatine contact is very rarely preserved in mosasaurs; however, in UALVP 24240, the right pterygoid is anteriorly firmly attached to the palatine along an obvious anteromedial-posterolateral suture line. Further, UALVP 24240 clearly demonstrates that the slender, elongate vomer contacts the palatine laterally and the pterygoid medially. The thin anterior process from the palatine body overlaps the vomer from the posterolateral side, while a similar process from the pterygoid extends anteriorly to medially overlap the vomer. Russell (1967) states that in *Platecarpus*, the vomers "cannot surely be distinguished from the vomerine process (of the palatine)" (p. 25). Holmes (1996) estimates the palatine-vomer suture in *Plioplatecarpus primaevus* to be at about the level of the fifth maxillary tooth. On the contrary, UALVP 24240 indicates that what has been referred to as the vomerine process (Russell, 1967) or vomerine bar (Holmes, 1996) of the palatine is for the most part the vomer proper with the palatine constituting merely its posterolateral corner dorsally.

While the lateral border of the vomerine process is nearly straight, the medial border is slightly curved inward and posteriorly continuous with the medial border of the pterygoid. Posteriorly, the vomerine process runs parallel to the septomaxilla; anteriorly, it extends beyond the posterior termination of the premaxillo-maxillary suture (Fig. 2-2).

The contact between the vomer and pterygoid on UALVP 24240 is both anatomically and evolutionarily of great importance as no other squamates, including other mosasaurs, are known to possess a contact between those two elements (Romer, 1956). The vomer-pterygoid contact of *Platecarpus* is present in basal lepidosaurs such as *Sphenodon* (Romer, 1956). Such a primitive palatal configuration in *Platecarpus* is intriguing and problematic because it hints at a much more complex phylogenetic history for not just mosasaurs, but all squamates.

**Septomaxilla**—The right and left septomaxillae are very well-preserved (Figs. 2-2, 2-3). Anteriorly, the element begins between the fifth and sixth maxillary tooth and ends posteriorly at the ninth tooth with a slender process inserting into the anterior ‘notch’ of the palatine. The ‘floor’ of the anterior portion of the nasal vestibule is open between the maxilla and the vomerine process. It is after the fifth maxillary tooth where the septomaxilla forms a delicate, gently concave surface with raised lateral and medial walls. In dorsal aspect, the septomaxillae extend posteriorly to the level of the base of the anterior processes of the frontal.

According to Holmes (1996), there is a robust, shield-shaped septomaxilla preserved on one specimen of *Plioplatecarpus primaevus* (RSM P1756. 1). It is described as forming the floor of the anterior part of the nasal vestibule with the maxilla (Holmes, 1996:cf. fig. 2A). In addition to *Plioplatecarpus* (Holmes, 1996), elongate strap-like septomaxillae in mosasaurs have been noted in *Plotosaurus* (Camp, 1942), possibly in *Tylosaurus* (Merriam, 1894; Huene, 1910), and again with some uncertainty, in YPM 40383 (Bell, 2005), a basal mosasauroid. UALVP 24240 provides the first evidence of septomaxillae in *Platecarpus*.

**Squamosal**—The squamosals are displaced and broken on both sides, and only parts of the postorbital processes are preserved (Fig. 2-2). The anterior extremities were either lost postmortem, or are concealed by overlying bones.

The morphology of the articulation with the quadrate and supratemporal cannot be determined.

**Quadrate**—Both quadrates are well preserved with the right preserving a complete and very delicate tympanic rim (Figs. 2-2, 2-3). Both quadrates are characterized by their typical mosasauroid C-shaped morphology formed by large supra- and infrastapedial processes. The infrastapedial process arises from the base of the rectangular mandibular condyle. The suprastapedial process and shaft form the margins of a vertically elongate, oblong stapedial notch that is about one third the height of the entire element. The distally tapered suprastapedial process slightly contacts the infrastapedial process.

The anterodorsal edge of the quadrate is strongly notched posteriorly, forming a concave border that continues ventrally to form a depressed area on the upper half of the element; this depressed area is the major insertion site for the quadrate head of the adductor mandibulae externus profundus (Russell, 1967) (Fig. 2-7A–D).

Although the medial surface of the quadrate is incompletely exposed, the stapedial pit is discernable on both sides. This pit is narrow and keyhole-shaped, with a long axis parallel to the quadrate shaft. This distinctive stapedial pit morphology, as well as the posteriorly-notched anterodorsal edge of the quadrate, are present on the left quadrate of the holotype (AMNH 1491), and a number of other specimens assignable to *P. planifrons* (Figs. 2-6B, 2-7A, B, D). These two characters are not found on the quadrate of AMNH 1820, *P. tympaniticus/ictericus* (Fig. 2-7C; see also fig. 25C in Russell, 1967). Despite the completeness of the quadrates, no identifiable extracolumellar elements are preserved.

**Stapes**—UALVP 24240 preserves parts of the right and left stapes (Fig. 2-3). The right stapes is preserved in three parts. The cup-shaped distal extremity of the stapes is on top of the quadrate ramus of the pterygoid, a thin, 10-mm-long portion of the shaft is preserved some distance anterior to the distal portion, and, near the basal tuber, there is a 20-mm-long section of the proximal end of the stapes that is flattened for most of its length, but further expands to a club shape at the proximal end. The left stapes is preserved in two pieces. The probable proximal portion is 15 mm long while the second piece is 27.5 mm long.

The morphological characteristics of the stapes of UALVP 24240 agree with those of the virtually complete stapes of NMC 40914 (*Platecarpus* sp.) and with Text-figure 23A in Russell (1967). Unfortunately, the proximal end of the element in the latter specimen remains inserted deeply into the base of the paroccipital process, obscuring its morphology.

**Prootic**—The articular surfaces of the parietal rami of the prootic are partially exposed as are the laterodorsal surfaces of the suspensorial rami of the prootic (Fig. 1-2). The nearly vertical sutural contact with the supratemporal is observable on both sides, as well as its long lateral contact with the opisthotic. The remainder of the element is not visible.

**Opisthotic-Exoccipital**—The opisthotic and exoccipital are fused in all mosasaurs. As preserved, only a few features of the opisthotic-exoccipital are observable (Fig. 2-2). The paroccipital processes flare out distally, where they also become thinnest and abut the supratemporals. Ventrally, the tongue-shaped, thin sheet of bone sheaths the posterolateral surface of the basal tuber of the basioccipital.

**Supratemporal**—Both relatively small, wedge-shaped supratemporals are preserved (Fig. 2-2). Dorsomedially, the supratemporal sends a thin, elongate process to the parietal, articulates laterally with the distal end of the paroccipital process, and posteriorly with the prootic. On the right supratemporal, a distinct, vertically oriented concavity is present on the posterolateral surface of the element. This concavity is the articulation for the squamosal.

**Basioccipital-Basisphenoid**—Both of the elements are well preserved and readily observable on the ventral side of the specimen (Fig. 2-3). The basal tubera of the basioccipital project ventrolaterally posterior to the posterolateral corners of the basisphenoid; the basioccipital is widest at this point. The anteroventral portion of the basal tuber is covered by the posterolateral ala of the basisphenoid; these alae are separated by a very shallow depression (not by a deep sulcus as postulated for *Platecarpus* cf. *P. somenensis* in Russell [1967]). The ventral portion of the basipterygoid processes of the basisphenoid are enclosed by the basisphenoid processes of the pterygoids. The parasphenoid is broken at its base but is otherwise completely preserved; its styloid, elongate body extends from the anterior part of the basisphenoid. The floor of the basisphenoid gently rises dorsally between the basipterygoid processes. There is no evidence of the parasphenoid ascending nearly vertically as postulated by Polcyn and Bell (2005a) for *Russellosaurus coheni*.

## Lower Jaw

**Dentary**—The dentary bears 12 marginal teeth (Fig. 2-2). Each tooth is bicarinate and curves posteromedially at about the middle height of the crown. The teeth show fine striations without faceting on the lingual side, whereas they show faceting with very faint or no striations on the labial side (cf. Cope, 1875; Nicholls, 1988). All the teeth are nearly equal in size except the twelfth, which is slightly smaller. Resorption pits are present posterolingual to each alveolus. Anteriorly, there is no edentulous prow as the dentary abruptly terminates in front of the first tooth. On the lateral face of the dentary are the foramina for the mandibular branches of the fifth cranial nerve (Fig. 2-3). Medially, the posterior two-thirds of the dentary is covered by the ala of the splenial; the splenial also covers the Meckelian groove for most of its length, although the groove is open at the tip of the dentary. The posterior limit of the dentary and splenial, where they articulate with the postdentary bones, produces the intramandibular joint.

**Splenial**—At the ventral limit of the intramandibular joint, the splenial forms the concave portion of a ball-and-socket joint with the angular (Fig. 2-3). It expands anterodorsally to form a thin ala covering the medial two thirds of the dentary. A large foramen, presumably for the inferior alveolar nerve, is present at the posteroventral corner of the ala. In lateral view, the splenial is only slightly exposed along the posteroventral margin of the dentary. The splenial does not contact the medial margin of the coronoid.

**Angular**—Anteriorly, the angular forms a convex articular facet for articulation with the splenial (Fig. 2-3). Posteriorly, the angular becomes a thin, strap-like element that wraps around the ventral margin of the surangular laterally, and the prearticular medially. The element is slightly shorter than the splenial, and terminates posteriorly as a tongue-shaped sheet of bone.

**Surangular**—The surangular is a robust, elongate element forming most of the lateral surface of the posterior part of the mandible (Figs. 2-2, 2-3). In cross-section, the surangular is crescent-shaped. The anterior half of the surangular articulates with the coronoid, forming a shallow concave dorsal border at that contact. Toward the posterior end, the surangular widens to form a small plateau immediately in front of the glenoid fossa. On the posterolateral corner of the plateau is the foramen for the cutaneous branch of the mandibular nerve. The surangular portion of the glenoid fossa constitutes 20% of the total area of the fossa.

**Coronoid**—The coronoid is a laterally compressed, saddle-shaped element with lateral and medial margins of unequal depth, the lateral margin being much shallower (Figs. 2-2, 2-3). The deeper medial wing would have contacted the dorsal border of the angular; however, the coronoid did not contact the splenial. Russell (1967) used the difference in angle formed between the descending posterior border of the lateral wing and the dorsal border of the surangular, to differentiate *Platecarpus* cf. *P. somenensis* from *P. coryphaeus* and *P. ictericus*. The state of this character cannot be determined for UALVP 24240.

**Articular-Prearticular**—The right retroarticular process preserves the original dorsal orientation of the glenoid fossa, even though the characteristic semi-circular portion of the process is broken and lost (Figs. 2-2, 2-3). The prearticular portion of the presumably fused, articular-prearticular is exposed on the medial side of the surangular; it is a vertically-oriented, thin strap of bone extending across the intramandibular joint and into the cavity between the splenial and dentary. The bone widely contacts the angular and surangular and likely was in contact with the ventral border of the medial wing of the coronoid at its dorsal margin (Russell, 1967:fig. 29). Lateroventrally on the retroarticular process there are two large, closely-spaced, foramina. Dorsally on the right retroarticular process, the foramen for the corda tympani is tentatively identified at the posteromedial corner of the preserved portion of the element, medially adjacent to the glenoid fossa. The articular comprises about 80% of the total area of the glenoid fossa, with the remainder formed by the surangular.

## Vertebrae

**Atlas-Axis**—Although the axis is slightly rotated to the right, all the associated atlas-axis elements are present (Fig. 2-3). In ventral aspect, the atlas intercentrum firmly attaches to the occipital condyle, the latter element being flanked by the paired atlas neural arches ventrally. Each neural arch bears a wing-like posteroventral projection for attachment of cervical ligaments and musculature. The posterior condyle of the axis is a dorsoventrally compressed oval. On the posteroventral surface of the axis, the axis hypapophysis bears a flat, circular articulation for a cervical intercentrum.

## DESCRIPTION: UALVP 40402

UALVP 40402 (Fig. 2-4) is less completely preserved than UALVP 24240, but does show some cranial features not preserved or exposed in UALVP 24240. As well, some characters exhibit important differences from those described for UALVP 24240.

### Skull

**Premaxilla**—The premaxilla is similar to that of UALVP 24240 (Fig. 2-4). The tongue-like posterior process gently bulges dorsally, expanding immediately anterior to the frontal processes. The premaxillo-maxillary suture terminates above the third maxillary tooth. There is no evidence of a predental rostrum.

**Maxilla**—The maxilla is deepest above the third maxillary tooth. There are only 10 maxillary teeth preserved; unfortunately, the posterior process is not well preserved and it cannot be determined if it possessed two extra teeth, although it seems likely. Each tooth crown bears well-developed lateral facets. A single row of maxillary foramina runs parallel to and immediately dorsal to the dental margin.

**Frontal**—The frontal is closely comparable to that of UALVP 24240. For example, the preorbital portion of the frontal table is wider than the interorbital portion (see UALVP 24240). One important difference is the presence of a distinct but very low-relief (< 5 mm) dorsal median ridge that extends posteriorly to the supraorbital embayment. The posterior part is weathered away, its margin being rough and incomplete.

**Parietal**—The parietal possesses a relatively small, circular parietal foramen that is completely enclosed within the parietal table. The suspensorial rami diverge at 90 degrees.

**Jugal**—The right jugal is exposed in lateral view and the posteroventral process is weakly developed.

**Pterygoid**—The right pterygoid preserves nine dental alveoli with/without teeth and is exposed in ventral view. The element has a well-developed, tongue-like basisphenoid process, a partially visible quadrate process, and an anterolaterally projecting ectopterygoid process.

**Postorbitofrontal**—The right postorbitofrontal is preserved in dorsal view. There is a shallow, rounded concavity that received the similarly-shaped posterolateral ala of the frontal. The squamosal process is medially rotated to expose its grooved articulation with the postorbital ramus of the squamosal. The proximal portion of the process is obscured.

**Squamosal**—One elongate element may be attributable to the squamosal.

**Quadrate**—Both quadrates are preserved. Unlike UALVP 24240, the distal end of the suprastapedial process does not taper medially, but rather expands with its distal extremity pointing ventrally. The anterodorsal border of the element is notched posteriorly, forming a shallow V-shaped outline. The element also possesses a delicate tympanic ala that is somewhat more elevated than that of UALVP 24240. The stapedial notch is vertically elongate and oblong in outline, and is about one third of the total height of the quadrate. The articular surface of the mandibular condyle is convex and nearly three times wider than long.

**Opisthotic-Exoccipital and Stapes**—Part of the right opisthotic-exoccipital is present between the right quadrate and the basioccipital. Along the medial concavity of the opisthotic is the shaft of the right stapes, the distal end of which is missing.

**Basioccipital-Basisphenoid**—The overall morphology of the basioccipital-basisphenoid complex is generally similar to that of UALVP 24240 and is visible in ventral view. The occipital tubera mark the widest point of these elements. The posterolateral processes of the basisphenoid, separated by a shallow depression, cover the anteroventral portion of the basal tubera. At the anterior margins of the basisphenoid, thin, wing-like basipterygoid processes project lateroventrally.

## Lower Jaw

**Dentary**—The left dentary is exposed in medial view and is covered posteriorly by the ala of the splenial (Fig. 2-4). Meckel's groove extends to the tip of the dentary, but due to preservation it is difficult to determine if it was open anteriorly. The marginal teeth are finely striated medially, and recurved.

**Splenial**—The left splenial shows the concave articular facet for the condyle of the angular. As in UALVP 24240, there is a large foramen on the medial side at the posteroventral corner of the ala, presumably for the entrance of the inferior alveolar nerve (Russell, 1967).

**Surangular-Articular**—The right surangular and articular are disarticulated from the remainder of the mandibular elements. The retroarticular process bears two foramina on the ventral surface. Forming a gentle arc, the lateral border of the process turns medially toward its distal end, where it meets the straight medial border.

## Vertebrae

**Atlas**—The left atlas neural arch as well as the odontoid (atlas centrum) are preserved though widely separated. Anteriorly the arch bears a smooth, flat, vertically elongate articulation surface for the occipital condyle. The elongate spinous process ascends anterodorsally over the condyle. Around the base of the spinous process is a small knob-like posterior projection, the "synapophyseal process" of Russell (1967:71).

The isolated atlas centrum appears to be completely preserved, but the anterior side of the element is not exposed. The atlas centrum is elevated along the vertical midline on the posterior articular surface, presumably to fit into the anterior concavity of the axis centrum.

**Axis**—The left side of the axis is exposed on UALVP 40402. The blade-like, elaborate spinous process is longer than high. Large, nearly circular postzygapophyses face nearly ventrally and slightly laterally. There is a small excavation on the medial wall of the base of the right postzygapophysis, here interpreted as a zygantrum. The axis intercentrum is missing.

**Third (C3) and Forth (C4) Cervical Vertebrae**—Between the prezygapophyses are a pair of elgongate zygosphenes and the neural arches are diagenetically compressed. The spinous process of C3 is complete and its dorsal end possesses a roughened plateau for the insertion of the spinalis capitis muscle (Russell, 1967). The articular surface of the hypapophysis faces posteroventrally where it articulates with the intercentrum of C4. The postzygapophyses on both vertebrae face ventrolaterally. On the right side of C3 is a small and inconspicuous zygantrum. The cotyle and condyle surfaces are elliptical in outline, and are more wide than high where the original shape is preserved.

## DESCRIPTION: YPM 40508

### Skull

**Premaxilla**—There is no predental rostrum, and the teeth and internarial bar are missing. On the left side of the dentigerous portion of the bone, there is a 2-cm-long scar excavated on the dorsal surface. The element is otherwise very similar to that of UALVP 24240.

**Maxilla**—Only the anterior halves of the maxillae are preserved. The element is deepest above the third marginal tooth, which coincides with the posterior termination of the sutural contact between the premaxilla, similar to the UALVP specimens. The anterior margin is vertical, creating a trapezoidal profile.

**Frontal**—The frontal of YPM 40508 is nearly completely preserved and complements the missing posterior portion of the frontal in UALVP 24240 (Fig. 2-5A, B). The frontal is nearly planar with a small, short median dorsal ridge represented as a slight sagittal bulge. The posterior border is nearly complete, preserving a shallow anterior median excavation between the posteromedian flanges. These flanges slope inward forming a slightly depressed area for the parietal articulations.

Ventrally, the frontal bears a ridge that separates the prefrontal and postorbitofrontal. Anterior to this ridge, the frontal is thin along its lateral margin; around the preorbital area where the frontal is widest, the lateral margin thickens and represents the lateral end of the ventral ridge. An identical pattern of thickening is observed in UALVP 24240 and the type of *P. planifrons*.

The supraorbital embayment of the lateral border is well developed, clearly indicating the greater width through the preorbital region than through the interorbital region. The posterolateral border is complete on the left side, where two smaller posterior projections are preserved laterally and inferiorly to the left posteromedian flange.

**Jugal**—The left jugal is similar to that of UALVP 24240. The posteroventral process is well developed forming a distinct keel. The vertical ramus does not taper dorsally. On the medial side, a shallow, semicircular articulation surface for the ectopterygoid is present anterior to the posteroventral process. The anterior portion of the postorbital process is partially broken as is the anterior one third of the horizontal ramus. The vertical ramus inclines slightly posteriorly at an angle of about 120 degrees.

**Pterygoid**—Both pterygoids are present but incomplete. The partial right pterygoid bears anterolaterally projecting ectopterygoid process. The left pterygoid preserves at least six alveoli anterior to the process; however, the complete number of teeth is unknown.

**Squamosal**—The preserved posterior portion of the left squamosal, approximately half of the postorbital ramus, shows a broad, nearly square articular surface with the supratemporal.

**Quadrate**—The left quadrate is nearly completely preserved (Fig. 2-6). The suprastapedial process is well developed, medially tapers toward the distal tip, and is approximately 70% of the height of the quadrate shaft. The infrastapedial process is weakly developed and does not contact the suprastapedial process. On the medial side, a distinct vertical ridge runs from the stapedial pit to the level of the infrastapedial process, and the stapedial pit is narrow and keyhole shaped. In dorsal view, the anterodorsal border of the quadrate curves posteriorly, forming a ‘notch’ (Fig. 2-7A).

## Lower Jaw

**Dentary**—Only the anterior part of the left dentary, bearing seven tooth positions, is preserved. The ventral portion of the anterior border of the element is incomplete. There is no predental rostrum anterior to the first tooth.

**Postdentary**—The tongue-like posterior end of the angular is sandwiched between the surangular and articular (see Fig. 2-3, UALVP 24240). There are small, but more numerous foramina (five) on the ventral surface of the retroarticular process in comparison with the UALVP specimens. As in UALVP 40402, the lateral border of the retroarticular process gently turns to meet the medial border at its distal end.

### Postcranium

**Vertebrae**—Four cervical vertebrae are preserved, all of which are similar to those of UALVP 40402. At least one of them shows a well-defined pair of zygosphenes. The centrum articulation surfaces are horizontally ellipsoid shaped.

## DISCUSSION AND CONCLUSIONS

### Taxonomy of *Platecarpus*: 1869–Present

*Platecarpus tympaniticus* was first erected by Cope (1869) based on a specimen consisting of a partial basioccipital-basisphenoid, a quadrate, the middle portion of a right pterygoid with teeth, a right humerus (that later turned out to be that of a turtle), several anterior vertebrae, and other bone fragments; these elements had been described and figured by Leidy (1865) as *Holcodus acutidens*, currently a nomen vanum (Russell, 1967) (Fig. 2-8). The specimen was collected near Columbus, Mississippi, USA, most likely from the upper Santonian or lower Campanian of the Eutaw Formation (Leidy, 1865; Kiernan, 2002), and is housed at the Academy of Natural Sciences of Philadelphia, Philadelphia, USA. All the material was considered to belong to a single individual (Leidy, 1865).

Since Cope (1869), nearly a dozen species of *Platecarpus* were erected from fossils found in North America (see Russell [1967] for the complete species list). When Russell (1967) revised the systematics of the mosasaurs of North America, he reduced the total number of *Platecarpus* species by half, retaining *P. tympaniticus* (generic type), *P. ictericus, P. coryphaeus, Platecarpus* cf. *P. somenensis*, and "*Platecarpus*" *intermedius*. Although Russell (1967) synonymized or discarded many names due to the paucity of material and diagnostic characters, he preserved *P. tympaniticus* even though the type is of almost no diagnostic value.

Subsequently, Bell (1993) synonymized *Platecarpus ictericus* and *P. coryphaeus* under *P. tympaniticus*, removed "*Platecarpus*" *intermedius*, and added *P. planifrons*. Bell (1993) also questioned the validity of *Platecarpus* cf. *P. somenensis*, noting that the type specimen from France lacked the diagnostic characters that unite the North American specimens assigned to *P. somenensis*, and suggested that use of the name should be abandoned. This view was maintained, and in all his subsequent work (Bell, 1997; Bell and Polcyn, 2005; Polcyn and Bell, 2005a), only *P. tympaniticus* and *P. planifrons* appear in mosasauroid phylogenies. In the most recent revision of Smoky Hill Chalk mosasaur biostratigraphy, Everhart (2001) followed Bell's (1997) classification scheme for the genus.

## Species Diagnoses

***Platecarpus tympaniticus*** **Cope, 1869**—As mentioned previously, Russell (1967) retained this taxon as the generic type, although the species is based only on the Mississippi specimen (upper Coniacian or lower Santonian) described by Leidy (1865) (Fig. 2-8). Russell (1967) recognized the specimen as *Platecarpus* because it possessed a "large suprastapedial process and delicate tympanic ala of the quadrate, and general form of the basioccipital and anterior vertebrae [referable to the genus *Platecarpus*]" (p. 153). He gives no species diagnosis except to differentiate it from *Platecarpus* cf. *P. somenensis* by having the ventroposterior (= posterolateral) processes of the basisphenoid separated only "by a shallow horizontal sulcus," and not by "a deep longitudinal cleft" (p. 153). Although Russell (1967:153) states that the preserved cranial material is "identical in form to corresponding elements of the Niobrara species *P. ictericus* and *P. coryphaeus*," he does not further specify what those elements are. Furthermore, despite the fact that *P. tympaniticus* has nomenclatural priority over any other species of *Platecarpus*, the quadrate bone of the generic type that Russell (1967) based on his assignment of the specimen to *Platecarpus* has never been illustrated or thoroughly described, making it very difficult to compare the generic type with congeners (c.f., Fig. 2-8). For instance, it is problematic to diagnose UALVP 24240, 40402, or YPM 40508 in comparison with the type materials of *P. tympaniticus* as there is insufficient diagnostic information provided by Russell (1967). Even though many subsequent researchers have proposed the synonymy of *Platecarpus ictericus* and *P. coryphaeus* with *P.*

*tympaniticus* (e.g., Nicholls, 1988; Bell, 1993 and 1997; Schumacher, 1993; Sheldon, 1996; Everhart, 2001; Bell and Polcyn, 2005; Polcyn and Bell, 2005a), these synonymies are questionable due to the lack of a character(s) diagnostic for *P. tympaniticus* as mentioned.

The lack of diagnostic information available from the type specimen of *Platecarpus tympaniticus* could also render the diagnoses for other congeners invalid. For instance, Bell's (1993) diagnostic characters for *P. planifrons* are based on a complete pterygoid tooth count, frontal dorsal surface, and the marginal teeth, none of which are preserved in the type specimen of *P. tympaniticus*. The only way to distinguish *P. planifrons* from *P. tympaniticus* is to introduce characters for the quadrate. ANSP 8487 (quadrate type specimen for *P. tympaniticus*) lacks all the diagnostic quadrate characters given here for *P. planifrons*: i.e., the lack of distinct posterior notching of the anterodorsal border (cf. Fig. 2-7C), the distal end of the suprastapedial process terminates transversally expanded, a broad, elliptical stapedial pit, and the smooth, gently rounded vertical ridge on the medial surface of the shaft (Konishi, pers. observ.)

Therefore, because of the absence of a formal diagnosis for *Platecarpus tympaniticus*, it seems most sensible to limit the use of the name *P. tympaniticus* to only the generic type from the upper Santonian/lower Campanian deposit of the Eutaw Formation, Columbus, Mississippi (Leidy, 1865). When Cope (1869) first assigned Leidy's (1865) specimen to *Platecarpus tympaniticus*, he did so with little description and no figures. It is therefore of paramount importance to redescribe the type specimen of *P. tympaniticus* and re-diagnose the taxon (Konishi in progress) before further synonymizations are considered.

***Platecarpus ictericus* (Cope, 1871) and *Platecarpus coryphaeus* (Cope, 1873)**—Russell (1967) used two characters to distinguish *P. ictericus* from *P. coryphaeus*: (1) "premaxillo-maxillary suture terminates posteriorly dorsal to midpoint between second and third maxillary tooth, where anterior portion of maxilla has greatest depth;" and (2) "exits for mandibular ramus of fifth nerve separate into two parallel rows anteriorly on dentary and terminated at ventroanterior margin of bone" (p. 155) (Fig. 2-9B).

In terms of the first diagnostic character above, Nicholls (1988) reported that in four *Platecarpus* specimens, the posterior termination of the suture varied from side to side depending on the developmental stage of the tooth. The second character distinguishing *P. ictericus* from *P. coryphaeus* is also problematic. The left dentary of UALVP 24240 shows an arrangement of foramina that is closer to that of *P. coryphaeus* (Fig. 2-9C), while the right dentary (reversed in the figure) shows an arrangement similar to that of *P. ictericus* (Fig. 2-9D). The right and left variation is so pronounced in UALVP 24240 that using Russell (1967), we would identify two different species of *Platecarpus*, not including *P. planifrons*, based on this character. These observations strongly indicate that *P. ictericus* and *P. coryphaeus* are morphologically indistinguishable; *P. ictericus* has seniority.

***Platecarpus* cf. *P. somenensis* Thevenin, 1896**—The species was erected based on a specimen found in France, consisting of the premaxilla, anterior portion of the maxilla, two pterygoids, the basioccipital and basisphenoid, two isolated maxillary teeth, and a right jugal. Russell (1967) referred *Platecarpus* specimens from the Lower Pierre Shale Formation (middle Campanian), South Dakota, to the taxon by diagnosing them as possessing large teeth and a "very heavy" posteroventral process on the jugal (p. 155). Russell (1967) also mentions the arrangement of the mandibular exits for the fifth nerve, which in this species separate anteriorly into "two parallel rows" (p. 155). This latter condition is identical to that in *P. ictericus* (Russell, 1967) and is of little taxonomic use. The heavy posteroventral process on the jugal is somewhat ambiguous since the expression "moderately large" was used for the same character in *P. coryphaeus* and *P. ictericus* by Russell (1967:153). In UALVP 24240 and YPM 40508, the posteroventral process on both jugals is present, posteriorly projecting as a pointed keel (Fig. 2-3). It is difficult to determine whether this is "heavy" or "moderately large," because it is posteriorly projecting more than in *P. ictericus* (Russell, 1967:figs. 37, 38), but certainly is not as thick/heavy as *Platecarpus* cf. *P. somenensis* (Thevenin, 1896:pl. 30). The degree of posterior projection of the process in both UALVP 24240 and YPM 40508 is comparable to that figured in Thevenin (1896). Therefore for this character, it is best to state that the posteroventral process on the jugal is present but thin in *P. ictericus* and *P. planifrons*, and present as well as thick/robust in *Platecarpus* cf. *P. somenensis*.

Although the validity of this species is problematic due to the absence of diagnostic characters uniting North American species with the French type (see Bell, 1993), this fact alone does not automatically invalidate the existence of the species within the Lower Pierre Shale Formation *Platecarpus* mosasaurs. While concurring with the basic claim of Bell (1993) that the use of the name must be abandoned sensu stricto, we further promote the formal restudy of this material in order to solve this problem properly. Therefore, we tentatively retain *Platecarpus* cf. *P. somenensis*, pending future work.

**"*Platecarpus*" *intermedius* (Leidy, 1870)**—Based on the species named by Leidy (1870) as *Clidastes intermedius*, Russell (1967:156) provisionally assigned the species to *Platecarpus* based on "the general heaviness of the dentary and its abrupt termination directly in front of the first tooth." Based on the limited cranial material of the type and the only specimen of the species, consisting of "an anterior portion of one [left] ramus of the lower jaw, a portion of the upper jaw [which is in fact a posterior portion of the right dentary], an axis and several [three] dorsal vertebrae" (Leidy, 1870:4), there are only two diagnostic characters (Russell, 1967). Namely, the number and position of nerve foramina on the dentary (cf. Fig. 2-9A, C), and secondly, short and inflated posterior dentary teeth. As already argued, the first character is of little or no value.

The second character from the "*P.*" *intermedius* type specimen, prompted Russell (1967) to point out similarities with *Globidens alabamaensis* (cf. Gilmore, 1912:pls. 39, 40). Polcyn and Bell (2005b) recently reassessed this material, along with new specimens from Texas, and suggested the nominal change of "*Platecarpus*" *intermedius* to *Globidens*. While the study by Polcyn and Bell (2005b) is still in progress, the size of these two presumed sub-adult specimens are comparable (Polcyn, pers. comm.). Hence, with our own observations of the type material, the current study is in accordance with Polcyn and Bell's (2005b) viewpoint that "*Platecarpus*" *intermedius* (Leidy 1870) likely belongs to the genus *Globidens*.

***Platecarpus planifrons*** **(Cope, 1874)**—The new osteological data presented here helps resolve the controversies concerning the validity of *Platecarpus planifrons* (Cope, 1874) (e.g., Russell, 1967; Bell, 1993, 1997). Despite the fact that the species was considered nomen vanum by Russell (1967), the taxon is clearly distinguishable from its presumed sister taxon, *P. tympaniticus* (or *P. ictericus*, see discussion above) (Bell, 1993, 1997), using the combination of cranial characters given previously (in particular, the frontal and quadrate).

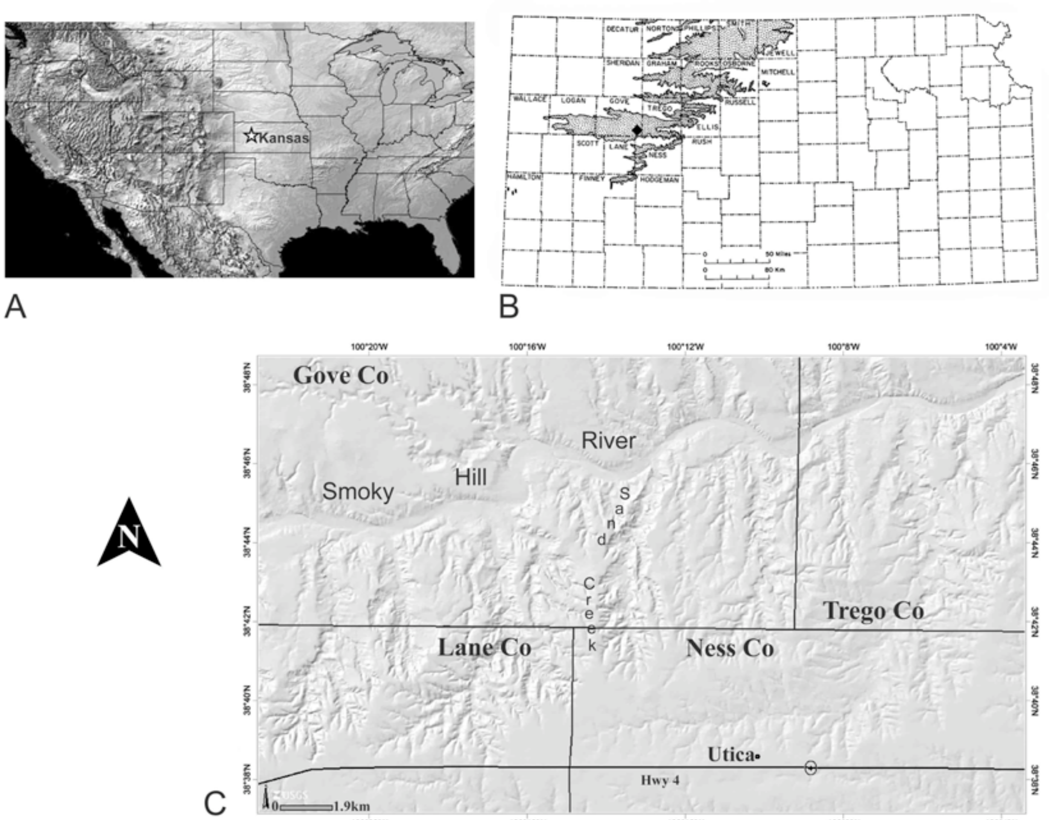
Bell (1993) postulated that there are more than 12 pterygoid teeth in *Platecarpus planifrons*. However, it is clear that in UALVP 24240 the number of teeth on the completely-preserved right pterygoid is only 10 (Fig. 2-3). As for UALVP 40402, the right pterygoid is nearly complete, yet there are only 9 tooth positions confirmed, the first one presumably overlain by the adjacent maxilla (Fig. 2-4). KU 14349, a nearly complete but dorsoventrally compressed *Platecarpus* skull assignable to *P. planifrons*, possesses 15 pterygoid teeth on its right side. Bell (1993) used this specimen to score the characters for *P. planifrons* in his final data matrix, presumably leading to his diagnostic character "more than 12 pterygoid teeth" (p. 203). With the absence of the complete pterygoid in the type specimen AMNH 1491, and the presence of only 10 teeth on the completely-preserved pterygoid in UALVP 24240, we suggest that the pterygoid tooth count in *P. planifrons* is more variable than previously thought.

It is noted that KU 14349, like UALVP 24240, does not possess a premaxillary rostrum. Since the type specimen AMNH 1491 preserves no premaxilla, it is parsimonious to conclude that *P. planifrons* lacks this feature all together. On this point we are in conflict with Bell's (1993, 1997) arguments for its presence. AMNH 1511, considered to be *P. planifrons* by Bell (1993, 1997), preserves a premaxilla with "a very short and obtuse" rostrum (Bell, 1993:51). Each quadrate of AMNH 1511 exhibits strong posterior notching of the anterodorsal border and a medially-tapering tip of the suprastapedial process, clearly indicating its referral to *P. planifrons*. Upon close examination, however, it was noted that the premaxilla does not articulate well with either of the associated maxillae (Konishi, pers. observ.) This observation casts some doubt on the fact that AMNH 1511 consists of a single individual, and it is for this reason that we recognize *P. planifrons* as not possessing a premaxillary rostrum despite the condition of AMNH 1511. Aside from the two cranial characters contradicting Bell's (1993, 1997) observations, this study verifies his recognition of the species as a valid taxon; thus, we find we are in agreement with Bell (1993; 1997) and refute Russell's (1967) notion of the species as a nomen vanum.

## ACKNOWLEDGMENTS

We dedicate this work to the memory of Osamu Shibue, whose mentorship and lifelong support have been and will continue to be, an inspiration to his grandson, TK. We further acknowledge L.A. Lindoe for his skillful preparation of both specimens and clever and artful construction of a display base. R. C. Fox kindly provided locality information on the UALVP specimens. We thank G. Bell for extensive discussions on all things mosasaur, including his long held opinion that UALVP 24240 was indeed *P. planifrons*. For reading and reviewing manuscripts, we thank M. V. H. Wilson, M. J. Everhart, R. Holmes, and an anonymous referee. TK also thanks D. Miao, D. Burnham, T. Daeschler, W. Joyce, D. Brinkman, and C. Mehling for collections assistance. Funding for this project was provided in part by NSERC operating grant (no. 238458-01) to MC.

FIGURE 2-1. Specimen locality for UALVP 24240 and 40402. **A**, map of United States with star indicating locality in western Kansas; **B**, distribution of Niobrara Chalk outcrop (stippled) in Kansas, black diamond indicates locality (modified from Hattin, 1982); **C**, Sand Creek, where the UALVP *Platecarpus* specimens were collected. **A** and **C** modified from USGS The National Map Viewer, http://nmviewogc.cr.usgs.gov/viewer.htm.


Kansas
A
DECATUR
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PHILLIPS
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JEWELL
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GRAHAM
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LOGAN
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TREGO
RUSSELL
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0
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B
100°20'W
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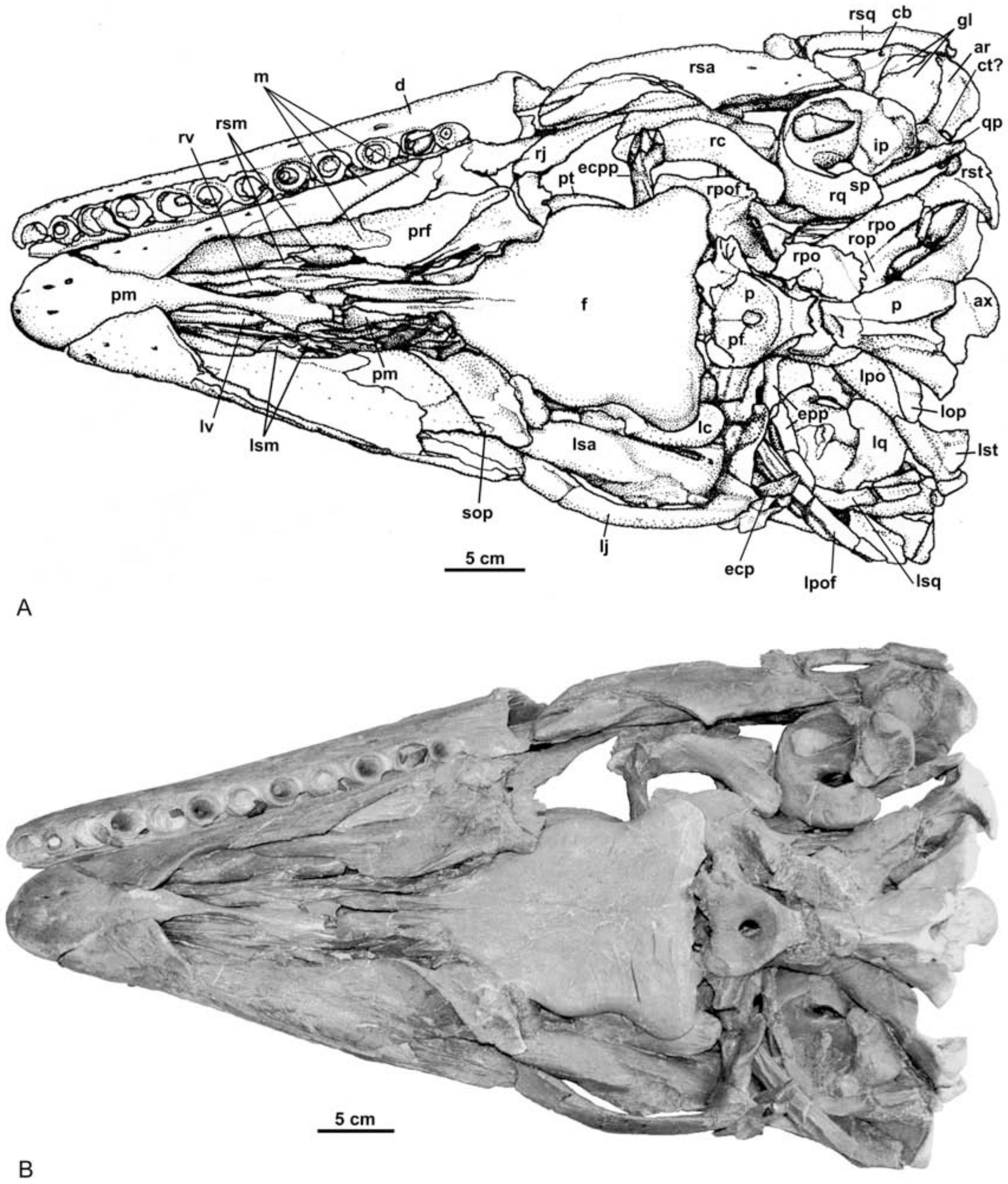
100°4'W
38°48'N
38°46'N
38°44'N
38°42'N
38°40'N
38°38'N
Gove Co
River
Smoky
Hill
Sand Creek
Trego Co
Lane Co
Ness Co
Utica
Hwy 4
USGS
0
1.9km
N
C

FIGURE 2-2. Dorsal view, *Platecarpus planifrons* (UALVP 24240). **A**, diagram; **B**, photograph. **Abbreviations**: **ar**, articular; **ax**, axis; **cb**, foramen for cutaneous branch of mandibular nerve; **ct**, corda tympani; **d**, dentary; **ecp**, ectopterygoid; **ecpp**, ectopterygoid process of pterygoid; **epp**, epipterygoid; **f**, frontal; **gl**, gleonid fossa; **ip**, infrastapedial process of quadrate; **lc**, left coronoid; **lj**, left jugal; **lop**, left opisthotic; **lpo**, left prootic; **lpof**, left postorbitofrontal; **lq**, left quadrate; **lsa**, left surangular; **lsm**, left septomaxilla; **lsq**, left squamosal; **lst**, left supratemporal; **lv**, left vomer; **m**, maxilla; **p**, parietal; **pf**, parietal foramen; **pm**, premaxilla; **prf**, prefrontal; **pt**, pterygoid; **qp**, quadrate process of pterygoid; **rc**, right coronoid; **rj**, right jugal; **rq**, right quadrate; **rop**, right opisthotic; **rpo**, right prootic; **rsa**, right surangular; **rsm**, right septomaxilla; **rsq**, right squamosal; **rst**, right supratemporal; **rv**, right vomer; **sop**, supraorbital process of prefrontal; **sp**, suprastapedial process of quadrate.


rsq
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lq
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lsm
lsa
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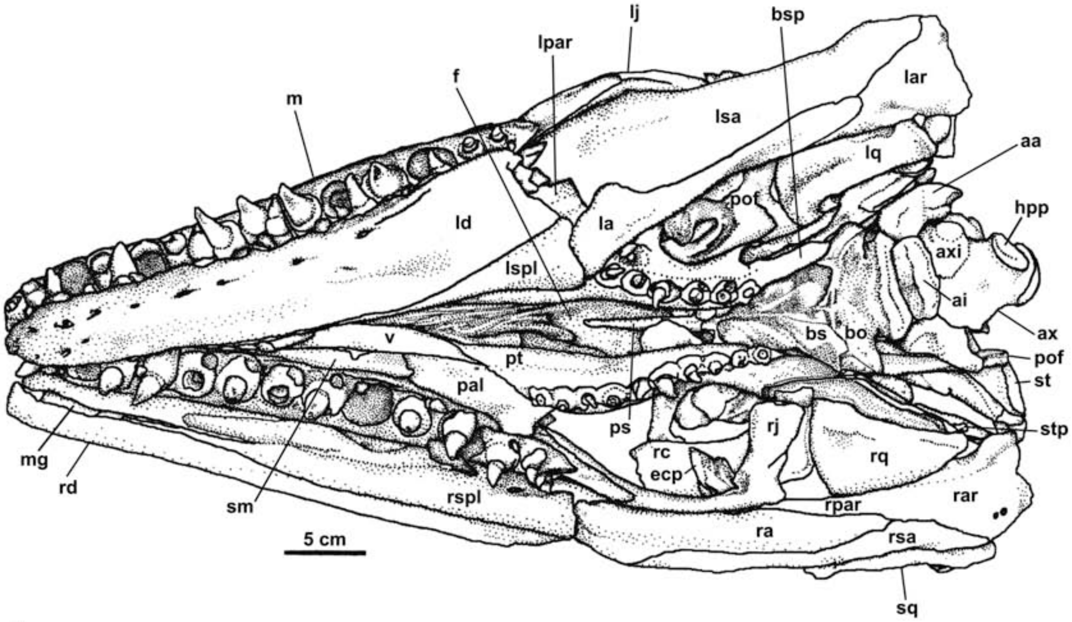
lj
5 cm
ecp
lpof
lsq
A
5 cm
B

FIGURE 2-3. Ventral view, *Platecarpus planifrons* (UALVP 24240). **A**, diagram; **B**, photograph. **Abbreviations**: **aa**, atlas neural arch; **ai**, atlas intercentrum; **ax**, axis; **axi**, axis intercentrum; **bo**, basioccipital; **bs**, basisphenoid, **bsp**, basisphenoid process of pterygoid; **ecp**, ectopterygoid; **f**, frontal; **hpp**, hypapophysis; **la**, left angular; **lar**, left articular; **ld**, left dentary; **lj**, left jugal; **lpar**, left prearticular; **lq**, left quadrate; **lsa**, left surangular; **lspl**, left splenial; **m**, maxilla; **mg**, Meckelian groove; **pal**, palatine; **pof**, postorbitofrontal; **ps,** parasphenoid; **pt**, pterygoid; **ra**, right angular; **rar**, right articular; **rc**, right coronoid; **rd**, right dentary; **rj**, right jugal; **rpar**, right prearticular; **rq**, right quadrate; **rsa**, right surangular; **rspl**, right splenial; **sm**, septomaxilla; **sq**, squamosal; **st**, supratemporal; **stp**, stapes; **v**, vomer.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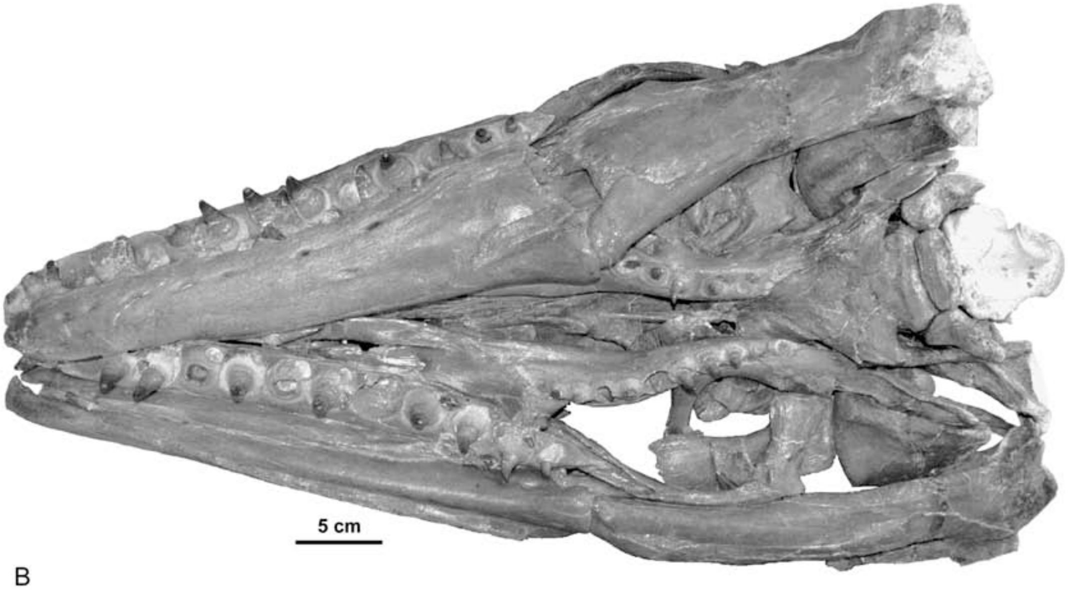
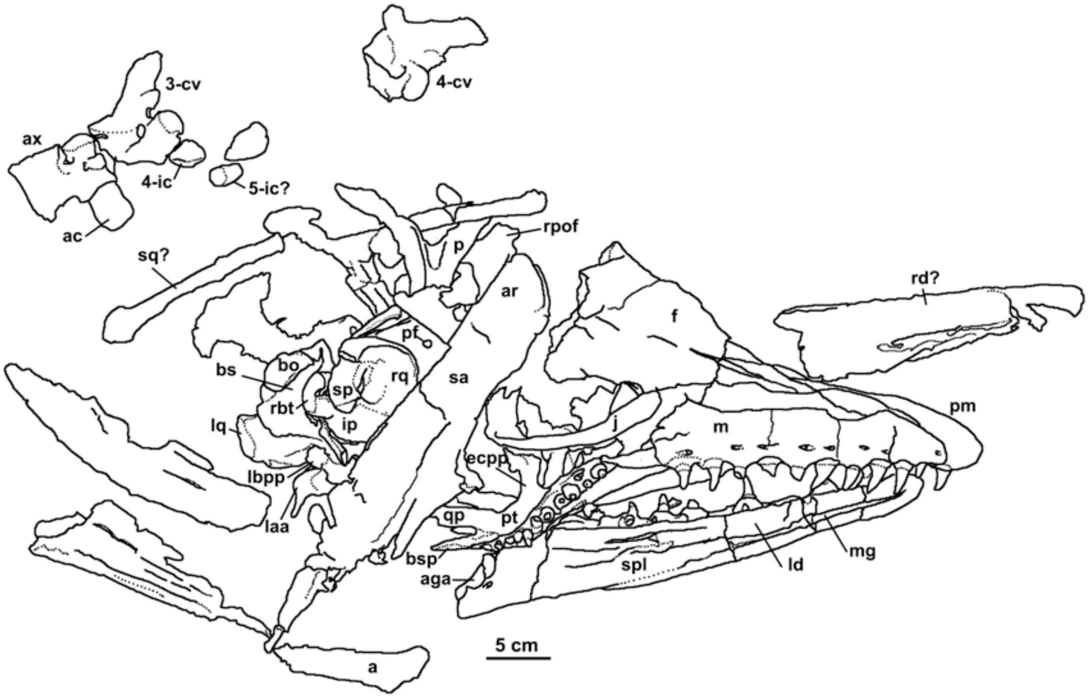
5 cm

A


5 cm

B

FIGURE 2-4. *Platecarpus planifrons* (UALVP 40402). **Abbreviations**: **3-cv**, third cervical vertebra; **4-cv**, fourth cervical vertebra; **4-ic**, fourth cervical vertebra intercentrum; **5-ic**, fifth cervical vertebra intercentrum; **a**, angular; **ac**, atlas centrum; **aga**, angular articulation facet of splenial; **ar**, articular; **ax**, axis; **bo**, basioccipital; **bs**, basisphenoid, **bsp**, basisphenoid process of pterygoid; **ecpp**, ectopterygoid process of pterygoid; **f**, frontal; **ip**, infrastapedial process of quadrate; **laa**, left atlas neural arch; **lbpp**, left basipterygoid process of basisphenoid; **ld**, left dentary; **lq**, left quadrate; **m**, maxilla; **mg**, Meckelian groove; **p**, parietal; **pf**, parietal foramen; **pm**, premaxilla; **pt**, pterygoid; **qp**, quadrate process of pterygoid; **rbt**, right basal tuber; **rd**, right dentary; **rpof**, right postorbitofrontal; **rq**, right quadrate; **sa**, surangular; **sp**, suprastapedial process of quadrate; **spl**, splenial; **sq**, squamosal.


4-cv
3-cv
ax
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5-ic?
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rpof
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ar
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f
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pm
ecpp
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qp
pt
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ld
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5 cm
a

FIGURE 2-5. Frontal of *Platecarpus planifrons* (YPM 40508). **A**, dorsal view; **B**, ventral view. **Abbreviations**: **apof**, articulation for postorbitofrontal; **aprf**, articulation for prefrontal; **ch**, cerebral hemisphere; **eb**, supraorbital embayment; **ob**, olfactory bulb; **pmf**, posteromedian flange; **vsrg**, ventral separation ridge.

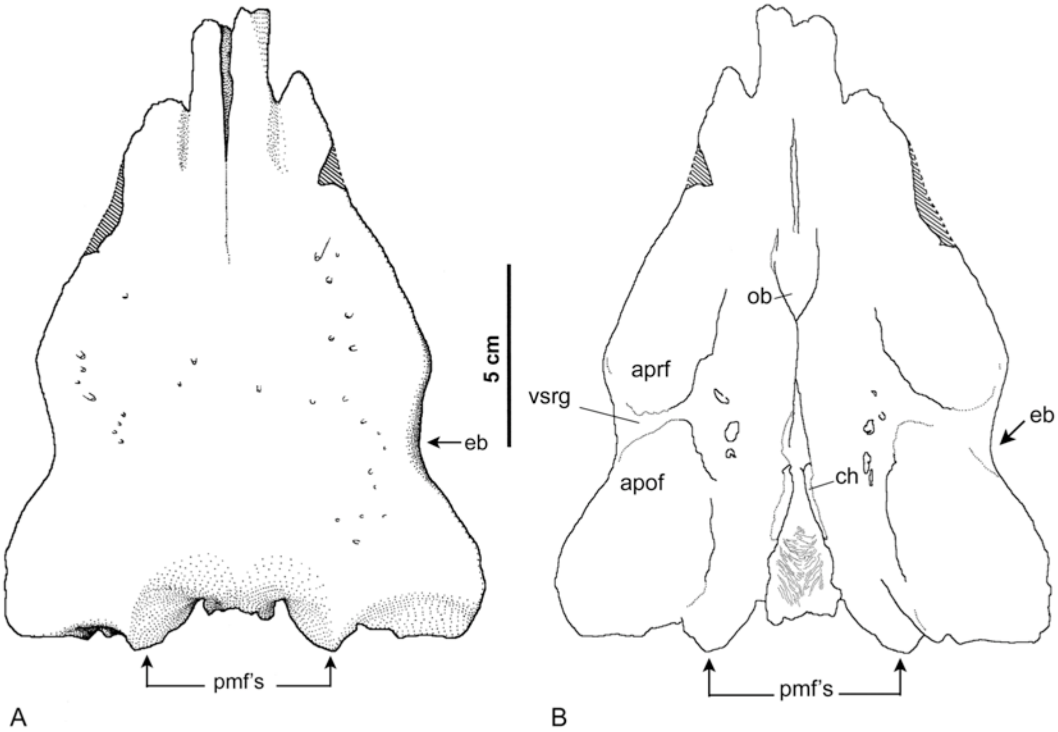
5 cm
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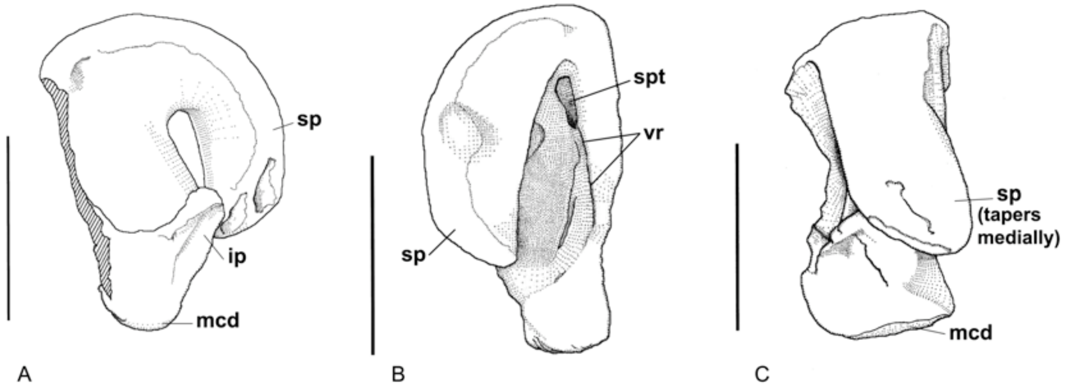
FIGURE 2-6. Left quadrate of *Platecarpus planifrons* (YPM 40508). **A**, lateral view; **B**, medial view; **C**, posterior view. **Abbreviations**: **mcd**, mandibular condyle; **spt**, stapedial pit; **vr**, medial vertical ridge. All the other abbreviations as in Fig. 2-2. Scale bars equal 5 cm.


sp
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mcd
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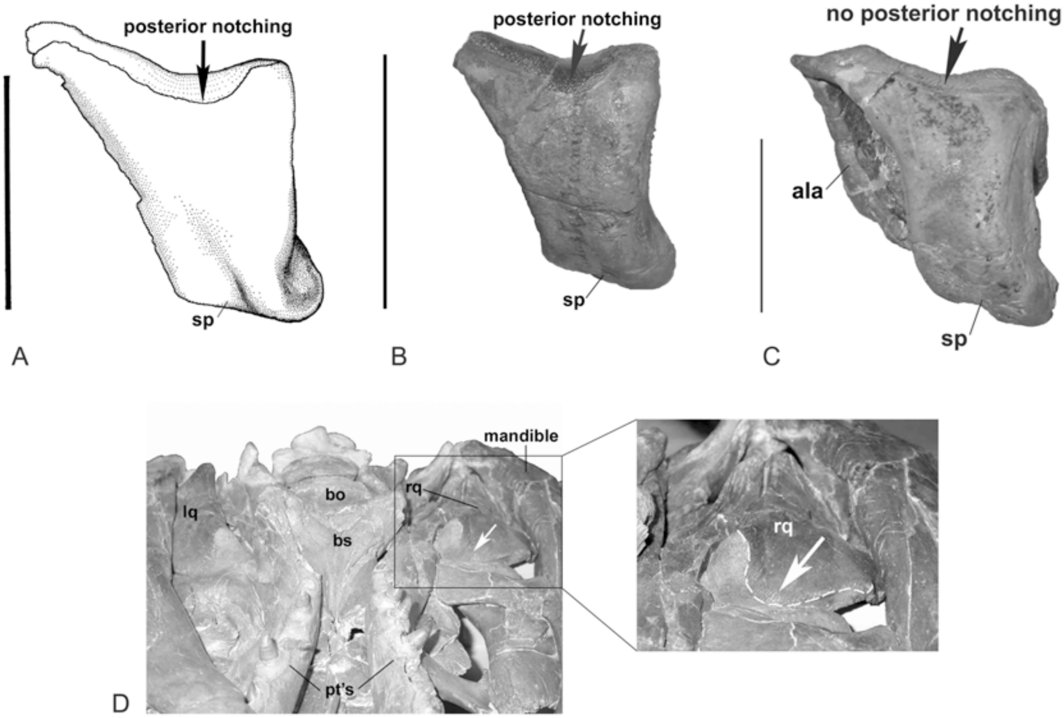
(tapers
medially)
mcd
C

FIGURE 2-7. Comparison of anterodorsal border of quadrates in four *Platecarpus* specimens. **A**, YPM 40508, *P. planifrons*; **B**, AMNH 1491, *P. planifrons* holotype; **C**, AMNH 1820, *P. ictericus*; **D**, UALVP 24240, *P. planifrons*, with the border indicated by the broken line in the blow-up image. Scale bars in **A**–**C** equal 5 cm. Abbreviations as in Figs. 2-2 and 2-3.


posterior notching
sp
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posterior notching
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B
no posterior notching
ala
sp
C
mandible
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rq
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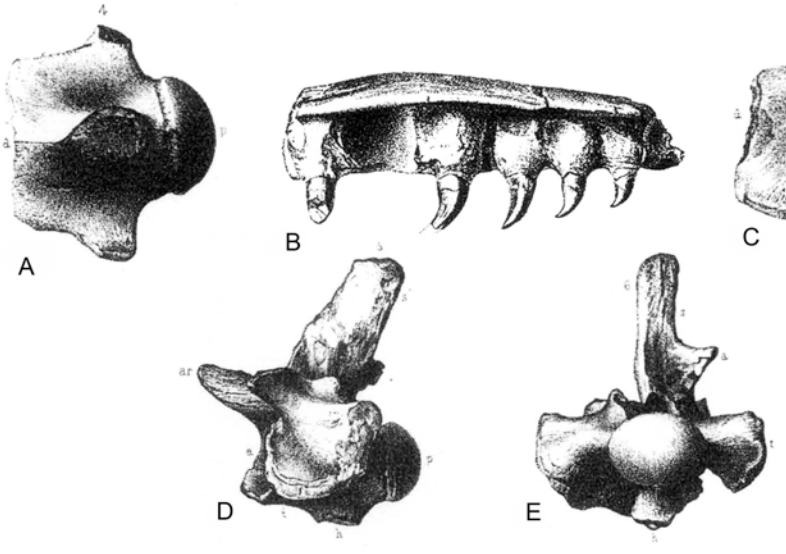
D

FIGURE 2-8. Type material of *Platecarpus tympaniticus* from Leidy, 1865. **A**, ANSP 8488, cervical vertebra in ventral view; **B**, ANSP 8491, right pterygoid; **C**, ANSP 8558, partial anterior dorsal vertebra in ventral view; **D** and **E**, ANSP 8559, cervical vertebra in left lateral (**D**) and posterior (**E**) views. Modified from Leidy, 1865. Not to scale.


A
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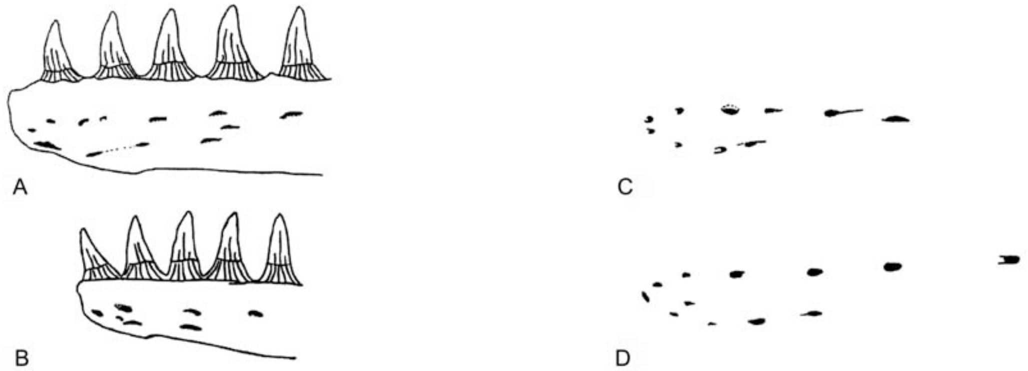
t
ar

FIGURE 2-9. Comparisons of the arrangement of the exits for the mandibular division of the fifth cranial nerve in *Platecarpus*. **A**, *P. coryphaeus* (sensu Russell, 1967) (AMNH 1511); **B**, *P. ictericus* (AMNH 1488, reversed); **C**, left dentary of UALVP 24240; **D**, right dentary of UALVP 24240 (reversed). **A** and **B** modified from Russell (1967:fig. 85). Not to scale.


A
C
B
D

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# CHAPTER THREE

# NEW MATERIAL OF THE MOSASAUR *PLIOPLATECARPUS NICHOLLSAE* CUTHBERTSON ET AL., 2007, CLARIFIES PROBLEMATIC FEATURES OF THE HOLOTYPE SPECIMEN

A nearly identical version of this chapter was published as: 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.

# INTRODUCTION

Since the late 19th century, the study of North American mosasaurs has centered around the well-preserved fauna from the Smoky Hill Chalk Member, Niobrara Chalk (upper Coniacian–lower Campanian) of west-central Kansas (e.g., Leidy, 1865; Cope, 1875; Williston, 1898; Russell, 1967a; Hattin, 1982; Everhart, 2001; Bell, 1997). Although mosasaurs are also known from younger formations elsewhere within the continent, such as the Pierre Shale, these fossils have received far less attention than those from the Niobrara Chalk. Consequently, our understanding of post-early Campanian mosasaur diversity and evolution in North America has been limited to a relatively small number of studies (Camp, 1942; Shannon, 1975; Nicholls, 1988; Wright and Shannon, 1988; Burnham, 1991; Holmes, 1996; Cuthbertson et al., 2007).

Assuming that younger mosasaur faunas are phylogenetically and evolutionarily connected to previous and spatially similar faunas, we have undertaken a broad scale research program examining a prominent group of mosasaurs, the plioplatecarpines (i.e., *Platecarpus* Cope, 1869, *Plioplatecarpus* Dollo, 1882, and *Ectenosaurus* Russell, 1967) (Russell, 1967a). This group of mosasaurs is known in abundance from numerous formations deposited in the Western Interior Basin of North America, such as the Niobrara Chalk (Kansas), Pierre Shale (Manitoba, South Dakota), Demopolis Chalk (Alabama), and Bearpaw Shale (Alberta, Saskatchewan, Montana), as well as the Craie Phosphatée de Ciply of Belgium and the Maastricht Formation of Belgium and the Netherlands (e.g., Russell, 1988; Lingham-Soliar, 1994). The taxonomy, relationships and palaeobiodiversity of plioplatecarpines remain largely unexplored with only a few recent and very focused studies representing the balance of research on *Plioplatecarpus* (Nicholls, 1988; Burnham, 1991; Lingham-Soliar, 1994; Holmes, 1996; Cuthbertson et al., 2007), *Platecarpus* (Konishi and Caldwell, 2007), and *Ectenosaurus* (Russell, 1967a).

From among the North American specimens of *Plioplatecarpus*, there are two recognized species: *Plioplatecarpus nichollsae* Cuthbertson et al., 2007 from the lower Campanian (possibly middle Campanian, see below) of Morden, Manitoba, Canada, and *Plio. primaevus* Russell, 1967 from the upper Campanian to lowermost Maastrichtian of Saskatchewan, Canada, and South Dakota, USA (Russell, 1967a; Holmes, 1996; Cuthbertson et al., 2007). Although there have been many other reports of *Plioplatecarpus* or *Plioplatecarpus*-like mosasaurs from North America, Holmes (1996) suggested that many of them may be synonymous with one of the nominal *Plioplatecarpus* species (e.g., UNO 8611-2, *Plioplatecarpus* sp. from the Demopolis Chalk Formation, east Gulf Coast, Alabama [Burnham, 1991]; CMN 10429, *Plioplatecarpus* sp. from the Mason River Formation, North West Territories [Russell, 1967b, 1988]).

Holmes (1996) also inferred that *Platecarpus somenensis* Thevenin, 1896 belonged to *Plioplatecarpus*, although its specific distinction within the genus was left unjustified. In the most recent review of the systematics of the genus *Platecarpus*, Konishi and Caldwell (2007) recognized the following four North American species: *Platecarpus tympaniticus* Cope, 1869, *Plat. ictericus* (Cope, 1871), *Plat. planifrons* (Cope, 1874), and *Plat.* cf. *P. somenensis*. While tentatively retaining *Plat.* cf. *P. somenensis* within the genus, Konishi and Caldwell (2007) also noted the necessity of the formal restudy of the material from the Pierre Shale as there are no shared diagnostic characters uniting the North American form and the holotype from the middle-upper Santonian phosphatic chalk of France (Nicholls, 1988; Bardet, 1990; cf. Bell, 1993). Konishi and Caldwell (2007) further stated that the absence of diagnosable *Plat. somenensis* material from North America does not automatically invalidate the presence of a distinct *Platecarpus* species from the lower Pierre Shale.

In Canada, a number of mosasaur specimens have been found in sediments deposited in the Late Cretaceous Western Interior Seaway, that once covered Alberta, Saskatchewan, Manitoba, and Northwest Territories (e.g., Russell, 1967b; Nicholls, 1988; Kyser et al., 1993; Tokaryk, 1993; Holmes, 1996; Holmes et al., 1999; Bullard, 2006; Cuthbertson et al., 2007). The lower unit of the Pembina Member around Morden, Manitoba has yielded a great number of marine vertebrate specimens including five currently identified mosasaur genera—*Hainosaurus* Dollo, 1885, *Tylosaurus* Marsh, 1872, *Clidastes* Cope, 1868, *Platecarpus*, and *Plioplatecarpus* (Nicholls, 1988; Cuthbertson et al., 2007) (Fig. 3-1). This lower unit of the Pembina Member, the second lowest member of the Pierre Shale in the area, is assigned to the *Baculites obtusus* ammonite zone (e.g., McNeil, 1984), which is earliest middle Campanian in age at around 80.5 Ma (Kauffman et al., 1993; Cobban, 1993; Ogg et al., 2004; Cobban et al., 2006). There are more than 200 catalogued mosasaur specimens, comprising more than one-third of the total number of marine reptile specimens collected in the area

(Nicholls, 1988). Among them, Nicholls (1988) assigned 83% of the identifiable mosasaur specimens to *Platecarpus*, which she classified into *Plat*. *tympaniticus*, *Plat*. *somenensis*, and *Platecarpus* sp. However, re-examination of these *Platecarpus* specimens indicates that most of them do not conform to the generic diagnosis for *Platecarpus* provided by Konishi and Caldwell (2007), nor do they conform to that for *Plioplatecarpus* sensu Holmes (1996).

In this study, we describe two plioplatecarpine specimens from the Morden district, one of which is exceptionally well preserved (i.e., an absence of selenite encrustation). Although Nicholls (1988) previously assigned both specimens to *Platecarpus tympaniticus*, we refer these materials to the recently established plioplatecarpine species *Plioplatecarpus nichollsae*, and use these additional specimens to clarify problematic morphologies in the holotype and original descriptions.

**Institutional Abbreviations—AMNH**, American Museum of Natural History, New York, USA; **BMNH**, Natural History Museum, London, United Kingdom; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **FHSM VP**, Sternberg Museum of Natural History, Hays, USA; **GSATC**, Geological Survey of Alabama Type Collection, Tuscaloosa, USA; **M**, Canadian Fossil Discovery Centre (previously Morden and District Museum), Morden, Canada; **P**, Royal Saskatchewan Museum, Regina, Canada; **RMM**, Red Mountain Museum, now housed at McWane Science Center, Birmingham, USA; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **UALVP**, University of Alberta

Laboratory for Vertebrate Paleontology, Edmonton, Canada; **UNO**, University of New Orleans, New Orleans, USA; **YPM**, Yale Peabody Museum of Natural History, New Haven, USA.

## MATERIALS

All of the vertebrate fossils collected from the vicinity of Morden were found in the lower unit of the Pembina Member, the lithology of which is characterized by an organic-rich, black, carbonaceous shale with numerous (20–30) interbedded bentonite layers (Nicholls, 1988). Selenite crystals are common in this lower unit of the Pembina Member, and almost all the vertebrate fossils collected from the Morden area are heavily encrusted with selenite (Nicholls, 1988). These crystals penetrate the fossils as well as coat the exterior, causing them to swell and crack, thereby making it difficult to observe fine anatomical details such as suture lines and bone margins in most cases. Nevertheless, mechanical removal of selenite crystals from M 83.10.18 has revealed a great deal of fine-scale anatomy. In contrast, TMP 83.24.01 is virtually selenite-free and is thus the specimen upon which the balance of this description is based. All other referred specimens are encrusted with selenite crystals to various degrees, but are still well enough preserved to show the features shared with M 83.10.18 and TMP 83.24.01.

## SYSTEMATIC PALAEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

MOSASAURIDAE Gervais, 1852

RUSSELLOSAURINA Polcyn and Bell, 2005

PLIOPLATECARPINI Russell, 1967a

*PLIOPLATECARPUS* Dollo, 1882

*PLIOPLATECARPUS NICHOLLSAE* Cuthbertson et al., 2007

(Figs. 3-2–3-15)

**Holotype**—CMN 52261, semi-articulated skeleton consisting of highly selenite-encrusted, overlapping skull elements, seven cervicals, 23 dorsal vertebrae, 11 pygal vertebrae, five caudal vertebrae, ribs, and relatively complete limb and girdle elements.

**Revised Diagnosis** (cf., Lingham-Soliar, 1994; Holmes, 1996; Cuthbertson et al., 2007)—Dentigerous portion of premaxilla with scalloped outline in dorsal view; first set of premaxillary teeth procumbent; premaxillo-maxillary suture low, posteriorly ascending approximately at 30 degrees; posterior terminus of this suture above posterior edge of second maxillary tooth; posterior margin of narial border between fifth and sixth maxillary teeth; three maxillary teeth posterior to anterior margin of orbit; lateral borders of frontal anterior to frontal alae straight, running parallel with each other forming nearly rectangular shield anteriorly; median dorsal keel on frontal well developed; pair of ventrolateral processes on frontal diverging anteriorly, flanking pair of parolfactory-bulb recesses; parietal foramen large, elongate oval with length greater than 1.6 times width; postorbital process of parietal extending laterally to or beyond posterolateral corner of frontal; postorbitofrontal with two distinct articular facets for frontal and parietal; basal tuber on basioccipital highly inflated; anterodorsal border of quadrate straight and oriented transversely; tympanic ala projecting laterally, forming right angle with long axis of suprastapedial process; suprastapedial process more than two-thirds total quadrate height; suprastapedial process wide with straight lateral margins; stapedial pit broadly ovate with straight lateral margins; posteroventral margin of quadrate shaft straight in side view; mandibular condyle transversely wide; surangular forming at least 50% of glenoid fossa; retroarticular process short and round; 12 maxillary and dentary teeth; incipient, non-functional zygosphenes and zygantra present at least on third cervical vertebra; scapular blade semicircular, semi-equal in size to coracoid blade; humeral pectoral crest robust; at least 11 pygal vertebrae.

**Type Locality and Horizon—**Bentonite mine about 19 km northwest of Morden, southern Manitoba (SE 1/4 Sec. 31, T3, R6), Canada; Pembina Member shale bed below uppermost bentonite seam with a radiometric age of 81 (+/-3) Ma (latest early Campanian) (Cuthbertson et al., 2007; Ogg et al., 2004).

**New Material, Locality, and Horizon—**TMP 83.24.01, well-preserved but disarticulated skull including braincase and first three cervical vertebrae. Collected in the Morden-Miami area, southern Manitoba, Canada (lowest middle

Campanian, Upper Cretaceous, Pembina Member, Pierre Shale Formation [McNeil, 1984; Nicholls, 1988; Kauffman et al., 1993; Cobban, 1993; Ogg et al., 2004; Cobban et al., 2006]). M 83.10.18, selenite-coated collection of isolated partial skull elements and right humerus. Collected near Miami Manitoba, North Cox site, NW 1/4 Sec. 35, T4, R7 (A.-M. Janzic, pers. comm.) (lowest middle Campanian, Upper Cretaceous, Pembina Member, Pierre Shale Formation) (Fig. 3-1).

**Referred Material, Locality and Horizon**—M 73.06.02, M 73.08.02, and M 84.07.18; locality as per Nicholls (1988), horizon lowest middle Campanian (Fig. 3-1).

## DESCRIPTION AND COMPARISONS

### Skull Elements

**Premaxilla**—There is no predental rostrum on the premaxilla, and the dentigerous portion is gently scalloped in dorsal view. The anterior-most teeth are procumbent as in *Plioplatecarpus primaevus* but not to the extent seen in *Plio. marshi* Dollo, 1882 (compare Lingham-Soliar, 1994:fig. 4B; Holmes, 1996:fig. 2C). The ventral median ridge that posteriorly contacts the vomers is set between the posterior pair of premaxillary teeth, and is longitudinally grooved on its ventral side. Posteriorly, the premaxillo-maxillary suture terminates above the posterior-quarter section of the second maxillary tooth (Fig. 3-2), while it is reported to terminate “directly above the gap between the second and third maxillary teeth” in the holotype (Cuthbertson et al., 2007:596). The slender, delicately proportioned internarial bar forms an inverted triangle in cross section, is attenuated around its midlength and widens towards both ends.

Cuthbertson et al. (2007) indicated that the long premaxillo-maxillary suture observed in this taxon is a primitive feature shared with *Platecarpus*. However, one specimen of *Plioplatecarpus houzeaui* Dollo, 1889 (IRSNB R37) suggests otherwise as the suture ends above the mid-point of the third maxillary tooth, although in another specimen (IRSNB 3101), it ends above the mid-point of the second tooth (Table 3-1). Based on the similarity of the premaxillary profile to IRSNB R37, it is also most likely that the suture ended above or slightly beyond the mid-point of the third maxillary tooth in the *Plio*. *marshi* holotype. As the premaxillo-maxillary suture in the above two *Plioplatecarpus* specimens is longer than that in *Platecarpus ictericus*, this refutes Cuthbertson et al.'s (2007) polarity claims for this character. Apparently, it is only *Plio. primaevus* which possesses an extremely short premaxillo-maxillary suture, posteriorly ending above the mid-point of the first maxillary tooth (Table 3-1). In *Plio*. *marshi*, the internarial bar does not constrict posteriorly as abruptly as in *Plio*. *nichollsae* or in *Platecarpus* (cf., Lingham-Soliar, 1994:fig. 4A).

**Maxilla**—The right and left maxillae of TMP 83.24.01 both lack the 12th tooth position postmortem. However, on M 83.10.18, the tooth row is complete with a tooth count of 12. The foramina for the nerve fibers of the maxillary ramus of the trigeminal nerve are large and increase in size posteriorly (Fig. 3-2).

The dorsal border of the maxilla overlaps the prefrontal with a thin, elongate, tongue-shaped flap of bone, superficially forming a sinusoidal sutural line between the two elements. The median border of this posterior flap does not form the posterolateral margin of the external naris and thus allows the underlying prefrontal to form the margin as in most other mosasaurs.

The anteriorly deepest portion of the maxilla occurs slightly posterior to the sutural contact with the premaxilla, above the anterior portion of the third maxillary tooth (Fig. 3-2). The lateral margin of the external naris is constricted posteriorly above the point between the fifth and sixth tooth positions (Fig. 3-2). In *Platecarpus*, such as *Platecarpus planifrons* (UALVP 24240), this posterior inflexion point of the maxilla is found above and behind the sixth maxillary tooth (for *Plat. ictericus* [FHSM VP-17017], this point occurs above the sixth tooth). In TMP 83.24.01, a greater dentigerous portion of the maxilla underlies the orbit (10th to 12th tooth positions) than in *Platecarpus* (cf., Russell, 1967:fig. 37; Fig. 3-2).

**Prefrontal—**The prefrontal in TMP 83.24.01 is well preserved. This triradiate element closely resembles that of *Platecarpus*. It bears an incipient supraorbital process/tuberosity at the anterodorsal corner of the orbit. There is a shallow, somewhat square-shaped ventral excavation at the end of the flat, expanded posterior process of the element that would have articulated with the anterior end of the postorbitofrontal. The dorsal surface of the anterior process is narrower and longitudinally sulcate more distinctly than in *Platecarpus*. This surface is separated from the nearly vertical, deep lateral wall, by a distinct ridge running above the maxillary-prefrontal suture (Fig. 3-2). This preorbital ridge is not as pronounced in *Plat. planifrons* (UALVP 24240) and *Plat. ictericus*

(AMNH 1820), where the dorsal and lateral surfaces of the element are somewhat more continuous. Although not completely preserved, the sutural contact between the prefrontal and maxilla appears longer and more shallowly inclined than in *Platecarpus* (Fig. 3-2; cf. Russell, 1967a:fig. 38). No well-preserved prefrontals are known for the other species of *Plioplatecarpus* (Lingham-Soliar, 1994; Holmes, 1996).

**Frontal**—Overall, the frontal is a broad, shield-shaped element, the lateral borders of which run nearly parallel to each other (Figs. 3-3, 3-4). Unlike *Plioplatecarpus primaevus*, the frontal exhibits no supraorbital emargination and consequently lacks “gently convex lateral margins” in front of the orbits (Holmes, 1996:675). Due in part to the lack of an interorbital constriction, the ratio between the longitudinal length of the parietal foramen and the minimum interorbital width is approximately 20 to 25% including the holotype, compared to nearly 50% for *Plio*. *primaevus* (Holmes, 1996). The supraorbital bulging is more pronounced than in *Platecarpus ictericus* (e.g., AMNH 1820), and is associated with a well-developed median dorsal keel (Fig. 3-4A). This keel rises approximately at the level of the orbit and extends anteriorly. The frontal shield has a straight overall profile as in *Platecarpus*, in contrast to the condition seen in *Plio*. *primaevus* and *Plio*. *houzeaui*, where the frontal table gently slopes forward anterior to the parietal foramen in lateral aspect (Holmes, 1996:fig. 2C). The posterolateral ala projects laterally instead of posterolaterally as in *Plio*. *primaevus* or *Plio*. *houzeaui*, and on its dorsal surface, a very shallow, ovoid depression is present, presumably marking the attachment site for the superficial musculature, cf. M. pseudotemporalis (Russell, 1967a). The frontal is widest across the alae.

The otherwise transversally straight posterodorsal margin of the frontal is broadly emarginate medially, enclosing the anterior portion of the parietal table in a squared outline (Figs. 3-3A, B; 3-4A). At the middle of this emargination, the frontal margin further recedes anteriorly, bordering the anterior half of the large, longitudinally elongate and oval parietal foramen that is nearly or completely formed by the parietal underneath (Figs. 3-3C, D; 3-4B). The aforementioned sutural outline results from medial and lateral thin overhanging flanges at the posterior edge of the frontal bone, anteriorly covering a large part of the parietal dorsal surface. On the holotype *Plio*. *nichollsae*, the medial flanges are most likely lost postmortem, asymmetrically exposing the anterior portion of the parietal table that surrounds the parietal foramen (Cuthbertson et al., 2007:figs. 4, 5). These posterior frontal flanges are completely absent on the ventral surface; as a result, the entire ventral surface of the parietal is exposed when the postorbitofrontal is removed (Fig. 3-4B). In this view, the suture connects the anterior edge of the parietal foramen and the tip of the frontal ala in an almost straight line. Flanking the ventral midline in front of the fronto-parietal suture, a pair of sickle-shaped depressions marks the roofs of the cerebral hemispheres (Russell, 1967a). Between these depressions, the olfactory tract originates and extends anteriorly. On TMP 83.24.01, about the posterior two-thirds of the tract is narrow and parallel-sided, but it gradually expands anteriorly to form the broad roof for the olfactory bulbs at the preorbital area. In *Platecarpus*, the olfactory tract remains narrow for its entire length, at the anterior end of which it abruptly expands to form the roof for the olfactory bulbs (Russell, 1967:fig. 4A; Konishi and Caldwell, 2007:fig. 5B). In all the other *Plioplatecarpus* taxa, the tract begins diverging from its posterior end and continues to diverge anteriorly for its entire length (Lingham-Soliar, 1994:fig. 5F, pl.5B; Holmes, 1996:fig. 4B). Flanking the broad roof for the olfactory bulbs is a pair of large oval depressions, hereafter referred to as parolfactory-bulb recesses (Figs. 3-3C, 3-4B). Laterally adjacent to this pair of large recesses, there are well-developed, anteriorly diverging ventro-lateral processes of the frontal (i.e., the descensus frontalis). Two well-preserved *Plio. primaevus* specimens, CMN 11835 and 11840, show nearly identical divergence and thickening of these processes. In CMN 11835, the posterior part of the left parolfactory-bulb recess can be discerned (Holmes, 1996:fig. 4B). The same characters are present on *Plio. houzeaui* and *Plio. marshi*, while in *Plat. planifrons* and *Plat. ictericus*, such depressions are absent or constricted, respectively (see Russell, 1967a:fig. 4; Konishi and Caldwell, 2007:fig. 5B). The presence of these characters seems to distinguish *Plioplatecarpus* from *Platecarpus*, and these features are most likely related to the broad, shield-shaped outline of the frontal for the former genus (cf., Holmes, 1996). Although the anterior part of the frontal is not completely preserved on any specimen assigned to *Plio*. *nichollsae* or to *Plio. primaevus* (Holmes, 1996; Cuthbertson et al., 2007; this study), based on the complete frontal of *Plio*. *houzeaui* (IRSNB 3108), it is hypothesized that in all the nominal *Plioplatecarpus* taxa, two widely separated anterolateral processes as well as the median premaxillary process(es) were present, with the former processes formed at the ends of the diverging ventro-lateral processes to form the anterior corners of the rectangular frontal shield (cf. Lingham-Soliar, 1994:pl. 6D). Contrastingly in *Platecarpus*, the ventro-lateral processes run parallel with each other anteriorly to form narrow-spaced anterolateral processes, resulting in the formation of a more triangular frontal outline.

**Parietal**—The lateral margins of the diamond-shaped parietal table converge posteriorly to form a well-developed parietal crest, a feature not observed in other *Plioplatecarpus* species though it is present in *Platecarpus*. Along the midline, the length of the parietal table exceeds that of the ramus portion of the element (Fig. 3-3A, B). This is not to the degree observed in other species of *Plioplatecarpus*, where the posterior edge of the ramus is either at the same level as the posterior border of the descensus parietalis (*Plio. houzeaui*), or anterior to this border (*Plio. primaevus*) (cf., Fig. 3-3C, D).

Although the absolute length of the parietal foramen is clearly greater than that of *Platecarpus planifrons* and *Plat. ictericus*, it is not as long as in *Plioplatecarpus primaevus* and *Plio. houzeaui* (not known in *Plio. marshi*). However, the average length to width ratio of the foramen for the taxon is 1.91, higher than any other *Platecarpus*/*Plioplatecarpus* mosasaur (Table 3-2). In addition, the foramen shape is unique in exhibiting an elongate oval; in all the other *Plioplatecarpus* species, the foramen is ovate with straight lateral margins.

The postorbital process is longer than half the width of the parietal table, and almost reaches the posterolateral corner of the frontal or extends further beyond this point (Figs. 3-3, 3-4). In TMP 83.24.01, the postorbital process forms a narrow plateau on the dorsal surface of the skull table behind the frontal (Fig. 3-3A, B). This participation by the postorbital process in forming the dorsal skull surface is a feature that unites this taxon with other *Plioplatecarpus* taxa such as *Plio. primaevus* (cf., Cuthbertson et al., 2007). In the latter taxon however, the process forms a much greater portion of the posterior edge of the skull table, such that the longitudinal thickness of the process equals that of the frontal ala, the character also found in *Plio. houzeaui* (Lingham-Soliar, 1994:pl. 6A; Holmes, 1996:fig. 2A). The left suspensorial ramus is nearly complete on TMP 83.24.01 and shows a gentle lateral curvature, but is not as laterally directed as in the reconstruction of the skull based on the holotype (Cuthbertson et al., 2007:fig. 6), where the suspensorial rami are incomplete and, in all probability, diagenetically deflected laterally to some extent (Cuthbertson et al., 2007:fig. 4A; cf., Fig. 3-4). Ventrally, the distal one-third of the left ramus of TMP 83.24.01 bears a finely grooved depression to articulate with the distal end of the anteromedial wing of the supratemporal to complete the arcade (Fig. 3-3C).

**Postorbitofrontal—**The postorbitofrontal is disarticulated in both TMP 83.24.01 and M 83.10.18, and is particularly well preserved in the former (Figs. 3-5, 3-6). The dorsal surface bears two wedge-shaped facets that are divided by a crest: a broad anterior articulation for the frontal and a narrow, posterior articulation surface for the parietal postorbital process. In *Platecarpus ictericus*, as a contrast to *Plioplatecarpus nichollsae*, the same surface virtually consists of a single broad concavity for articulation with the frontal ala, although a minute wedge-shaped notch is found posteromedially adjacent to the former concavity to have received a short parietal postorbital process (e.g., AMNH 1820:Fig. 3-5D). In this species, the process is less than half the parietal table width and does not participate in the dorsal surface of the skull table. The jugal process is complete on TMP 83.24.01 and shows a well-developed anteroventral projection and is more complex in its articulations with the jugal than was suggested by Cuthbertson et al.'s (2007:599) "peg and slot" joint (Fig. 3-6). Holmes (1996:674) lists the "extremely short" postorbital (= jugal) process of the postorbitofrontal as a diagnostic character for the genus *Plioplatecarpus*; however, the anteroventral projection noted here is extremely well developed in *Plio. houzeaui* (IRSNB R36 [Lingham-Soliar, 1994:pl. 7E]), suggesting that the short, truncated jugal process of the postorbitofrontal is unique to *Plio. primaevus* and UNO 8611-2, a plioplatecarpine mosasaur from Alabama, USA, described as *Plioplatecarpus* sp. (Burnham, 1991). The left postorbitofrontal of M 83.10.18 preserves a largely complete squamosal process, which is long and slender (Fig. 3-5C). According to Cuthbertson et al. (2007:fig. 6), the length of the reconstructed squamosal process of the holotype is about 21% of the distance across the frontal alae, although the same ratio is 76% using the left postorbitofrontal of M 83.10.18. Adding to the observation made for the parietal suspensorial rami, this also indicates that the lateral border of the supratemporal fenestra was of comparable length to that of *Platecarpus*, contrary to Cuthbertson et al.'s (2007) suggestion that it was uniquely short for *Plio. nichollsae* among plioplatecarpines. It is also noted that in the holotype, the virtually complete left squamosal process of the element is severely bent at its mid-length (rather than "at its distal tip" [Cuthbertson et al., 2007:599]), making the lateral border of the fenestra appear unusually short (Cuthbertson et al., 2007:fig. 5A).

**Jugal**—Although none of the specimens assigned to *Plioplatecarpus nichollsae* preserves jugals, all the plioplatecarpine specimens collected from the Morden district that preserve their jugals consistently show that they are more *Platecarpus*-like in their morphology (i.e., M 73.01.02, M 75.01.06, M 75.04.06, and M 84.08.18). The jugal process of the postorbitofrontal in M 75.04.06 is very similar to that of TMP 83.24.01, and its jugal bears a small posteroventral process and an ascending ramus that is distally both slightly expanded and concave laterally, to receive the anteroventral projection of the postorbitofrontal (as in *Platecarpus*). As well, on M 84.08.18, where the horizontal ramus is nearly complete, the ascending ramus length is less than 50% of the former as in *Platecarpus*. In *Plioplatecarpus*, including UNO 8611-2, the jugal morphology is markedly different from the above conditions: namely, the lack of the posteroventral process, and a distally attenuated ascending ramus whose length is greater than 50% of the horizontal ramus length (cf., Burnham, 1991:fig. 7; Lingham-Soliar, 1994:pl. 7C, D). Hence in all probability, the jugal morphology of *Plio*. *nichollsae* is comparable to that in *Platecarpus*, although the posteroventral process is less developed (absent in M 75. 01. 06) and the ascending ramus is somewhat less expanded distally than in *Platecarpus*.

**Quadrate**—The quadrate most closely resembles that of *Platecarpus*, in particular *Plat*. *ictericus* (compare Russell, 1967a:fig. 25 and Konishi and

Caldwell, 2007:fig. 6). The anterodorsal border is transversely straight, and the ala projects laterally with a relatively flat anterior surface without any conspicuous bulging. In *Plioplatecarpus*, there is anterolateral bulging of the alar surface, which is especially clear in dorsal aspect, and the dorsal rim of the ala projects anterolaterally in this aspect. The rim of the ala describes a semicircle although it is reconstructed more as rectangular in outline on AMNH 1820, a specimen of *Plat. ictericus* (Russell, 1967a:fig. 24B). In the holotype of *Plat. tympaniticus*, a virtually undistorted right tympanic alar rim bears a nearly perfect semicircular outline as in TMP 83.24.01. Indeed, the rim is the only preserved part of the quadrate ala in AMNH 1820 and has been distorted as well; therefore, it is most likely that *Plat. ictericus* also had a quadrate ala whose margin was circular rather than rectangular (contra Russell, 1967a). Similar to *Platecarpus*, but unlike *Plioplatecarpus*, the posteroventral extension of the ala curves upward to form a distinct infrastapedial process above the condyle, instead of projecting posteriorly (e.g., Holmes, 1996; Figs. 3-7, 3-8). The suprastapedial process in *Plio. nichollsae* is among the most well developed in mosasaurs (cf. *Platecarpus*), where it is more than two-thirds the length of the quadrate shaft (Fig. 3-7). As in *Plat. ictericus*, the process is wide and bears parallel lateral borders which diverge at the distal end to form a broad, blunt terminus. In other *Plioplatecarpus* taxa, in contrast, the lateral borders of the suprastapedial process are often gently constricted (e.g., CMN 11835; IRSNB R36; IRSNB 1739) and the process is also absolutely narrower than that belonging to similar-sized quadrates of *Platecarpus*.

Cuthbertson et al. (2007) suggested that the “pointed suprastapedial process” is symplesiomorphic for *Plio. nichollsae* and *Platecarpus*. However, the morphology of the distal end of the suprastapedial process varies both intra- and interspecifically within *Platecarpus*, where in *Plat. ictericus*, for example, more than 60% of the specimens in the YPM and AMNH collections show the rounded as opposed to pointed (22%) distal extremity. More importantly, the remainder of the observed quadrates (six individuals) do not fall into either type. This observation indicates that the distal morphology of the suprastapedial process serves no taxonomic use for *Platecarpus*, and refutes Cuthbertson et al.’s (2007) assertion. Nevertheless, it is the case that both *Plio*. *nichollsae* and *Plat*. *ictericus* share the distally expanded suprastapedial process as described above (cf. Konishi and Caldwell, 2007).

In M 83.10.18 the right quadrate is preserved with a nearly complete extracolumella passing through the stapedial notch and expanding outward to fill the entire space of the quadrate conch (Fig. 3-8G). The expanded portion of the extracolumella is only partially preserved on TMP 83.24.01 (Fig. 3-8A), most likely due to the removal of the large outer portion during its preparation. Due to the presence of the extracolumella, it is difficult to determine whether or not the posterior eminence/swelling of the quadrate shaft sensu Holmes (1996) and Cuthbertson et al. (2007) is present on TMP 83.24.01. In addition, the posterior border of the exposed ventral portion of the shaft remains rather straight as in *Platecarpus,* but is not at all similar to other *Plioplatecarpus* taxa where this border itself is often gently curved outward (swollen) (e.g., Lingham-Soliar, 1994:pl. 8F, G; Holmes, 1996:fig. 7C) (Fig. 3-7).

Many isolated quadrates of *Platecarpus* cf. *P. ictericus* show a notch for the passage of the extracolumella at the anterodorsal corner of the stapedial notch. In fact, the anterodorsal corner of the stapedial notch is never swollen in *Plioplatecarpus* either, as the space was necessary to allow the extracolumella to pass through the otherwise nearly closed stapedial notch. In this regard, we consider Holmes' (1996) and Cuthbertson et al.'s (2007) definition that the prominent swelling on the "posterior surface of (the) quadrate shaft" being a *Plioplatecarpus* synapomorphy misleading. Such a swelling is limited at the ventral portion of the posterior border of the quadrate shaft in both *Platecarpus* and *Plioplatecarpus*. Thus, the most discernible feature that distinguishes *Plio. primaevus*, *Plio. houzeaui*, and *Plio. marshi* from *Platecarpus* is the presence of the prominent convexity of the posterior border on the ventral portion of the quadrate shaft. As is shown in Cuthbertson el al. (2007:fig. 7), the posteroventral border of the quadrate shaft is straight on the holotype, much as in TMP 83.24.01 or in *Platecarpus*, including the holotype of *Plat. tympaniticus*. In this view, the quadrate shaft morphology of *Plio. nichollsae* is better aligned with that in *Platecarpus* than *Plioplatecarpus* (contra Cuthbertson et al., 2007).

The mandibular condyle is wide and assumes the outline of a curved teardrop shape, as in *Platecarpus*, where the pointed medial end gently curves anteriorly (Fig. 3-8F). As described in Cuthbertson et al. (2007), it is in a marked contrast to the medio-laterally narrow triangular outline of the mandibular condyle in other *Plioplatecarpus* species. The median vertical ridge (Fig. 3-8B, I) is gently domed and straight as in *Plat. ictericus*, but not in other *Plioplatecarpus* taxa, in which it gently curves posteriorly following the anterior border of the large stapedial pit at the corner of the stapedial notch. This character seems to be associated with the fact that in those *Plioplatecarpus* species, the long axis of the stapedial pit inclines further posterodorsally from the long axis of the quadrate shaft compared to *Platecarpus* and *Plio. nichollsae* (Fig. 3-8B). The outline of the stapedial pit on the new material is a broad ovate with straight lateral borders, but not as broad as those of *Plio. houzeaui* or *Plio. marshi*, in which it is an even broader oval with a somewhat curved lateral border (e.g., IRSNB R36, R38, R40).

**Squamosal**—The squamosal is complete on the right side of TMP 83.24.01 (Fig. 3-9). The overall morphology of the squamosal is reminiscent of *Platecarpus ictericus* (e.g., AMNH 1820), except for the posterior edge whose outline is gently rounded in this specimen, compared to the somewhat rectangular outline in the former. The medial wall of the long postorbitofrontal process becomes progressively deeper posteriorly than the lateral wall, forming a groove for the articulation of the postorbitofrontal squamosal process. Unlike in *Plioplatecarpus houzeaui* (IRSNB R36) (Lingham-Soliar, 1994:pl. 7E), where the distal end of the latter process reaches the posterior margin of the squamosal, this groove shallows and diminishes at the posterior end of the postorbitofrontal process. This also indicates that the lateral border of the supratemporal fenestra was virtually equal to the full length of the squamosal process of the postorbitofrontal, a further suggestion that the supratemporal fenestra length was not shortened in any unusual manner in *Plio. nichollsae*. Posterior to this slender postorbitofrontal process, the squamosal expands to form a club-shaped distal terminus. Projecting anterodorsally, the short parietal process vaguely forms a low parallelogram in outline. Ventrally, the anterior edge of the elongate, concave quadrate articulation surface projects forward, forming the anteroventral quadrate process. The process is not as well developed as in IRSNB R36, a *Plio. houzeaui* specimen (Lingam-Soliar, 1994:pl. 7E).

**Supratemporal—**The left supratemporal of TMP 83.24.01 is in articulation with the paroccipital process (Figs. 3-9–3-11). Anteromedially, the element sends a long, dorsally grooved, wing-like process whose main plane lies horizontal. Judging from the size of the corresponding articulation concavity on the suspensorial ramus, the distal half of this anteromedial wing of the supratemporal must have been overlapped by the former. The broad, medially grooved anterior process of the supratemporal abuts the anterior surface of the distal end of the paroccipital process. At its anterior end, the process contacts the prootic with a U-shaped suture line (Fig. 3-9). At the posterior end of this process, the main body of the supratemporal thickens to produce a low, lateral eminence that is roughly three-sided pyramid in shape; a medial concavity on the distal squamosal body fit onto this eminence. Posteroventrally attached to the main body is a vertically oval, smooth condyle, whose surface projects posterolaterally beyond the distal corner of the paroccipital process. In a well-preserved *Plioplatecarpus houzeaui* braincase (IRSNB R37), where two intact supratemporals are attached to the paroccipital processes, there is an additional flap of bone that projects medioventrally from this condyle and wraps around the disto-ventral border of the paroccipital process on each side; the character is apparently unique to this species among plioplatecarpines. This oval condyle is much narrower in *Platecarpus ictericus* and projects only slightly beyond the distal edge of the paroccipital process (Russell, 1967a:figs. 17, 20). Anteirorly, this condyle forms a pronounced concavity (much deeper than in *Platecarpus*), and is here interpreted to have received the distomedial eminence on the long quadrate suprastapedial process (Fig. 3-9).

**Prootic—** The braincase is well preserved in TMP 83.24.01, including a prootic that is mostly complete in its original three-dimensional state (Fig. 3-9). The trigeminal notch is smoothly U-shaped. The parietal processes rise more vertically from the trigeminal notch, as opposed to their more anterior orientation in *Clidastes propython* as figured in Russell (1967a:fig. 12). The anteroventral basisphenoidal process is broad and hatchet-shaped, compared with the less expanded, somewhat crescent-shaped process in *Plat. ictericus* (e.g., AMNH 1488; 1566; 1820), and forms the thick anterolateral wall of the braincase on each side (Fig. 3-9; cf. Camp, 1942:fig. 19). The sutural contact with the basisphenoid is obscured by complete co-ossification between these two elements. The otosphenoidal crest, which is the posterior flange of the basisphenoidal process, covers the exit for the cranial nerve VII near its posterodorsal corner. The thickest portion of the prootic is marked by the region of the otic capsule near the internal suture with the opisthotic. In front of this suture a large, elliptical foramen for the shared entrance of cranial nerves VII and VIII pierces the inner prootic wall. At least two separate foramina are discernable within this foramen (cf. Russell, 1967a:fig. 13). Posterolaterally, and paralleling the long axis of the parietal suspensorial ramus above, the prootic sends a thin and elongate process along the anterior surface of the paroccipital process, distally contacting the prootic process of the supratemporal (Fig. 3-9A).

**Opisthotic-Exoccipital**—A large part of the opisthotic forms prominent paroccipital processes that diverge posterolaterally from each other at approximately 90 degrees. The long axis of the paroccipital processes remains nearly horizontal, similar to *Platecarpus* and other *Plioplatecarpus* taxa. Although the comparable portion is not often preserved in other plioplatecarpine specimens, the expanded distal end of the paroccipital process bears a well-developed ventral process (Fig. 3-11). The region of the braincase that is surrounded by the opisthotic is narrower than the anterior portion that is surrounded by the prootic (Fig. 3-9). Although the inner wall of the braincase is largely discernible, no cranial foramina can be observed due to infilling by matrix. On the lateral surface, the surrounding bones obliterate the internal auditory meatus, and the fenestra rotunda is obscured by postmortem damage on the bone surface. A thin, tongue-like process descends ventrally and slightly laterally beneath the internal auditory meatus region to distally wrap around the dorsolateral surface of the basal tuber. Immediately behind this process, the shared opening for cranial nerves X, XI, and XII pierces the lateral wall of the opisthotic as in *Platecarpus* (cf. Camp, 1942:fig. 19) and *Plioplatecarpus* (Holmes, 1996). In condylar view, the exoccipital of *Plio. nichollsae* is deeper than that of *Plat. ictericus*, as the border with the occipital condyle is shifted ventrally, so that the suture between the two elements is lateroventrally inclined. This feature is observed to a greater extent in *Plio. primaevus* (compare Russell, 1967a:fig. 17; Holmes, 1996:fig. 3; Fig. 3-11).

**Supraoccipital**—The supraoccipital is mostly complete and forms the posterior apex of the V-shaped braincase wall in dorsal view, capping the otic capsules (Fig. 3-9). On the external surface, the midsagittal crest is extremely well developed as it rises almost vertically in the form of a thickened keel above the foramen magnum, a condition that seems to be shared only with *Plio. primaevu*s among plioplatecarpine mosasaurs (Holmes, 1996:fig. 5A; cf. Russell, 1967a:fig. 19; Fig. 3-11).

**Basioccipital**—The occipital condyle in condylar view is proportionally smaller than that of *Platecarpus ictericus* but larger than in *Plioplatecarpus primaevus* (Fig. 3-11; cf. Russell, 1967:fig.17; Holmes, 1996:fig. 3). The pitted condylar surface is sulcate along its mid-sagittal line. Amongst the plioplatecarpines, the basal tubera are probably the most developed and bulbous. In comparison with *Plat. ictericus*, the tubera expanded further medioventrally so that they are more closely spaced with each other (Figs. 3-10, 3-11), and these inflated tubera can be noted on the holotype as well (Cuthbertson et al., 2007:fig. 5B). This expansion also stretched the pitted surface on each tuber medioventrally so it is clearly visible in ventral aspect. In *Plat. planifrons* and *Plat. ictericus*, this pitted muscle insertion site occurs only on the lateral surface of the tubera (Russell, 1967a). Between the tubera, as known in most

*Plioplatecarpus* specimens and also reported on the holotype of *Plio. nichollsae* (Cuthbertson et al., 2007), the floor of the basioccipital shows a region of non/poor ossification, marked by a large opening with an irregular border (Fig. 3-10). Although the floor of the medullary cavity is not exposed due to the infilling matrix, this ventral opening must have been dorsally connected to the canals for the basilar artery that run through the basioccipital. Anteriorly, the latero-ventral face of each basal tuber is wrapped around by a thin, fan-shaped posterolateral process from the basisphenoid, much as in *Platecarpus* and *Plioplatecarpus*.

**Basisphenoid—**The floor of the basisphenoid between the posterolateral processes has been crushed and pushed against the roof of the element postmortem (Fig. 3-10). In well-preserved *Plioplatecarpus primaevus* and *Plio. marshi* specimens, there is a bilobate canal for the basilar artery longitudinally piercing the floor of this region of the basisphenoid (cf. Holmes, 1996:fig. 3). The basipterygoid processes are either broken or obscured by the pterygoid basisphenoid processes on TMP 83.24.01. Anteriorly, the basisphenoid narrows to form the parasphenoid rostrum. On the left lateral side of this projection, the anterior portion of the vidian canal is exposed in front of the alar process. The sella turcica region does not preserve fine anatomical details. The base of the parasphenoid process is preserved, projecting from the anterior edge of this rostrum. The process is sulcate on both the dorsal and ventral surface (Figs. 3-9, 3-10).

**Pterygoid—**The pterygoid is largely complete, except for the missing ectopterygoid processes (Fig. 3-10). On the left side, a set of 11 small pterygoid teeth is preserved, which appears to be a complete count. The pterygoid teeth barely differ in size, especially compared to UALVP 24240, a *Platecarpus planifrons* specimen with 10 pterygoid teeth that steadily increase in size toward the middle of the tooth row (Konishi and Caldwell, 2007). Although a count of at least 12 pterygoid teeth has been suggested for the holotype by Cuthbertson et al. (2007), the pterygoid tooth count in *Plat. planifrons* is known to range from 10 to 15 (Konishi and Caldwell, 2007), and *Plat. ictericus* specimens variably exhibit 11 (AMNH 1820) to 13 (AMNH 1566) pterygoid teeth. Hence, the difference in the pterygoid tooth count between the new specimen and the holotype of *Plioplatecarpus nichollsae* is considered to fall well within the range of intraspecific variation for this trait in plioplatecarpine mosasaurs. The quadrate rami expand and diverge posteriorly with a similar interangle to that formed by the suspensoria above (Fig. 3-10). Both the lateral and medial edges of the process curl dorsally to form a shallow trough. The basisphenoid process is about one-quarter the length of the quadrate ramus and edentulous. Anteriorly, the posterior end of the vomer is attached to each pterygoid in TMP 83.24.01, though its suture is much obliterated postmortem. In contrast, the broad, obliquely oriented suture with the palatine is largely complete on the left side (Fig. 3-10). The ectopterygoid processes are largely missing on TMP 83.24.01, but the preserved posterior border on each process suggests anterior inclination of the process. On the holotype, the preserved portion of the ectopterygoid process projects more laterally than in *Platecarpus* and TMP 83.24.01, although a certain degree of postmortem distortion is possible (Cuthbertson et al., 2007:fig. 5B).

**Palatine**—Both palatines of TMP 83.24.01 are preserved still attached to the posteromedial portion of the median buttress of the maxilla, although each element has rotated about 90 degrees from horizontal. On the left palatine, a slender vomerine process projects anteriorly from the medial side, though it is not clear if the process is composed of the vomer, palatine, or both. The lateral border of the process forms the posteromedial border of the choana, whose posterior margin is formed by the gently concave anterior margin of the main palatine body. The gently convex and somewhat scalloped posterior border of the palatine is medially sutured to the pterygoid posteriorly. Compared to *Platecarpus ictericus*, the palatine is more distinctly notched at its posterolateral corner immediately adjacent to its lateral contact with the maxilla (Russell, 1967a:fig. 6). This notched border continues forward as a sulcus on the ventral surface of the bone for about 1 cm. As Russell (1967a) stated, there is no sign of the palatine foramen, which in *Varanus* enters the same region as the notch in TMP 83.24.01. It is a possibility, therefore, that this distinct notch and the ventral groove on the posterolateral corner of the palatine in *Plioplatecarpus nichollsae*, and possibly in other plioplatecarpines, functioned as the palatine foramen in *Varanus*, passing the maxillary branch of the cranial nerve V, inferior orbital artery, and vena maxillaris, even though there seems no obvious foramen on the maxilla for them to enter anterior to the groove (Bahl, 1937; Russell, 1967a). The palatine abuts the maxilla between the eighth and 11th maxillary teeth, while in *Plat. planifrons*, it does between the ninth and the 11th teeth.

**Vomer**—Konishi and Caldwell (2007) reported a clear sutural contact between the vomer and pterygoid on a well-preserved *Platecarpus planifrons* specimen. As mentioned above, however, only the distal ends of the vomers are attached to the pterygoids in TMP 83.24.01, and the sutural contact between the two elements has been obliterated postmortem. Holmes (1996:fig. 2B) showed widely separated vomerine processes throughout their length in *Plioplatecarpus primaevus*, based on the specimen P1756.1. However, the well-preserved anterior portion of the vomerine processes (of the vomer) of TMP 83.24.01 show that the processes are tightly spaced, and also bear considerably longer ventral oblique crests that extend for the length of three and a half tooth positions anteriorly (Fig. 3-12). This contrasts with the approximately two tooth positions in *Plio. primaevus* (Holmes, 1996:fig. 2B). These characters are also discernible on the articulated skull of another Morden plioplatecarpine specimen, TMP 84.162.01, and also in the reconstruction of *Plat. ictericus* by Russell (1967a:fig. 84). Indeed, Russell (1967a:25) states that in *Clidastes*, *Tylosaurus*, and *Platecarpus*, the vomers (and vomerine processes) are "more closely appressed along the midline of the skull…than in *Varanus*." Re-examination of P1756.1 shows that the right vomerine process has been broken anteriorly and dislocated posteriorly, and the posterior portion of the ventral oblique crest on the left process is also missing postmortem. We thus suggest that what appears to be a marked difference in the form of vomerine processes between *Plio. primaevus* and *Plio. nichollsae* can be best attributed to the postmortem alteration of these elements in P1756.1, and that these mosasaurs likely shared similar vomer morphology, including the long ventral oblique crest that occupies approximately the anterior half of the vomerine process. The vomerine process as preserved does not show parasagittal rotation in its posterior segment (TMP 83.24.01), contrary to Holmes' (1996) suggestion. However, the completely preserved right vomerine process of TMP 84.162.01, which remains in articulation with the pterygoid and palatine, exhibits such rotation posteriorly. Anteriorly, the vomerine processes fuse at the level of the second maxillary tooth and connect to the ventrally sulcate vomerine process of the premaxilla in TMP 83.24.01.

**Epipterygoid**—The right epipterygoid is preserved in its entirety positioned against the quadrate ramus of the pterygoid with virtually no postmortem damage, although the left counterpart is broken into three parts with its distal extremity missing (Fig. 3-9). Measuring about 65mm, the epipterygoid is spatula-shaped at its ventral extremity, becoming gradually cylindrical up to 75% of its length distally, at which point it deflects and tapers steadily to end in a rounded point. The surface of the element is smooth, except for the dorsal terminus, which exhibits numerous, fine longitudinal grooves suggesting the presence of a cartilaginous cap in life. Russell (1967a) describes an epipterygoid in *Platecarpus* as having "a small, rounded, ventral termination" and a flattened dorsal termination (p. 45). In *Plotosaurus bennisoni*, it is also the dorsal end of the bone that expands to "a thin blade" (Camp, 1942:30). In *Varanus* (e.g., TMP 1990.7.33, *V. exanthematicus*), the epipterygoid is well developed and has a somewhat expanded dorsal extremity (pers. observ.). On the contrary, the flattened end of both right and left epipterygoids preserved on TMP 83.24.01

inserts into the shallow dorsal pocket on the pterygoid at the base of the basisphenoid process, while the slender, cylindrical end is free from any articulation on both sides (cf. Camp, 1942; Russell, 1967a). As this occurs on both sides, the observation made here seems as natural as it can be anomalous.

## Mandibular Elements

**Dentary**—As in the holotype, M 83.10.18 exhibits 12 marginal teeth (Cuthbertson et al., 2007). There is no edentulous prow preceding the first dentary tooth. The medial parapet is subequal in height to the lateral wall of the dentary. The dentary only slightly deepens posteriorly, resulting in its slender proportion that is shared with both *Platecarpus* and *Plioplatecarpus*. Heavy encrustation of selenite crystal renders further anatomical detail of the element unobservable.

**Postdentary Bones**—The surangular, prearticular, and articular including the retroarticular process, are preserved in articulation in M 83.10.18, while only the glenoid area is preserved with TMP 83.24.01 (Fig. 3-13). Anteriorly, the surangular consistently tapers past the deepest portion of the element, which occurs approximately at the posterior limit of the coronoid buttress. This gradual anterior tapering of the surangular is absent in *Platecarpus*: it either ends abruptly with a more squared outline as in *Plat. planifrons* (UALVP 24240), or tapers more rapidly as in *Plat. ictericus* (e.g., Russell, 1967a:fig. 38; AMNH 1821). The ventral margin posterior to the coronoid buttress is slightly concave. The dorsal margin is raised immediately posterior to the coronoid buttress, and posteriorly the margin is shallowly concave. Also in contrast with *Platecarpus*, in which the surangular contribution to the glenoid fossa is smaller than that of the articular, it is subequal or even slightly larger in *Plioplatecarpus nichollsae* (M 83.10.18 and TMP 83.24.01:Fig. 3-13). The form of the retroarticular process most resembles that of *Platecarpus ictericus*, being short and round with a slightly longer lateral border than the medial one.

## Marginal Dentition

Most of the marginal dentition on TMP 83.24.01 has been damaged but is selenite free. In general, the lateral surface of the tooth crown is strongly faceted/fluted with four to five facets lacking striations, while the medial surface bears numerous fine striations with some weak facets (Fig. 3-2). Typical of plioplatecarpine mosasaurs, a cross section of the base of the crown is nearly circular. The tooth crown becomes rather slender distally and curves posteromedially at about its mid-height. Unlike *Platecarpus*, the posterior carinae are extremely faint to absent on the maxillary teeth of TMP 83.24.01. Compared to *Plat. ictericus*, the exposed portion of the root below the dental margin is highly inflated rather than possessing the gradually tapering, concave surface that is distally continuous with the crown surface (cf., Russell, 1967a:fig. 37). Inflation of the tooth base makes the marginal teeth in *Plioplatecarpus nichollsae* appear large, especially in larger specimens such as M 83.10.18.

## Postcranial Elements

**Atlas—**This ring-shaped element is completely preserved with little postmortem distortion, and is largely similar to, but slightly different from, that in both *Platecarpus ictericus* (AMNH 2005) and *Plioplatecarpus primaevus* (Holmes, 1996:fig. 9) (Fig. 3-14A–E). The posterior face of the odontoid (atlas centrum) rigidly abuts on the anterior surface of the axis centrum. The odontoid anteroventral and anterolateral surfaces are smooth and continuous, anteriorly forming a gentle convexity. The odontoid dorsal surface is semicircular in outline. This contrasts the condition in *Plat. ictericus*, in which the dorsal surface is somewhat anteriorly pointed due to the presence of a weak, mid-sagittal keel on the anterodorsal surface. In *Plio. primaevus* (CMN 11835), the dorsal surface is similarly semicircular as in *Plio. nichollsae*. Although the general description of the mosasaur atlas intercentrum by Russell (1967a:71) matches the element in *Plio. nichollsae*, the ventral tubercle is highly developed and dome-like with a rugose surface (Fig. 3-14A, C). This tubercle is nothing but a low keel along the ventral midline in *Plat. ictericus* (AMNH 2005), while it is as well developed in *Plio. primaevus* as in *Plio. nichollsae* (cf. Holmes, 1996:fig. 9A). The general morphology of the atlas neural arch is in accordance with that described for *Platecarpus* in Russell (1967a). The arches flank the occipital condyle and odontoid anteriorly and posteriorly, respectively. The articulation surface accommodating the occipital condyle faces anteromedially, and is smoothly concave and broadly oval in outline, gradually widening ventrally. Behind this facet, the main body of the arch tapers posteriorly, terminating in a well-developed synapophyseal process at its posteroventral corner. Anterodorsally, each arch sends a spinous process that curves toward the dorsal midline but without meeting the counterpart at its distal end along the midline. Distally, the spinous process expands slightly and twists medially, and also bears longitudinal grooves (Fig. 3-14D). The anterior border of the process projects directly above the anterior condylar surface without notching (cf. Russell, 1967a). There is a well-developed posterodorsally directed tuberosity with longitudinal grooves on the posterior border of the spinous process at its base. As in *Plat. planifrons* and probably in *Plat. ictericus*, a deep longitudinal groove runs immediately medial to this tuberosity (Fig. 3-14D). In *Plio. primaevus*, the overall atlas neural arch morphology is nearly identical to that of *Plio. nichollsae*, except that the posterior tubercle at the mid point of the posterior border is shorter (cf. Holmes, 1996:fig. 9A).

**Axis**—The axis is well preserved in TMP 83.24.01, exhibiting an overall similarity to that of *Platecarpus* and *Plioplatecarpus primaevus* (Fig. 3-14A–E). In comparison with the former taxon, the element is proportionately anteroposteriorly shorter with a proportionately taller neural arch-spine complex. The pronounced anterior process on the neural spine is less developed in TMP 83.24.01 than in *Plat. ictericus* (AMNH 2005, pers. observ.; cf. Russell, 1967a:fig. 40; Fig. 3-14C). In comparison to the same species, the neural arch is anteroposteriorly shortened and is more erect, rather than tilting posteriorly. The postzygapophysis faces more ventrally than in *Plat. ictericus*, and its articulation facet is less oval and more circular as in *Plio. primaevus* (Holmes, 1996:fig. 9A).

On the medial surface of the postzygapophysis, an incipient zygantra is marked as a small notch, which is shorter than the one in *Plat. ictericus* (AMNH 2005). For the *Plio. primaevus* specimens (CMN 11835 and P1756.1), there seem no well-defined zygantra, and they have been reported absent in *Plio. houzeaui* (Lingham-Soliar, 1994). Compared to *Plat. planifrons* and *Plat. ictericus*, the centrum condyle is less convex, as in *Plio. primaevus* (Holmes, 1996:fig. 9A; cf., Lindgren et al., 2007). The hypapophysis is extremely short, bearing a nearly circular facet as in the latter species, while it is deeper with a somewhat triangular articular facet in *Plat. ictericus* (AMNH 2005). The third intercentrum (axis peduncle; not figured) is dorsally flat so as to articulate with the axis hypapophysis, and ventrally presents a three-faced projection whose surface is pitted and ribbed for the attachment of cervical muscles (see Russell, 1967a:fig. 41). At the distal extremity, the peduncle is slightly bifurcated. The wing-like transverse processes are anteroposteriorly short as in *Plio. primaevus*, resulting in less posterior extension of the synapophyseal surface in comparison with *Plat. ictericus* (Holmes, 1996). The axis intercentrum bears a rugose, button-like ventromedian tuberosity, which is represented only as a smooth mid-sagittal keel on *Plat. ictericus*. In *Plio. primaevus*, this process is equally rugose but is developed along the entire midline of the element (cf. Holmes, 1996:fig. 9A; Fig. 3-14B, C, E).

**Post Atlas-Axis Cervical Vertebra**—One anterior, most likely the third, cervical vertebra is well preserved on TMP 83.24.01 (Fig. 3-14F–J). The neural spine is anteroposteriorly about half the length of that of the axis, and its anterior border is sharply keeled. The spine inclines posteriorly at about 70 degrees from horizontal. As in the axis, the neural spine widens posteriorly in horizontal cross section, and its distal end forms a rugose triangular surface for the insertion of the spinalis capitis muscle (Russell, 1967a). The posterior face of the neural spine is slightly narrower than that in the axis, and bears a shallow median sulcus dorsally, which ventrally changes into a median keel around the mid-height of the spine. In the axis, only the latter is present (Fig. 3-14B, G). The post-zygapophyseal facet faces more laterally than in axis. Otherwise, the facet is circular and there is an incipient zygantrum on the medial surface of the base of the process as in the preceding vertebra. Each neural arch tapers posteriorly in horizontal cross section, while it broadens in the axis. The prezygapophysis projects out from the anteroventral corner of the neural arch extending anterolaterally, with its facet facing mediodorsally at about 30 degrees from horizontal. As in *Platecarpus*, *Plioplatecarpus primaevus*, and *Plio*. *houzeaui*, a well-developed round ridge runs along the lateral face of the process to connect it to the synapophysis (Fig. 3-14H). This ridge is absent on the *Plio*. *marshi* holotype (IRSNB R38). Overall, the transverse processes are lateroventrally declined. At the distal end of the process, the synapophyseal facet faces posterolaterally and slightly ventrally, and is small and round (cf., Russell, 1967a). Its pitted surface indicates the presence of a cartilaginous layer between the facet and the cervical rib in life. Another ridge anteriorly connects this synapophyseal facet with the lateroventral corner of the cotylar rim, forming the lateroventral border of the vertebra (Fig. 3-14F). It is hypothesized that levator costae muscles originated along this ridge and the posterior edge of each synapophysis (Russell, 1967a). As in the holotype, no zygosphenes are apparent on this vertebra (Cuthbertson et al., 2007). The centrum condyle is even less convex than that of the axis. On the ventral side, the hypapophysis is deeper and its facet faces slightly more posteriorly than in the axis. The central articulation surfaces are transversely elliptical and do not tilt forward.

**Humerus—**The right humerus of M 83.10.18 exhibits a robust pectoral crest, a shared character with *Plioplatecarpus*, excepting *Plio. houzeaui* for which no humerus is known (e.g., Lingham-Soliar, 1994; Holmes, 1996; Cuthbertson et al., 2007). The dorsolateral border of the humerus is straight as in *Platecarpus*, while it is gently convex in *Plio. primaevus* (CMN 11835) and *Plio. marshi* (IRSNB R38) (Fig. 3-15). Contrary to the suggestion by Cuthbertson et al. (2007), the ectepicondyle as well as entepicondyle are well developed on M 83.10.18. In the *Plio. primaevus* specimen CMN 11835, the two humeri show different degree of ectepicondylar development, the left one possessing a more distinct ectepicondyle (cf. Holmes, 1996:fig. 15A, B). Indeed, while Cuthbertson et al. (2007) reported a lack of a distinct ectepicondyle in CMN 52261 (holotype) presumably based on its right humerus (fig. 2; mislabeled as left in fig. 3), the left counterpart (fig. 2; mislabeled as right in fig. 3) does show a well-developed ectepicondyle, similar in morphology to that of *Plio. primaevus* (Holmes, 1996:fig. 15A, B). Thus, what appears to be the weak development of the ectepicondyle on CMN 52261 seems best attributed to a postmortem artifact. These observations make it clear that *Plio. nichollsae* most likely possessed a humerus with its width across the entepicondyle and ectepicondyle greater than the length of the element (contra Cuthbertson et al., 2007), and that overall the distal portion of the humerus of this taxon is more comparable to that of other *Plioplatecarpus* species than *Platecarpus* (cf. Russell, 1967a:fig. 53).

## DISCUSSION

### Morphological Re-characterization of *Plioplatecarpus nichollsae* and Phylogenetic Implications

Both TMP 83.23.01 and M. 83.10.18 are assignable to *Plioplatecarpus nichollsae* Cuthbertson et al., 2007 under the revised species diagnosis we proposed here. Although several new diagnostic features such as a pair of parolfactory-bulb recesses cannot be confirmed on the holotype due to the state of its preservation, the majority of the characteristics are shared between the new material and the holotype as follows: procumbent first pair of premaxillary teeth; low premaxilla-maxillary suture posteriorly terminating above posterior edge of second maxillary tooth; posterior end of external naris occurring above point between fifth and sixth maxillary teeth; rectangular frontal shield lacking supraorbital embayment; well-developed frontal median dorsal keel; large, elongate oval parietal foramen; highly inflated basal tubera; long and wide suprastapedial process with parallel lateral margins; ovate stapedial pit with straight lateral borders; straight posteroventral margin of quadrate shaft; transversely wide mandibular condyle; 12 maxillary and dentary teeth; and robust humeral pectoral crest. Because no other nominal plioplatecarpine taxa exhibit a combination of the aforementioned characteristics, we can confidently assign the new material to *Plioplatecarpus nichollsae* (see also the foregoing section for fine anatomical comparisons made among various plioplatecarpine taxa).

Even under the revised diagnosis and morphological re-characterization provided for *Plioplatecarpus nichollsae*, it is readily recognizable that some morphological characters of the taxon are shared with *Platecarpus*, some with *Plioplatecarpus*, and yet others are autapomorphic characters that often fall between these two genera in the degree of their development, as Cuthbertson et al. (2007) previously suggested. According to observation of all the available lower Pierre Shale (= Pembina Member in Canada and Sharon Springs Member in USA) plioplatecarpine material by the first author, no specimens of *Platecarpus ictericus* or *Plio*. *primaevus* had been identified (contra Russell, 1967; Nicholls, 1988). Instead, the plioplatecarpine specimens in these members are, without exception, characterized by possessing at least the following three characters: the widely separated frontal anterolateral processes; the posteromedian border of the frontal embayed around the anterior-half margin of the parietal foramen dorsally, typically forming the anterior margin of the foramen itself (contra Cuthbertson et al., 2007); and the quadrate that is morphologically virtually identical to that of *Plat*. *ictericus* (e.g., AMNH 2182, SDSMT 30139, 45331, TMP 84.162.01). While formal taxonomic study of most of these specimens and their incorporation into a global plioplatecarpine phylogenetic analysis are still underway, *Plioplatecarpus nichollsae* under the revised diagnosis morphologically conforms to this unique plioplatecarpine assemblage from the lower Pierre Shale exposures in North America that exhibits more synapomorphies with post-middle Campanian *Plioplatecarpus* taxa than does *Platecarpus*. In addition to their 'morphological intermediacy', these mosasaurs including *Plio. nichollsae* are also found stratigraphically between *Platecarpus* and *Plio. primaevus* (e.g., McNeil, 1984; Cobban et al., 2006). Based on these facts, it seems reasonable to assume that the lower Pierre Shale plioplatecarpines likely represent an evolutionary link between *Platecarpus* and stratigraphically younger *Plioplatecarpus* taxa, regardless of their current taxonomy.

Given this assumed order of evolution from *Platecarpus* to *Plioplatecarpus nichollsae* to post-middle Campanian *Plioplatecarpus* taxa, we note that Cuthbertson et al.'s (2007:604) hypothesis that the "increased size of the (parietal) foramen in *Plioplatecarpus* (in relation to *Platecarpus*) is the result of forward migration of its anterior border into the frontal" needs some re-evaluation. Although they have argued that the posterior border of the foramen shows the same positional relationship with the anterior limit of the supratemporal fenestra and posterolateral corners of the frontal in both *Platecarpus* and *Plioplatecarpus* (Cuthbertson et al., 2007), it is not the case according to their figure 11 and our own observation of the respective specimens. We argue that in the process of evolutionary enlargement of the parietal foramen in these plioplatecarpine taxa, the posterior as well as the anterior border of the foramen migrated anteriorly in relation to the frontal. This is apparent in Cuthbertson et al.'s (2007) figure 11, where the posterior rim of the parietal foramen occurs at the level of the anterior border of the supratemporal fenestra in *Plat. ictericus* (fig.

11A), between this border and the posterolateral corner of the frontal in *Plio. nichollsae* (fig. 11C), and at the level of the posterolateral corner of the frontal in *Plio. primaevus* (fig. 11B). The observation based on Cuthbertson et al. (2007:fig.11C) also holds true for TMP 83.24.01 (Fig. 3-3A, B) and M. 83.10.18 (Fig. 3-4A), augmenting our proposal here.

The nature of the “thickened ventral rim of the naris” reported as the species’ autapomorphy is currently uncertain (Cuthbertson et al., 2007:603). We failed to observe any signs of such thickening on virtually selenite-free TMP 83.24.01 or M 83.10.18, and the feature is less likely associated with ontogeny as the holotype is the smallest of the three (Cuthbertson et al., 2007). One unnumbered maxillary specimen representing a larger plioplatecarpine individual from the Morden area exhibits such thickening of the anteroventral narial margin, but it is not medially convex as reported on CMN 52261 by Cuthbertson et al. (2007). This feature is hence regarded intraspecifically variable if it is real, but selenite-induced swelling of the bone may result in such thickening as well.

Re-characterization of *Plioplatecarpus nichollsae* provided in this study helps facilitate our understanding of its contemporaries both morphologically and phylogenetically, which will in turn help resolve the interrelationships among the members of the tribe Plioplatecarpini.

## Systematic Notes on Other *Plioplatecarpus* Taxa

Although Burnham (1991) described UNO 8611-2 from the Campanian/Maastrichtian boundary of the Demopolis Formation in western

Alabama as a new species of *Plioplatecarpus*, he refrained from establishing a new species based on the specimen. However, our observations of the east Gulf plioplatecarpine mosasaurs strongly argue for the specific distinction of this specimen and RMM 7071 within the genus *Plioplatecarpus*, contrary to Holmes' (1996) view that UNO 8611-2 exhibits "little to distinguish it from *Plioplatecarpus primaevus*" except for "somewhat pachyostotic ribs and a lack of a quadrate eminence" (p. 686). For instance, the quadrate eminence is consistently absent in UNO 8611-2 and RMM 7071, which renders the possible postmortem loss of this feature in the former specimen unlikely (cf., Burnham, 1991). The outline of the preorbital margins of the frontal resembles that of *Platecarpus* cf. *P*. *somenensis* from North America: i.e., round and broadly expanded with widely separated anterolateral frontal processes (compare Nicholls, 1988:fig. 11A; Burnham, 1991:fig. 10; Holmes, 1996:fig. 4A). The interorbital width is wider than the width across these anterolateral processes as well, unlike in *Plio*. *primaevus*, in which the former dimension is less than the latter (Holmes, 1996).

All the specimens of *Plioplatecarpus primaevus* have been recovered from upper Campanian to lowermost Maastrichtian strata in the Western Interior Basin of North America, while the European materials are all Maastrichtian in age (e.g., Lingham-Soliar, 1994; Holmes, 1996). As for the European *Plioplatecarpus* species, we here point out that *Plio*. *marshi* and *Plio*. *houzeaui* are morphologically less distinct from each other than previously considered (e.g., Lingham-Soliar, 1994; cf. Jagt, 2005). For example, Lingham-Soliar (1994:figs.

3, 5C-E, 6) reconstructed *Plio*. *marshi* as possessing a low-profile maxilla with a significant posterior edentulous portion, based on IRSNB 1622. However, this element is in fact a right dentary (of *Pliopaltecarpus* sp., cf., *Plio*. *marshi*), and the 'maxillary fragment' identified for the holotype (IRSNB R38) by him is also the posterior portion of the right dentary (Lingham-Soliar, 1994:fig. 5A, B). Our identification of these elements as a dentary is supported by the presence of the Meckelian groove on the medial surface, a slightly more elevated medial wall than the lateral wall, and the posterior edentulous portion, which is found in the dentary of *Plio*. *houzeaui* as well (e.g., IRSNB R35 = holotype). In light of our re-identification of the "maxilla" (Lingham-Soliar, 1994:183) of *Plio*. *marshi* as a dentary, there seem no well-preserved maxillae for the species. However, close examination of one of the most complete and best-preserved specimens of *Plioplatecarpus* IRSNB R37 (e.g., Lingham-Soliar, 1994:fig. 16) indicates that this specimen, identified by Lingham-Soliar (1994) as *Plio*. *houzeaui*, has a maxilla whose form is comparable to that attributed to *Plio*. *houzeaui* (IRSNB 3101)—i.e., a short, low triangular element posteriorly sending an elongate, fully dentigerous ramus—while it also possesses a medial dentary wall that is higher than the lateral wall, and a median dorsal ridge on the premaxilla, both of which occur in the holotype of *Plio*. *marshi*. This observation could suggest that IRSNB R37 is assignable to *Plio*. *marshi* (cf. Table 3-1), and indicates that fewer osteological differences exist between *Plio*. *marshi* and *Plio*. *houzeaui* than previously hypothesized (e.g., Lingham-Soliar, 1994). In the specific diagnosis for *Plio*. *houzeaui*, Lingham-Soliar (1994) states that it "is smaller than *P*.

*marshi*" (p. 193), and he also regarded that the quadrate morphology is virtually indistinguishable between the two species. Although it is plausible that specimens of *Plio*. *marshi* represent larger (adult) individuals of *Plio*. *houzeaui*, further study of all the European *Plioplatecarpus* material is necessary before such systematic revisions can be made. For example, the frontal morphology of the holotype of *Plio*. *marshi* presents short, round alae that appear too distinct from any other congener for *Plio*. *houzeaui* to be considered synonymous with the former taxon. Nevertheless, revisions to both generic- and specific-level diagnoses for *Plioplatecarpus*, including UNO 8611-2, are necessary, before we consider any taxonomic revision for this currently monophyletic taxon.

## Systematic Notes on *Platecarpus somenensis*

Thevenin (1896) erected this taxon based on the partial skull remains recovered from the middle-upper Santonian phosphatic chalk exposure in France. Thereafter, all the subsequent specimens assigned to the species only came from the lower middle Campanian Pierre Shale in North America (e.g., Russell, 1967; Nicholls, 1988; Cobban et al., 2006). It was Bell (1993) who pointed out the fact that the French holotype and the North American specimens do not share diagnostic characters, and suggested the abandonment of the use of the name and necessity to establish a new taxon based on the North American specimens alone. In revising the *Platecarpus* taxonomy, Konishi and Caldwell (2007) primarily agreed with Bell's (1993) notion, but did not proceed with the formal taxonomic revision to the North American *Platecarpus somenensis* specimens and tentatively retained this taxon as a species of *Platecarpus*. However, observations on the specimens of *Plioplatecarpus nichollsae* described above suggest that these two taxa seem to share more characters than with any other plioplatecarpine taxon. According to Russell (1967a:155), the anteriorly deepest portion of the maxilla in *Platecarpus* cf. *P. somenensis* occurs "…dorsal to third maxillary tooth…", posterior to the point where the premaxillo-maxillary suture ends posteriorly "…above midpoint between second and third maxillary tooth…". This condition is nearly identical to that observed in TMP 83.24.01, and although Cuthbertson et al. (2007) did not distinguish these two points on the holotype, the suture nevertheless terminates posteriorly "directly above the gap between the second and third maxillary teeth" (p. 596). Both Russell (1967a:155) and Nicholls (1988:53) clearly stated that the "very large" parietal foramen in *Plat. somenensis* is broadly bordered by the frontal anteriorly (cf., Figs. 3-3, 3-4). Moreover, Nicholls (1988) observed that *Plat. somenensis* possesses a "slightly spatulate (= scalloped)" premaxilla, "often procumbent" tooth crowns, and a "very high" median dorsal ridge on the frontal (pp. 52-53), all of which are shared with the new *Plioplatecarpus nichollsae* specimens. In his unpublished master's thesis, Shannon (1975) assigned GSATC 220 to *Platecarpus* cf. *P. somenensis*. Upon examination of the material, the fragmentary frontal clearly showed anteriorly diverging ventro-lateral processes flanking a pair of parolfactory-bulb recesses (GSATC 220). As none of these characters uniting 'North American' *Platecarpus somenensis* and *Plioplatecarpus nichollsae* are found in *Platecarpus*, and as many of these characters are shared with other species of *Plioplatecarpus*, it seems most reasonable to consider the *Plat. somenensis* specimens from North America to be assigned to *Plioplatecarpus* (contra Konishi and Caldwell, 2007). However, a formal taxonomic revision of *Platecarpus somenensis* requires a number of successive analyses, including a reassessment of the European type material, a detailed examination of North American material assigned to that European species, finally followed by a comparison of the North American material to *Plioplatecarpus* species, in particular, *Plio. nichollsae*.

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FIGURE 3-1. Geographic locality and stratigraphic horizon of referred mosasaur specimens in the study, indicated by arrows. Detailed map of southern Manitoba (Morden-Miami area) shows general specimen locality in shaded ellipse, which corresponds to quarry numbers 1 to 18 in Nicholls (1988). Specimens come from the Pembina Member of the Pierre Shale Formation assigned to *Baculites obtusus* ammonite zone (ca. 80.5 Ma), lowermost middle Campanian (Nicholls, 1988; Ogg et al., 2004). Maps modified from Young and Moore (1994) and Nicholls (1988), stratigraphic column after Young and Moore (1994).

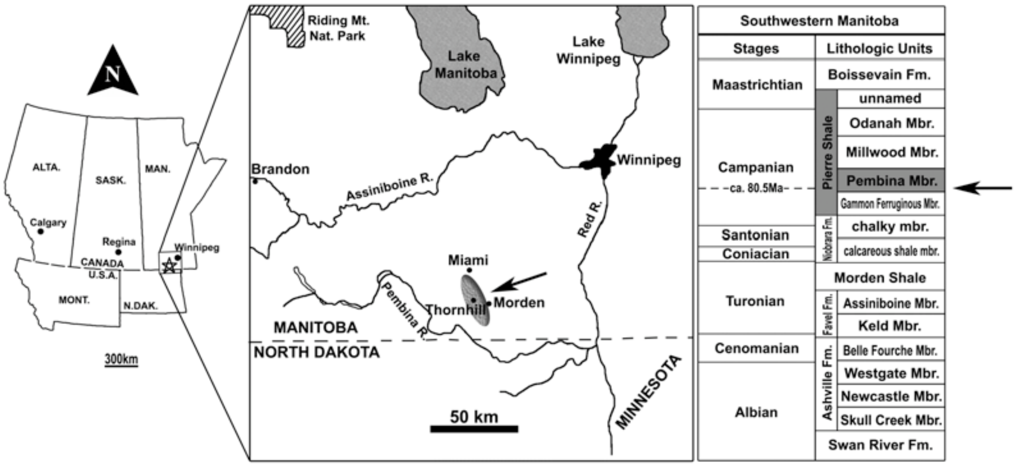

N
ALTA.
SASK.
MAN.
Calgary
Regina
Winnipeg
CANADA
U.S.A.
MONT.
N.DAK.
300km
Riding Mt.
Nat. Park
Lake
Manitoba
Lake
Winnipeg
Brandon
Assiniboine R.
Winnipeg
Red R.
Miami
Thornhill
Morden
Pembina R.
MANITOBA
NORTH DAKOTA
MINNESOTA
50 km
Southwestern Manitoba
Stages
Lithologic Units
Maastrichtian
Campanian
ca. 80.5Ma
Santonian
Coniacian
Turonian
Cenomanian
Albian
Boissevain Fm.
Pierre Shale
unnamed
Odanah Mbr.
Millwood Mbr.
Pembina Mbr.
Gammon Ferruginous Mbr.
Niobrara Fm.
chalky mbr.
calcareous shale mbr.
Morden Shale
Favel Fm.
Assiniboine Mbr.
Keld Mbr.
Ashville Fm.
Belle Fourche Mbr.
Westgate Mbr.
Newcastle Mbr.
Skull Creek Mbr.
Swan River Fm.

FIGURE 3-2. TMP 83.24.01, *Plioplatecarpus nichollsae* premaxilla and maxilla in lateral view. **A**, diagram; **B**, photograph. **Abbreviations**: **12alv**, alveolus for 12th maxillary tooth; **m**, maxilla; **pal**, palatine; **pifx**, posterior inflexion point of dorsal maxillary border; **pm**, premaxilla; **prf**, prefrontal; **prg**, preorbital ridge; **pst**, posterior termination point of premaxillo-maxillary suture; **sop**, supraorbital process/tuberosity on prefrontal; **vp**, vomerine process of premaxilla. Scale bar equals 5 cm.

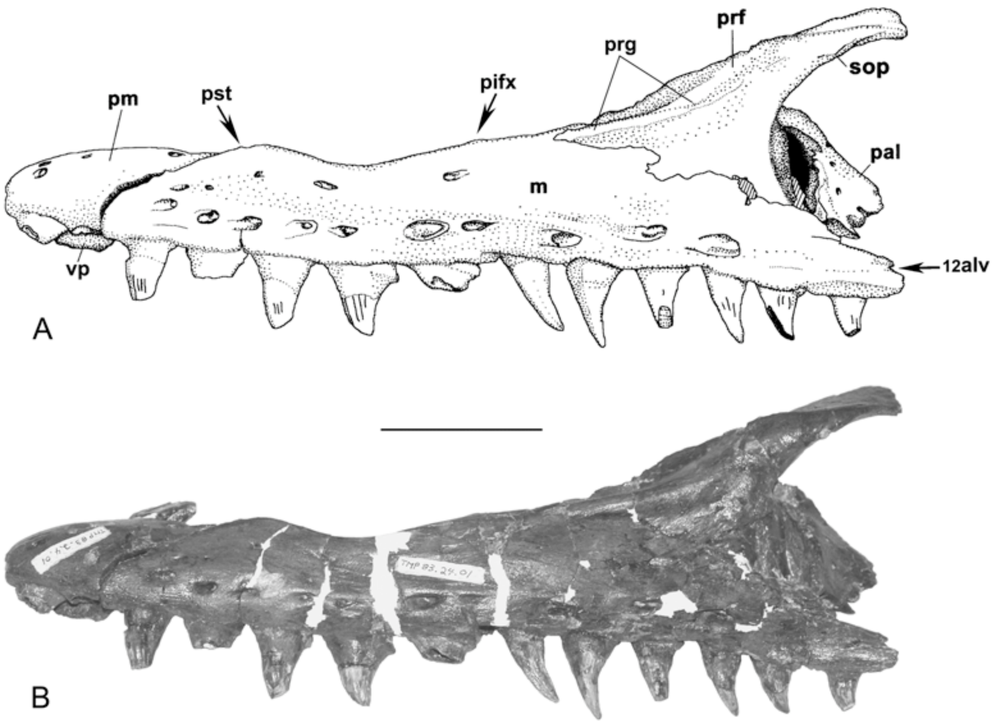

pm
pst
pifx
prg
prf
sop
pal
m
vp
12alv
A
TMP 83.24.01
B

TABLE 3-1. Comparison of premaxillo-maxillary suture length among *Platecarpus* and *Plioplatecarpus*, indicated by position of the posterior sutural termination point.

| Taxon | Posterior termination point of pmx-mx suture | Specimen* |
|---|---|---|
| *Plioplatecarpus primaevus* | Above point between 1st and 2nd maxillary teeth | NMC 11835 |
| *Plioplatecarpus nichollsae* | Around posterior edge of 2nd maxillary tooth | TMP 83.24.01,<br>CMN 52261 (holotype) |
| *Platecarpus ictericus* | Above point between 2nd and 3rd maxillary teeth | AMNH 1820 |
| *Platecarpus planifrons* | Above mid-point of 3rd maxillary tooth | UALVP 24240 |
| *Plioplatecarpus houzeaui* | Above mid-point of 2nd to mid-point of 3rd maxillary teeth | IRSNB 3101,<br>IRSNB R37 |
| *Plioplatecarpus marshi* | Above mid-point of 3rd maxillary tooth or beyond | IRSNB R38 (holotype) |

*All specimens directly observed by the senior author.

FIGURE 3-3. TMP 83.24.01, *Plioplatecarpus nichollsae* skull table. **A**, dorsal view (diagram); **B**, dorsal view (photo); **C**, ventral view (diagram); **D**, ventral view (photo). **Abbreviations**: **aj**, articulation for jugal; **apo**, articulation for prootic; **aprf**, articulation for prefrontal; **ast**, articulation for supratemporal; **che**, partial roof for cerebral hemisphere; **dpf**, descensus processus frontalis; **dpp**, descensus processus parietalis; **f**, frontal; **lpof**, left postorbitofrontal; **mdk**, median dorsal keel; **ob**, olfactory bulbs; **otr**, olfactory tract; **p**, parietal; **pf**, parietal foramen; **pla**, frontal posterolateral ala; **pobr**, parolfactory-bulb recess; **pop**, postorbital process of parietal; **pvmk**, posteroventral median keel; **rpof**, right postorbitofrontal; **sr**, suspensorial ramus. Arrows in **C** indicate fronto-parietal suture on ventral side. Scale bars equal 5 cm.

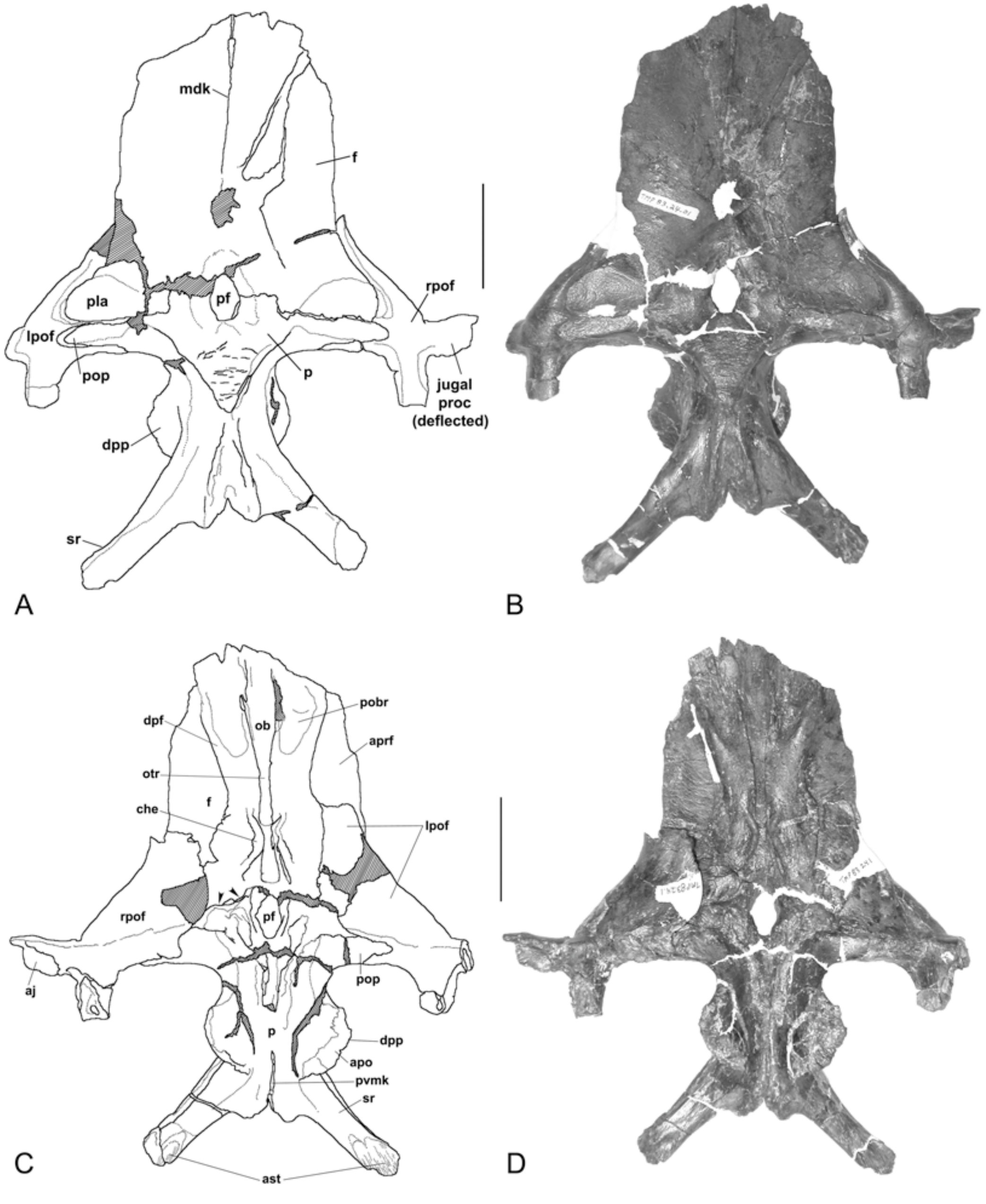

mdk
f
pla
pf
rpof
lpof
pop
p
jugal proc (deflected)
dpp
sr
A
B
pobr
dpf
ob
aprf
otr
f
che
lpof
rpof
pf
aj
pop
p
dpp
apo
pvmk
sr
ast
C
D

FIGURE 3-4. M 83.10.18, *Plioplatecarpus nichollsae* skull table. **A**, dorsal view; **B**, ventral view. **Abbreviations**: **apof**, articulation for postorbitofrontal; **rpobr**, right parolfactory-bulb recess; **sob**, supraorbital bulging. All the other abbreviations as in Figure 3-3. White broken lines indicate sutural contact between frontal and parietal; note the difference between the two sides. Scale bar equals 5 cm.

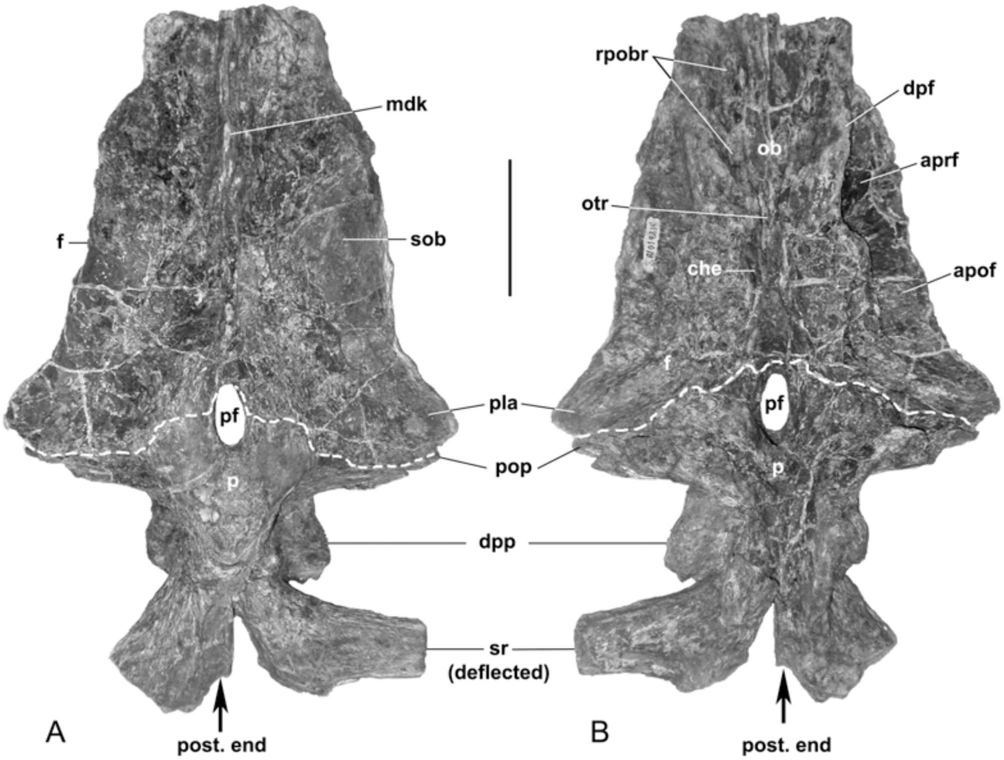

mdk
f
sob
pf
pla
pop
p
dpp
sr
(deflected)
A
post. end
rpobr
dpf
ob
aprf
otr
che
apof
f
pf
p
B
post. end

TABLE 3-2: Parietal foramen (PF) length to width ratio in *Platecarpus* and *Plioplatecarpus* taxa.

| Taxa and specimens | PF length to width ratio | Average |
|---|---|---|
| *Platecarpus planifrons* | | |
| UALVP 24240 | 1.27 | 1.27 |
| *Platecarpus ictericus* | | |
| AMNH 1820 | 1.18 | 1.18 |
| *Plioplatecarpus nichollsae* | | |
| CMN 52261 | 2.20 | 1.91 |
| TMP 83.24.01 | 1.63 | |
| M 83.10.18 | 1.95 | |
| M 84.07.18 | 1.87 | |
| *Plioplatecarpus primaevus* | | |
| CMN 11835 | 1.67 | 1.64 |
| CMN 11840 | 1.60 | |
| *Plioplatecarpus houzeaui* | | |
| IRSNB R36 | 1.82 | 1.82 |

FIGURE 3-5. Plioplatecarpine postorbitofrontals in dorsal view. **A**, TMP 83.24.01, *Plioplatecarpus nichollsae*, right postorbitofrontal (diagram); **B**, same (photo); **C**, M 83.10.18, *Plio. nichollsae*, left postorbitofrontal; **D**, AMNH 1820, *Platecarpus ictericus*, right postorbitofrontal (reversed). **Abbreviations**: **apla**, articulation for frontal posterolateral ala; **apop**, articulation for postorbital process of parietal; **jp**, jugal process; **sqp**, squamosal process. Scale bars equal 5 cm.

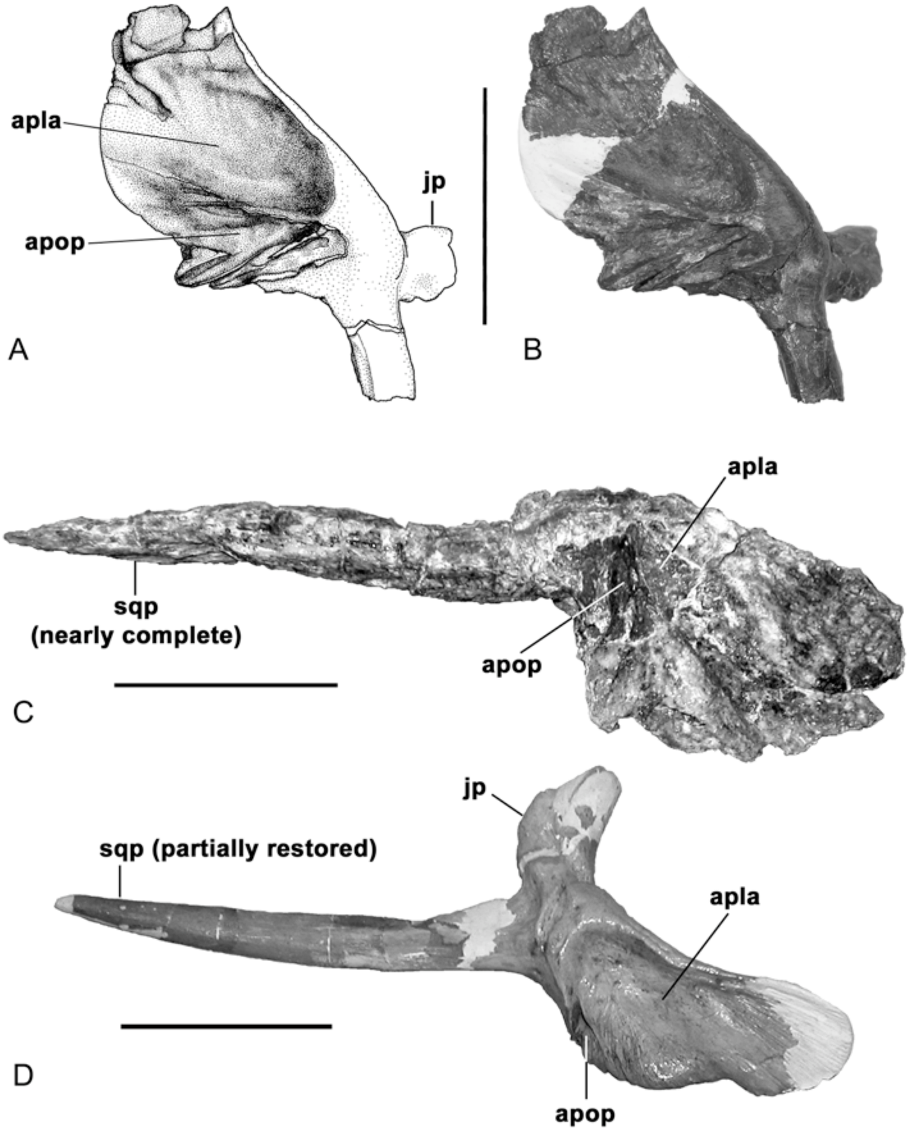

apla
jp
apop
A
B
apla
sqp
(nearly complete)
apop
C
jp
sqp (partially restored)
apla
D
apop

FIGURE 3-6. TMP 83.24.01, *Plioplatecarpus nichollsae* right postorbitofrontal in lateral view. **Abbreviation**: **avp**, anteroventral projection of jugal process.

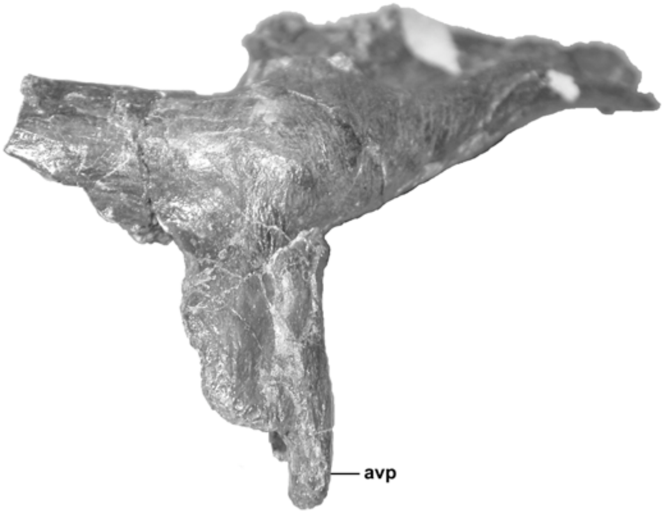

avp

FIGURE 3-7. TMP 83.24.01, *Plioplatecarpus nichollsae* left quadrate in posterolateral view. **A**, diagram; **B**, photo. **Abbreviations**: **ecl**, extracolumella (partial); **ip**, infrastapedial process; **mcd**, mandibular condyle; **qs**, quadrate shaft; **sp**, suprastapedial process. Scale bar equals 5 cm.

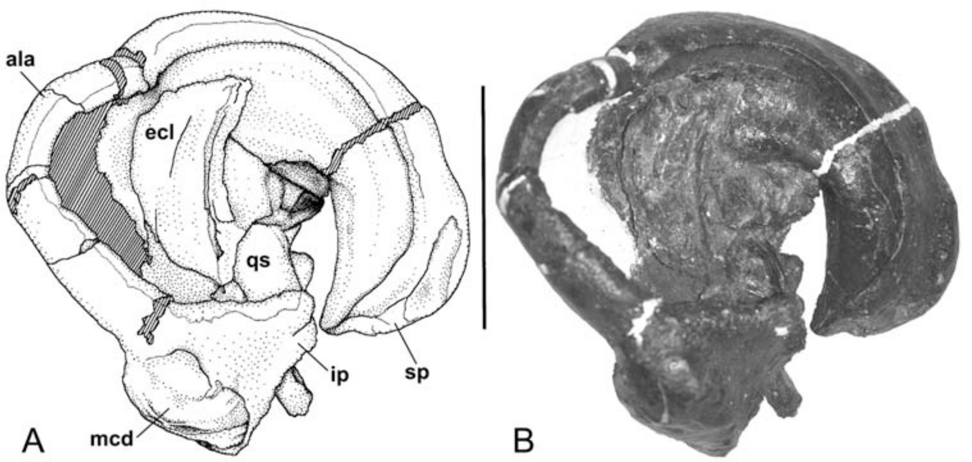

ala
ecl
qs
ip
sp
mcd
A
B

FIGURE 3-8. *Plioplatecarpus nichollsae* quadrates. (**A**-**F**) TMP 83.24.01 left quadrate. **A**, lateral view; **B**, medial view; **C**, anterior view; **D**, posterior view; **E**, dorsal view; **F**, ventral view. (**G-I**) M83.10.18 right quadrate (reversed). **G**, lateral view; **H**, dorsal view; **I**, medial view. **Abbreviations**: **ant-df**, anterior deflection of mandibular condylar surface; **ccd**, cephalic condyle; **spt**, stapedial pit; **vr**, medial vertical ridge. All the other abbreviations as in Figure 7. Note nearly complete extracolumella on M83.10.18. Scale bars equal 5 cm.

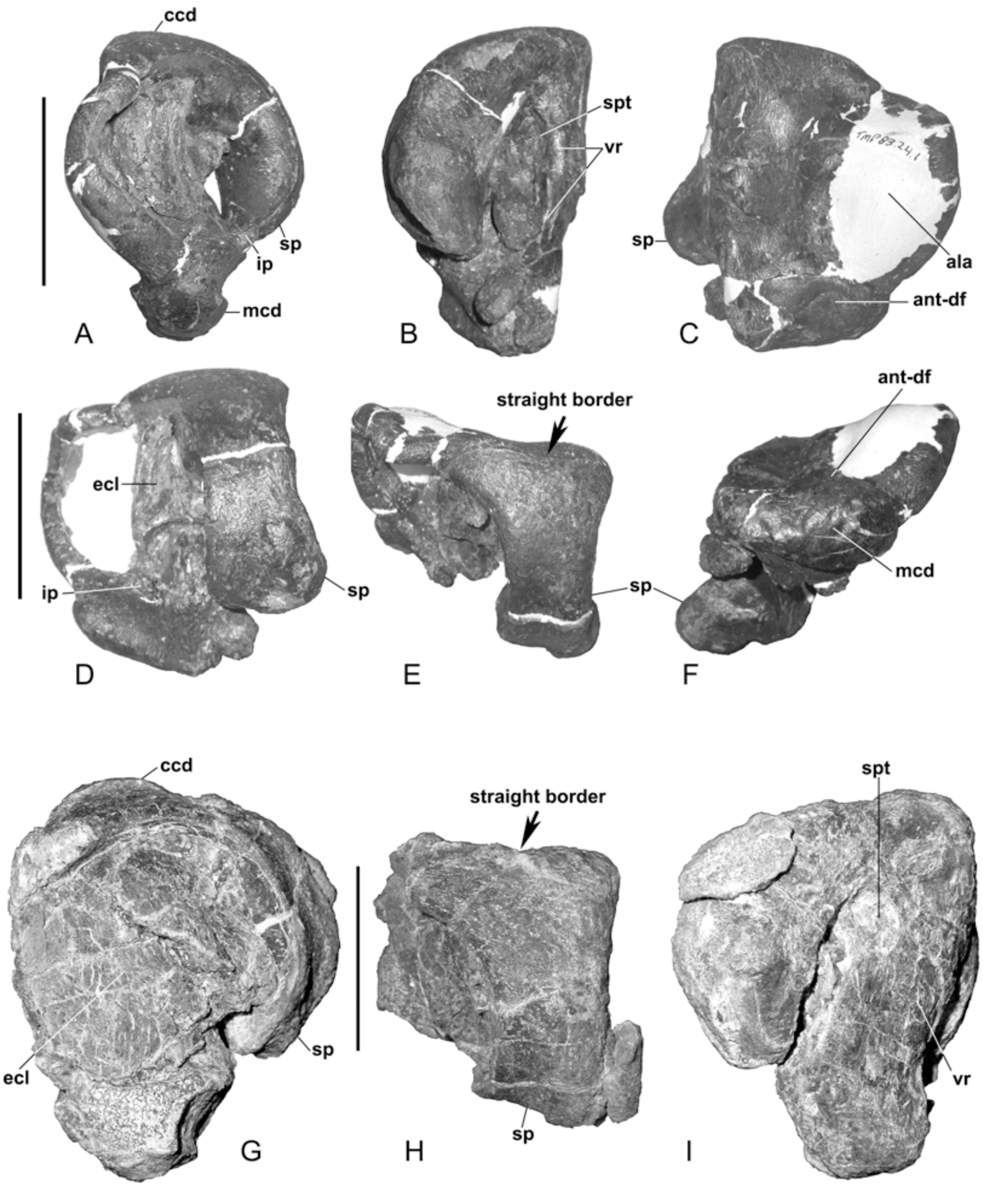

ccd
sp
ip
mcd
A
spt
vr
B
TMP 83.24.1
sp
ala
ant-df
C
ecl
ip
sp
D
straight border
sp
E
ant-df
mcd
F
ccd
ecl
sp
G
straight border
sp
H
spt
vr
I

FIGURE 3-9. TMP 83.24.01, *Plioplatecarpus nichollsae* braincase in dorsal view. **A**, diagram; **B**, photo. **Abbreviations**: **ap**, articulation for parietal; **aq**, articulation for quadrate; **asq**, articulation for squamosal; **asr**, articulation for suspensorial ramus; **lepp**, left epipterygoid; **lpo**, left prootic; **lpopr**, left paroccipital process; **lpt**, left pterygoid; **lsq**, left squamosal; **lst**, left supratemporal; **prpo**, prootic process of supratemporal; **ps**, parasphenoid; **repp**, right epipterygoid; **rpo**, right prootic; **rpopr**, right paroccipital process; **rpt**, right pterygoid; **rq**, right quadrate; **rsq**, right squamosal; **rst**, right supratemporal; **so**, supraoccipital. Scale bars equal 5 cm.

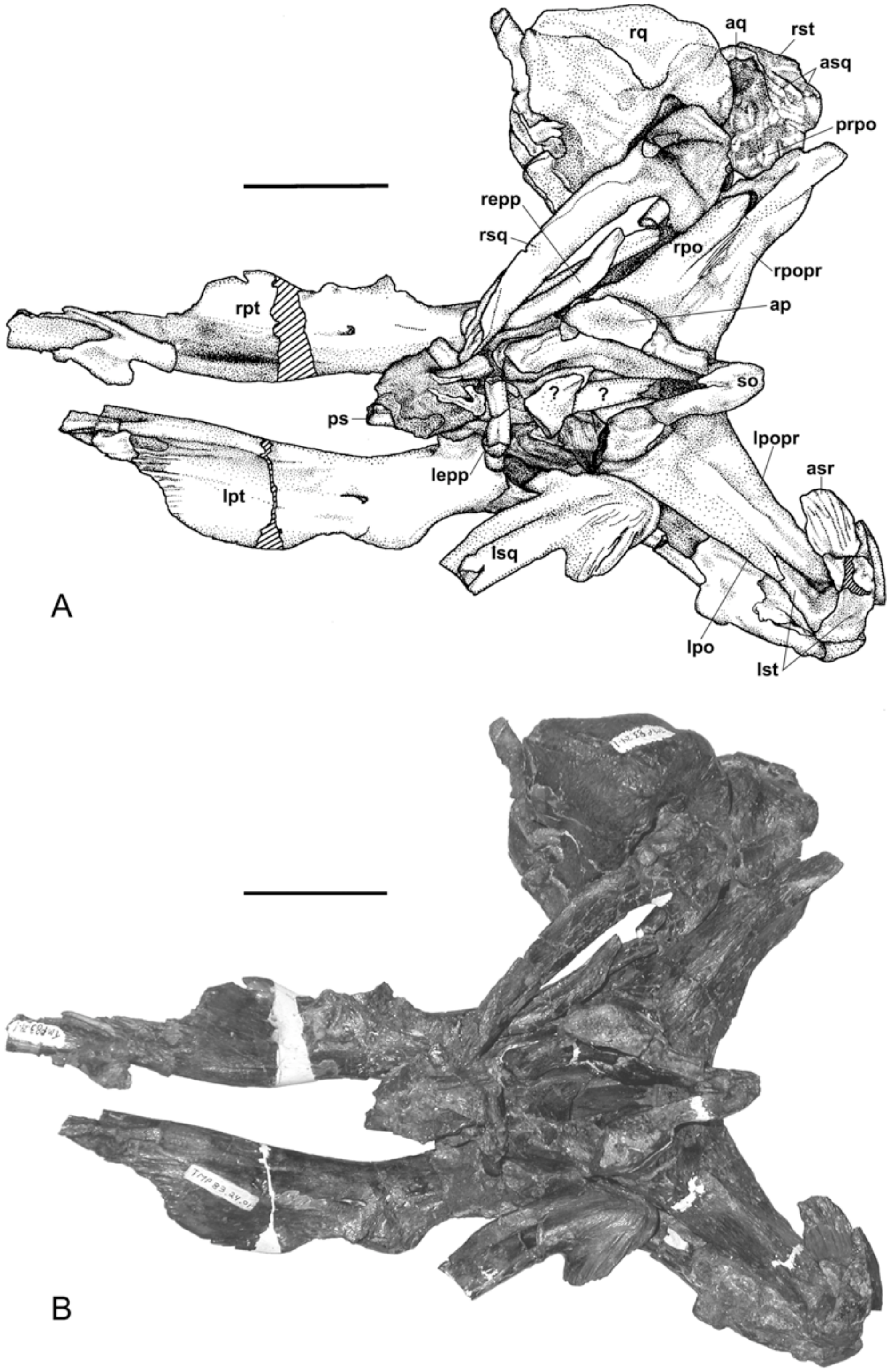

rq
aq
rst
asq
prpo
repp
rsq
rpo
rpopr
rpt
ap
so
?
?
ps
lpopr
asr
lepp
lpt
lsq
lpo
lst
A
B

FIGURE 3-10. TMP 83.24.01, *Plioplatecarpus nichollsae* braincase in ventral view. **A**, diagram; **B**, photo. **Abbreviations**: **aop**, supratemporal articulation for opisthotic; **bo**, basioccipital; **bs**, basisphenoid; **bsp**, basisphenoid process; **bt**, basal tuber; **ecl**, extracolumella (partial); **ecp**, ectopterygoid process; **lqr**, left quadrate ramus; **mcd**, mandibular condyle; **ocd**, occipital condyle; **rqr**, right quadrate ramus; **sp**, suprastapedial process. All the other abbreviations as in Figure 3-9. Scale bars equal 5 cm.

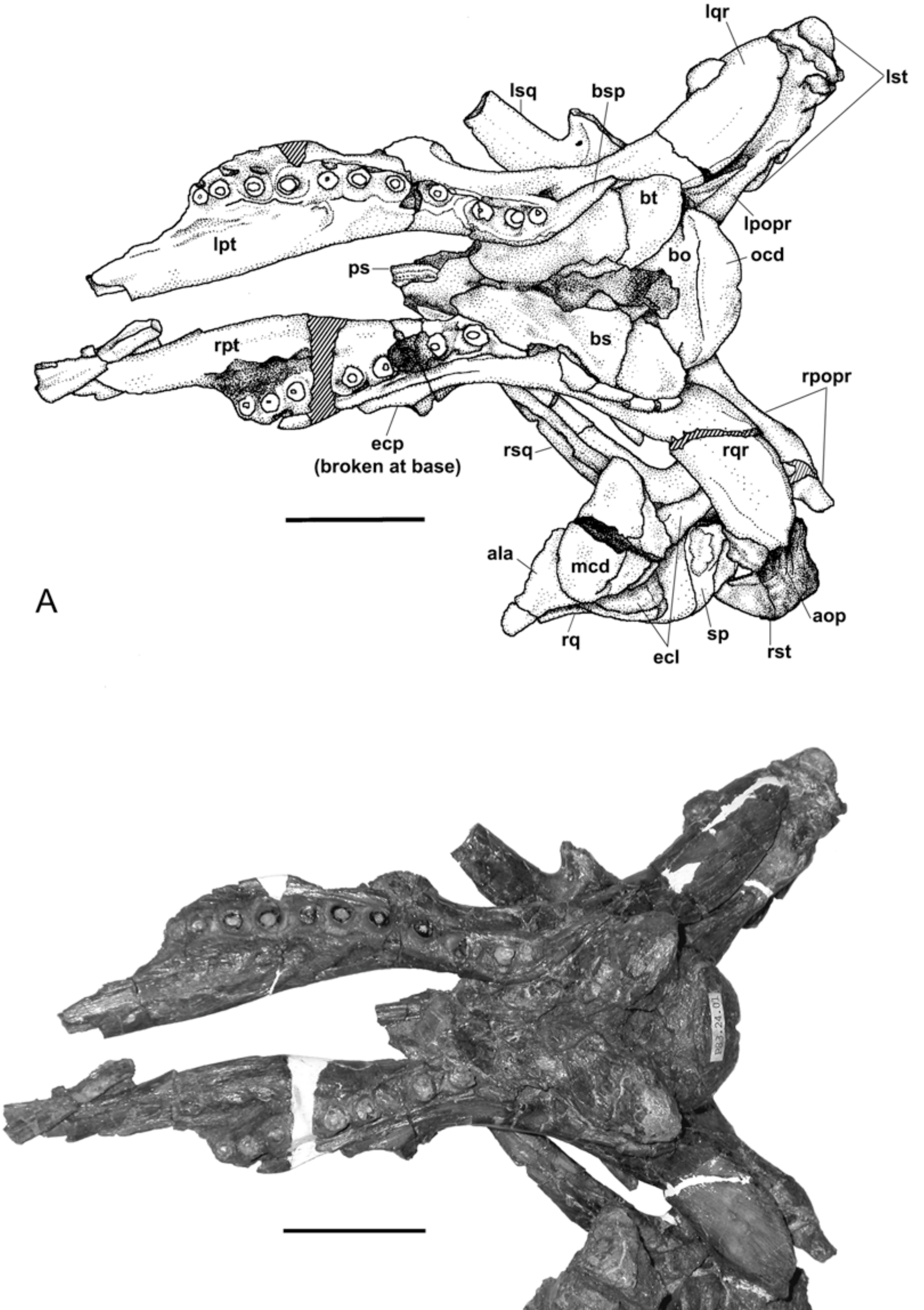

lqr
lst
lsq
bsp
bt
lpopr
lpt
ps
bo
ocd
rpt
bs
rpopr
ecp
(broken at base)
rsq
rqr
ala
mcd
aop
rq
ecl
sp
rst
A
B

FIGURE 3-11. TMP 83.24.01. *Plioplatecarpus nichollsae* braincase in condylar view. **Abbreviations**: **amp**, anteromedial process of supratemporal; **lbt**, left basal tuber; **leo**, left exoccipital; **lqcd**, left quadrate condyle (of supratemporal); **msc**, midsagittal crest of supraoccipital; **rbt**, right basal tuber; **reo**, right exoccipital; **rqcd**, right quadrate condyle; **vpr**, disto-ventral process of paroccipital process. All the other abbreviations as in Figures 3-9 and 3-10. Dashed lines indicate sutures between exoccipitals and occipital condyle. Quadrates removed from the image. Scale bar equals 5 cm.

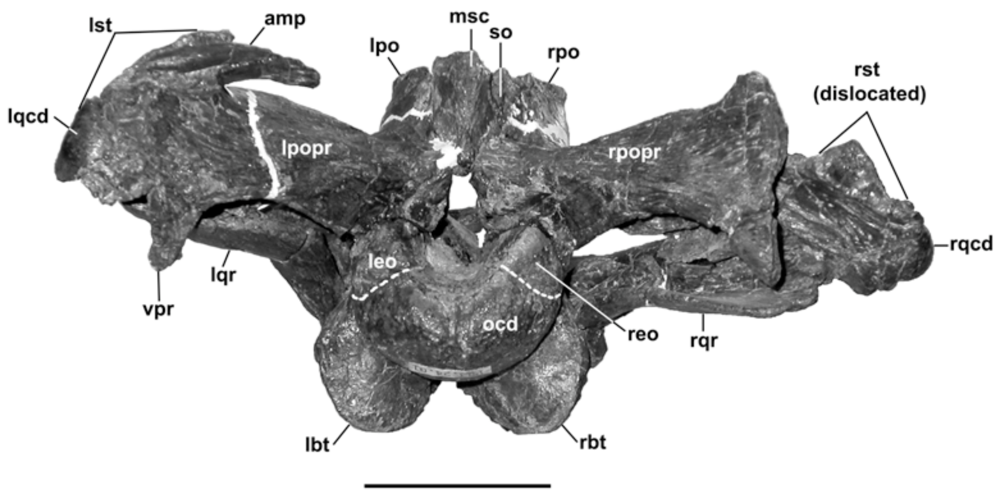

lst
amp
lqcd
lpo
msc
so
rpo
rst
(dislocated)
lpopr
rpopr
rqcd
leo
lqr
vpr
ocd
reo
rqr
lbt
rbt

FIGURE 3-12. TMP 83.24.01, *Plioplatecarpus nichollsae* anterior portion of vomers in ventral view. **Abbreviation**: **voc**, ventral oblique crest of vomer. Broken lines indicate approximate outline of missing posterior portion of right element. Note they are closely spaced. Scale bar equals 5 cm.

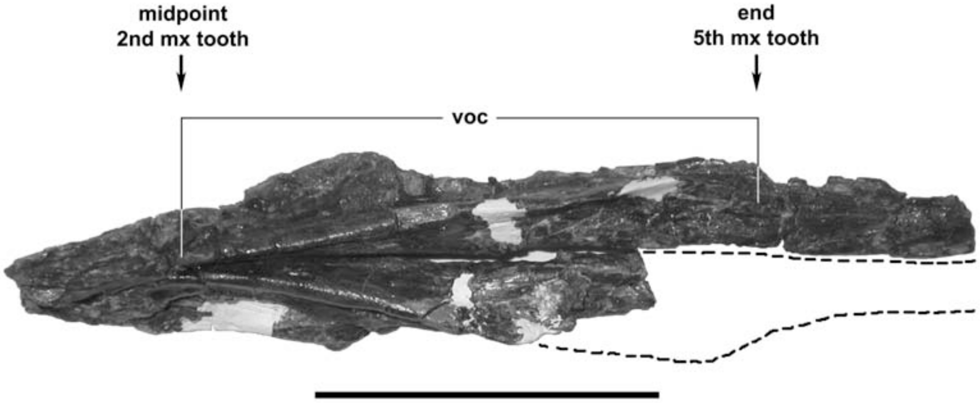

midpoint
2nd mx tooth
end
5th mx tooth
voc

FIGURE 3-13. TMP 83.24.01, right glenoid fossa of *Plioplatecarpus nichollsae*. **Abbreviations**: **ar**, articular; **gl**, glenoid fossa; **sa**, surangular. Broken line indicates boundary between surangular and articular. Note the surangular forming more than 50% of the glenoid fossa. Scale bar equals 5 cm.

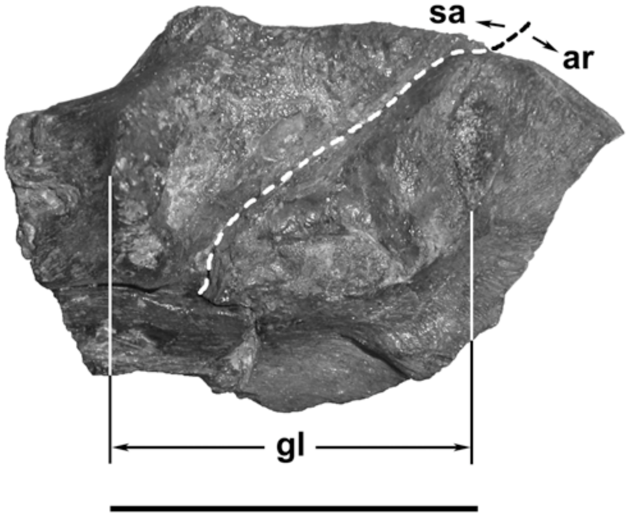

sa
ar
gl

FIGURE 3-14. TMP 83.24.01, *Plioplatecarpus nichollsae* anterior cervical vertebrae. (**A**-**E**) atlas-axis complex. **A**, anterior view; **B**, posterior view; **C**, left lateral view; **D**, dorsal view; **E**, ventral view. (**F**-**J**) third(?) cervical vertebra. **F**, anterior view; **G**, posterior view; **H**, right lateral view; **I**, dorsal view; **J**, ventral view. **Abbreviations**: **aa**, atlas neural arch; **ai**, atlas intercentrum; **ai-tub**, atlas intercentrum tuberosity; **asyn**, atlas synapophysial process; **axi**, axis intercentrum; **axi-tub**, axis intercentrum tuberosity; **axns**, axis neural spine; **cdl**, condyle; **ctl**, cotyle; **gv**, groove medial to atlas neural arch posterodorsal tuberosity; **hyp**, hypapophysis; **mak**, median anterior keel; **mpg**, median posterior groove; **mpk**, median posterior keel; **ns**, neural spine; **od**, odontoid (= atlas centrum); **poz**, postzygapophysis; **prz**, prezygapophysis; **sc-ins**, spinalis capitis muscle insertion surface; **syn**, synapophysis. Scale bars equal 5 cm.

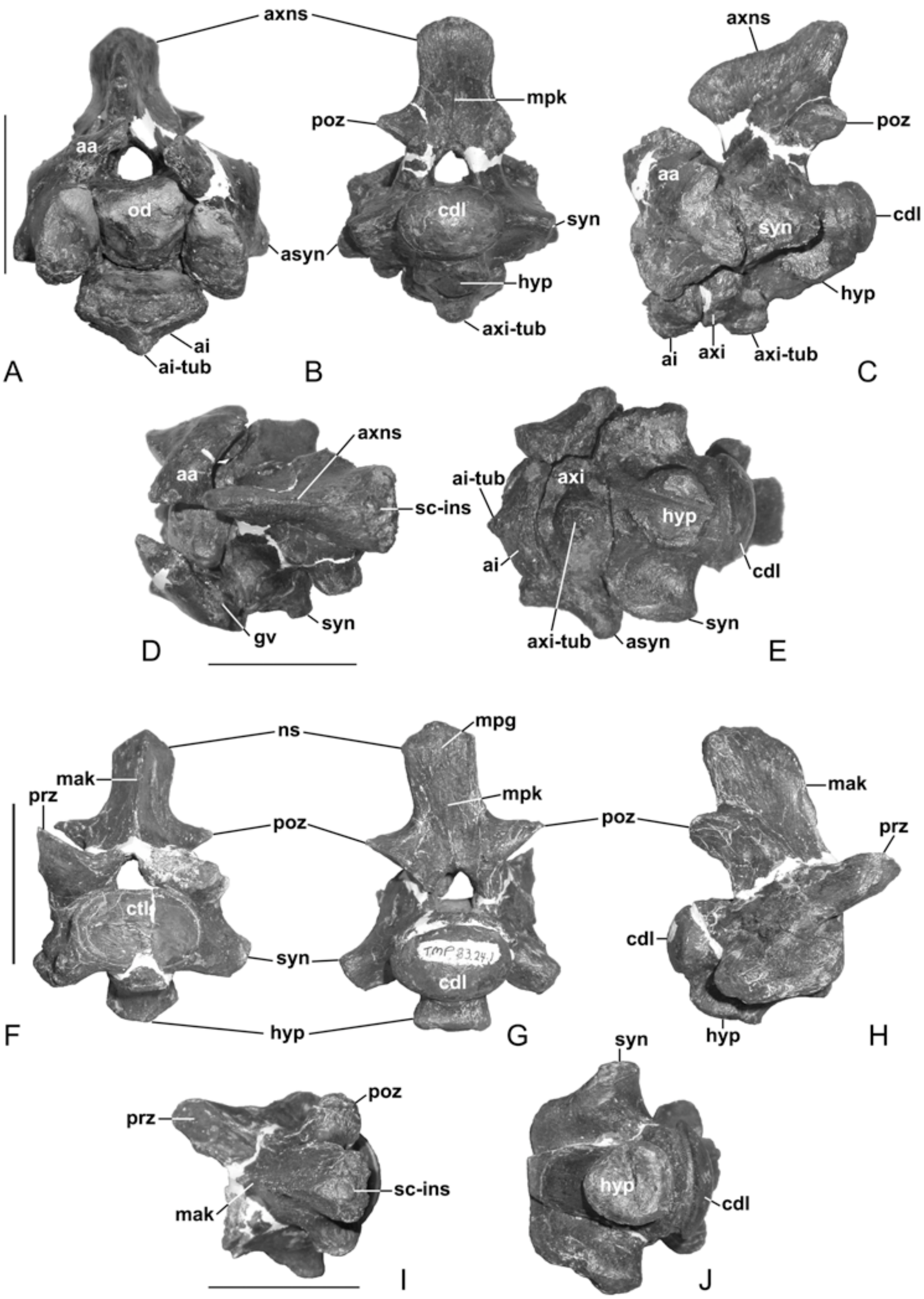
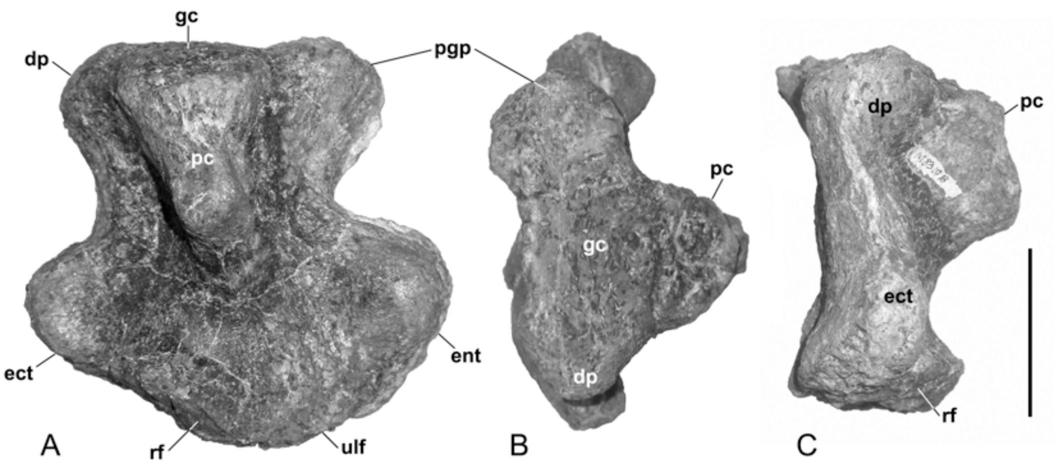

axns
aa
od
mpk
poz
cdl
syn
asyn
hyp
axi-tub
ai
ai-tub
axi
A
B
C
sc-ins
gv
D
E
ns
mpg
mak
prz
ctl
TMP 83.24.1
F
G
H
I
J

FIGURE 3-15. M 83.10.18, *Plioplatecarpus nichollsae* right humerus. **A**, medial view; **B**, dorsal view; **C**, anterior view. **Abbreviations**: **dp**, deltoid process; **ect**, ectepicondyle; **ent**; entepicondyle; **gc**, glenoid condyle; **pc**, pectoral crest; **pgp**, postglenoid process; **rf**, radial facet; **ulf**, ulnar facet. Scale bar equals 5 cm.


gc
dp
pgp
pc
ect
ent
rf
ulf
A
gc
pc
dp
B
dp
pc
ect
rf
C

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# CHAPTER FOUR

# REDESCRIPTION OF THE HOLOTYPE OF *PLATECARPUS TYMPANITICUS* COPE, 1869 (MOSASAURIDAE: PLIOPLATECARPINAE), AND THE ISSUE OF GENERIC NOMENCLATURE

To be submitted as: Konishi, T., and M. W. Caldwell. Redescription of the holotype of *Platecarpus tympaniticus* Cope, 1869 (Mosasauridae: Plioplatecarpinae), and the issue of generic nomenclature. Journal of Vertebate Paleontology.

# INTRODUCTION

*"It is a pity that little or nothing has been added to our knowledge of the southern and eastern species of this group [=* Platecarpus*] within the last twenty years [in North America]. Perhaps we may expect more definite knowledge concerning them in the immediate future"*—S. W. Williston (1897:185).

From Late Cretaceous strata of the Western Interior Basin in North America, over 3000 specimens of large, carnivorous marine reptile mosasaurs (Squamata: Mosasauridae) have been discovered since the early part of the 19th century (e.g., Russell, 1967, 1988; Nicholls, 1988; Kiernan, 2002; pers. observ.). Although the earliest description of a mosasaur specimen from the continent dates back to 1834 when a mosasaur snout was assigned to "*Ichthyosaurus*" *missouriensis* by Harlan (Caldwell and Bell, 2005), the sudden increase in the number of specimens collected occurred during the late 19th century, when E. D. Cope and O. C. Marsh began competing, i.e., the famous fossil feuds, over naming new fossil vertebrate taxa (e.g., Bell, 1997a; Everhart, 2005). Consequently, numerous fossil vertebrate species were erected by the two from the late 1860s to early 1880s, and among them were a number of mosasaur taxa (e.g., Cope, 1869, 1870a, 1871a, 1874; Marsh, 1872, 1880). Due to the intense nature of the competition, however, the holotype materials tended to be poor in quality, and their descriptions often lacked figures of the specimen (e.g., Cope, 1869, 1870b, 1871b; Marsh, 1880).

The holotype and only specimen of the mosasaur *Platecarpus tympaniticus*, the generic type, typifies this issue (Cope, 1869). The specimen was collected from the Tombigbee Sand Member of the Eutaw Formation near Columbus, Mississippi, U.S.A., and is late Santonian to earliest Campanian in age (ca. 84 to 83 Ma) (Leidy, 1865; Cope, 1869; Russell, 1967; Kiernan, 2002; Ogg et al., 2004). The holotype originally included a chelonian humerus as well as mosasaurid cranial fragments and three anterior vertebrae (Leidy, 1865; Cope, 1869; pers. observ.). Leidy (1865) provided the first description of the holotype with some specimen illustrations and various measurements, and provisionally referred the material to *Holcodus acutidens* Gibbes, 1851. However, since this taxon was earlier established based only on three teeth that also included a crocodilian tooth (Gibbes, 1851; Leidy, 1865), Cope (1869) erected *Platecarpus tympaniticus* to which he assigned 'Leidy's holotype'. In proposing this new taxon, Cope (1869) merely devoted half a page to the holotype description and the species diagnosis, and in this case, neither measurements nor figures were included (cf. Konishi and Caldwell, 2007). Six years later, Cope (1875) figured the right quadrate of the holotype (reversed in his figure) for the first time (contra Konishi and Caldwell, 2007), but no further description was provided.

While the holotype of *Platecarpus tympaniticus* continued to be the only specimen of the genus reported from Late Cretaceous strata of the eastern Gulf, as many as 17 additional species of *Platecarpus* were recognized between 1870 and 1898, based on the material collected almost exclusively from western Kansas, U.S.A. (Cope, 1874; Merriam, 1894; Thevenin, 1896; Williston, 1898). During this period, Cope named a total of eight *Platecarpus* species (Cope, 1874) while Marsh named four, though the latter used the name *Lestosaurus* instead (Marsh, 1872; Russell, 1967). Although not finding the high number of species assigned to *Platecarpus* particularly problematic, Williston (1897) first addressed the taxonomic issues concerning the genus *Platecarpus*, stating that the congeneric status of *Platecarpus tympaniticus* from Mississippi with the "Kansas species" assigned to this genus had yet to be established conclusively (p. 185). Williston (1897:185) based his argument on the fact that "very little of the skeleton has been described" of *P. tympaniticus*: at the same time, he also acknowledged that there is a high degree of similarity in the quadrate morphology between the Mississippi and Kansas forms, and that the quadrate of *Platecarpus* is highly characteristic among mosasaurs. Subsequently, in his synthetic work on the systematics of European and North American mosasaurs, Williston (1898) reiterated these issues concerning *Platecarpus* almost word by word, retained the genus, and assigned a total of fourteen species to it. Williston (1898) neither included nor re-described *Platecarpus tympaniticus*, merely hoping that the knowledge of the east Gulf species would increase "in the immediate future" (p. 180).

Thus, the question of whether or not *Platecarpus tympaniticus* is congeneric with other species assigned to the genus was raised by Williston (1897, 1898), but never answered. Seventy years later, the question was resurrected by Russell (1967) who recognized only five species of *Platecarpus* from North America, but considered that the fragmentary holotype and only specimen of *P. tympaniticus* was diagnosable at the generic level (quadrate characters and general braincase and vertebral morphology). Consequently, Russell (1967) supported the nomenclatural seniority of *Platecarpus* Cope, 1869, over *Lestosaurus* Marsh, 1872 (cf. Cope, 1874; Williston, 1898). He also invalidated *Holcodus* Gibbes, 1851, thereby recognizing *Platecarpus* as the oldest available generic name between the two (Russell, 1967). However, Russell (1967) did not provide a species diagnosis for *P. tympaniticus*. Instead, he only acknowledged that the cranial material of the holotype is morphologically identical to corresponding elements of the two species from Kansas: *P. ictericus* (Cope, 1870a), and *P. coryphaeus* (Cope, 1871a). He further suggested that one of them might be a junior synonym of the generic type once the "anterior portions of the skull of *P. tympaniticus* are discovered in the Eutaw Formation" (Russell, 1967:153). However, this simply indicated that the holotype of *P. tympaniticus* is not diagnosable to the species level by itself, potentially making it a nomen dubium.

Reviewing the taxonomy of *Platecarpus*, Konishi and Caldwell (2007) realized the above issue and urged that redescription of the *Platecarpus tympaniticus* holotype and re-diagnosis of all other species are necessary before the nomenclatural seniority of the species over any other congener could be considered (Nichols, 1988; Bell, 1993, 1997b; Schumacher, 1993; Sheldon, 1996; Everhart, 2001; Bell and Polcyn 2005; Polcyn and Bell, 2005a). Konishi and Caldwell (2007) also concluded that *P. coryphaeus* is a junior synonym of *P. ictericus*, as they did not consider Russell's (1967) proposed characters separating them to be significant taxonomically. In addition, Konishi and Caldwell (2007) suggested that another valid species of *Platecarpus* from North America, *P. planifrons* (Cope, 1874), could be clearly distinguished from the holotype of *P. tympaniticus* using quadrate characters.

While a study presented in Chapter 5 of this thesis strongly demonstrates that *P. planifrons* likely belongs to a distinct genus closely related to *Platecarpus*, the synonymy of *P. ictericus* and *P. coryphaeus* still seems certain. At the same time, Konishi and Caldwell (2009) reported that the quadrate morphology of *Plioplatecarpus nichollsae* Cuthbertson et al., 2007, is virtually indistinguishable from that of *Platecarpus ictericus*. Following Russell (1967) and Konishi and Caldwell (2007, 2009), the quadrate of the holotype *Platecarpus tympaniticus* can diagnose both *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, challenging Williston (1897, 1898) and Russell's (1967) belief that the quadrate of *Platecarpus* is very characteristic among mosasaurs, and by inference should diagnose the genus. We therefore need to describe the holotype of *Platecarpus tympaniticus* fully including the quadrate, and compare it particularly with the aforementioned two plioplatecarpine taxa in order to examine whether *Platecarpus tympaniticus* is a valid taxon or not.

**Institutional Abbreviations**—**ALMNH PV**, Alabama Museum of Natural History, Tuscaloosa, Alabama, USA; **AMNH**, American Museum of Natural History, New York, New York, USA; **ANSP**, Academy of Natural Sciences Philadelphia, Philadelphia, Pennsylvania, USA; **BMNH R**, The Natural History

Museum, London, United Kingdom; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **FHSM VP**, Fort Hays Sternberg Museum of Natural History, Hays, Kansas, USA; **FM UC**, Field Museum, Chicago, Illinois, USA; **KU**, University of Kansas Natural History Museum, Lawrence, Kansas, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **RMM**, McWane Science Center (former Red Mountain Museum), Birmingham, Alabama, USA; **UW**, University of Wisconsin-Madison Geology Museum, Madison, Wisconsin, USA; **YPM**, Yale University Peabody Museum of Natural History, New Havens, Connecticut, USA.

## MATERIALS AND METHODS

The holotype of *Platecarpus tympaniticus* is comprised of nine numbered specimens, all attributed to a single individual (Leidy, 1865): ANSP 8484, a partial left surangular; ANSP 8487, a right quadrate; ANSP 8488, a nearly complete anterior cervical vertebra; ANSP 8491, a partial right pterygoid; ANSP 8558, a partial posteriormost cervical vertebra; ANSP 8559, a partial posterior cervical vertebra; ANSP 8562, a partial basioccipital-basisphenoid complex; and ANSP 8488, jaw fragments associated with a block of matrix. All elements have been regarded as pertaining to the same individual (Leidy, 1865). ANSP 8491, the partial pterygoid, is currently missing but figured in Leidy (1865:pl. XI, fig. 14; see also Konishi and Caldwell [2007:fig. 8B]). These elements were photographed and the description given here is based on observation of the material. Outline drawings of ANSP 8487 (the quadrate) and 8562 (the braincase) were produced from photographs using Adobe Photoshop 7.0 for Windows, printed out and hand-stippled, and then scanned a second time to create the respective figures.

## DESCRIPTIONS AND COMPARISONS

### Cranial Elements

**Right Quadrate (ANSP 8487: Fig. 4-1; Cope, 1875:pl. XXXVII, fig. 11)**—the element is relatively complete and undistorted. It is approximately as wide as it is anteroposteriorly elongate, owing mainly to the great lateral expansion of the tympanic ala (Cope, 1869; Fig. 4-1). The suprastapedial process is laterally unconstricted and elongate, its length being about two-thirds the height of the quadrate shaft. The process exhibits a rounded expansion at its distal end (Fig. 4-1B). The anterior border of the cephalic condyle is not markedly notched posteriorly, and its anteromedial corner is gently rounded in dorsal view, similar to *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, but differing from *Platecarpus planifrons* where the same corner develops into an acute crest (Fig. 4-1D; Konishi and Caldwell, 2007:fig. 7; Konishi and Caldwell, 2009:fig. 8E). In dorsal aspect, the quadrate ala extends laterally from the quadrate shaft, forming a right angle with the long axis of the suprastapedial process, most similar to *Platecarpus ictericus* and *Plioplatecarpus nichollsae* but less so to *P. planifrons* (same figure references as above). An undistorted rim of the ala forms a nearly perfect semi-circle (Fig. 4-1A).

On the medial surface, the quadrate bears a gently domed medial vertical ridge that extends approximately along the dorsal two-thirds of the shaft (Fig. 4-1C). This condition differs in *Platecarpus planifrons*, where a thin, well-developed vertical crest is present in the same region (Konishi and Caldwell, 2007:fig. 6B). Immediately below this ridge, the medial face of the mandibular condyle is shallowly excavated, most presumably for the loose articulation with the quadrate ramus of the pterygoid. The broadly oval stapedial pit has straight lateral borders, typical of the condition in *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, while it is keyhole shaped in *Platecarpus planifrons* (Konishi and Caldwell, 2007:fig. 6B).

In ventral view, the mandibular condyle is transversely elongate (Fig. 4-1E). The anterior deflection of the condylar surface has been damaged, and as a consequence the anterior condylar border is incomplete. However, the condyle most likely formed a curved teardrop-shape in outline similar to *Platecarpus ictericus* and *Plioplatecarpus nichollsae*. The posteroventral border of the quadrate shaft is straight in medial view (Fig. 4-1C; Konishi and Caldwell, 2009:fig. 7). The degree of development of the infrastapedial process is unclear as the posteroventral portion of the tympanic ala is most likely incomplete and covered by matrix. In both *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, the infrastapedial process extends posterodorsally immediately lateral to the posteroventral corner of the quadrate shaft. In many specimens of *Platecarpus ictericus*, the process is long and contacts the disto-lateral corner of the suprastapedial process, while in the well-preserved quadrate of *P. nichollsae*

(TMP 83.24.01), the process is small and widely separated from the suprastapedial process (compare Russell, 1967:figs. 24B, 25A; Konishi and Caldwell, 2009:figs. 7, 8D). Whether this difference is taxonomic or not cannot be determined conclusively until more specimens of the latter taxon become available in the future.

Overall, no major features separate the quadrate morphology of the holotype of *Platecarpus tympaniticus* from that of *P. ictericus* or *Plioplatecarpus nichollsae*, and any minor differences are those that vary intraspecifically in each of the latter two species.

**Basioccipital-Basisphenoid (ANSP 8562: Fig. 4-2)**—Although the basioccipital-basisphenoid complex is not very distorted, the smooth bone surface in general indicates a certain degree of weathering, and its dorsal portion has been severely broken. The relatively well-preserved ventral surface is solid except for some small foramina. The paired basal tubera are not very inflated and are well separated from each other, a condition more similar to *Platecarpus planifrons* and *P. ictericus* than to *Plioplatecarpus nichollsae* (Konishi and Caldwell, 2009). Between the pair of posterolateral processes of the basisphenoid is a single ventral foramen with an irregular outline, situated at the sutural contact between the basisphenoid and basioccipital (Fig. 4-2D). Anterior to this foramen, a distinct longitudinal sulcus separates the posterolateral processes of the basisphenoid, extending forward and gradually shallowing along its course.

When viewed laterally, the distal surface of the basal tubera is distinctly notched dorsally, forming a C-shape. The descending process of the opisthotic wraps the dorsolateral portion of the tuber. Due to surface erosion, no exits for any cranial nerves can be discerned on the lateral wall of the opisthotic (Fig. 4-2E).

In posterior aspect, the surface of the occipital condyle is only shallowly sulcate along the vertical midline, likely reflecting some erosion (Fig. 2B). The overall orientation of the shallowly concave sutural surface between the basioccipital and exoccipital is horizontal, as seen in *Platecarpus ictericus* (e.g., AMNH 1820; Russell, 1967:fig. 17). In *Plioplatecarpus nichollsae* and *P. primaevus*, the suture slants lateroventrally (Konishi and Caldwell, 2009). In comparison to *Plioplatecarpus nichollsae*, the wide separation of the paired basal tubera in ANSP 8562 is obvious in posterior aspect as well (Fig. 4-2B; Russell, 1967:fig. 17; Konishi and Caldwell, 2009:fig. 11). The foramen magnum is taller than wide. Little more can be said about other parts of the braincase.

**Pterygoid (ANSP 8491: Leidy, 1865:pl. XI, fig. 14; Konishi and Caldwell, 2007:fig. 8B)**—As Konishi and Caldwell (2007) pointed out, the partial right pterygoid bearing five teeth and three vacant alveoli, as described by Leidy (1865), is currently missing. According to Leidy (1865:72), this partial pterygoid measured “three inches [= 7.6 cm] long,” a comparable size to be considered as part of the holotype material. Each of the preserved pterygoid teeth has “a circular base, and are strongly curved backward” (Leidy, 1865:73). These teeth are also divided approximately into two halves by two carinae, one occurring on the medial and the other occurring on the lateral surface of each crown (Leidy, 1865). According to Leidy (1865), the teeth were also striated on both anterior and posterior faces. These fine surface features on each pterygoid tooth crown are common to the specimens of *Platecarpus planifrons*, *P. ictericus*, and *Plioplatecarpus nichollsae* examined. Although Leidy (1865) considered it to be the left pterygoid, his description as well as figure indicate that it came from the right side, particularly based on the position of the resorption pits (Leidy, 1865:pl. XI, fig. 14; Konishi and Caldwell, 2007).

**Surangular (ANSP 8484)**—The partial left surangular deepens anteriorly as in *Platecarpus* and *Plioplatecarpus nichollsae*. The dorsal border is gradually elevated anteriorly to form a coronoid buttress, whereas the same border generally remains horizontal in *Platecarpus planifrons*. The element bears a distinct horizontal ridge on the medial surface forming an overhanging shelf at its mid-height, under which the prearticular would have fitted. The lateral cortical surface is variably eroded, and the ventral, anterior, and posterior borders are all incomplete. The glenoid portion of the surangular is missing.

## Postcranium

**Cervical Vertebrae (ANSP 8488, 8558-59: Leidy, 1865:pl. VII, figs. 4–7; Konishi and Caldwell, 2007:fig. 8A, C–E)**—All three vertebrae are figured in Leidy (1865). ANSP 8488 and 8559 bear well-developed hypapophyses with a distinct facet for an intercentrum. On the former vertebra, the facet is broadly drop-shaped with its apex pointing anteriorly, while it is smaller with a longitudinally elongate elliptical outline on the latter. Along with the fact that the synapophyseal facets are taller in ANSP 8559 than in 8488, the latter must have come from a more anterior part of the cervical column. In ANSP 8558, although the “hypapophysis is a mere rudiment” (Leidy, 1865:38), and apparently lacked an associated intercentrum, its articular cotyle fits well with the articular condyle of ANSP 8559, indicating that they are adjoining vertebrae. Compared with a complete cervical series of cf. *Platecarpus ictericus* (AMNH 2005 and YPM 24900), ANSP 8488 is probably the fourth and ANSP 8559 is the fifth or sixth vertebra. In AMNH 2005 and YPM 24900, the last intercentrum-bearing cervical is the sixth, with the seventh exhibiting only a rudimentary median ventral tuberosity (Russell, 1967:fig. 40). As ANSP 8559 most probably articulated with ANSP 8558, they are interpreted here as the sixth and seventh cervical vertebrae, respectively. In the holotype *Plioplatecarpus nichollsae* (CMN 52261), the seventh cervical vertebra clearly articulated with an intercentrum (Cuthbertson et al., 2007).

In all vertebrae, the intervertebral joint surface exhibits strong curvature as in *Platecarpus ictericus*, but not in *Plioplatecarpus nichollsae* (Leidy, 1865:pl. VII, figs. 4, 5; Konishi and Caldwell, 2009:fig. 14H). The articular surface is transversely oval, where the articular condyle width exceeds its height by 30% and 25% in ANSP 8488 and ANSP 8559, respectively (the condyle is incomplete in the last cervical, ANSP 8558). The neural spine is more erect and taller in the posterior one. A distinct rounded crest connects the well-developed prezygapophysis with the synapophysis where preserved. From the ventral corner of the synapophyseal facet, a horizontal ridge extends anteriorly to connect itself to the lateroventral corner of the cotylar rim. Each postzygapophyseal facet faces lateroventrally at approximately 60 degrees from the horizontal (Leidy, 1865:pl. VII, fig. 6). The presence of zygosphenes cannot be confirmed in any vertebra due to preservational artifacts, but a shallow, posteriorly facing oval depression at the base of the right postzygapophysis on ANSP 8559 indicates the presence of zygantra in the posterior cervicals.

## TAXONOMIC DISCUSSION

The fragmentary nature of the holotype of *Platecarpus tympaniticus* has created a taxonomic problem for well over a century (e.g., Williston, 1897; Russell, 1967; Konishi and Caldwell, 2007). It has made it difficult for this taxon to be diagnosed against other plioplatecarpine species, inclusive of new taxa such as *Plioplatecarpus nichollsae*. No dermal skull elements such as a frontal and/or a parietal are preserved with the holotype material. According to our re-description, morphology of the well-preserved right quadrate ANSP 8487 (Fig. 4-1) cannot be discriminated taxonomically from that of *Platecarpus ictericus* (late Santonian to early Campanian) and *Plioplatecarpus nichollsae* (earliest middle Campanian) (Gill and Cobban, 1965; Nicholls, 1988; Ogg et al., 2004; Everhart, 2005; Cuthbertson et al., 2007; Konishi, 2008; Konishi and Caldwell, 2009). As both the pterygoid and surangular are poorly preserved in the holotype, the partial basioccipital-basisphenoid complex (ANSP 8562) and three cervical vertebrae (ANSP 8488, 8558-59) are the only elements of the specimen that assist in determining its species-level identity.

The preserved portion of the basioccipital-basisphenoid complex (Fig. 4-2) shows a couple of important characters that characterize *Platecarpus ictericus* but not *Plioplatecarpus nichollsae*. In posterior view, the suture between the exoccipital and occipital condyle is relatively horizontal in orientation (Fig. 2B). In *Plioplatecarpus nichollsae* as well as in *P. primaevus*, the suture is lateroventrally inclined, thereby decreasing the relative area of the occipital condyle exposed in condylar view (Konishi and Caldwell, 2009:fig. 11). In *P. nichollsae*, a pair of bulbous basal tubera protrudes more ventrally and towards the midline, a defining feature of this species (Konishi and Caldwell, 2009). In ANSP 8562 as well as in the holotypes of *Platecarpus ictericus* (AMNH 1559) and *P. coryphaeus* (AMNH 1566), the tubera are not inflated, are more widely separated from each other along the midline, and project more laterally (Fig. 4-2; cf. Russell, 1967:fig. 17).

When the general morphology of the cervical vertebrae is considered, the significant curvature of the intervertebral joint as seen in the holotype of *Platecarpus tympaniticus* is shared with *Platecarpus ictericus*, but not with *Plioplatecarpus nichollsae* (compare Leidy, 1865:pl. VII, figs. 4, 5; AMNH 1559 [*Plat. ictericus* holotype]; Konishi and Caldwell, 2009:fig. 14H [*Plio. nichollsae*]). In fact, the decrease in the intervertebral joint curvature in the cervical column is a shared derived character among the most derived plioplatecarpines, occurring in *Plioplatecarpus nichollsae* and all the other nominal *Plioplatecarpus* species (Holmes, 1996; Konishi and Caldwell, 2009; pers. observ.).

In addition, one of Russell's (1967) diagnostic characters for the genus *Platecarpus* was that the total number of intercentrum-bearing cervical vertebrae should be five; i.e., from the axis to the sixth vertebra. According to our comparative observations, ANSP 8558 was identified as the seventh cervical vertebra, while its hypapophysis is a rudimentary projection lacking an articular facet for the eighth intercentrum. In contrast, a fully articulating hypapophysis is present on the same vertebra in the holotype of *Plioplatecarpus nichollsae* (Cuthbertson et al., 2007). This indicates not only that the holotype of *Platecarpus tympaniticus* exhibits the condition that Russell (1967) identified as diagnostic of *Platecarpus*, but also that based on this character, it is distinct from *Plioplatecarpus nichollsae*.

Based on the suite of quadrate, basioccipital, and vertebral characters that we identified above, it seems most likely that the holotype and only specimen of *Platecarpus tympaniticus* is indistinguishable from *P. ictericus* but is distinct from all other known plioplatecarpines. Based on nearly 500 plioplatecarpine specimens, it is found that little morphological evidence contradicts the synonymy of the two taxa (we likewise find no reasonable support for distinguishing *P. ictericus* and *P. coryphaeus* [cf. Konishi and Caldwell, 2007]).

The conclusion derived here is also in accordance with the age of the holotype of *Platecarpus tympaniticus* as late Santonian/earliest Campanian (ca. 84 to 83 Ma) (Kiernan, 2002; Ogg et al., 2004). Although based on a small sample size, Konishi (2008) suggested that in the Smoky Hill Chalk Member exposed in west-central Kansas, *P. ictericus* is known from the strata at Marker Unit 11 or above (late Santonain to early Campanian [ca. 84 to 81 Ma]) (Hattin, 1982; Ogg et al., 2004; Everhart, 2005). On the other hand, *Plioplatecarpus nichollsae* occurs in the lowermost middle Campanian (ca. 80.5 Ma) (Gill and Cobban, 1965; Nicholls, 1988; Ogg et al., 2004), adding support for the conclusion that *Platecarpus ictericus* is conspecific with *Platecarpus tympaniticus*.

Finally, although much fewer in number in comparison to those from western Kansas, several mosasaur specimens that are morphologically comparable to the holotype of *Platecarpus tympaniticus* have been collected from the lower part of the lower unnamed member of the Mooreville Chalk, early Campanian in age, in west-central Alabama (e.g., ALMNH PV 985.0021; RMM 1903; 7070 [in part]) (Kiernan, 2002; Mancini and Puckett, 2005). As *Platecarpus planifrons* contemporaneously occurred in both western Kansas and central Alabama (Konishi, 2008), this indicates that *P. tympaniticus* also simultaneously inhabited the Western Interior Seaway south of Kansas to the Gulf of Mexico. Hence, palaeobiogeographic evidence also seems to support the notion that *P. tympaniticus* is a senior synonym of *P. ictericus*.

## CONCLUSIONS

Although Konishi and Caldwell (2007) suggested that the holotype of *Platecarpus tympaniticus* may not be diagnosable as a senior synonym of *Platecarpus ictericus*, the above re-description of the holotype, and a character comparison with other, closely related plioplatecarpine species, indicated that the specimen exhibited characters that also diagnose *P. ictericus* to the exclusion of any other mosasaur. As well, the stratigraphic occurrence of the Mississippi holotype also conforms to the known taxon range zone of *Platecarpus ictericus* in Kansas, and since a couple of plioplatecarpine specimens from the equivalent horizons in Alabama are indistinguishable in form to the holotype, it is concluded that *Platecarpus tympaniticus* Cope, 1869, is a senior synonym of *Platecarpus ictericus* Cope, 1870a. Following Konishi and Caldwell's (2007) taxonomy of *Platecarpus*, it would be reasonable to conclude that there are two species within the genus, i.e., *P. tympaniticus* (generic type) and *P. planifrons* (Cope, 1874). However, the global plioplatecarpine phylogenetic analysis presented in Chapter 5 indicates that *Platecarpus planifrons* should be considered a distinct genus from *Platecarpus*. Consequently, we recognize the genus *Platecarpus* to be monotypic.

## SYSTEMATIC PALAEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

MOSASAURIDAE Gervais, 1852

RUSSELLOSAURINA Bell and Polcyn, 2005

PLIOPLATECARPINAE Dollo, 1884

*PLATECARPUS* Cope, 1869

*Platecarpus* Cope, 1869:264.

*Holcodus* Cope, 1871b:269.

*Liodon* Cope, 1871b:273 (in part).

*Lestosaurus* Marsh, 1872:454.

*Holosaurus* Marsh, 1880:87.

**Generic Type**—*Platecarpus tympaniticus* Cope, 1869, by monotypy.

**Diagnosis**—As for species.

### *PLATECARPUS TYMPANITICUS* Cope, 1869

(Figs. 4-1–4-2)

?*Holcodus acutidens* Gibbes, 1851: Leidy, 1865:118, pl. VII, figs. 4-7, pl. XI, fig. 14 (nomen dubium).

*Platecarpus tympaniticus* Cope, 1869:265.

*Liodon ictericus* Cope, 1870a:572 (first usage).

*Liodon mudgei* Cope, 1870a:572 (first usage).

*Liodon ictericus* Cope, 1870a: Cope, 1870b:577 (original description).

*Liodon mudgei* Cope, 1870a: Cope, 1870b:581 (original description).

*Holcodus coryphaeus* Cope, 1871a:298 (first usage).

*Holcodus ictericus* (Cope, 1870a): Cope, 1871a:298 (new combination).

*Liodon curtirostris* Cope, 1871a:298 (first usage).

*Holcodus coryphaeus* Cope, 1871a: Cope, 1871b:269 (original description).

*Holcodus mudgei* (Cope, 1870a): Cope, 1871b:273 (new combination).

*Liodon curtirostris* Cope, 1871a: Cope, 1871b:273 (original description).

*Lestosaurus simus* Marsh, 1872:455, pl. X, pl. XII, fig. 2.

*Lestosaurus felix* Marsh, 1872:457, pl. XIII, fig. 4.

*Lestosaurus latifrons* Marsh, 1872:458, pl. XIII, fig. 3.

*Lestosaurus gracilis* Marsh, 1872:460.

*Lestosaurus curtirostris* (Cope, 1871a): Marsh, 1872:461 (new combination).

*Lestosaurus ictericus* (Cope, 1870a): Marsh, 1872:461 (new combination).

*Lestosaurus coryphaeus* (Cope, 1871a): Marsh, 1872:461 (new combination).

*Rhinosaurus mudgei* (Cope, 1870a): Marsh, 1872:463 (new combination).

*Platecarpus ictericus* (Cope, 1870a): Cope, 1874:35 (new combination).

*Platecarpus coryphaeus* (Cope, 1871a): Cope, 1874:35 (new combination).

*Platecarpus felix* (Marsh, 1872): Cope, 1874:35 (new combination).

*Platecarpus curtirostris* (Cope, 1871a): Cope, 1874:36 (new combination).

*Platecarpus simus* (Marsh, 1872): Cope, 1874:36 (new combination).

*Platecarpus latifrons* (Marsh, 1872): Cope, 1874:36 (new combination).

*Platecarpus gracilis* (Marsh, 1872): Cope, 1874:36 (new combination).

*Platecarpus mudgei* (Cope, 1870a): Cope, 1874:36 (new combination).

*Platecarpus coryphaeus* (Cope, 1871a): Cope, 1875:142, pl. XV, fig. 1, pl. XVI, fig. 3, pl. XVII, fig. 6, pl. XX, figs. 4-7, pl. XXI, figs. 1, 2, pl. XXXVI, fig. 6, pl. XXXVII, fig. 9.

*Platecarpus ictericus* (Cope, 1870a): Cope, 1875:144, pl. XV, fig. 2, pl. XVII, figs. 3, 4, pl. XVIII, fig. 6, pl. XIX, figs. 7-10, pl. XX, figs. 1-3, pl. XXV, figs. 1-25(27), pl. XXXVI, fig. 7, pl. XXXVII, fig. 8.

*Platecarpus curtirostris* (Cope, 1871a): Cope, 1875:150, pl. XV, fig. 3, pl. XVI, figs. 4, 5, pl. XVII, fig. 2, pl. XVIII, figs. 7, 8, pl. XXI, figs. 7-13, pl. XXXVI, fig. 5, pl. XXXVII, fig. 10.

*Platecarpus mudgei* (Cope, 1870a): Cope, 1875:157, pl. XVI, fig. 2, pl. XVII, fig. 5, pl. XXVI, figs. 2, 3, pl. XXXVII, fig. 7 (reversed).

*Platecarpus tympaniticus* Cope, 1869: Cope, 1875:pl. XXXVII, fig. 11 (reversed).

*Holosaurus abruptus* Marsh, 1880:87.

**Holotype**—ANSP 8484 (partial left surangular), 8487 (right quadrate), 8488 (nearly complete anterior cervical vertebra), 8491 (partial right pterygoid), 8558 (partial posteriormost cervical vertebra), 8559 (partial posterior cervical vertebra), and 8562 (partial basioccipital-basisphenoid complex), and jaw fragments associated with the matrix that contains ANSP 8488. All elements are considered to be from one individual. ANSP 8491 is currently missing.

**Type Locality and Horizon**—From “a greenish sandstone,” which most likely corresponds to the Tombigbee Sand Member of the Eutaw Formation, near Columbus, Mississippi, USA (Leidy, 1865:35). Horizon is upper Santonian to lowermost Campanian (ca. 84 to 83 Ma) (Kiernan, 2002; Ogg et al., 2004).

**Referred Material, Locality, and Horizon**—ALMNH PV 985.0021, from Greene County, Alabama, USA; lower Mooreville Formation, lower Campanian (Kiernan, 2002). AMNH 202; 1488; 1501 (*P. mudgei* holotype); 1512; 1528; 1550; 1559 (*P. ictericus* holotype); 1563 (*P. curtirostris* holotype); 1566 (*P. coryphaeus* holotype); 1820; 1821; 2005; 2006; 6159; 14788, from western Kansas (Wallace, Logan, Gove, and Lane Counties), USA; Smoky Hill Chalk Member, middle Coniacian to lower Campanian (Hattin, 1982; Ogg et al., 2004), but most likely from the upper section above the Marker Unit 11 of Hattin (1982), upper Santonian to lower Campanian (Bennett, 2002; Everhart, 2005; Konishi, 2008). BMNH R-2833, from Logan County, western Kansas, USA; Smoky Hill Chalk Member, horizon as per AMNH specimens. CMN 40914, from Logan County, western Kansas; Smoky Hill Chalk Member, horizon as per AMNH specimens. FHSM VP-322; 2075; 17017, from western Kansas (Logan and Gove Counties), USA; Smoky Hill Chalk Member, horizon is upper Santonian for VP-322 (MU 12) and VP-17017 (MU 15-16), as per AMNH specimens for VP-2075 (Schumacher, 1993; Everhart, 2005). FM UC-600, from 20 miles (32 km) northeast of Scott City, Scott County, western Kansas; Smoky Hill Chalk Member, horizon as per AMNH specimens. KU 1001; 1007; 1021; 1031; 1046; 1063; 1135; 1196; 1230; 5042; 14287; 14340; 55219; 85586; 85588, from western Kansas (Logan and Gove Counties), USA; Smoky Hill Chalk Member, horizon as per AMNH specimens. LACM 128319, from NW ¼ Section 15, T 15 S, R 34 W, Logan County, Kansas, USA; Smoky Hill Chalk Member, horizon as per AMNH specimens. RMM 1903; 7070 (in part), from western Alabama (Greene and Hale Counties), USA; lowermost Mooreville Chalk Formation, lower Campanian (Kiernan, 2002; Mancini and Puckett, 2005). YPM 884; 1112; 1114; 1175; 1256 (*Lestosaurus latifrons* holotype); 1258 (*Lestosaurus simus* holotype); 1264 (*Lestosaurus gracilis* holotype); 1267; 1269; 1277 (*Lestosaurus felix* holotype); 1284; 1350A (*Holosaurus abruptus* holotype); 3690;

3997; 4003; 24900; 24903; 24904; 24905; 24915; 24918; 24921; 24929; 24931; 40393; 40463; 40472; 40473; 40497; 40498; 40561; 40573; 40587; 40610; 40632; 40653; 40669; 40673; 40683; 40691; 40693; 40712; 40718; 40719; 40819, from western Kansas (Wallace, Logan, Gove, ?Lane, and Graham Counties), USA; Smoky Hill Chalk Member, horizon as per AMNH specimens. The above list comprises the specimens that were directly examined, and is by no means complete.

**Emended Diagnosis**—Size moderate, mandible seldom reaching 70 cm in length; no predental rostrum on premaxilla; first pair of premaxillary teeth procumbent; premaxillo-maxillary suture posteriorly ascending in straight line; premaxillo-maxillary suture short, posteriorly terminating above second or third maxillary tooth; 12 maxillary teeth; prefrontal posteriorly contacting postorbitofrontal above orbit; frontal supraorbital border may be thickened lateral to prefrontal-postorbitofrontal contact; pair of broadly shallow parasagittal excavations flanking median dorsal keel on dorsal frontal surface; ventrolateral processes of frontal running parallel with each other; parietal foramen ovoid, its anterior border occurring within one foramen length from fronto-parietal suture; parietal table triangular, wider than long; parietal table lateral borders slightly convex, seldom concave; parietal crest typically obtuse angled; parietal postorbital process short, not reaching anterolateral corner of upper temporal fenestra; same process not forming dorsal plateau posterior to frontal ala; posteroventral jugal process acute, pointing posteriorly; 10 to 13 pterygoid teeth, may be more; ectopterygoid process projecting anterolaterally from dentigerous body of pterygoid; quadrate cephalic condyle anterior border straight; same condyle with round, obtuse anteromedial corner; stapedial pit oval with straight sides; medial vertical ridge broadly rounded; quadrate shaft with or without slight posteroventral bulging; mandibular condyle transversely wide, teardrop-shaped in outline with its apex pointing anteromedially; quadrate ala projecting laterally nearly perpendicular to long axis of suprastapedial process in dorsal view; quadrate alar surface relatively planar; suprastapedial process long, at least two-thirds the quadrate height; process distally terminating in rounded expansion; infrastapedial process may or may not be present; basal tubera not inflated; basal tubera widely separated from each other; 12 dentary teeth; virtually no edentulous prow anterior to first dentary tooth; no extensive edentulous portion posterior to last dentary tooth on dentary; coronoid process moderately developed; coronoid posterior border posteriorly descending at about 45 degrees from horizontal; surangular anteriorly constantly diverging with straight dorsal and ventral borders; articular portion of glenoid fossa larger than surangular portion; retroarticular process rounded; cervical intervertebral joints curved; eighth intercentrum (peduncle) absent on seventh cervical centrum; zygosphenes and zygantra rudimentary; zygapophyses functional throughout pre-pygal series; 20 to 22 dorsal vertebrae; pygal vertebrae five to six; approximately 90 caudal vertebrae (FHSM VP-322; LACM 128319); scapula anteroventral border forming obtuse angle with long axis of scapular neck; more than half the length of scapula posteroventral border anteriorly embayed; coracoid fan-shaped, may be notched; scapula and coracoid sub-equal in size; humerus length slightly exceeding distal width; pectoral crest narrow; radius hatchet-shaped to nearly semi-circular; carpals typically four; tarsals three; phalanges cylindrical; paddle spread, base of fifth digit divergent from the others at 60 degrees or greater; hyperphalangy minimal; marginal teeth posteromedially recurved at around mid-height; marginal teeth faceted laterally and finely striated medially; teeth subcircular in cross-section at base.

**Taxonomic Remarks—**The following *Platecarpus* taxa are considered nomina dubia due to the lack of diagnostic characters in the holotypes.

*Platecarpus latispinus* (Cope, 1871c): nomen dubium.
*Platecarpus tectulus* (Cope, 1871b): nomen dubium.
*Platecarpus glandiferus* (Cope, 1871b): nomen dubium.
*Platecarpus affinis* (Leidy, 1873s): nomen dubium.

All the other species formerly assigned or referred to the genus are re-assigned to different mosasaur genera by various later workers and/or this study, as indicated.

*Platecarpus intermedius* (Leidy, 1870): to *Globidens* sp. (Kiernan, 2002; Polcyn and Bell, 2005b; Konishi and Caldwell, 2007).
*Platecarpus crassartus* (Cope, 1871c): to *Plioplatecarpus* sp., cf. *P. primaevus* (Lingham-Soliar and Nolf, 1989; pers. observ.).

*Platecarpus planifrons* (Cope, 1874): to Plioplatecarpinae gen. nov. (pers. observ.).

*Platecarpus anguliferus* (Cope, 1874): to *Tylosaurus* sp. (pers. observ.).

*Platecarpus clidastoides* (Merriam, 1894): to *Ectenosaurus clidastoides* (Russell, 1967).

*Platecarpus oxyrhinus* (Merriam, 1894): to *Ectenosaurus clidastoides* (Russell, 1967).

*Platecarpus somenensis* Thevenin, 1896: to Plioplatecarpinae gen. nov. (pers. observ.).

*Platecarpus brachycephalus* Loomis, 1915: to Plioplatecarpinae gen. nov. (pers. observ.).

*Platecarpus ptychodus* Arambourg, 1952: to cf. Russellosaurina gen. et sp. indet. (pers. observ.).

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FIGURE 4-1. *Platecarpus tympaniticus* holotype right quadrate, ANSP 8487. **A**, anterior; **B**, posterior; **C**, medial; **D**, dorsal; **E**, ventral views. **Abbreviations**: **ala**, tympanic ala; **ccd**, cephalic condyle; **fm**, anterior foramen; **isp**, infrastapedial process; **M**, matrix; **mcd**, mandibular condyle; **qs**, quadrate shaft; **sp**, suprastapedial process; **spt**, stapedial pit. Cross-hatched area in **A** indicates broken surface. Scale bars equal 5 cm.

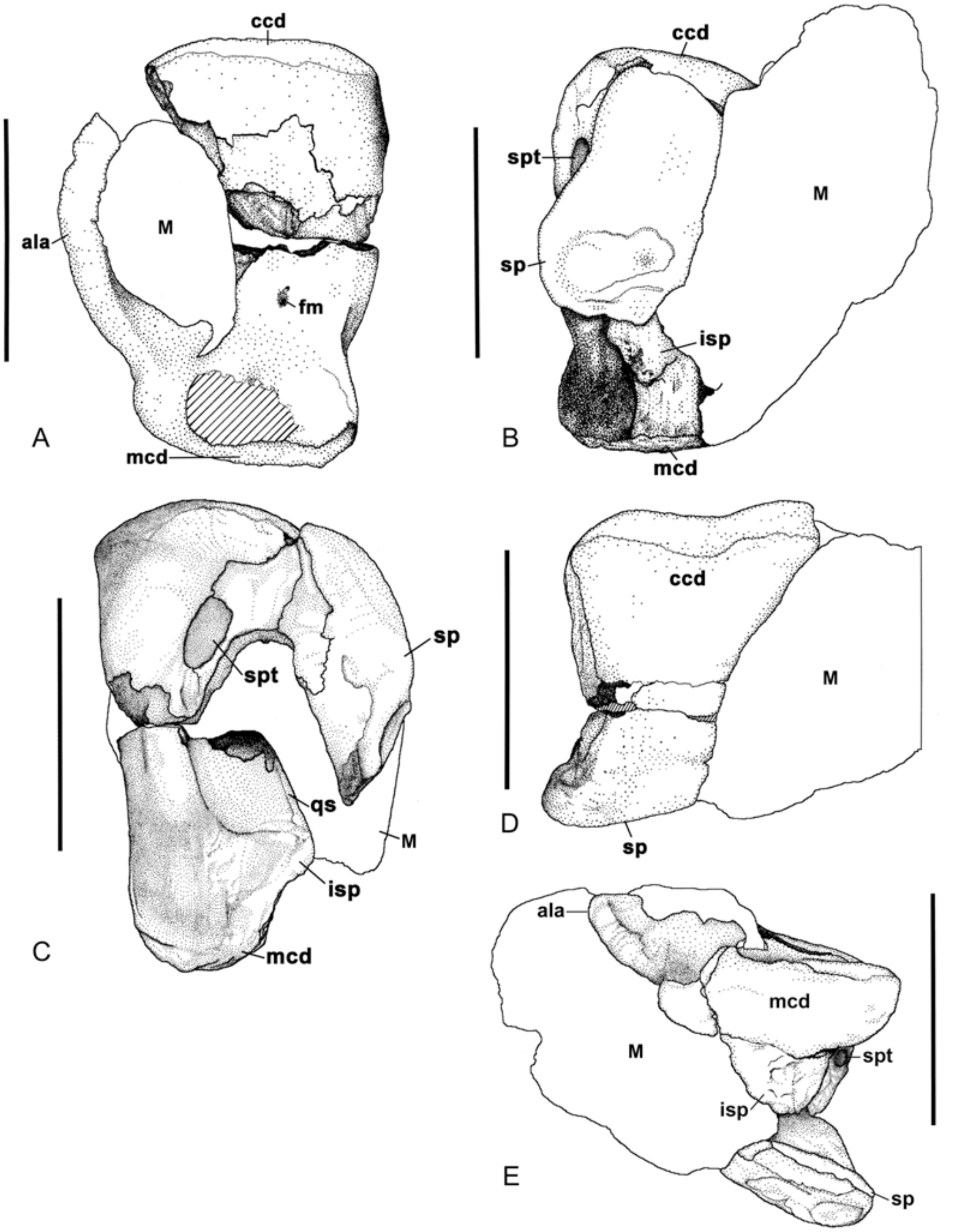
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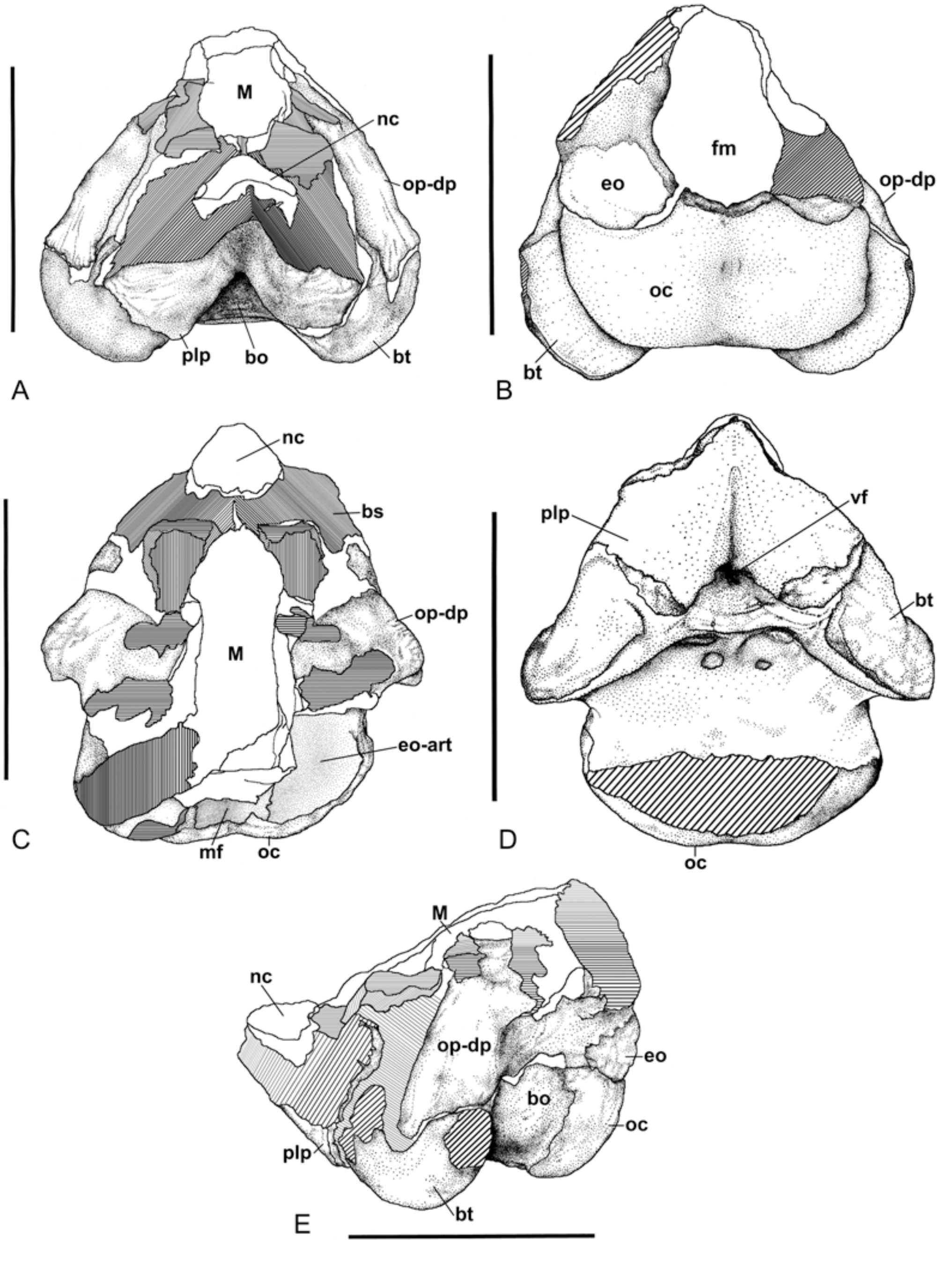
FIGURE 4-2. *Platecarpus tympaniticus* holotype partial braincase, ANSP 8562. **A**, anterior; **B**, posterior; **C**, dorsal; **D**, ventral; **E**, left lateral views. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **bt**, basal tuber; **eo**, exoccipital; **eo-art**; articulation surface for exoccipital on basioccipital; **fm**, foramen magnum; **M**, matrix; **mf**, medullary floor; **nc**, neural canal; **oc**, occipital condyle; **op-dp**, descending process of opisthotic; **plp**, posterolateral process of basisphenoid; **vf**, ventral foramen. Cross-hatched areas indicate broken surfaces. Scale bars equal 5 cm.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# CHAPTER FIVE

# A NEW PLIOPLATECARPINE MOSASAUR FROM THE LOWER MIDDLE CAMPANIAN OF NORTH AMERICA, AND AN ANALYSIS OF PLIOPLATECARPINE PHYLOGENY

To be submitted as: 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.

# INTRODUCTION

Plioplatecarpines, a group of medium-sized russellosaurine mosasaurs (Squamata: Mosasauridae), are represented by at least 500 specimens in North America alone (e.g., Russell, 1967; Polcyn and Bell, 2005; pers. obs.). Within North America, their fossil remains are distributed from the middle late Coniacian (*Platecarpus planifrons*) to earliest Maastrichtian (*Plioplatecarpus primaevus*), and are presently known from four genera comprising about 10 species (Russell, 1967; Hattin, 1982; Wright and Shannon, 1988; Schumacher, 1993; Holmes, 1996; Bell, 1997; Everhart, 2001; Cuthbertson et al., 2007; Konishi and Caldwell, 2007; Konishi, 2008a, 2008b; Polcyn and Everhart, 2008; Konishi and Caldwell, 2009). Two other plioplatecarpine species, *Plioplatecarpus houzeaui* and *Plio. marshi*, are found in Maastrichtian strata in Belgium and the Netherlands, and *Angolasaurus bocagei* comes from upper Turonian strata in northern Angola (e.g., Lingham-Soliar, 1994a, b; Bell and Polcyn, 2005; Jacobs et al., 2006).

Numerous mosasaur specimens from other parts of the world have also been referred to as plioplatecarpines, including those from the Iberian Peninsula (Bardet et al., 1999), North Africa (e.g, Arambourg, 1952; Bardet et al., 2000), Western Africa (e.g., Lingham-Soliar, 1991), Australia (e.g., Kear et al., 2005), Antarctica (e.g., Martin et al., 2002), and Atlantic South America (e.g., Bengtson and Lindgren, 2005; Fernández et al., 2008). However, because of the fragmentary nature of these specimens, only a very few can be diagnosed down to the generic level and none to the species level. The suggested generic assignment of *Platecarpus ptychodon* Arambourg, 1952 from North Africa is questionable, based on its general tooth morphology (Arambourg, 1952:pl. XXXIX, fig. 1–7). Our recent examination of the holotype of *Platecarpus somenensis* Thevenin, 1896 in France suggests that it is neither *Platecarpus* nor *Plioplatecarpus*, if it is indeed a plioplatecarpine mosasaur at all (cf. Konishi and Caldwell, 2009; Caldwell et al., in prep.).

Although many mosasaur specimens from numerous world localities have been assigned to the plioplatecarpines, their taxonomic definition has been historically unstable. In 1967, Russell re-diagnosed and re-defined the subfamily Plioplatecarpinae, in which he included two new tribes, Plioplatecarpini (*Platecarpus*, *Plioplatecarpus*, and *Ectenosaurus*) and Prognathodontini (*Prognathodon* and *Plesiotylosaurus*). Apparently removing the genera *Ectenosaurus* and *Plesiotylosaurus*, Lingham-Soliar (1994a) modified Russell's (1967) diagnosis for the subfamily. It remains unclear, however, whether or not *Prognathodon* was included in Plioplatecarpinae under Lingham-Soliar's (1994a) diagnosis; the subfamily was characterized as having a maximum of 14 dentary teeth, a character of *Prognathodon*, yet it was also diagnosed as exhibiting haemal arches unfused to the caudal centra, a non-*Prognathodon* character (e.g., Lingham-Soliar and Nolf, 1989). However, a subsequent global phylogenetic analysis on mosasauroids by Bell (1997) recognized the constituent genera of Russell's (1967) Prognathodontini, *Prognathodon* and *Plesiotylosaurus*, as belonging to Tribe Globidensini within the subfamily Mosasaurinae, while *Ectenosaurus* was retained within Tribe Plioplatecarpini as its basal-most member. Bell (1997) also proposed inclusion of Plioplatecarpini in his informal

"Russellosaurinae"; consequently, he did not use the name Plioplatecarpinae. Although Bell's (1997) major phylogenetic rearrangement of plioplatecarpines has since been widely supported by most researchers (e.g., Bell and Polcyn, 2005; Polcyn and Bell, 2005; Caldwell and Palci, 2007; Polcyn and Everhart, 2008; but see Dutchak and Caldwell, 2009), no formal re-diagnosis and re-definition of Plioplatecarpini or Plioplatecarpinae has been proposed, making the referral of any mosasaur specimen to this taxon difficult and ambiguous.

According to Bell (1993, 1997), Bell and Polcyn (2005), Polcyn and Bell (2005), Cuthbertson et al. (2007), Caldwell and Palci (2007), and Polcyn and Everhart (2008), the relationships among the derived members of the plioplatecarpines, namely *Platecarpus* and *Plioplatecarpus*, are largely unresolved, since the genus *Platecarpus* is either paraphyletic at best or polyphyletic at the worst (cf. Cuthbertson et al., 2007). At the same time, Bell's (1993) phylogenetic analysis included two specimens of *Platecarpus tympaniticus*, FMNH UC-600 and DMNH 8769, that also formed a paraphyletic clade nested within the paraphyletic genus *Platecarpus*. This finding suggested that at least part of the phylogenetic uncertainty for the genus stems from our historic inability to diagnose the genus and/or the species constituting it.

Konishi and Caldwell (2007) reviewed the taxonomy of *Platecarpus* from North America and concluded that at least three species of *Platecarpus* were recognized: *P. tympaniticus* (generic type), *P. ictericus*, and *P. planifrons*. While they (2007) questioned the validity of *P. tympaniticus*, arguing that the holotype, the only confirmed specimen of the taxon, cannot be diagnosed against its congeners without redescription, conclusions drawn in this thesis (Chapter 4) establish the validity of this taxon and propose the synonymy of *P. ictericus* with *P. tympaniticus*. Meanwhile, one of Bell's (1993) two specimens of *P. tympaniticus*, DMNH 8769, had been examined, and it was determined to belong to none of the *Platecarpus* species recognized by Konishi and Caldwell (2007), nor to any nominal *Plioplatecarpus* species reported from North America (Holmes, 1996; Cuthbertson et al., 2007; Konishi and Caldwell, 2009).

TMP 84.162.01, a plioplatecarpine specimen from the lowermost middle Campanian of Morden, Manitoba, Canada, was also identified as *Platecarpus tympaniticus* by Nicholls (1988). Unlike other more typical Morden specimens, TMP 84.162.01 is virtually selenite-free and preserves superb details of all the cranial elements, including orbitosphenoids. The material includes an articulated skull with the first three cervical vertebrae, both lower jaws, and a left scapula. Our reexamination of the material made it clear that it was distinct from any other known plioplatecarpine species, and that it was morphologically closest to DMNH 8769, and also to AMNH 2182 (a specimen formerly identified as *Plioplatecarpus* sp. by Bell [1993, 1997]).

In this study, we first establish a new plioplatecarpine taxon based on a focused description of TMP 84.162.01 and DMNH 8769. We then present a novel phylogenetic analysis encompassing all the known plioplatecarpine species including the new taxon, and propose revised taxonomic frameworks and diagnoses for existing species, genera, and the subfamily.

**Institutional Abbreviations—ALMNH PV**, Alabama Museum of Natural History, Tuscaloosa, Alabama, USA; **AMNH (FR)**, American Museum of Natural History, New York, USA; **BNNH**, The Natural History Museum, London, UK; **CDM**, Courtenay and District Museum, Courtenay, British Columbia, Canada; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **DMNH**, Museum of Nature and Science, Dallas, USA; **FHSM VP**, Fort Hays Sternberg Museum, Hays, Kansas, USA; **FMNH**, Field Museum of Natural History, Chicago, USA; **GSATC,** Geological Survey of Alabama Type Collection, Tuscaloosa, Alabama, USA; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **KU**, The University of Kansas Natural History Museum, Lawrence, Kansas, USA; **LACM**, Los Angeles County Museum, Los Angeles, USA; **RMM**, Red Mountain Museum (currently McWane Science Center), Birmingham, Alabama, USA; **RSM P**, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; **SDSMT**, South Dakota School of Mines and Technology, Rapid City, USA; **SMU**, Southern Methodist University, Dallas, Texas, USA; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **UNO**, University of New Orleans, New Orleans, USA; **USNM**, Smithsonian National Museum of Natural History, Washington D. C., USA; **YPM**, Yale Peabody Museum of Natural History, New Havens, USA.

## MATERIALS AND METHODS

Specimens were photographed using a Nikon D-100 and/or Nikon Coolpix 4500 digital cameras. Some of these photo images were traced using Adobe Photoshop 7.0 for Windows to generate line drawings. Two of these images were further stippled using the same program. On TMP 84.162.01, measurements were made in mm using calipers and a tape measure.

## SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

MOSASAURIDAE Gervais, 1852

RUSSELLOSAURINA Polcyn and Bell, 2005

PLIOPLATECARPINAE Dollo, 1884

Plioplatecarpidae Dollo, 1884:653.
“mosasauriens microrhynques” Dollo, 1890:163.
Platecarpinae Williston, 1897:177.
Plioplatecarpini Russell, 1967:148.

**Emended Diagnosis**—(cf. Russell, 1967; Bell, 1993; Lingham-Soliar, 1994a) russellosaurines generally of medium size, mandible length rarely reaching 1000 mm; quadrate ala laterally expanded with uniformly curved border, thin in the middle; distinct alar concavity immediately dorsal to mandibular condyle; suprastapedial process elongate, at least reaching midheight of quadrate; process often ending with blunt terminus; canal(s) for basilar artery through basisphenoid and basioccipital exiting as large opening(s) on medullary floor near foramen magnum; jaws slender; a few large foramina on lateroventral/ventral face of retroarticular process; marginal dentition slender, distally tapering and posteromedially recurved at mid-height of crown; two carinae on marginal tooth crown aligned in anteroposterior orientation, dividing crown surface approximately into two halves; marginal tooth crown medially striated, laterally faceted or fluted to various degrees; tooth crown with subcircular basal cross section; haemal-arch-bearing caudal centra short horizontally, often taller than long.

**Remarks**—The emended diagnosis for Plioplatecarpinae Dollo, 1884 (Russell, 1967) supports Bell's (1997) global mosasaur phylogeny by exclusion of the Prognathodontini and *Halisaurus* from Plioplatecarpinae. As a consequence, the tribe Plioplatecarpini Russell, 1967, becomes the only tribe within the Plioplatecarpinae, and the distinction of the former from the latter is unnecessary. Following Bell and Polcyn (2005), Polcyn and Bell (2005), and this study, *Yaguarasaurus columbianus* is not included in the clade based on its close phylogenetic affinity with *Tethysaurus nopcsai* and *Russellosaurus coheni*, two basal russellosaurine genera (contra Páramo [1994] and Páramo-Fonseca [2000]).

### *LATOPLATECARPUS*, gen. nov.

(Figs. 5-2–5-20, 5-22)

**Generic Type**—*Latoplatecarpus willistoni* sp. nov.

**Diagnosis**—(cf. Cuthbertson et al., 2007; Konishi and Caldwell, 2009) Autapomorphies of taxon within Plioplatecarpinae: dorsal border of internarial bar anteriorly elevated, producing distinctly bulging profile immediately posterior to dentigerous rostrum; parietal foramen pyriform; posterolateral borders of parietal table gently concave or straight, never convex; parietal crest distinct, often acuminate; posteroventral process of jugal blunt, obtusely angled; vertical ramus of jugal distally tapering but retaining distinct concavity for postorbitofrontal articulation; basal tubera highly bulbous, approaching each other toward midline; scapular blade semicircular. Differing from *Plioplatecarpus* in: skull table lacking arched profile; parietal crest present; descensus processus parietalis posterior border originating anterior to parietal fossa; jugal process present; jugal horizontal ramus at least twice as long as vertical ramus; quadrate ala planar; quadrate mandibular condyle wider than long; surangular progressively deepening anteriorly; scapula subequal in size to coracoid; anteroventral border of scapular blade shorter than length of articular condyle; proximal articular surface of humerus planar; proximodorsal border of humerus straight. Differing from *Platecarpus tympaniticus* in: premaxillo-maxillary suture posteriorly terminating anterior to anteriorly deepest portion of maxilla; ventrolateral processes of frontal anteriorly diverging, flanking pair of parolfactory-bulb recesses; parietal postorbital process laterally extending for nearly entire length of anterior border of upper temporal opening; same process variably forming dorsal skull surface posterior to frontal ala; dorsal surface of anteromedial process of postorbitofrontal bearing two distinct articular concavities for frontal and parietal postorbital process anteriorly and posteriorly, respectively; coronoid posterior process low; surangular forming at least 50% of glenoid fossa; pygal count more than 10; anteroventral border of scapular blade extending sub-perpendicular to condylar neck; humeral pectoral crest enormous; distance across ectepicondyle and entepicondyle exceeding humerus length; phalanges dumbbell shaped.

**Etymology**—"*Lato*", derived from a Latin adjective *latus* meaning wide or extensive, referring to widely separated anterolateral processes of frontal, produced by anteriorly diverging frontal ventrolateral processes, and "*platecarpus*", referring to the close evolutionary affinity of the new genus to *Platecarpus*, in particular referring to the virtually identical quadrate morphology between the two.

### *LATOPLATECARPUS WILLISTONI*, sp. nov.

**Holotype**—TMP 84.162.01, an articulated skull and mandibles including the first three cervical vertebrae and left scapula, belonging to a relatively small individual (50 cm snout-supratemporal length).

**Type Locality and Horizon**—Found in the vicinity of Morden, southern Manitoba, Canada, from the lowermost middle Campanian *Baculites obtusus* ammonite zone of the Pembina Member, lower Pierre Shale Formation, approximately 80.5 Ma (e.g., Gill and Cobban, 1965; Nicholls, 1988; Ogg et al., 2004; cf., Konishi and Caldwell, 2009; Fig. 5-1).

**Diagnosis**—Frontal ala acuminate; parietal foramen length : width ratio less than 1.5; splenial-angular contact via single vertical ridge-and-groove articulation; surangular dorsal border as well as ventral border straight; intervertebral joints with high degree of curvature.

**Etymology—**"*willistoni*" honors Samuel W. Williston, whose first synthetic work on mosasaur systematics and anatomy in 1898 founded a framework for our modern understanding of these unique fossil squamates, particularly those found in the Western Interior Basin of North America, where the new genus is well represented.

**Referred Specimens**—AMNH 2182, mostly complete, semi-articulated skull with partial rostrum; DMNH 8769, disarticulated but nearly complete and well-preserved skull elements, partial mandibles, seven cervical, seven dorsal, and eight intermediate caudal vertebrae, and ribs; SDSMT 30139, well-preserved skull, mandibles, nearly complete presacral and 11 intermediate caudal vertebrae in articulation, both pectoral girdles, and interclavicle.

**Referred Specimens, Locality, and Horizon**—AMNH 2182 comes from Mule Creek Junction ("N half section 7, T38N, R60W" [Russell, 1967:211]) in Niobrara County, eastern Wyoming, "near base of" the Pierre Shale Formation and most likely Sharon Springs Member, lowermost middle Campanian (*Baculites obtusus* Ammonite zone) (Gill and Cobban, 1966; Russell, 1967:211; Hicks et al., 1999). DMNH 8769 collected from 1.5 mi (2.4 km) east of Route 34, south side of North Sulphur River, Hunt County, northeastern Texas; collected from the Ozan Formation, stratigraphically equivalent with, or slightly older than, the Wolfe City Sand, whose absolute age is estimated to be about 80 to 79 Ma, which is early middle Campanian containing *B. mclearni* Ammonite zone (Cobban and Kennedy, 1993; Mancini and Puckett, 2005, and references therein). SDSMT 30139 collected from “twenty-three miles (23 mi/37 km) west of Edgemont” (museum label) (and 1 mi/1.6 km north of Red Bird [Russell, 1967]), Niobrara County, Wyoming, from the lower part of the Pierre Shale Formation and most likely from the Sharon Springs Member, horizon is lowermost middle Campanian (*B. obtusus* and *B. mclearni* Ammonite zones) (e.g., Gill and Cobban, 1966; Hicks et al., 1999). Hence, the majority of the referred specimens as well as the holotype are confidently assigned to the lowermost middle Campanian *B. obtusus* and *B. mclearni* ammonite zones (80.6 to 80.0 Ma in age [Ogg et al., 2004]), here considered to be closely representing the new species’ taxon range zone.

## Descriptions and Comparisons: Skull

**Premaxilla**—In both the holotype and DMNH 8769, the anterior dentigerous portion of the premaxilla exhibits a somewhat trapezoidal outline without any rostral projections (Figs. 5-3, 5-4). Whereas the anterior border is straight in dorsal aspect, it is slightly notched along the midline on the ventral side (Fig. 5-4, arrow). Anteriorly on this wide dentigerous portion, there are two irregular rows of foramina piercing the broadly convex dorsal surface parasagittally. The premaxilla is widest at its anterior-most contact with the maxillae, posterior to which the element tapers. On both sides, the premaxilla remains in contact with the maxillae up to the point above the mid-section of the second maxillary tooth in the holotype (cf., Nicholls, 1988), and above the posterior quarter section of the second maxillary tooth in DMNH 8769. Between the external nares, the premaxilla further narrows to form a slender internarial bar, which in cross-section forms an inverted triangle. In DMNH 8769, the internarial bar is unusually highly compressed around its middle portion, where the narrow dorsal surface becomes a narrow ridge before it re-expands posteriorly. In lateral aspect, the portion immediately anterior to this compressed section of the narial bar distinctly arches dorsally, while the inferior border of the bar remains straight along its length (Fig. 5-5). Such dorsal arching also exists to a lesser extent in the holotype and *Plioplatecarpus nichollsae*, while it is absent in *Platecarpus planifrons* (UALVP 24240) and the *Plioplatecarpus marshi* holotype (IRSNB R38). In TMP 83.24.01 (*Plioplatecarpus nichollsae*), the lateral constriction of the bar is nearly as pronounced, but distinct dorsal surface persists throughout its length (it diminishes in DMNH 8769). In the holotype, the internarial bar is much more robust (Fig. 5-3). The internarial bar posteriorly dilates again and overlaps the anteromedian processes of the frontal. In the holotype, one of these processes reaches the mid-portion of the internarial bar as a thin strap of bone, extending along its ventrolateral margin (see below).

In DMNH 8769, the two empty alveoli for the first set of the premaxillary teeth are each inclined anteroventrally, indicating that the first tooth pair was procumbent. The well-preserved second premaxillary tooth projects slightly anterolaterally on each side, and the crown surface is strongly fluted laterally and finely striated medially (Fig. 5-5). Between the second right and left premaxillary teeth, a keel-like vomerine process (of the premaxilla) projects ventrally and posteriorly. It is ventrally sulcate as in *Plioplatecarpus nichollsae*, and probably in other plioplatecarpines.

**Maxilla**—Each maxilla bears 12 alveoli, and the right maxilla of the holotype is complete to its distal extremity, extending posteriorly to the midpoint of the orbit (Figs. 5-3, 5-4). The anteriorly deepest portion of the maxilla occurs above the posterior edge of the second tooth in both the holotype and DMNH 8769, clearly posterior to the posterior end of the premaxillo-maxillary suture (cf., Russell, 1967; Konishi and Caldwell, 2009; Figs. 5-3, 5-5). The dorsal border of the maxilla is broadly embayed posterior to the second maxillary tooth to form the curved anterolateral border of the external naris. On both specimens, the posterior limit of this embayment occurs above the gap between the fifth and sixth maxillary teeth, as in *Plioplatecarpus nichollsae* (TMP 83.24.01), posterior to which the external naris continues as a narrow, parallel-sided opening (Fig. 5-3, arrow). No apparent thickening or convexity is discernible along the rim of the narial expansion, as noted in the holotype *P. nichollsae* (Cuthbertson et al., 2007; see Konishi and Caldwell, 2009).

In a specimen referable to *Platecarpus planifrons* (FHSM VP-2116), the depth of the maxilla measured at the point of the deepest narial embayment exceeds the length of the fully-erupted maxillary tooth by about 15 %; this is in contrast to the condition found in the *Latoplatecarpus willistoni* holotype, where the corresponding maxillary depth is shorter than the fully-erupted maxillary tooth

(3rd right) by about 23 % (Fig. 5-3), indicating a significantly lower profile of the maxilla. This trend is also confirmed when the anteriorly deepest portion of the maxilla is considered. In UALVP 24240 (*Platecarpus planifrons*), this portion is 21.0 % of the entire maxillary length on the left side, while the same ratio is 15.4 % in TMP 84.162.01 (the holotype), measured on the right side (cf. Fig. 5-3). Based on the reconstruction of *Plioplatecarpus primaevus* in Holmes (1996:fig. 2C), this ratio is 14.0 % in this taxon, while it is about 13.5 % in *Plioplatecarpus houzeaui* (IRSNB 3101; Lingham-Soliar, 1994a:fig. 18A).

Along the dental margin of the holotype left maxilla, the sparsely spaced exits for the fifth cranial nerve become progressively larger posteriorly, the last one ending above the eighth tooth (Fig. 5-4). On the opposite side, the size difference of these foramina is less distinct, and they are more tightly spaced and seem to be concentrated in the anterior-half of the element (Fig. 5-3). In a well-preserved specimen of *Plioplatecarpus nichollsae* TMP 83.24.01, the same exits extend as far back as the ninth maxillary tooth on both sides.

In the holotype, dorsally a thin flap of bone, a posterodorsal process of the maxilla, extends posteriorly to overlap the prefrontal along its dorsal sulcus (see below). The medial border of the process does not reach the posterolateral border of the external naris, which is formed by the underlying prefrontal. As mentioned above, the posterior extension of the maxilla beyond the anterior orbital margin is extensive in *Latoplatecarpus willistoni*. With the right prefrontal slightly pushed forward postmortem against the maxilla in the holotype, the anterior orbital margin occurs above the anterior margin of the 10th maxillary tooth. This suggests that at least the last two and a half tooth positions underlie the orbit, the condition comparable to that in *Plioplatecarpus nichollsae* (TMP 83.24.01), where the anterior orbital border is situated above the midsection of the 10th maxillary tooth (with a total of 12 maxillary tooth count) (Konishi and Caldwell, 2009:fig. 2).

**Prefrontal**—The holotype right prefrontal largely retains its original shape and topological relationship with adjacent bones (Fig. 5-3). Compared to TMP 83.24.01, *Plioplatecarpus nichollsae*, it possesses a significantly greater exposure of its anterodorsal surface lateral to the frontal margin. In TMP 83.24.01 (*P. nichollsae*), this area is extremely narrow with subparallel borders, while in the holotype of *Latoplatecarpus willistoni*, its medial border (= frontal margin) runs anteromedially to form an anteriorly diverging, triangular dorsal surface (Fig. 5-3), more comparable to the condition seen in *Platecarpus tympaniticus*. This apparent difference in the degree of dorsal exposure lateral to the frontal seems directly correlated with the morphology of the latter element. In *Plioplatecarpus nichollsae*, the preorbital borders of the frontal remain subparallel with each other, while they converge anteriorly in the new taxon as in *Platecarpus tympaniticus* and *P. planifrons* (but to a lesser degree; see frontal below). However, this anterodorsal surface of the prefrontal is longitudinally sulcate for reception of the posterodorsal process of the maxilla, and is distinctly separated from the vertical lateral wall by a pronounced preorbital ridge that extends horizontally above the maxillo-prefrontal suture. This condition is similar to that found in *P. nichollsae* but different from *Platecarpus tympaniticus* and *P. planifrons*, where the dorsal and lateral walls are somewhat more continuous (Konishi and Caldwell, 2009). The suture with the maxilla is inclined posteriorly at a low angle, approximately at 20 degrees from the maxillary dental margin. An incipient supraorbital tuberosity is present along the lateral margin of the supraorbital ramus on both the holotype and DMNH 8769, whose distal extremity bears a shallow ventral excavation into which the postorbitofrontal fits from underneath (Figs. 5-4, 5-6). It may be noted that the dorsolateral surface of DMNH 8769, in spite of the anteromedially oriented frontal margin, is proportionately narrower than in the holotype (see below).

**Frontal**—The holotype frontal is virtually complete, though slightly compressed, while the DMNH 8769 frontal experienced little distortion (Figs. 5-3, 5-7). Distinct from all known plioplatecarpine taxa, the posterolateral alae each forms an acuminate corner of the skull table, with a transversally straight posterior margin (holotype) or with a considerably excavated posterior margin by the adjacent postorbital process of the parietal (DMNH 8769) (Figs. 5-3, 5-7). Unlike in *Platecarpus planifrons*, the ventral separation ridge is absent and the supraorbital border is not thickened (Konishi and Caldwell, 2007; Konishi, 2008b). Uniting the new taxon to all the *Plioplatecarpus* species and *Platecarpus* cf. *P. somenensis*, is a robust, anteriorly diverging descensus processus frontalis observable fully in DMNH 8769, and partially on the left side with the lateral half of the parolfactory-bulb recess exposed on the holotype (Figs. 5-4, 5-7B).

Although the overall morphology of the frontal is triangular in the holotype, this contrasts with the similarly triangular frontal outline in *Platecarpus*.

Even though the preorbital borders of *Latoplatecarpus willistoni* converge anteriorly, including DMNH 8769 (Fig. 5-7), they do not do so as much as in *Platecarpus*, the difference arising from the more widely spaced anterolateral processes of the element in the new taxon. For example, in UALVP 24240, *Platecarpus planifrons*, the distance between the anterolateral processes is about 36 % that of the interorbital width, and in AMNH 1820, a *Platecarpus tympaniticus* specimen with a relatively short interorbital distance, the same ratio is about 39 % (Russell, 1967:fig. 4A). In TMP 84.162.01, the holotype of *Latoplatecarpus willistoni*, the distance between the anterolateral processes is at least 50 % of the interorbital width, taking into account that the anterior portion of the frontal experienced more lateral compression. This is in accordance with the presence of anteriorly diverging ventro-lateral processes (descensus processus frontalis) on the ventral frontal surface, where the processes distally form the anterolateral processes; in specimens of *Platecarpus*, the ventro-lateral processes run parallel with each other, thus leading to narrowly spaced anterolateral processes (Konishi and Caldwell, 2009).

A pronounced median dorsal keel originates as far back as the level of the orbit in both the holotype and DMNH 8769; in the former, the keel progressively becomes more pronounced anteriorly, reaching 4 mm in maximum height. Parasagittal to the keel, the frontal is longitudinally sulcate as a result of distinct supraorbital bulging, producing a low M-shaped cross-section between the orbits.

Posteriorly on the holotype, the frontal bears two distinct median embayments in dorsal aspect; the broader median embayment demarcates its sutural contact with the invading parietal table, while the smaller one forms the anterior half of the parietal foramen (Fig. 5-3). In DMNH 8769, the latter embayment is at least incipiently developed, as a pair of posteromedian flanges inside the former embayment surrounds, if not borders, the anterior half of the parietal foramen (Fig. 5-7A). Ventrally, the fronto-parietal suture is invisible due to the underlying postorbitofrontal that broadly clasps two elements at the posterolateral corner of the skull table (Figs. 5-4, 5-7B).

**Parietal**—Overall, the parietal is well preserved though the suspensorial ramus is only preserved on the left side in the holotype specimen. A pentagonal parietal table bears a large parietal foramen and a distinct parietal crest anteriorly and posteriorly, respectively (Figs. 5-3, 5-7A). In the holotype and in the referred specimen AMNH 2182, the anterior half border of the parietal foramen is superficially formed by the frontal, while the parietal continues to form the basal rim of the foramen anteriorly as a thin ring of bone underneath the frontal (Fig. 5-3). Consequently, it is inferred that the foramen is completely enclosed by the parietal in ventral aspect (cf. Konishi and Caldwell 2009:fig. 4B). In the holotype, the length : width ratio of the foramen is 1.48 (19.3 mm x 13.0 mm) and it is 1.36 (15.4 mm x 11.3 mm) in DMNH 8769, less than in *Plioplatecarpus nichollsae* (1.64 to 2.20) (Konishi and Caldwell, 2009:table 2). The outline of the parietal table in *Latoplatecarpus willistoni* is nearly identical to *Plioplatecarpus nichollsae*. Although the postorbital processes that extend laterally from the table are either missing or obliterated postmortem in the holotype (Fig. 5-3; cf. Konishi and Caldwell, 2009:fig. 3A, B), they are clearly present and visible dorsally in

DMNH 8769. It is indeed noteworthy that in the latter specimen, these postorbital processes are asymmetrically exposed on the dorsal surface of the skull table, where the left process is distally more expanded than the right counterpart (Fig. 5-7A). Therefore, as with *Plioplatecarpus nichollsae*, the degree of the dorsal exposure of the parietal postorbital processes seems to have varied intraspecifically in the new taxon, sometimes differing even in the same individual. In posterior aspect, the postorbital process exhibits lateral bifurcation to clasp the parietal process from the postorbitofrontal, with which it forms a V-shaped sutural contact (Fig. 5-8).

The left suspensorial ramus in the holotype is nearly complete, approximately the distal 25 % of which is inferred to have been in contact with the supratemporal. The left descensus processus parietalis is intact, with a depth that is slightly less than half the parietal table width. The columnar end of the left epipterygoid attaches to the medial face of the posteroventral corner of this process (Fig. 5-4). On both the holotype and DMNH 8769, the posterior margin of the descending process of the parietal is located at a short distance anterior to the parietal fossa (i.e., the base of the suspensorial rami [Bahl, 1937:142]) (Fig. 5-7B, dashed line). In DMNH 8769, there is a posteroventral median keel between the descending parietal processes. The last two characters mentioned are likewise found in *Plioplatecarpus nichollsae* (Konishi and Caldwell, 2009).

**Postorbitofrontal**—The right postorbitofrontal of the holotype had been dislocated from its original position, partially revealing its articulation surface with the frontal and parietal (Fig. 5-3). Reflecting the outline of the frontal ala, the broadly wedge-shaped anterior process of the postorbitofrontal bears a frontal facet that has a pointed (i.e., acuminate) posterolateral corner. Although the anterior process suffered some surface obliteration, there is a well-developed straight ridge extending anteromedially across the entire dorsal face of the process, posterior to which the postorbital process of the parietal would have articulated from above, much as in *Plioplatecarpus nichollsae* (Konishi and Caldwell, 2009:fig. 5A–C). Consequently, although the postorbital processes of the parietal are not well preserved on the holotype, they most likely participated in forming posterolateral corners of the skull table as in DMNH 8769. However, unlike in *Plioplatecarpus nichollsae* (TMP 83.24.01), this narrow parietal articulation surface does not fully extend to the posterolateral corner of the anterior process, on the holotype being only approximately two-thirds as wide as the anteriorly adjacent frontal facet (cf. Konishi and Caldwell, 2009:fig. 5A, B).

To complement the holotype, the well-preserved and articulated skull table of DMNH 8769 provides some insight into the complex nature of the topological relationship among the postorbitofrontal, frontal, and parietal in this taxon. At the posterolateral corner of the skull roof, the fan-shaped postorbitofrontal anterior process clasps the frontal ala and the dorsal ramus of the postorbital process of the parietal from underneath (Fig. 5-7). In addition to this, the medially projecting parietal process of the postorbitofrontal along the anterior border of the supratemporal fenestra is tightly sutured between the dorsal and ventral rami of the parietal postorbital process (Fig. 5-8; see parietal above). The latter ramus also ventrally abuts the posterior margin of the wing-like anterior process of the postorbitofrontal, presumably preventing the latter from dislocating posteriorly (Fig. 5-7B). Indeed, it is typical of disarticulated *Plioplatecarpus* specimens that the frontal, parietal, and a pair of postorbitofrontals are preserved as one unit in original articulation (e.g., *P. nichollsae*: CMN 52261, TMP 83.24.01; *P. primaevus*: CMN 11835, 11840; *P. houzeaui*: IRSNB 3108, 3130), while these elements are typically found in isolation in disarticulated specimens of all the other plioplatecarpine taxa, including *Platecarpus* (e.g., *Selmasaurus johnsoni*: FMNH VP-13910 [holotype]; *S. russelli*: GSATC 221 [holotype]; *Platecarpus planifrons*: AMNH 1491 [holotype], FHSM VP-13907; *Plat. tympaniticus*: AMNH 1820, YPM 1256). Consequently, it is highly probable that the structural complexity by which the three skull roof elements articulate with one another in *Latoplatecarpus willistoni*, particularly as a result of the extensive 'interlocking' between the parietal and postorbitofrontal, played a major role in providing a structural rigidity in the skull roof, whatever evolutionary advantages such a structural modification may have provided to the plioplatecarpine lineage.

In the holotype, the jugal process, extending ventrally at the lateral corner of the anterior process, is partially damaged but the distal end of the long anteroventral projection is preserved, revealing its morphological resemblance to that in *Plioplatecarpus nichollsae* but not in *Plioplatecarpus primaevus* (in the latter, this process is truncated and cup shaped [Holmes, 1996; Konishi and Caldwell, 2009:fig. 6]). This condition is also discernible in DMNH 8769, in which the process is complete. On the ventral surface of the skull roof, the anterior extremity of the anterior process underlies the prefrontal. On the left side of the holotype, the long squamosal process is 109 mm in length, still maintains its articulation with the squamosal, and extends past the anterior border of the quadrate process of the squamosal (cf. Lingham-Soliar, 1994a). The same condition occurs in DMNH 8769 as well (Fig. 5-9), but unlike in *Plioplatecarpus houzeaui* (IRSNB R36), the process does not reach the posterior border of the squamosal (Lingham-Soliar, 1994a).

**Orbitosphenoid**—A rare occurrence of paired orbitosphenoids is reported on TMP 84.162.01 (the holotype) (Fig. 5-10). The pair is lying on one side against the skull table immediately posterior to the frontal-parietal suture. Overall the element is laterally flattened. The expanded dorsal portion is only visible on the left element, from which a slender, curved ramus that would have encircled the posterodorsal portion of an optic chiasma extends ventroanteriorly. In life, the distal extremity of the ramus would have approached the same of the counterpart towards the midline, as in *Varanus* (Bahl, 1937). Dorsally, it is possible that the expanded proximal body along its dorsal border was connected by the cartilaginous pila preoptica of Bahl (1937:149) to a narrow curved groove, found on either side of the triangular boss at the posteroventral face of the frontal (Bell, pers. comm.). This groove has often been referred to as an impression for a cerebral hemisphere in the literature (e.g., Russell, 1967).

**Pterygoid**—The right pterygoid of the holotype bears 15 (or 16) small teeth, the highest count in plioplatecarpine mosasaurs with the exception of KU 14349, a *Platecarpus planifrons* specimen from the Niobrara Chalk of Kansas (Konishi and Caldwell, 2007) (Fig. 5-4). The teeth are closely spaced, and unique in that the additional teeth are born on a basisphenoid process, which is usually almost or completely edentulous in plioplatecarpines, including KU 14349 and DMNH 8769 (Russell, 1967:fig. 84; Konishi and Caldwell, 2007:fig. 3). On the holotype, however, as many as six alveoli line the basisphenoid process to its distal extremity. In a stark contrast, only nine widely spaced teeth and/or alveoli are present on each pterygoid of DMNH 8769, with the posterior-most one located on the proximal portion of the basisphenoid process on the left side (Fig. 5-11). Apparently, the corresponding position on the counterpart is edentulous. The pterygoid tooth count in *Latoplatecarpus willistoni*, like in many other plioplatecarpine taxa, is thus intraspecifically highly variable (Konishi and Caldwell, 2007; Konishi and Caldwell, 2009).

The ectopterygoid process in the holotype is well developed and projects anterolaterally from the long axis of the element, much as in *Platecarpus tympaniticus* and *P. planifrons*. The process consists of an expanded, rugose distal terminus and a flat, stalk-like basal region, the former of which would have articulated with an ectopterygoid with a significant overlap (Fig. 5-10B, C). On DMNH 8769, a conspicuous groove runs along the dorsal surface of the basal portion of the ectopterygoid process. Anteriorly, the pterygoid forms an oblique sutural contact with both the vomer and palatine (cf., Konishi and Caldwell, 2007). Posteriorly, the quadrate ramus of the holotype continues to expand towards the distal end, and is slightly more than 2.5 times as long as the basisphenoid process. In *Plioplatecarpus nichollsae*, it is reported that this ramus is about four times as long as the basisphenoid process (Konishi and Caldwell, 2009). On DMNH 8769, the ramus is nearly straight, posteriorly terminating in a rather blunt, squared-off edge (Fig. 5-11).

**Epipterygoid**—The left epipterygoid in the holotype is preserved almost in situ so that both ends still maintain their articulations with the parietal and base of the pterygoid basisphenoid process (Fig. 5-10). In accordance with the observation made in *Plioplatecarpus nichollsae* by Konishi and Caldwell (2009), the parietal end is columnar, while the pterygoid end is somewhat flattened, contradicting many previous hypotheses about the orientation of the epipterygoid in mosasaur skulls (e.g., Camp, 1942; Russell, 1967; Fig. 5-10B, C). Unlike *P. nichollsae* (TMP 83.24.01), the dorsal end does not decrease in diameter, with no indication of a distal cartilaginous cap; i.e., no fine grooves are preserved. The right counterpart is missing the dorsal terminus, but like the left, its ventral end is flattened, and inserts into the dorsal notch between the basisphenoid process and quadrate ramus of the pterygoid (Fig. 5-3).

**Palatine**—The right palatine is the better preserved of the two in the holotype. Laterally, it abuts the maxilla between the mid-section of the eighth and eleventh tooth. Its posterolateral corner is significantly notched as in *Plioplatecarpus nichollsae*, continuing anteriorly as a conspicuous groove gouged along the ventral surface of the bone, running parallel with the dental margin of the maxilla for about the length of one alveolus (Fig. 5-4). As Konishi and Caldwell (2009) suggested, it is a possibility that this distinct notch and groove served a similar function to the palatine foramen found in this region in *Varanus* (cf., Russell, 1967). In DMNH 8769, the posterior margin of the bone is evenly scalloped instead of bearing a single large notch at the lateral end, and oriented anteromedially rather than being round.

On the holotype, the long, anteromedially oblique border forms a long suture with the vomer and pterygoid (Fig. 5-4). The suture with the vomer is via a thin splint of bone that delicately braces the posterolateral border of the vomer, partially contributing to the formation of the vomerine process. This anteromedial extension of the palatine also demarcates the posteromedial border of the choana, whose posterior border is formed by the shallowly concave anterior border of the palatine (Fig. 5-4). In dorsal aspect, the posterior end of the "J-shaped ridge" (Russell, 1967:24–25) forms the anteroventral floor of the orbit (Fig. 5-3).

**Vomer**—As observed in *Platecarpus planifrons* by Konishi and Caldwell (2007), the vomer in TMP 84.162.01 shows that it is in contact with the pterygoid posteromedially, as well as with the palatine posterolaterally (Fig. 5-4). This topological relationship effectively places the slender posterior portion of the vomer between the two bones. The vomer posteriorly extends as far back as the level of the posterior end of the ninth maxillary tooth, beyond the anterior border of the choana. Thus, the vomer fully comprises the vomerine process (cf., Russell, 1967; Holmes, 1996; Konishi and Caldwell, 2007). As Holmes (1996) observed in *Plioplatecarpus primaevus*, approximately the posterior half of the vomerine process rotates so that its main plane is oriented parasagittally. The two vomerine processes run parallel with and close to each other, leaving virtually no space in between (cf. Holmes, 1996; Konishi and Caldwell, 2009). Anteriorly, the ventral oblique crests are well developed, extending from the anterior margin of the third to the posterior margin of the fifth maxillary teeth, and converging anteriorly. In *Plioplatecarpus nichollsae*, this crest is found between the mid-section of the second and the posterior margin of the fifth maxillary teeth (Konishi and Caldwell, 2009:fig. 12).

Anterior to the third maxillary tooth position, the vomer re-expands for a short distance and immediately tapers again, contacting the vomerine process of the premaxilla. This anterior-most segment of the vomer is about 1.5-tooth-positions long, and it is likely fused to the counterpart posterior to its contact with the premaxilla. Both the aperture for the Jacobson's organ and the vomerine aperture, were not identified with confidence, although Russell (1967:fig. 84) indicates the former to be situated laterally adjacent to the posterior end of this anterior-most segment in *Platecarpus tympaniticus*.

**Squamosal**—The left squamosal in the holotype is preserved in its entirety and largely in situ (Fig. 5-4), and in DMNH 8769 the left squamosal is in articulation with the postorbitofrontal, while the right one is in articulation with both the supratemporal medially and quadrate ventrally (Figs. 5-9, 5-13B, F). Anteriorly, the slender postorbital process extends as far forward as the base of the jugal process of the postorbitofrontal. Although the longitudinal walls of the process diminish in height anteriorly, the medial wall is significantly taller than the lateral one in the holotype (cf. Konishi and Caldwell, 2009). In marked contrast, the medial wall in DMNH 8769 progressively becomes shallower anteriorly, while its lateral wall maintains the same depth along most of its length

(Fig. 5-9), exhibiting some intraspecific variations in this character. The parietal process in both specimens is low and roughly triangular in outline.

Most notably, the posterior portion of the squamosal process of the postorbitofrontal extends well beyond the anterior limit of the squamosal quadrate process in both specimens (Figs. 5-9, 5-12). Almost the entire medial surface of the vaguely triangular quadrate process is broadly concave, and receives a mirror-image lateral convexity of the supratemporal. The foot-shaped ventral portion of the quadrate process is ventrally excavated to form a longitudinally elongate ovate concavity, with which a mirror-image eminence found on the disto-medial portion of the quadrate suprastapedial process articulates (see quadrate below; Fig. 5-12).

**Supratemporal**—In the holotype skull, only the posterior surface of the element is exposed on the left side, whereas it is largely exposed on the other side excepting the medial surface that is in articulation with the distolateral portion of the paroccipital process. Missing the parietal process, the lateral surface of the preserved middle portion of the right supratemporal (hereafter referred to as a main body) is convex and grooved in an anterodorsal direction for its articulation with the squamosal. The main body anteriorly sends a short prootic process along the distolateral end of the paroccipital process, distally forming a U-shaped sutural contact with the prootic, much as in *Plioplatecarpus nichollsae* (Konishi and Caldwell, 2009). Extending as far ventrally as the posteroventral corner of the opisthotic, the main body of the supratemporal ventrally sends a process vertically oval in outline with a cup-shaped anterior face, hereafter referred to as a ventral process (variably referred to by Fernández and Martin [2009] as "ventrally directed expansion" [p. 721], "medio-ventral expansion" [p. 722], and "posteroventral expansion" [p. 724] of the supratemporal). On the left side, this cup-shaped ventral process articulates with the distomedial portion of the elongate suprastapedial process of the quadrate (Fig. 5-12). Although the squamosal is slightly displaced from its original articulation with the quadrate on this side, the more elongate and nearly horizontally oriented quadrate articulation of the squamosal and the anterior concavity of the ventral process of the supratemporal together create a continuous, large single semi-arc-shaped concavity, into which the suprastapedial process of the quadrate would fit (pers. observ. of FMNH PR-467; see quadrate below). Dorsally, the main body of the left supratemporal sends an elongate, rectangular, sheet-like parietal process, anterodorsally and slightly medially. This process articulated with the parietal suspensorial ramus from underneath.

**Quadrate**—The virtually undistorted right quadrate of the holotype measures 97 mm in height, which is both proportionately and absolutely large compared with *Platecarpus* of similar skull size. In *Platecarpus planifrons* (UALVP 24240), the average quadrate height of 90.5 mm constitutes about 93 % that of the holotype of *Latoplatecarpus willistoni*, while its skull length is about 10 % longer. AMNH 1820 and 1821, a skull and mandibles most likely belonging to a single individual of *Platecarpus tympaniticus*, possesses quadrates that are 92 mm in height, while its mandible is nearly 8 % longer than TMP 84.162.01 (Russell, 1967:table 1). The overall morphology of the quadrate of the new plioplatecarpine is nearly identical to that of *Plat. tympaniticus* and

*Plioplatecarpus nichollsae* (cf., Konishi and Caldwell, 2009). In particular, the suprastapedial process of prominent proportion is 75 % that of the height of the quadrate on the right side of the holotype. The process is broad and distally expanded, and lacks any lateral constriction.

There are two eminences along the dorsomedial border of the suprastapedial process readily discernible in DMNH 8769 (Fig. 5-13A, E), both occurring in the posteriorly sloping portion of the process that is posterior to the cephalic condyle. The distal one is the most pronounced of the two, and it also bulges medially to form a button-like prominence near the distomedial end of the process. The outline of this prominence matches that of the ventral process of the supratemporal described above, and it is inferred here that these two parts articulated with each other, as it was also hypothesized by Fernández and Martin (2009) for *Taniwhasaurus antarcticus*. Almost immediately anterior to this distal prominence is a narrower, less prominent eminence without a medial bulge. The relative size as well as the elongate ovoid outline of the eminence, in addition to its topological relationship with the former eminence, no doubt makes it a site for the squamosal articulation (Fig. 5-13).

Except in the recent reconstruction of the quadratic suspensorium in *Taniwhasaurus antarcticus* by Fernández and Martin (2009:fig. 5A, B), all the existing restorations of mosasaur skulls known to the authors had shown the supratemporal and squamosal articulating to the quadrate at the broadly convex cephalic condyle (e.g., Russell, 1967:fig. 20; Holmes, 1996:fig. 2C). In this view, the quadrates were positioned upright in mosasaur skulls. The observations made on the quadrates of *Latoplatecarpus willistoni* create a problem, as the supratemporal and squamosal articulate with the distal portion of the long suprastapedial process, which necessitates a quadrate to rotate forward from the presumed upright position, in order to maintain the horizontal orientation of the upper temporal (= postorbital) process of the squamosal. However, we believe such was the case in many plioplatecarpines and possibly other groups of mosasaurs, including *Platecarpus planifrons* (e.g., AMNH 1491; FHSM VP-2116, 2296), *Platecarpus tympaniticus* (e.g., AMNH 1820; LACM 128319), and *Plioplatecarpus nichollsae* (TMP 83.24.01; Konishi and Caldwell 2009:fig. 7), based not only on the similar eminences consistently observed on their quadrates, but also on an anteriorly inclined orientation of the quadrates preserved in well-articulated skulls such as TMP 84.162.01 (*Latoplatecarpus willistoni*), FHSM VP-2116 (*Platecarpus planifrons*), and LACM 128319 (*P. tympaniticus*). In modern squamates, the orientation of the quadrates in the resting position (= jaws closed) varies from anteriorly inclined (e.g., *Dracaena*, *Naja*), vertical (e.g., *Tupinambis*, *Lanthanotus*, *Python*), to posteriorly inclined (most others) (Romer, 1956; Dalrymple, 1979; Estes et al., 1988; pers. observ.). In addition, in all cases but a few, it is the posterodorsal portion of the quadrate (i.e., the suprastapedial proper) that articulates with the squamosal and/or supratemporal in extant squamates, rather than the anterodorsal corner, that is, the cephalic condyle (Estes et al., 1988).

The conch of the left quadrate in the holotype of *Latoplatecarpus willistoni* is completely filled with the round expansion of the extracolumella, which is as thick as the depth of the conch itself (Fig. 5-12). The tympanic rim is better preserved on the right side, although part of the ala has been pushed inward and slightly deformed, resulting in a straighter lateral outline of the rim rather than circular (cf. Konishi and Caldwell, 2009). The anterior cephalic border lacks a posterior embayment, and the tympanic ala projects laterally rather than anterolaterally, features shared with *Platecarpus tympaniticus* and *Plioplatecarpus nichollsae* but not with all the other nominal *Plioplatecarpus* species. The alar surface lacks any conspicuous bulging as well except above the mandibular condyle, where the surface is distinctly depressed. The mandibular condyle is about twice as wide as it is long with a curved teardrop-shaped outline, its apex pointing medioanteriorly. Where the mandibular condyle attains its maximum anteroposterior dimension, the anterior extension of the smooth condylar surface forms a 'lip', visible in anterior aspect at the ventral edge of the quadrate (cf. Konishi and Caldwell, 2009:fig. 8C).

**Jugal**—The gracile left jugal in DMNH 8769 is nearly complete without distortion, missing only the distal extremities postmortem. The long horizontal (= infraorbital) ramus is at least twice as long as the vertical ramus, exhibiting a gentle ventral curvature and gradually expanding distally (Fig. 5-14). On the medial surface of the ramus, the shallowly concave articulation facet for the maxilla anteriorly occupies a little over half the length of the ramus. Posteriorly, this facet meets the anterior end of the much shallower and dorsoventrally narrower articulation facet for an ectopterygoid, an indication that the maxilla and ectopterygoid contacted each other at their extremities (cf. Bell, 1993). Located distolaterally on the vertical (= postorbital) ramus is a laterally and slightly anteriorly facing articulation concavity for reception of the jugal process of the postorbitofrontal from above. Unlike in *Platecarpus*, however, this articular end lacks any antero-posterior expansion, and is the narrowest portion of the ramus as in *Plioplatecarpus houzeaui*, although it is not as thin and rod-like as in the latter taxon (Fig. 5-14; Lingham-Soliar, 1994a:pl. 7C, D). At the posteroventral corner of the jugal, an obtuse-angled, moderately developed jugal process can be seen. It lacks a distinct posterior keel that characterizes jugals in *Platecarpus*, but can be separated from the condition in post-middle Campanian *Plioplatecarpus* spp. where the jugal process is lacking altogether. This gentle posteroventral process morphology is highly comparable to those of plioplatecarpines found in the Western Interior Basin of equivalent age, including a specimen referred to *Platecarpus* sp., cf. *P. somenensis* from Alabama (Shannon, 1975; Konishi and Caldwell, 2009; pers. observ.).

**Prootic**—As part of the well-preserved, minimally distorted brain case of DMNH 8769, the triradiate prootic is virtually complete on both sides (Fig. 5-15). Forming a thick anterolateral wall of the braincase on each side of the midline, a broadly square-shaped parietal process bears a sinusoidal dorsal border, whose finely grooved surface articulated with the descending process of the parietal from above (Fig. 5-15B). The trigeminal notch exhibits a rounded outline as seen in *Platecarpus tympaniticus* (AMNH 1820), rather than a square-shaped outline seen in *Plioplatecarpus nichollsae* (TMP 83.24.01) (Konishi and Caldwell, 2009). Although not readily discernible, the outline of this notch is predicted to have been more square-shaped in the holotype, because of the 'hatchet-shaped' anteroventral basisphenoidal process (of the prootic) as found in *Plioplatecarpus nichollsae*. In this respect, DMNH 8769 differs from the holotype and *P. nichollsae* in possessing a less square-shaped basisphenoidal process similar to the one in *Platecarpus tympaniticus* (e.g., AMNH 1488, 1566, and 1820) (Fig. 5-15). The suture between the process and the alar process of the basisphenoid is well demarcated since the latter is apparently preserved as a calcified cartilage in DMNH 8769. In this specimen, the crista prootica (otosphenoidal crest) barely covers the exit for the seventh cranial nerve and is less developed than in some specimens of *P. tympaniticus* (e.g., AMNH 1820), though it may be due partially to its small size, i.e., ontogeny (see discussion below). In addition, the posterior-most border of the basisphenoidal process is so abbreviated that a large fenestra rotunda is nearly completely exposed on the lateral wall of the opisthotic behind (Fig. 5-15A). The exit for the seventh cranial nerve in the holotype is exposed on the lateral surface of the posterodorsal corner of the basisphenoidal process, although a small crista prootica may have partially covered the foramen but been lost postmortem (Fig. 5-4). In both specimens, the third, suspensorial ramus of the prootic extends posteriorly along the lateral wall of the opisthotic, and distally forms a shallowly U-shaped suture with the supratemporal.

**Opisthotic-Exoccipital**—In the well-preserved braincase of DMNH 8769, most notably, the aforementioned fenestra rotunda, which is a shared opening for the cranial nerve IX (Bahl, 1937; Russell, 1967), is larger in diameter than the fenestra ovalis, as in *Varanus*. On the left side, the delicate stapes is intact and preserved along the ventral sulcus of the paroccipital process of the opisthotic (Fig. 5-15A, D). At the distal end of the process, the opisthotic develops a keel-like, downward projection medially adjacent to the ventral process of the supratemporal (Fig. 5-15C). It is possible that part of this keel laterally contacted the distomedial surface of the quadrate suprastapedial process. As in Russell's (1967) reconstruction, there is a small wedge-shaped gap between this keel and the ventral process of the supratemporal (Fig. 5-15C). On the left side of the holotype, this gap is filled by what appears to be a mass of calcified cartilage, which measures approximately 23 mm high and 26 mm wide (Fig. 5-12). This large mass caps the distal-most portion of the medial border of the suprastapedial process ventral to the supratemporal. Thus, the distal two-thirds of the suprastapedial process of the quadrate in this taxon was possibly supported by three bony and one cartilaginous elements collectively forming the posterolateral corner of the supratemporal fenestra.

As in most plioplatecarpines, the jugular foramen in DMNH 8769 is found medial to the posterior flange of the tongue-like process that distally cradles the dorsolateral surface of the basal tuber (Fig. 5-15A). Although in Holmes' (1996:fig. 6) reconstruction of the braincase of *Plioplatecarpus primaevus* there is no such a flange, and the jugular foramen is located on the same bone surface as the fenestra rotunda, this is most likely a postmortem artifact as this region is highly weathered on the original specimen, CMN 11840. A similar flange is clearly preserved on the holotype of *Plioplatecarpus marshi* and BMNH 5868 (*Plioplatecarpus* sp.) (Lingham-Soliar, 1994a:fig. 8, pl. 1B; pers. observ.). In posterodorsal aspect, the opisthotic portion of the paroccipital process contacts the supraoccipital proximally with a straight suture perpendicular to the axis of the process (Fig. 5-15C). As noted by Konishi and Caldwell (2009), the suture between the exoccipital and the occipital condyle is more lateroventrally inclined in *Plioplatecarpus nichollsae* than in *Platecarpus tympaniticus* (cf. Konishi and Caldwell, 2009:fig. 11).

**Supraoccipital**—The supraoccipital appears completely fused to the paroccipital processes in the holotype, while the sutural distinction is evident in DMNH 8769, the smaller individual of the two. In the latter, the virtually undistorted supraoccipital possesses a pronounced median dorsal keel bearing a pair of low ridges running along its dorsal edge (Fig. 5-15C). The highly developed nature of this supraoccipital median keel is reminiscent of that found in both *Plioplatecarpus nichollsae* and *P. primaevus* (Konishi and Caldwell, 2009). On each side of the keel, the external surface of the bone bears two conspicuous sulci that run parallel with the keel. A pair of short, dorsoventrally flattened processes diverges laterally and slightly ventrally from the midline to form the roof of the foramen magnum, which is vertically elongate ovoid. Each of these processes is distally squared off in outline, and broadly contacts the opisthotic by a straight transverse suture (see above).

**Basioccipital**—In the holotype, the partially exposed articular surface of the occipital condyle is strongly pitted. In posterior view, the occipital condyle is shallow in DMNH 8769. Ventrally in both specimens, a pair of significantly inflated basal tubera grows ventromedially toward each other, much as in

*Plioplatecarpus nichollsae* (Fig. 5-4; Konishi and Caldwell, 2009:figs. 10, 11). Compared to AMNH 1820, a *Platecarpus tympaniticus* specimen, the pitted distal surface is much more expanded and extends further toward the midline. Compared with *P. tympaniticus* (AMNH 1820), a greater portion of the anteroventral surface of the tuber is covered by the posterolateral wing from the basisphenoid. In all respects, the morphology of the basal tubera in *Latoplatecarpus willistoni* is identical to that in *Plioplatecarpus nichollsae* as described by Konishi and Caldwell (2009), and it distinguishes these two taxa from *Platecarpus* spp. Unlike in *Plioplatecarpus nichollsae* and other *Plioplatecarpus* taxa however, there is no unossified region on the floor of the basioccipital between the two tubera, including in DMNH 8769. Nevertheless, in the holotype, the broad posteroventral area between the tubera is split along the midline from lateral compression, suggesting that the floor of the element was rather thin along the midline, likely due to the downward expansion and/or migration of the canal for the basilar artery that runs through the basioccipital. Although the preservation makes it impossible to confirm the dorsal exit of the canal on the floor of the medullary cavity in the holotype, a large, bilobate exit for the basilar artery pierces the medullary floor for its entire breadth just inside the foramen magnum in DMNH 8769 (Fig. 5-15C).

**Basisphenoid-Parasphenoid**—A pair of posterolateral wings of the basisphenoid embraces extensively the anterior half portion of the basal tubera ventrally and laterally. In DMNH 8769, these wings are not separated by a deep longitudinal cleft, but instead by numerous fine longitudinal grooves. The alar process is largely overlapped laterally by a large, descending basisphenoidal process of the prootic, and it appears cartilaginous on both sides as mentioned earlier (Fig. 5-15A, B). The alar process overhangs the anterior portion of the wide vidian canal, which curves upward posteriorly. Flanked by the pair of basisphenoid processes of the pterygoids, the parasphenoid rostrum in the holotype gently narrows anteriorly; the basipterygoid processes have been obscured by the pterygoids. Around the level of the base of the basisphenoid processes (of the pterygoids), the anterior extremity of the parasphenoid rostrum is further narrowed (Fig. 5-4). This anterior segment measures approximately 20 mm in length. A long, virtually complete parasphenoid extends further anteriorly from the anterior end of the rostrum to the level of the first pterygoid tooth without notable dorsal deflection, although there is a postmortem break between its base and the rostrum (Fig. 5-4). This styloid process extends for about 77 mm, similar in length to the interpterygoidal vacuity.

## Descriptions and Comparisons: Lower Jaw

**Dentary**—There are 12 alveoli in each dentary (Figs. 5-16, 5-17). Anteriorly, no conspicuous predental rostrum is present, and at least the first and second teeth are inclined somewhat anteriorly as indicated by DMNH 8769. The dentary is gracile in this taxon, and it curves slightly upward posteriorly in DMNH 8769. The estimated maximum depth of the dentary is about 23 % of the entire length of the bone in the holotype. This value is comparable to 21 % in *Platecarpus tympaniticus* (FMNH UC-600). The meckelian groove steadily narrows anteriorly, barely reaching the anterior margin of the bone. In the holotype, a concentration of very small foramina is found anteriorly on the lateral surface under the first two alveoli. Posterior to this portion, however, there are only two or three exits for the mandibular branch of the fifth cranial nerve, therefore a large part of the lateral dentary wall is smooth. In DMNH 8769, the same foramina are more numerous and more broadly distributed on the outer surface of the bone, found on the anterior one-third of the jaw. Posterior to the last tooth, a small portion of the jaw is edentulous in both specimens for a little over one alveolar length. On the right seventh tooth in DMNH 8769, the exposed root portion comprises nearly 30% of the entire tooth height, and is bulbous (Fig. 5-17).

**Splenial**—In the holotype the splenial is largely complete on both sides, reaching as far anteriorly as the level beneath the fourth alveolus on the right side. The virtually undistorted posterior border of the medial wing of the left splenial is broadly notched, as the posterodorsal corner of the wing extends posteriorly (Fig. 5-16B). The posterior margin of the deep medial wing is also notched in DMNH 8769, though to a much lesser extent (Fig. 5-18B). These observations contrast with the anterodorsally gently inclined, linear posterior border of the wing as reconstructed by Russell (1967:fig. 29) for *Platecarpus tympaniticus* or by Holmes (1996:fig. 8) for *Plioplatecarpus primaevus*. Indeed, the equally well-preserved medial splenial wing of FMNH UC-600 assignable to *Platecarpus tympaniticus* exhibits exactly the same embayment along its posterior border. A very small notch seems to be present near the dorsal end of the posterior margin of the wing in *Plioplatecarpus primaevus* (P 1756.1) as well. For its entire length, the expanded wing covers the meckelian groove medially. The large, horizontally ellipsoid posteroventral foramen, well preserved in the holotype, measures 7.0 mm x 3.8 mm in diameter, and occurs approximately 25 mm anterior to the base of the intramandibular joint on the medial surface (Fig. 5-16B). The foramen likely allowed the passage for the inferior alveolar nerve (Bahl, 1937). The lateral wing of the splenial is best preserved in the right side of DMNH 8769, with its virtually complete dorsal border (Fig. 5-18C). Between the medial and lateral wings of the splenial runs a blade-like anterior extension of the prearticular (Fig. 5-18A, B).

At the posteroventral corner, the splenial thickens to form a vertically ovoid, cup-shaped articulation surface to receive the anterior end of the angular. This articulation cotyle for the angular is U-shaped in outline with a vertical median groove in the center, similar to the condition in *Platecarpus* (Russell, 1967:fig. 28). In addition, fine, numerous U-shaped concentric grooves are found on this articulation surface in DMNH 8769. Also, near the right articulation cotyle of this specimen, the splenial exhibits an anomalous bone growth forming a lump along its ventral border (Fig. 5-18C, arrow).

**Angular**—The anterior articular condyle of the angular is similar in its outline to that of the angular articulation cotyle of the splenial. In DMNH 8769, the splenial articulation facet is V-shaped in outline. The splenial facet is convex overall, and bears a vertical median keel to fit into the splenial cotyle in front. Laterally in the articulated holotype mandible, the angular is narrowly exposed along the anteroventral border of the surangular. Medially, the angular bears a wedge-shaped wing that covers the ventromedial portion of the anterior half of the surangular and prearticular. This wing is approximately half as deep as the medial wing of the splenial, and dorsally does not contact the coronoid. In the holotype, the intact anterior border of this medial wing is distinctly notched posteriorly, forming the border for a large angular foramen (7.9 mm x 5.9 mm, horizontally ovate), which allows the passage for the angular branch of the inferior alveolar nerve (Bahl, 1937). The foramen is larger than the one for the splenial branch of the same nerve already mentioned, and the anterodorsal corner of the wing completely forms its dorsal border, except the foramen is open anteriorly (cf. Holmes, 1996:fig. 8). No such anterodorsal overhanging portion of the medial angular wing is present in Russell's (1967:fig. 29) reconstruction of the mandible for *Platecarpus tympaniticus*; however, as the specimen he based his reconstruction on (AMNH 1821) has incomplete angulars, it is possible that such an overhanging structure existed in this taxon as well but was not preserved. In *Platecarpus planifrons* (UALVP 24240) on the other hand, the angular foramen is proportionately smaller and is completely surrounded by the angular. Unlike in *Varanus*, the angular is definitely larger than the coronoid in the new taxon (Bahl, 1937) (see coronoid below).

**Surangular**—Overall, the surangular is comparable in morphology to that of *Platecarpus tympaniticus* in exhibiting outline that deepens anteriorly (Figs. 5-16, 5-18C). The dorsal border is horizontally straight, except at both ends where it gently rises to form a coronoid buttress anteriorly and the anterior rim of the glenoid fossa posteriorly (Fig. 5-19A). In both the holotype and DMNH 8769, the anterior surangular foramen and its anterior fossa are positioned below the anterior 38 % portion of the coronoid suture (Figs. 5-16A, 5-18C, 5-19A). In *Platecarpus planifrons*, this foramen (and the fossa) is present beneath the anterior one-fifth (FHSM VP-2116) to one-fourth (UALVP 24240) portion of the coronoid suture, and in one specimen of *P. tympaniticus* (AMNH 1821), underneath slightly less than the anterior one-third portion of the suture. It is possible then that this increase in the relative length of the anterior surangular foramen and associated groove within the derived plioplatecarpine mosasaurs was related to the anterior extension of the surangular itself. When the position of the anterior terminus of the element relative to the splenio-angular joint is considered, only the anterior one-fifth or smaller portion of the coronoid suture is found anterior to the joint in *Platecarpus planifrons* (e.g., FMNH VP-2116, UALVP 24240), while greater than one-third of the anterior portion of the same suture extends beyond the joint in *Latoplatecarpus willistoni*. In *P. tympaniticus* (FMNH UC 600), a slightly smaller portion (30 %) of the coronoid suture is found anterior to the intramandibular joint, while in the holotype of *Plioplatecarpus houzeaui*, more than 65% (two-thirds) of the coronoid suture extends anterior to the splenio-angular joint.

From the level of the lateral margin of the glenoid fossa, a long, straight ridge runs anteroventrally in a shallow angle across the broad lateral face of the element, along which the adductor mandibulae externus medialis and superficialis muscles may have inserted from the supratemporal arcade, as in extant *Varanus*

(Russell, 1967:fig. 33). A minute foramen for the cutaneous branch of the mandibular nerve is located immediately lateral to the anterolateral corner of the glenoid fossa (in the holotype). As in *Plioplatecarpus nichollsae*, but unlike in *Platecarpus*, the surangular constitutes nearly or slightly more than 50 % of the total glenoid area (Fig. 5-20A, B, E). This is mainly because of the more posterior extension of the surangular-articular suture on the glenoid surface, the posterolateral corner of which the suture reaches. In *Platecarpus* (Fig. 5-20C, D), the same suture ends posteriorly well before reaching this corner of the fossa, which results in a surangular comprising only about 20 to 30 % of the total glenoid fossa (Konishi and Caldwell, 2007).

**Coronoid**—On the right side of the holotype, the coronoid is virtually undistorted, still in articulation with the surangular along its ventral border and with the dorsal border of the prearticular along the anteroventral margin of the medial wing (Fig. 5-19). The depth of the lateral wing is only about 30 % that of the medial wing, and both are absolutely and proportionately shallower than in *Platecarpus*. For instance, the lateral wing height is about 74 % that of the medial one in UALVP 24240 (*P. planifrons*), and 78 % in FHSM VP-17017 (*P. tympaniticus*), in both cases clearly exceeding 50 %. The absolute and relative decrease in the lateral coronoid wing height becomes further pronounced in the more derived members of the genus *Plioplatecarpus*. In the holotype of *Plioplatecarpus houzeaui* (IRSNB R35), the ventral as well as dorsal border of the lateral wing are no longer curved but are straight, forming the anteriorly thinning, small, wedge-shaped lateral face (cf., Lingham-Soliar, 1994a:fig. 23). Around the midpoint of the element, the lateral wing is 27 % as deep as that of the maximum depth of the medial wing, and anterior to the midpoint this ratio steadily decreases. In *P. primaevus* from North America, the overall morphology of the coronoid is nearly identical to that in the former European taxon, with the similar height ratio between the two wings (ca. 22 %) (Holmes, 1996:fig. 8; pers. observ. of P 1756.1). If this general trend in decreasing the lateral wing height of the coronoid indeed reflects evolution, then the condition in DMNH 8769 is somewhat intermediate between *Platecarpus* and the holotype of *Latoplatecarpus willistoni*: whereas the depth of the shallow lateral wing of the holotype coronoid remains the same throughout its length, in DMNH 8769 the lateral wing deepens towards the middle of the element as in *P. tympaniticus*, and the deepest portion measures about two-thirds that of the medial wing (Fig. 5-18D).

The posterior coronoid process (processus messetericus in Bahl, 1937) is unique in the holotype of *L. willistoni* in exhibiting a dorsally rounded, significantly low-angled (~ 40 degrees from horizontal) posterior border (Fig. 5-19: arrow head). However, as this process is sharply angled dorsally in DMNH 8769 and in all species of *Platecarpus* and *Plioplatecarpus* with a possible exception of *P. nichollsae*, the low, rounded profile of the process in the holotype of *Latoplatecarpus willistoni* is less likely to be of evolutionary significance. Nevertheless, the angle of the posterior border of the process from the horizontal seems to exhibit a general trend of decreasing among the derived plioplatecarpine mosasaurs. In *Platecarpus planifrons*, the border is oriented vertically, it is about 60 degrees from the horizontal in *P. tympaniticus*, and about 55 degrees in

*Plioplatecarpus primaevus* and *P. houzeaui*, all measured in lateral aspect. Based on measurements from the figures in Cuthbertson et al. (2007:fig. 5B), the right coronoid in the holotype of *P. nichollsae* may exhibit a similarly low-angled posterior border to that in TMP 84.162.01, at about 50 degrees from the horizontal. This remains a tentative estimation however, as the element is photographed in latero-ventral aspect. More importantly however, *Platecarpus*, *Latoplatecarpus willistoni*, and *Plioplatecarpus nichollsae* all exhibit a markedly concave dorsal margin of the coronoid, whereas it is (nearly) straight in both *P. primaevus* and *P. houzeaui* (compare Russell, 1967:fig. 37; Lingham-Soliar, 1994a:fig. 23; Holmes, 1996:fig. 8; Konishi and Caldwell, 2007:fig. 2; Cuthbertson et al., 2007:fig. 4B). Regardless of the specific morphology of the processus messetericus, therefore, it seems that the process indeed underwent evolutionary reduction in the course of plioplatecarpine evolution.

**Articular-Prearticular**—The articular, consisting of the round retroarticular process and the posteromedial portion of the glenoid fossa, lies in the horizontal plane, while the anteriorly extending, slender and blade-like prearticular lies in the para-sagittal plane medial to the surangular. There, it is dorso-ventrally constricted medial to the posterior half of the surangular, but it expands anteriorly to attain its maximum depth around the intramandibular joint (e.g., Fig. 5-18B). Beyond the joint, it extends anteriorly to insert into the space between the medial and lateral wings of the splenial within the Meckelian groove (Figs. 5-16B, 5-18B). The dorsal border of the prearticular is shallowly concave where it is dorso-ventrally compressed (Fig. 5-18B). The overall outline of the retroarticular process is similar to that of *Platecarpus tympaniticus*, where the round lateral border meets a straight medial border at the posteromedial corner of the process (Fig. 5-20A, C, E). However, the lateral border in the new species appears more rounded than in *P. tympaniticus*. As in *Plioplatecarpus nichollsae*, the surangular-articular suture on the glenoid surface extends posteriorly to reach the posterolateral corner of the glenoid fossa (Fig. 5-20A, B, E). As a partial consequence of this, the outline of the articular portion of the glenoid fossa is more crescent shaped instead of semicircular as seen in *Platecarpus* taxa (Fig. 5-20C, D).

**Descriptions and Comparisons: Dentition**

In the holotype of *Latoplatecarpus willistoni*, most of the marginal dentition has been reconstructed except for a few teeth. The third right maxillary tooth is original and is the longest in the entire jaw (Fig. 5-3). The crown morphology of this particular tooth is comparable to that of *Plioplatecarpus marshi* (cf. Lingham-Soliar [1994a:fig. 12]), in exhibiting not only the main posteromedial curvature but also a slight anterior deflection near the apex, which is flattened laterally (cf. Nicholls, 1988; Fig. 5-3B). This tooth lacks a clearly-defined posterior carina. In fact, in DMNH 8769, at least the first seven maxillary teeth lack the posterior carinae, and the twelfth tooth on the left maxilla also lacks one. Nevertheless, as expected for plioplatecarpines, where present, the two carinae are oriented in a fore-and-aft direction and subequally divide the crown into two halves (e.g., 10th right maxillary tooth, holotype). In DMNH 8769, about four facets are present on the lateral face of each crown while the medial surface is finely striated. The base of the crown is consistently sub-circular in cross section along the length of the jaw in both specimens. As in *Plioplatecarpus nichollsae* (TMP 83.24.01), the bulbous distal portion of the root is greatly exposed beyond the dental margin, generally constituting about one-third the entire tooth height (Figs. 5-5, 5-17; Konishi and Caldwell, 2009:fig. 2). This phenomenon is most likely related to the relative reduction in jaw depth, rather than an increase in individual tooth size, based on comparison with more basal plioplatecarpines such as *Platecarpus* (see maxilla above). Interestingly, in DMNH 8769, all the erupted teeth seem to show the same degree of development and are fully erupted except for postmortem breakage, exhibiting no signs of a postero-anterior, wave-like tooth replacement pattern suggested for many amniote groups by Edmund (1960).

Most pterygoid tooth crowns are reconstructed out of plaster in the holotype, but one original tooth crown (right third) is short and abruptly recurved at mid-height, distally bears a distinct wear facet and has a crown height of 7.5 mm. Although only the lateral carina is discernible, the posterior crown surface is distinctly striated while anteriorly the surface is smooth. An identical condition is found also in *Plioplatecarpus nichollsae* (TMP 83.24.01). In *Platecarpus planifrons* (UALVP 24240), similarly shaped pterygoid teeth bear distinct, transversely oriented carinae more than half the height of the crown; in the same taxon, the crown is smooth or faintly faceted anteriorly and finely striated posteriorly. In the holotype of *Latoplatecarpus willistoni*, the crown is sub-circular in basal cross section as in the marginal dentition.

## Descriptions and Comparisons: Postcranium

**Cervical Vertebrae**—In DMNH 8769, a complete set of seven cervicals are preserved, while only the three anterior-most cervicals are preserved articulated with the skull of the holotype. Consequently, unless specified, the following description of the cervical column is based on the former specimen, while the figure references are drawn to the holotype. The odontoid (atlas centrum) lacks a median vertical ridge on the anterior surface and dorsally exhibits a semi-circular outline, which is also discernible in the holotype. This condition is also found in *Plioplatecarpus nichollsae* and *P. primaevus*, whereas such a ridge exists along the anterior surface of the odontoid in *Platecarpus tympaniticus* (e.g., AMNH 2005) (Konishi and Caldwell, 2009). The ventral face of the atlas intercentrum is a transversely elongate rectangle in outline, and each side slopes medioventrally in a shallow angle to form a mid-sagittal, button-like tuberosity bearing a rugose surface (Fig. 5-4). The tuberosity is lower than in *Plioplatecarpus nichollsae* (TMP 83.24.01), while no such a tuberosity is present on the same element in *Platecarpus tympaniticus* (AMNH 2005) or in *P. planifrons* (UALVP 24240) (Konishi and Caldwell, 2009). A pair of atlas neural arches flanks the preceding two elements. The overall morphology is nearly identical to that described for *Plioplatecarpus nichollsae* (TMP 83.24.01). The distal end of the spinous process is intact and rotated slightly anterolaterally as well as it is expanded. A prominent, posterodorsally directed tuberosity projects at the base of the spinous process along its posterior border. The exposed articulation surface with the axis centrum is smooth, slightly concave, and is a broad triangle in outline with its apex pointing posteriorly, which has not been described in *P. nichollsae*.

The overall axis morphology is virtually indistinguishable from that of *Plioplatecarpus nichollsae* (Konishi and Caldwell, 2009:fig. 14A–E), except for the greater curvature of the central condyle, which is even greater than that of a *Platecarpus tympaniticus* specimen examined (AMNH 2005). As in *Plioplatecarpus nichollsae*, the neural arch and the neural spine are relatively short antero-posteriorly, particularly in comparison with *Platecarpus tympaniticus* (AMNH 2005). The anterior border of the neural arch rises nearly straight from the anterior edge of the central body in the new taxon as in *Plioplatecarpus nichollsae*, whereas the border is distinctly notched in *Platecarpus tympaniticus* (AMNH 2005), partially due to the greater anterior overhanging of the neural spine (cf. Russell, 1967:fig. 40). The synapophyseal facet is also antero-posteriorly short as in *Plioplatecarpus nichollsae* or *P. primaevus*, its length about half as long as that of the centrum. The same facet in *Platecarpus tympaniticus* measures about two-thirds the centrum length (AMNH 2005). Preserved only in the holotype, the ventral face of the axis intercentrum is as wide as that of the atlas, but it is nearly 1.5 times longer than the atlas (Fig. 5-4). A prominent ventral tuberosity must have been present on the axis, as indicated by its broken base occupying the posterior two-thirds of the surface along the midline. This condition is identical to that observed in *Plioplatecarpus nichollsae* and differs from either *Platecarpus tympaniticus* or *Plioplatecarpus primaevus* (see Konishi and Caldwell, 2009). Interestingly however, UALVP 24240 (*Platecarpus planifrons*) bears a nearly identical ventral tuberosity on its axis intercentrum. In the holotype of *Latoplatecarpus willistoni*, the densely pitted hypapophyseal surface is only slightly tilted posterodorsally on the ventral surface of the axis centrum and is triangular in outline with its apex pointing forward (Fig. 5-4). The latter condition is different in DMNH 8769, in exhibiting a more circular outline of the hypapophyseal facet, although its anterior rim is pointed.

The depth of the synapophyseal facet, as well as the width of the articular condyle, steadily increase from c2 to c7: consequently, the centrum of the seventh cervical vertebra is more than 20 % wider than the axis centrum (Fig. 5-21). On the other hand, the hypapophyseal facet gradually decreases in size posteriorly and is smallest on the seventh cervical vertebra, although the facet is still distinctly present and fully articulated with the eighth intercentrum (peduncle). Incipient zygantra are present at least posterior to c4, are not observable on c5 and c6, and absent on c7. Although the region is well preserved, there is no trace of zygosphenes on c3. When in articulation, the cervical vertebrae exhibit a moderate ventral curvature, consistent with the observation made in *Plioplatecarpus primaevus* (Holmes, 1996) and a specimen of *Platecarpus tympaniticus* (LACM 128319). The neural spines are well preserved only on c3 and c4; between the two, the horizontal length as well as the width of the spine decrease posteriorly, while the spine slightly increases in height posteriorly.

**Dorsal Vertebrae**—The anterior-most seven dorsal vertebrae are preserved in DMNH 8769, where the width of the centrum continues to increase posteriorly: the seventh dorsal vertebra (= 14th in the entire vertebral column) is approximately 38 % wider than the axis across the articulation condyle, the trend also found in two specimens of post-middle Campanian *Plioplatecarpus* (Fig. 5-21). On the presumed first dorsal vertebra, the synapophyseal facet is both taller and longitudinally longer than the last cervical. Posterior to the first dorsal, the height of the facet progressively decreases while the facet slightly increases its longitudinal dimension. In all the preserved dorsal vertebrae, zygapophyses are well developed, but neither zygantra nor zygosphenes are present. A couple of neural spines are preserved; they appear to increase in height while decreasing in horizontal dimension gradually caudally. Hypapophyses are lacking from all the dorsal vertebrae preserved. Throughout the preserved anterior section of the vertebral column, the angle formed between the prezygapophyseal facet and horizontal plane fluctuates between approximately 45 and 60 degrees.

**Caudal Vertebrae**—A total of eight, anterior intermediate caudal vertebrae are preserved in DMNH 8769. On each vertebra, a pair of cup-shaped haemapophyses clearly articulated with a haemal arch-spine complex, a russellosaurine feature (Polcyn and Bell, 2005).

**Scapula**—Although partially encrusted with selenite crystals, the left scapula (Fig. 5-22) of the holotype retains its overall morphology, including the minimally distorted articulation condyle. The anteroventral and posteroventral borders of the scapular blade are aligned in a nearly straight line, forming a nearly semicircular blade outline, similar to *Plioplatecarpus primaevus* and the two European *Plioplatecarpus* taxa (see Lingham-Soliar, 1994a:fig. 26B; Holmes, 1996:fig. 14). In contrast with these three taxa but similar to *Platecarpus tympaniticus* and *Plioplatecarpus nichollsae*, the horizontal dimension of the articulation condyle is both relatively and absolutely greater in the new taxon (compare Russell, 1967:fig. 44; Cuthbertson et al., 2007:figs. 2, 8B; Fig. 5-22, this study). The length of the condylar surface is about 35 % that of the antero-posterior length of the blade in the new taxon, while it ranges from 38 % to 42 % in *Platecarpus tympaniticus*. On the other hand, it is about 25 % in *Plioplatecarpus primaevus* and 22 % in *P. houzeaui* (pers. observ.). The holotype of *P. nichollsae* possesses an even greater proportion of about 48 %, although its degree of postmortem distortion is unknown. As well, as in *Platecarpus* and *Plioplatecarpus nichollsae*, the base of the articulation condyle is situated more anteriorly in relation to the blade than in stratigraphically younger *P. primaevus*, *P. houzeaui*, and *P. marshi*. Namely, the horizontal length of the anteroventral border of the blade is less than that of the articular condyle (Fig. 5-22A, B). In *Platecarpus planifrons*, there is little anterior projection of the scapular blade beyond the anterior border of the articular condyle (e.g., FHSM VP-2116). In *P. tympaniticus*, the ratio between the blade length anterior to the condyle and that posterior to the condyle is 1 : 2.7 on average based on various AMNH and YPM specimens examined. On the holotype of *Latoplatecarpus willistoni*, this ratio is 1 : 2.5, while in three other plioplatecarpine specimens from the lower Pierre Shale Formation, including the holotype of *Plioplatecarpus nichollsae*, the ratio is 1 :

2.7 (AMNH 14800, CMN 52261, and FMNH PR465). Hence in all the above taxa, the portion of the scapular blade poster to the articular condyle is at least 2.5 times longer than the portion anterior to it. In contrast, in the upper Campanian-lowermost Maastrichtian *P. primaevus*, this ratio dramatically increases to 1 : 1.7 (USNM 18254 = holotype) to 1 : 1.5 (CMN 11835), and in the lower Maastrichtian *P. houzeaui* (IRSNB 3101) and the upper Maastrichtian *P. marshi* (IRSNB R38 = holotype), further to 1 : 1.1 and 1 : 1, respectively. In the last two taxa, the stalk-like condyle is situated near/at the mid-portion of the blade along its ventral border. As the anterior part of the blade further expanded forward in these two taxa, the height of the blade did not seem to increase in proportion: as a result, the scapular blade became horizontally elongate in outline (Lingham-Soliar, 1992; cf. Lingham-Soliar, 1994a:fig. 15).

Although Cuthbertson et al. (2007:601) describes that the posterior scapular blade of the left scapula in the holotype of *Plioplatecarpus nichollsae* "tapers dorsally" at its posterior end as in *Platecarpus* (*tympaniticus*), the same feature is less distinct in the right scapula, which exhibits more posterior elongation of the posterior blade with a nearly horizontal ventral border similar to *Latoplatecarpus willistoni* (TMP 84.162.01) or *Plioplatecarpus primaevus* (compare Cuthbertson et al., 2007:figs. 2, 8; Fig. 5-22, this study). Furthermore, on both scapulae, the dorsal border of the blade is proportionally much longer and describes a nearly complete semicircle as in the new taxon and other lower Pierre Shale plioplatecarpine specimens mentioned above, and contrasts with the condition in *Platecarpus tympaniticus*, where the same border describes a much shorter arc (cf. Russell, 1967:fig. 44). Based on the near horizontal anteroventral margin of the blade mentioned by Cuthbertson et al. (2007) and included in the generic diagnosis of *Latoplatecarpus* above, the right scapula of the holotype of *Plioplatecarpus nichollsae* is highly reminiscent of the left scapula of TMP 84.162.01 described herein. In all respects, therefore, the scapular morphology of the new taxon is most comparable to that of *Plioplatecarpus nichollsae* and other lower Pierre Shale forms among derived plioplatecarpines.

The broadly pear-shaped condylar articular surface is rugose and heavily pitted, consisting of a narrow, smaller coracoid articulation area anteromedially, and a broadly oval glenoid surface posterolaterally (Fig. 5-22C).

**Ribs**—Based solely on DMNH 8769, ribs are flat proximally and become rounder distally (cf. Burnham, 1991; Holmes, 1996; Cuthbertson et al., 2007). In *Platecarpus* (e.g., FHSM VP-2116 [*P. planifrons*]; LACM 128319 [*P. tympaniticus*]), each thoracic rib bears a longitudinal groove on its anterior face along the proximal half or greater portion of the shaft, resulting in a flattened overall rib morphology. On at least one thoracic rib in DMNH 8769, such a groove is only weakly developed and confined to the head region, resulting in a slightly more rounded shaft. In cross-section, the rib is highly dense with reduced porosity within the medullary cavity. Occurrence of the preceeding two conditions suggests that *Latoplatecarpus willistoni* exhibited some degree of pachyosteosclerosis sensu Houssaye et al. (2008) in its ribs. In one specimen referable to *Platecarpus tympaniticus* (ALMNH PV 985.0021), the rib appears more porous in cross-section.

## Phylogenetic Analysis

Based on a novel character set consisting of 72 cranial and 25 postcranial characters, derived with some reference to the characters of Bell (1997), and Bell and Polcyn (2005), and 17 ingroup taxa, we conducted a series of phylogenetic analyses using MacClade version 4.03 (Maddison and Maddison, 2001) and PAUP 4.0b10 (Swofford, 2002) for Macintosh (Appendices 1–3). Encompassing the known diversity of russellosaurine mosasaurs sensu Polcyn and Bell (2005), the 17 ingroup taxa consisted of three monotypic genera of anatomically primitive mosasauroids, two species of *Tylosaurus* representing tylosaurines, and all the known nominal species of mosasaurs that have been recognized as pertaining to Plioplatecarpinae and/or Plioplatecarpini in the literature prior to this study (e.g., Russell, 1967; Wright and Shannon, 1988; Lingham-Soliar, 1994a; 1994b; Holmes, 1996; Cuthbertson et al., 2007; Konishi and Caldwell, 2007; Polcyn and Everhart, 2008; Konishi and Caldwell, 2009; Chapter 4; this chapter). Members of Prognathodontini sensu Russell (1967) and the genus *Halisaurus* were not considered to be plioplatecarpines (contra Russell, 1967; see above), and two mosasaurine taxa, *Clidastes propython* and *Kourisodon puntledgensis* were used as outgroups.

Using a branch-and-bound search algorithm, a total of nine most parsimonious trees (MPTs) were found: tree length (TL) of 243, consistency index (CI) of 0.7160, retention index (RI) of 0.7723, and rescaled consistency index (RC) of 0.5530. The 50 % majority-rule consensus tree of those nine MPTs (Fig. 5-23A) recovered the following relationships within the ingroup taxa: a = (b

+ (c + d)), where ‘a’ represents Russellosaurina, ‘b’ represents three anatomically primitive Turonian trans-Atlantic taxa, ‘c’ represents Tylosaurinae, and ‘d’, Plioplatecarpinae. Within Plioplatecarpinae, *Ectenosaurus clidastoides* was found at the basal-most position, and the interrelationships among the rest of the plioplatecarpines were resolved as follows: (*Angolasaurus bocagei*, ((*Selmasaurus russelli*, *S. johnsoni*), (*Platecarpus planifrons*, (*P. tympaniticus*, (*Latoplatecarpus willistoni*, (*Plioplatecarpus nichollsae*, *Platecarpus* sp., cf. *P. somenensis*, (*Plioplatecarpus primaevus*, (*P. houzeaui*, *P. marshi*))))))) (Fig. 5-23A). Among the nine MPTs, *Platecarpus* was consistently found to be polyphyletic. In addition, the 50 % majority-rule consensus tree did not resolve the relationships among *Plioplatecarpus nichollsae*, *Platecarpus* sp., cf. *P. somenensis*, and the clade consisting of the three post-middle Campanian species of *Plioplatecarpus*.

## Phylogenetic Discussions-I: Basal Position of *Ectenosaurus*

The basal position of *Ectenosaurus clidastoides* within plioplatecarpines (Fig. 5-23A) was recovered in six of the nine shortest trees (MPTs), while the remaining three trees showed its sister-group relationship to the clade composed of three anatomically primitive Turonian taxa (hereafter tentatively referred to as a ‘tethysaur-clade’), and all the other plioplatecarpine taxa. In those three MPTs, the tylosaurines were always recovered as the basal-most russellosaurines. However, such a topology is considered highly unlikely when accounting for the fact that *Tethysaurus*, one of the constituent taxa of the ‘tethysaur-clade’, exhibits terrestrial limb morphology that is simply not known for any other more derived russellosaurine taxon, and unfortunately for *Yaguarasaurus* and *Russellosaurus* there are no known appendicular elements (Páramo, 1991, 1994; Bardet et al., 2003; Bell and Polcyn, 2005; Polcyn and Bell, 2005; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009). Hence, we do support the basal position of *Ectenosaurus clidastoides* within the plioplatecarpines, and consider its aberrant anatomy (e.g., an elongate snout) as reflecting its high degree of ecological specialization, rather than some sort of phylogenetically primitive states within Russellosaurina. In our preferred tree topology (cf. Fig. 5-23B), the plioplatecarpine clade including *Ectenosaurus* possesses the following synapomorphies: a parietal table longer than wide (19(1)), an acute posteroventral process of the jugal (28(2)), and a thin quadrate ala (34(0)), among which only the last character remains unchanged throughout the clade.

The plioplatecarpines, with the exclusion of *Ectenosaurus*, share the following synapomorphies: 12 maxillary teeth (6(0)), and lack of the median dorsal keel on the frontal (11(0)). As a specimen of *Plioplatecarpus marshi* (IRSNB R37) possesses 13 maxillary teeth, there is a state change in the branch leading to this taxon. According to Lingham-Soliar’s (1994a) emended diagnosis for Plioplatecarpinae, they have “maximum twelve teeth on maxilla” (p. 180). While the majority of the constituent taxa of plioplatecarpines are indeed characterized by possessing only 12 maxillary teeth, none of the plioplatecarpine specimens that we examined showed fewer than 12 maxillary teeth, with the single possible exception of the holotype (FHSM VP-13910) of *Selmasaurus* *russelli*. This specimen has a complete dentary tooth count of 11, although its maxillary teeth are incompletely preserved (Polcyn and Everhart, 2008). Thus, together with the condition found in *Ectenosaurus clidastoides*, and at least one specimen of *Plioplatecarpus marshi* exhibiting more than 12 maxillary teeth, we are unable to find a support for Lingham-Soliar’s (1994a) maxillary tooth count character as diagnostic of the group.

In the 50 % majority-rule consensus tree, *Angolasaurus bocagei* is sister to *Selmasaurus* and the other, more derived plioplatecarpines. In our preferred hypothesis, contact between the quadrate suprastapedial and infrastapedial processes (37(2)) defined the branch ancestral to *Selmasaurus* and the more derived plioplatecarpines, while these processes were primitively separate in *Angolasaurus*. The two species of *Selmasaurus* were united by the following synapomorphies: an inverted teardrop-shaped parietal foramen (21(5)), an inverted teardrop-shaped stapedial pit outline (41(7)), and a medially bending quadrate shaft (95(1)). Together, *Selmasaurus* formed a sister clade to *Platecarpus planifrons* and the more derived plioplatecarpines (Fig. 5-23A).

## Phylogenetic Discussions-II: A Revised Taxonomy for *Platecarpus planifrons*

The paraphyletic clade consisting of *P. planifrons* and *P. tympaniticus* nested within plioplatecarpine mosasaurs has been recognized since Bell (1993). Konishi and Caldwell (2007) revised the alpha-level taxonomy of the genus, recognizing *P. planifrons* and *P. ictericus* as two valid species, while tentatively retaining *P. somenensis* and *P. tympaniticus* pending future investigation. Based on the thorough redescription of the holotype and only specimen of *P. tympaniticus* however, this thesis (Chapter 4) proposes that this taxon should be valid and become a senior synonym of *P. ictericus*. Following this suggestion rather than that of Konishi and Caldwell (2007), we have used the name *P. tympaniticus* in place of *P. ictericus* in the current phylogenetic analysis.

As is apparent from the phylogeny in the current study, as many as nine character changes (eight cranial and one postcranial) are present in the branch ancestral to *Platecarpus tympaniticus* and the other, more derived plioplatecarpines (Fig. 5-23B). Indeed, the number of these character changes is about twice that found in the branch ancestral to *P. planifrons* and the more derived plioplatecarpines; we consider this to be a strong indication that a generic distinction is present between *P. planifrons* and *P. tympaniticus* just as there is between the former species and *Selmasaurus*. Such a notion is also well supported by examination of chronostratigraphic data for these two taxa, where the beginnings of their known taxon range zones are separated by approximately 3.5 million years (Fig. 5-23C). Since *Platecarpus tympaniticus* Cope, 1869 has nomenclatural seniority, we here propose an assignment of *Platecarpus planifrons* (Cope, 1874) to a new genus (cf. Fig. 5-24; see the following Systematic Paleontology section).

## Phylogenetic Discussions-III: Distinction between *Platecarpus tympaniticus* and *Latoplatecarpus willistoni*

There are eight key morphological changes that take place on the branch ancestral to *Latoplatecarpus willistoni* and the other, more derived members of the group, one of which is the widely separated anterolateral processes of the frontal (10(2)). As Konishi and Caldwell (2009) suggested, this feature is associated with the anterior divergence of a pair of ventrolateral processes and the presence of paired parolfactory-bulb recesses, both found underneath the frontal. There is no reversal of this character within this derived plioplatecarpine clade, and we consider it one of the most reliable characters distinguishing these plioplatecarpines from more primitive *Platecarpus tympaniticus*. A number of important character changes as well as corroboration of stratigraphic data find strong support for the generic distinction of *L. willistoni* from *Platecarpus* (Fig. 5-23B, C). The paraphyletic clade consisting of FMNH UC-600 and DMNH 8769 nested within Bell's (1993) paraphyletic *Platecarpus* or Bell and Polcyn (2005) and Polcyn and Bell's (2005) polyphyletic *Platecarpus* is thus resolved, as a result of recognition of the latter specimen as pertaining to the new genus.

We here also point out that AMNH 2182, also diagnosable as *Latoplatecarpus willistoni*, has been miscoded in Bell's (1997) analysis to represent its anatomy inaccurately. Among the four characters coded differently between this specimen and DMNH 8769 by Bell (1997), the character no. 50 (posteroventrally ascending tympanic rim morphology), and 62 (quadrate mandibular condyle morphology), should be coded identically between the two specimens. Another character (character no. 33), an "inconspicuous, low and narrowly rounded" transverse ridge across the dorsal surface of the postorbitofrontal, is coded absent for AMNH 2182 and present for DMNH 8769 (Bell, 1997:308). However, the bone surface of the former specimen is too poorly preserved to allow any reliable scoring for such a fine character. The remaining character (character no. 24) is the only one whose original coding for AMNH 2182 can be retained, i.e., the large parietal foramen straddling the frontal-parietal suture and anteriorly deeply invading the frontal (Bell, 1997). However, while the parietal foramen in DMNH 8769 does not deeply invade the frontal anteriorly, we argue that the condition in this specimen is not sufficiently different to be coded otherwise (contra Bell, 1997). In particular, although the posteromedian flanges of the frontal (= "median frontal sutural flange" in Bell, 1997:306) do not approach each other in DMNH 8769 to border directly the anterior half of the parietal foramen as they do in *Plioplatecarpus nichollsae*, the flanges nevertheless laterally surround this portion of the parietal foramen (Fig. 5-7). This is in a marked contrast with *Platecarpus tympaniticus*, in which the parietal foramen is occasionally bordered anteriorly by the frontal on the dorsal surface as well (e.g., LACM 128319). Such specimens however lack the posteromedian flanges, and it is the anterior half of the parietal table that is broadly surrounded by the frontal posterolateral flanges (= "lateral sutural flange of frontal" in Bell, 1997:306), including the entire parietal foramen (as opposed to only the posterior half of it as in DMNH 8769 or TMP 84.162.01). Consequently, character no. 18 in our own phylogenetic analysis was coded the same in both AMNH 2182 and DMNH 8769, and we suggest that the former be assigned to *Latoplatecarpus willistoni* as well, not *Plioplatecarpus* as it was long proposed since Bell (1993).

### Phylogenetic Discussions-IV: The Problem of *Platecarpus* sp., cf. *P. somenensis*

In our preferred tree topology (Fig. 5-23B), only a single character change occurs on the branch ancestral to the clade consisting of *Platecarpus somenensis*, *Plioplatecarpus nichollsae*, and the three post-middle Campanian plioplatecarpines. This character change constitutes a change in the articulation surface morphology of the intramandibular joint from smoothly keeled to obliquely grooved (57(0) to (1)). This character was scored as unknown for *P. nichollsae* and *P. primaevus*, and a further character transformation occurred in *P. marshi* (57(1) to (2)).

As Konishi and Caldwell (2009) suggested, it is clearly indicated in our current phylogenetic analysis that North American specimens referred to *Platecarpus somenensis* are best referred to the genus *Plioplatecarpus*, and we further propose here that they be considered conspecific with *P. nichollsae* for the following reasons.

First, all the North American specimens previously recognized as *Platecarpus somenensis* and examined for our phylogenetic analysis, except for FMNH PR-466 (see below), are unusually large. For example, a mandible of the largest specimen examined (FMNH PR-465) measures a little over 1000 mm long, about 40 % larger than the average and presumably fully matured *Platecarpus tympaniticus* specimens (e.g., FMNH UC-600, ca. 580 mm). It is noteworthy that the mandible is even larger than that pertaining to the largest-known specimen of *Tylosaurus kansasensis* (FHSM VP-13742, 980 mm) (Everhart, 2005; pers. observ.). There seems little doubt, therefore, that these specimens of *Platecarpus somenensis* represent mature mosasaur individuals, and in the case of FMNH PR-465, probably fully matured. Assuming that the large size of those specimens represents their late ontogenetic stage, it is reasonable to predict that they belong to the same taxon represented by smaller plioplatecarpine specimens from the similar geographic and temporal ranges and with similar anatomy, such as *Plioplatecarpus nichollsae*.

Second, according to our phylogenetic analysis, the least stable relationship among derived plioplatecarpines (= the clade indicated by an asterisk in Fig. 5-23A) was found between *Platecarpus somenensis* and *Plioplatecarpus nichollsae*, where the following three topologies were recovered in equal frequency among nine MPTs; (*Platecarpus somenensis*, (*Plioplatecarpus nichollsae*, post-middle Campanian *Plioplatecarpus* spp.)), (*Plioplatecarpus nichollsae*, (*Platecarpus somenensis*, post-middle Campanian *Plioplatecarpus* spp.)), and (post-middle Campanian *Plioplatecarpus* spp., (*Platecarpus somenensis*, *Plioplatecarpus nichollsae*)). Although we prefer the last topology since very few changes separate *P. nichollsae* and *Platecarpus somenensis* while more than 15 character changes separate the three post-middle Campanian species of *Plioplatecarpus* from either *P. nichollsae* or *Platecarpus somenensis*, there is no character supporting the clade comprising *Plioplatecarpus nichollsae* and *Platecarpus somenensis* either (Fig. 5-23B).

A single character change that occurs on the branch leading to *Platecarpus somenensis* represents a transformation from a triangular, moderately developed parietal process of the squamosal to a rectangular, well-developed one (50(1) to (2)). However, it is noted that in the same individual FMNH PR-467, in which the above condition was observed, the crista prootica (otosphenoidal crest) was unusually well developed covering the openings for the ninth as well as the seventh cranial nerve on the braincase, while no other plioplatecarpines we examined, including specimens of *Plioplatecarpus nichollsae*, exhibited such strong crest development. This likely indicates that the large animal size or late ontogenetic stage is contributing to the high degree of crest development, rather than that the feature represents an evolutionary novelty. On FMNH PR-467, we can also observe that the floor of the basioccipital is well ossified, measuring at least 5 mm in thickness. The same region in small specimens of *Plioplatecarpus nichollsae* (CMN 52261, TMP 83.24.01), on the other hand, is broken or unossified (Cuthbertson et al., 2007:fig. 5B; Konishi and Caldwell, 2009:fig. 10). The poorly ossified nature of the basioccipital floor, whether resulting in the irregular breakage or natural openings, is also typical of the post middle-Campanian species of *Plioplatecarpus*, including at least one large specimen (*Plioplatecarpus primaevus* [e.g., CMN 11840], *P. houzeaui* [e.g., IRSNB 3108], and *P. marshi* [e.g., IRSNB R38 = holotype]). Such openings are almost always absent in this region of *Platecarpus* and *Latoplatecarpus willistoni*, represented by specimens of various sizes (Fig. 5-15D). Consequently, this may indicate that the ossification in this region of the braincase became heterochronically delayed among most derived plioplatecarpines, and in this view, the well-ossified basioccipital floor in FMNH PR-467 indicates its individual maturity, supported also by its large body size. We consider, therefore, that the highly developed parietal process of the squamosal as well as the otosphenoidal crest found only in *Platecarpus somenensis* (i.e., FMNH PR-467) are a result of individual maturity.

Two of the three autapomorphic characters for *Plioplatecarpus nichollsae* relate to the absence of interorbital constriction (13(0)) and parallel-sided frontal preorbital margins (14(2)). We have little direct evidence to suggest that the frontal morphology changes according to ontogeny in any kind of mosasaurs: however, the two frontal characters above are linked with each other, as the interorbital constriction would result if the preorbital borders expand laterally, as seen in *Platecarpus somenensis* (FMNH PR-467). Therefore, if we assume that the preorbital borders expanded laterally according to the ontogeny of *Plioplatecarpus nichollsae* (see below), it becomes possible that this species would possess anteriorly expanded frontal preorbital borders with interorbital constriction later in their ontogeny. In fact, FMNH PR-466, while referred to *Platecarpus somenensis* by Russell (1967), is a small specimen that is about 70 % of FMNH PR-467 in linear dimension (maxilla length 295 mm and 421 mm, repectively). Interestingly, not only is the specimen small in size, it also lacks preorbital expansion of the frontal and exhibits an overall triangular frontal outline, even though the frontal anterolateral processes are widely separated, as in FMNH PR-467. As FMNH PR-466 (the small specimen) was collected from exactly the same locality and horizon as FMNH PR-465 and PR-467 (the large specimens), in the lower Pierre Shale in the southwestern corner of South Dakota, it is highly suggestive that the former specimen is a small individual of the taxon represented by the latter two. In lieu of the fact that both the holotype CMN 52261 (maxilla 235 mm long) and referred specimen TMP 83.24.01 (maxilla < 270 mm long) of *Plioplatecarpus nichollsae* represent small mosasaur individuals without interorbital constriction and preorbital expansion, we here propose that this species, often represented by small specimens, and large plioplatecarpine specimens referred to *Platecarpus somenensis* from the lower Pierre Shale Formation of North America, be considered conspecific.

Finally, although the third autapomorphic state of *Plioplatecarpus nichollsae*, namely the moderately developed posteroventral bulge along the quadrate shaft (38(2)) based on the holotype can be contrasted with its absence (38(0)) coded for *Platecarpus somenensis* based on FMNH PR-467, we argue that such an eminence also occurs in some *Platecarpus* cf. *P. tympaniticus* specimens form the Niobrara Chalk (e.g., AMNH 1563 [= "*P. curtirostris*" holotype], YPM 40544, 40691), while others lack them as in FMNH PR-467 (e.g., AMNH 1559 [= "*P. ictericus*" holotype], 1820). In fact, despite the obvious size difference, the well-preserved quadrates of FMNH PR-467 (*Platecarpus somenensis*) and TMP 83.24.01 (*Plioplatecarpus nichollsae*) are morphologically indistinguishable, excepting the subtle difference in the outline of the posteroventral border of the quadrate shaft (Konishi pers. observ.). Hence, we do not consider that the presence of such a moderate eminence in the holotype of *Plioplatecarpus* *nichollsae* and its absence in the specimen of *Platecarpus somenensis* coded in our analysis would provide sufficient evidence against synonymyzing the two.

As all the published specimens of *Platecarpus somenensis* from the lower Pierre Shale Formation of North America were referred specimens (Russell, 1967), and because the French holotype is neither *Plioplatecarpus* nor *Platecarpus* according to our recent observation, the name *Plioplatecarpus nichollsae* Cuthbertson et al., 2007 is consequently assigned to these North American specimens thus far referred to as *Platecarpus somenensis*.

### Phylogenetic Discussions-V: A New Generic Assignment of ***Plioplatecarpus nichollsae*** Cuthbertson et al., 2007

As a result of synonymizing the aforementioned two taxa, a new tree topology results, in which all the terminal taxa representing the derived plioplatecarpines in Figure 5-23B form a Hennigian comb. Such a topology is still consistent with our discussion of the generic identity of *Plioplatecarpus nichollsae*, as *Plioplatecarpus* maintains monophyly. However, while as many as 17 character changes occurred in the branch ancestral to the three post-middle Campanian species of *Plioplatecarpus*, only one character change (splenio-angular articulation surface: 57(0) to (1)) was found on the branch ancestral to *Plioplatecarpus nichollsae* and the other congeners. When the stratigraphic and geographic data are mapped onto the tree topology presented in Figure 5-23B, not only is the number of the character changes so high, but the temporal segregation between the known first occurrence of *Plioplatecarpus nichollsae* and that of *P.*

*primaevus* is greatest among the derived members of Plioplatecarpinae, while the former species and *Latoplatecarpus willistoni* are contemporaneous (Fig. 5-23C).

Upon running a new parsimony analysis in which we merged character states between *Plioplatecarpus nichollsae* and "*Platecarpus somenensis*" from the former analysis to represent one species within the matrix, and with the exclusion of character 57, nine MPTs of 237 steps were found. While a strict consensus tree produced a basal polytomy at the node ancestral to *Latoplatecarpus willistoni* and four *Plioplatecarpus* spp., three MPTs recovered the topology ((*Latoplatecarpus willistoni*, *Plioplatecarpus nichollsae*), three most derived *Plioplatecarpus* spp.) and yet another three, (*Plioplatecarpus nichollsae*, (*Latoplatecarpus willistoni*, three most derived *Plioplatecarpus* spp.)), suggesting that the generic assignment of *Plioplatecarpus nichollsae* would also require re-consideration. We further investigated this issue, and ran another phylogenetic analysis, in which we retained character 57. This also produced the same number of MPTs of 239 steps, in which the aforementioned tree topologies resulted in the same frequencies (one-third each), including our preferred hypothesis that forms a basis for the interrelationships presented in Figure 5-24: that is, *Latoplatecarpus willistoni* and *Plioplatecarpus nichollsae* are congeneric and sister to each other, and they are both generically distinct from the post-middle Campanian species of *Plioplatecarpus* primarily because the branch ancestral to the latter three speicies has as many as 17 unambiguous character changes in our first analysis (Fig. 5-23B). We also point out that presence or absence of character 57, the intramandibular joint surface morphology, did not alter the resulting tree topologies at all in the new analyses, indicating that this character is not a defining character of a clade consisting of *Plioplatecarpus nichollsae*, *P. primaevus*, *P. houzeaui*, and *P. marshi* to the exclusion of *Latoplatecarpus willistoni*, which suggests that the generic distinction between *L. willistoni* and *Plioplatecarpus nichollsae* is rather artificial. As well, the greatest number of morphological changes does not occur between the latter two taxa but between *P. nichollsae* and all the other nominal species of *Plioplatecarpus*, and this seems to well justify the generic distinction to be placed between *P. nichollsae* and the post-middle Campanian species of *Plioplatecarpus*, and as such we refute assignment of *Latoplatecarpus* to *Plioplatecarpus* as well.

Hence, by compiling all the available data based on chronostratigraphy, paleobiogeography, morphology, and phylogeny of the derived plioplatecarpine mosasaurs, we have little doubt that *Latoplatecarpus willistoni* is generically distinct from post-middle Campanian *Plioplatecarpus* species, while there is far more evidence to support referral of *Plioplatecarpus nichollsae* to the former genus than to the latter (Fig. 5-24). At the same time, we support the three post-middle Campanian species of *Plioplatecarpus* as congeners, especially based on the highest number of synapomorphies in our phylogeny—based mainly on quadrate, jugal, and dermal skull roof characters—that unite these species together, coupled with the nearly five million years of the stratigraphic gap between the last known occurrence of the pre-late Campanian plioplatecarpines and the earliest known occurrence of *Plioplatecarpus primaevus* in the middle late Campanian.

## *LATOPLATECARPUS NICHOLLSAE* (Cuthbertson et al., 2007)

*Plioplatecarpus nichollsae* Cuthbertson, Mallon, Campione, and Holmes, 2007:595, figs. 2-7, 8b, 9, 11c (original description).

**Holotype**—CMN 52261.

**Emended Diagnosis** (cf. Cuthbertson et al., 2007; Konishi and Caldwell, 2009)—Preorbital borders of frontal straight or laterally expanded, exhibiting various degrees of interorbital constriction; frontal ala distally rounded; parietal foramen length : width ratio at least 1.5, typically more than 1.6; surangular dorsal border slightly curved; intervertebral joints with low degree of curvature; at least 11 pygal vertebrae; adult body size among largest in plioplatecarpines, with mandible occasionally reaching 1 m in total length, amounting to total body length of over 9 m.

**Referred Specimens**—FMNH PR-465, 466, 467, 674; M 73.06.02, 73.08.02, 83.10.18, 84.07.18; TMP 83.24.01.

**Distribution**—Western Interior Basin of North America in Manitoba (Pembina Member, Pierre Shale Formation), Wyoming and South Dakota (Sharron Springs Member, Pierre Shale Formation), and Alabama (lower Demopolis Chalk Formation), lower middle Campanian.

**Remarks**—The foregoing anatomical comparisons with other plioplatecarpines as well as a series of the following phylogenetic analyses both justify the generic re-assignment of the species to the new genus. Also, note that all the specimens from the lower Pierre Shale Formation previously referred to as

*Platecarpus* cf. *P. somenensis* in the published literature are assigned to this species.

## *PLESIOPLATECARPUS*, gen. nov.

**Generic Type**—*Plesioplatecarpus planifrons* (Cope, 1874), by monotypy.

**Diagnosis**—As for species.

**Etymology**—"Plesio" means near in Latin, and "platecarpus," referring to its close evolutionary affinity to the more derived *Platecarpus*.

## *PLESIOPLATECARPUS PLANIFRONS* (Cope, 1874)

*Clidastes planifrons* Cope, 1874:31 (original description).

*Platecarpus planifrons* (Cope, 1874): Williston, 1898:188 (new combination).

**Holotype**—AMNH 1491.

**Diagnosis**—As per Konishi (2008b).

**Referred Specimens**—FHSM VP-2077, 2116, 2181, 2277, 2296, 13907; KU 14349, 75037; MSC 9515; UALVP 24240, 40402; YPM 1429, 24936, 40434, 40440, 40450, 40493, 40508, 40517, 40638, 40646.

**Distribution**—Western Interior Basin of North America in Kansas (Smoky Hill Chalk Member, Niobrara Chalk) and Alabama (Tombigbee Sand Member, Eutaw Formation), upper middle Coniacian to middle Santonian (cf. Konishi, 2008b).

## NOTES ON PALEOBIOGEOGRAPHY AND FUNCTIONAL ANATOMY

When incorporating known biostratigraphic and biogeographic data in one of our preferred phylogenetic hypotheses, some trends emerge (Fig. 5-23C). In particular, no single species depicted here shows a geographic distribution across the Atlantic Basin with the possible exception of *Plioplatecarpus marshi* (see Mulder, 1999). In addition, only *Plioplatecarpus* is found on both sides of the basin at the generic level.

Considering the well-sampled nature of mosasaur specimens in both North America and Western Europe, and the presence of numerous, temporally overlapping strata between the two continents (e.g., Russell, 1967), this species-level, trans-Atlantic segregation among large, hydropedal mosasaurs is intriguing. It is noteworthy that in the Turonian (ca. 93.5 to 90 Ma), three anatomically primitive russellosaurines *Tethysaurus*, *Russellosaurus*, and *Yaguarasaurus* have been found from Morocco, Texas, and Colombia, respectively, clearly exhibiting trans-Atlantic distribution near the paleoequator (Páramo, 1994; Bardet et al., 2003; Polcyn and Bell, 2005). Although these three primitive mosasaurs are currently recognized as pertaining to separate genera, more than five synapomorphies define the clade containing them in our phylogeny, showing strong support for their monophyly within Russellosaurina and suggesting that these taxa may even constitute fewer genera than three (cf. Bell and Polcyn, 2005). This could suggest that during the Turonian, this anatomically primitive russellosaurine lineage quickly dispersed near the paleoequator across the then much more confined Atlantic Basin, despite their primitive terrestrial limb morphology that indicates a lesser degree of aquatic adaptation particularly compared to the later lineages (Bardet et al., 2003). As both the North Atlantic Ocean and South Atlantic Ocean continued to expand in the post-Turonian time (e.g., Stille et al., 1996), this rapid initial radiation of russellosaurines might have been followed by endemic speciation events on either side of the Atlantic Basin. In the Northern Hemisphere for plioplatecarpines, this possibly led to specific- and generic-level, trans-Atlantic segregation until later in the Maastrichtian age (Fig. 5-23C). This observation seems consistent with some other contemporary mosasaur taxa such as the mosasaurine *Prognathodon*, as it was not until the latest Campanian that the genus started exhibiting a fully trans-Atlantic distribution (e.g., Christiansen and Bonde, 2002; Lucas et al., 2005; Schulp, 2006; Schulp et al., 2008).

By and throughout the Maastrichtian however, some mosasaurs, including *Plioplatecarpus*, had evolved novel anatomical features to become increasingly pelagic. These included stiffening of a greater portion of their body by increasing the angle of the zygapophyseal facets, limiting the zygapophysis-bearing vertebrae to the cervical and anterior dorsal series, elongation of the dorsal neural spines for providing greater area of epaxial muscle attachment to attain a deeper and more rigid body, and increasing the number of pygal vertebrae to increase the rigidity in the proximal tail region (e.g., Burnham, 1991; Lingham-Soliar, 1994a; Holmes, 1996; Lindgren et al., 2008; pers. observ. of various *Plioplatecarpus* specimens). In addition, CMN 21853, *Plioplatecarpus* sp., from lower Maastrichtian strata in southern Alberta, Canada, exhibits the highest degree of hyperphalangy among derived plioplatecarpines, exhibiting a greater degree of secondary adaptation to aquatic life (exact phalangeal counts not known in the other congeners from the Maastrichtian) (Holmes et al., 1999). Furthermore, the overall C-shaped outline of the jugal (i.e., infraorbital rim) as well as the arched frontal (i.e., supraorbital rim) found exclusively in *P. primaevus* and *P. houzeaui* (only the former character is currently known for *P. marshi*) clearly indicate an increase in their relative orbit size. Parvipelvian ichthyosaurs, characterized by possessing deep, tuna-like bodies for cruising habits, also possessed improportionately large eyeballs for their body length (Motani et al., 1999; Motani, 2002). Among them, similarly arched supraorbital rims can be also found in members of genera such as *Leptonectes*, *Stenopterygius*, *Ichthyosaurus*, and *Ophthalmosaurus* (Motani, 1999; McGowan and Motani, 2003).

Accumulation of those novel osteological characters in *Plioplatecarpus* would no doubt make them faster, long-distance swimmers in comparison to predecessors such as *Platecarpus tympaniticus*. The latter became large (ca. 7 m) and was clearly a hydropedal (i.e., paddle-bearing) mosasaur, but had a low pygal count of approximately five (Russell, 1967) and a flexible torso region with well-developed zygapophyses, probably employing a carangiform swimming style ideal for maneuvering but less suited for cruising (e.g., Lindgren et al., 2007). As early as the early Maastrichtian, *Plioplatecarpus houzeaui* and *P. marshi* attained as many as 15 pygal vertebrae, while possibly reducing the prepygal vertebrae to ca. 22 (Lingham-Soliar, 1994a; pers. observ.). With the reduced number of zygapophysis-bearing dorsals, hyperphalangy, and increase in the relative orbit size, *Plioplatecarpus* exhibits remarkable convergence in these traits with the mosasaurine *Plotosaurus*, that is also hypothesized to have been capable of sustained, and also likely fast, cruising (Lindgren et al., 2007; Lindgren et al., 2008). Although the latter taxon is so far only known from the eastern Pacific Basin of late early to early late Maastrichtian age (Lindgren et al., 2008), continuous expansion of the North Atlantic Basin throughout the Late Cretaceous must have provided a similar open-water niche to be exploited by mosasaurs inhabiting the Western Interior Basin of North America. By the Maastrichtian, *Plioplatecarpus*, the most derived lineage of plioplatecarpine mosasaurs, may have played a similar ecological role in the North Atlantic Ocean to that played by *Plotosaurus* in the Pacific Ocean.

## ACKNOWLEDGEMENTS

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FIGURE 5-1. Locality and stratigraphic position of TMP 84.162.01, holotype of *Latoplatecarpus willistoni* gen. et sp. nov. The oval area in southern Manitoba indicates part of Pembina Mountain that has yielded a great concentration of marine reptile fossils, including TMP 84.162.01. **Abbreviations**: **ALTA.**, Alberta; **MAN.**, Manitoba; **MONT.**, Montana; **N. DAK.**, North Dakota; **SASK.**, Saskatchewan. Figure adopted from figure 1 in Konishi and Caldwell (2009).

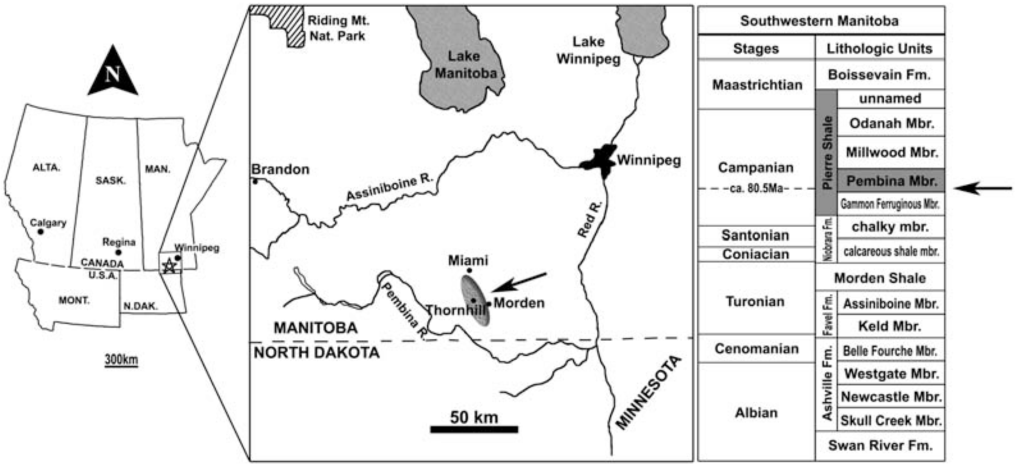

N
ALTA.
SASK.
MAN.
Calgary
Regina
Winnipeg
CANADA
U.S.A.
MONT.
N.DAK.
300km
Riding Mt. Nat. Park
Lake Manitoba
Lake Winnipeg
Winnipeg
Brandon
Assiniboine R.
Red R.
Miami
Thornhill
Morden
Pembina R.
MANITOBA
NORTH DAKOTA
MINNESOTA
50 km
Southwestern Manitoba
Stages
Lithologic Units
Maastrichtian
Campanian
ca. 80.5Ma
Santonian
Coniacian
Turonian
Cenomanian
Albian
Boissevain Fm.
Pierre Shale
unnamed
Odanah Mbr.
Millwood Mbr.
Pembina Mbr.
Gammon Ferruginous Mbr.
Niobrara Fm.
chalky mbr.
calcareous shale mbr.
Morden Shale
Favel Fm.
Assiniboine Mbr.
Keld Mbr.
Ashville Fm.
Belle Fourche Mbr.
Westgate Mbr.
Newcastle Mbr.
Skull Creek Mbr.
Swan River Fm.

FIGURE 5-2. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. Skull and right mandible in loose articulation. Note that mandible is longer than skull. Scale bar equals 10 cm.

FIGURE 5-3. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. skull in dorsal view. **A**, line drawing; **B**, photograph. **Abbreviations**: **ac**, atlas centrum (odontoid); **art-pm**; articular surface with premaxilla; **3-ns**; neural spine (broken) on third vertebra; **3-tr**, transverse process on third vertebra; **ax-poz**, axis postzygapophysis; **ax-tr**, axis transverse process; **ctl**, cartilaginous mass; **ecl**, extracolumella; **ecpp**, ectopterygoid process; **epp**, epipterygoid; **f**, frontal; **ip**, infrastapedial process; **jp**, jugal process of postorbitofrontal; **laa**, left atlas neural arch; **lm**, left maxilla; **lop**, left opisthotic; **lpof**, left postorbitofrontal; **lprf**, left prefrontal; **lq**, left quadrate; **lqr**, left quadrate ramus of pterygoid; **lsq**, left squamosal; **lst**, left supratemporal; **lv**, left vomer; **mcd**, mandibular condyle; **mdk**, median dorsal keel on frontal; **ns**, neural spine; **oc**, occipital condyle; **p**, parietal; **pal**, palatine; **pf**, parietal foramen; **pm**, premaxilla; **pop**, postorbital process of parietal; **popr**, paroccipital process; **ps**, parasphenoid; **pt**, pterygoid; **pt-t**, pterygoid teeth; **raa**, right atlas neural arch; **rm**, right maxilla; **rop**, right opisthotic; **rpo**, right prootic; **rpof**, right postorbitofrontal; **rprf**, right prefrontal; **rqr**, right quadrate ramus of pterygoid; **rst**, right supratemporal; **rv**, right vomer; **so**, supraoccipital; **sp**, suprastapedial process. Arrow indicates posterior constriction of external naris.

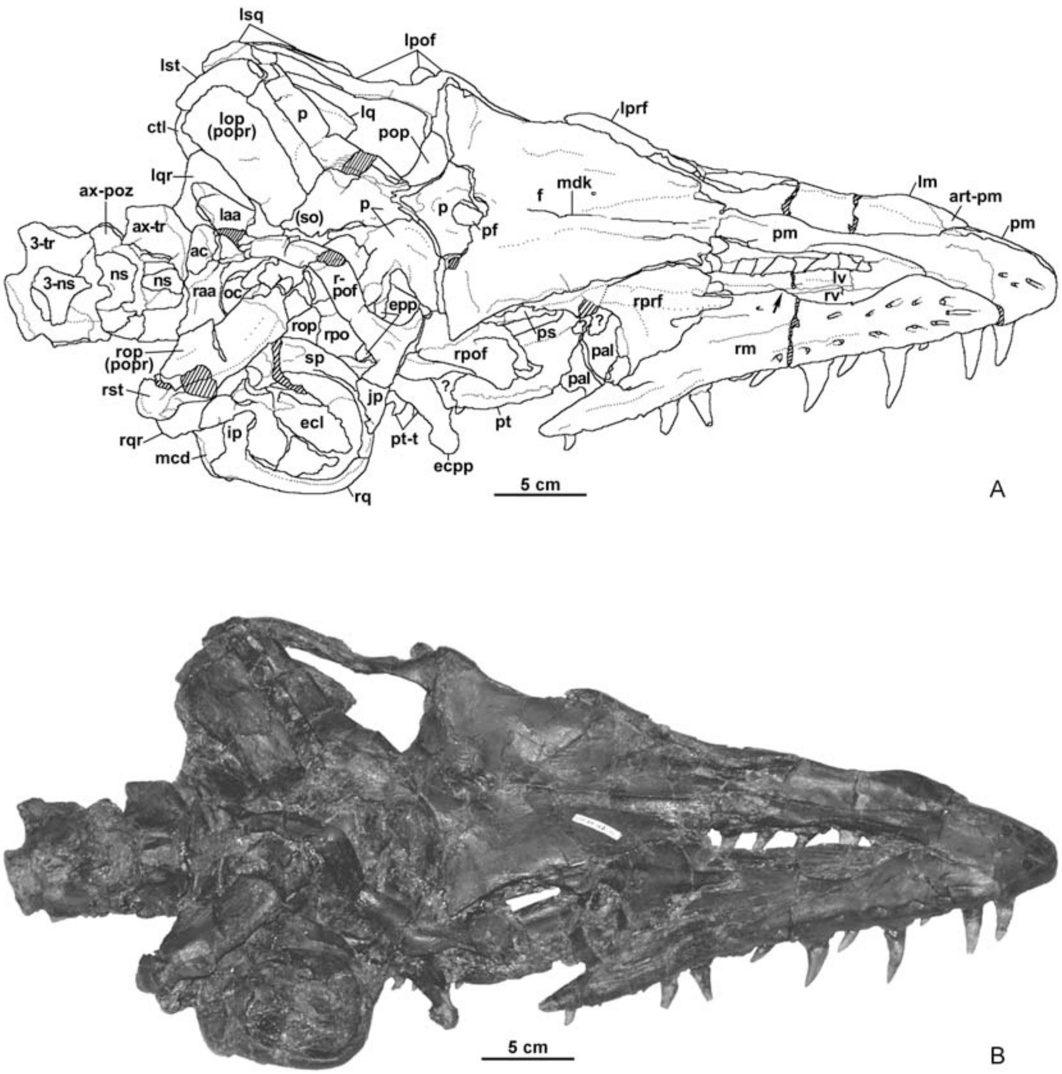

lsq
lpof
lst
lop
(popr)
p
lq
pop
lprf
ctl
lqr
ax-poz
ax-tr
laa
(so)
p
p
f
mdk
pf
lm
art-pm
pm
pm
3-tr
3-ns
ns
ns
ac
raa
oc
r-
pof
epp
rprf
lv
rv
rop
rpo
ps
rop
(popr)
sp
rpof
pal
pal
rm
rst
?
?
rqr
ip
ecl
jp
pt-t
pt
mcd
ecpp
rq
5 cm
A
5 cm
B

FIGURE 5-4. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. skull in ventral view. **A**, line drawing; **B**, photograph. **Abbreviations**: **3-cv**, third cervical vertebra; **3-prez**, prezygapophysis on third vertebra; **aa**, atlas neural spine; **ai**, atlas intercentrum; **ax**, axis; **axi**, axis intercentrum; **ax-syn**, axis synapophysis; **bo**, basioccipital; **bs**, basisphenoid; **ctl**, cartilaginous mass; **ecl**, extracolumella; **epp**, epipterygoid; **f**, frontal; **hyp**, hypapophysis; **ldpf**; left descensus processus frontalis; **lecpp**, left ectopterygoid process; **ljp**, left jugal process of postorbitofrontal; **lm**, left maxilla; **lpal**, left palatine; **lpof**, left postorbitofrontal; **lprf**, left prefrontal; **lpt**, left pterygoid; **lqr**, left quadrate ramus of pterygoid; **lst**, left supratemporal; **lv**, left vomer; mcd, mandibular condyle; **os**, orbitosphenoid; **p**, parietal; **pm**, premaxilla; **po**, prootic; **ps**, parasphenoid; **q-rim**, quadrate alar rim; **recpp**, right ectopterygoid process; **rm**, right maxilla; **rpal**, right palatine; **rpt**, right pterygoid; **rq**, right quadrate; **rqr**, right quadrate ramus of pterygoid; **rst**, right supratemporal; **rv**, right vomer; **sq**, squamosal. Arrow indicates anterior dent on premaxilla resulting in scalloped outline of the element.

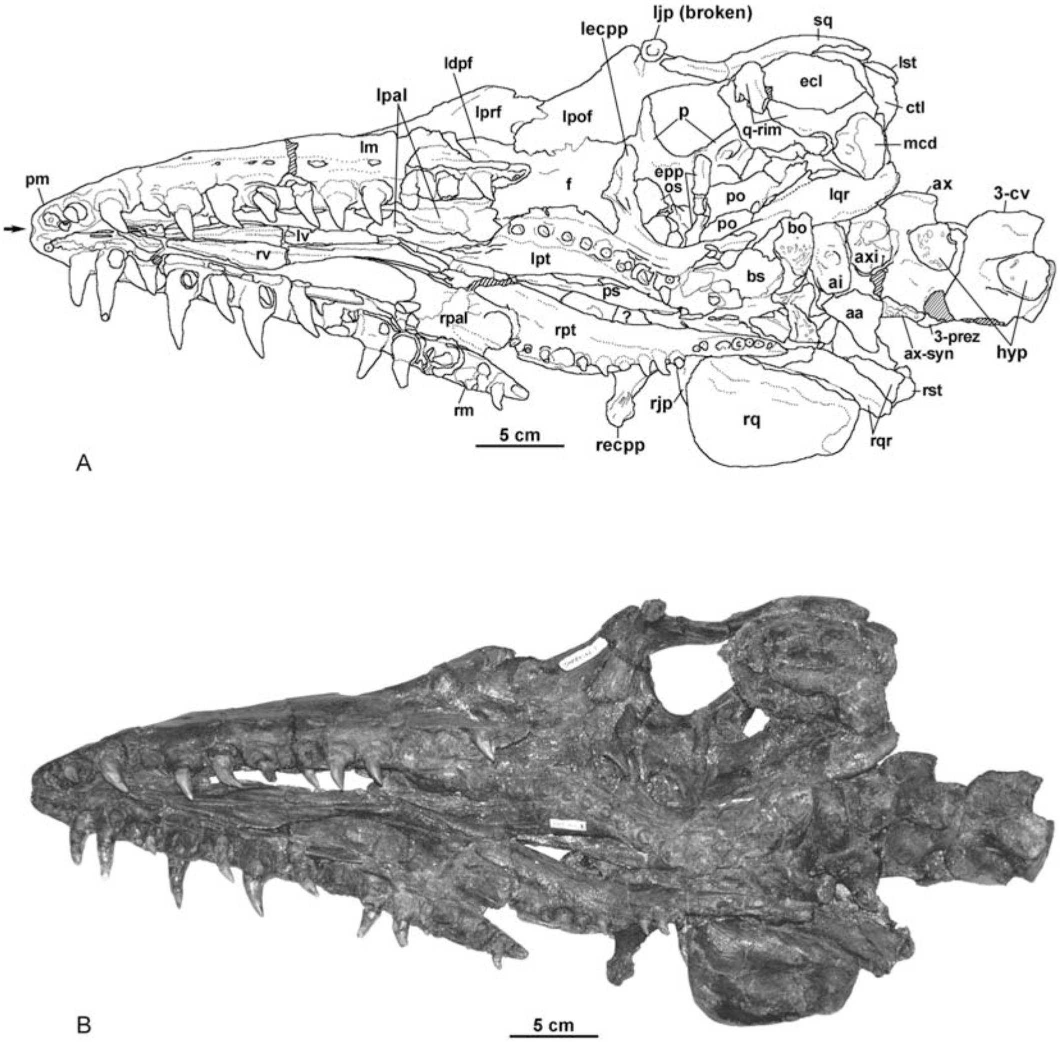

ljp (broken)
sq
lecpp
lst
ecl
ldpf
ctl
lpal
lprf
lpof
p
q-rim
mcd
lm
f
epp
os
po
lqr
ax
3-cv
pm
po
bo
axi
lv
rv
lpt
bs
ai
ps
?
aa
rpal
rpt
3-prez
ax-syn
hyp
rst
rjp
rm
rq
rqr
recpp
5 cm
A
5 cm
B

FIGURE 5-5. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. premaxilla and left maxilla in left lateral view. **Abbreviations**: **m**, maxillary tooth; **p**, premaxillary tooth. Numbers indicate tooth numbers. Arrow indicates dorsal bulge along internarial bar. Scale bar equals 5 cm.

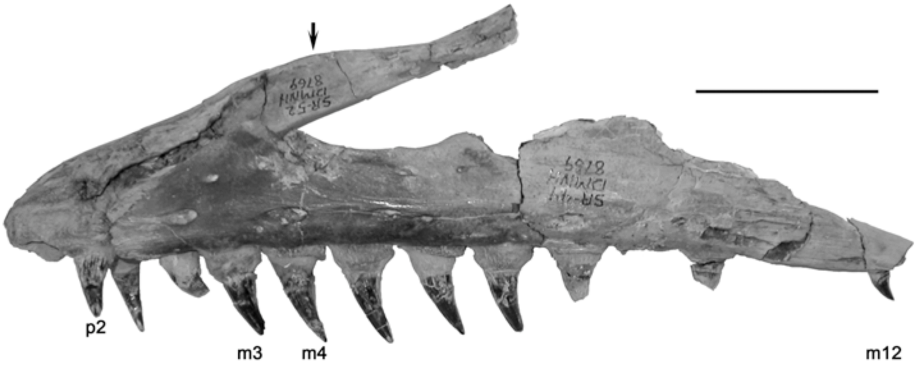

SR-52
DMNH
8769
SR-??
DMNH
8769
p2
m3
m4
m12

FIGURE 5-6. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. right prefrontal in dorsal view. **Abbreviations**: **af**, articulation for frontal; **am**, articulation for maxilla; **sop**, supraorbital process. Scale bar equals 5 cm.


am
sop
af

FIGURE 5-7. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. skull table. **A**, dorsal view; **B**, ventral view. Abbreviations: **ala**, frontal ala; **aprf**, prefrontal articulation surface; **dpf**, descensus processus frontalis; **dpp**, descensus processus parietalis; **eb**, supraorbital embayment; **f**, frontal; **jp**, jugal process; **ob**, olfactory bulb; **obsa**, orbitosphenoid articulation groove; **oc**, olfactory canal; **p**, parietal; **pc**, parietal crest; **pf**, parietal foramen; **pmvk**, posteromedial ventral keel of parietal; **pobr**, parolfactory bulb recess; **pof**, postorbitofrontal; **pop-dr**, postorbital process dorsal ramus; **pop-vr**, postorbital process ventral ramus. Arrow indicates the inferred level of posterior end of parietal along midline. Scale bar equals 5 cm.

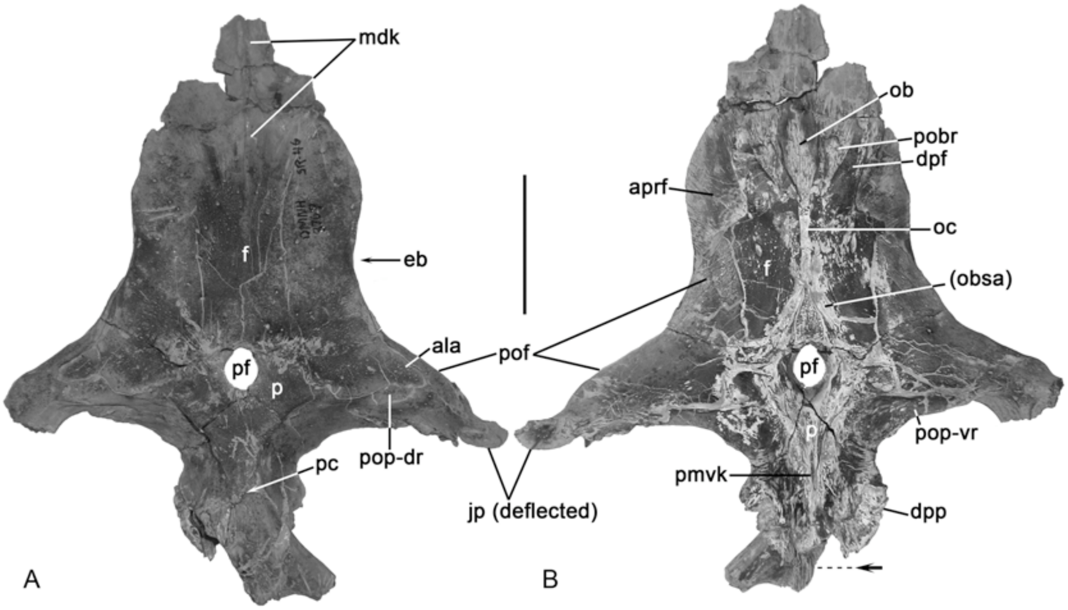

mdk
f
eb
ala
pf
p
pop-dr
pc
pof
jp (deflected)
A
B
ob
pobr
dpf
aprf
oc
f
(obsa)
pf
p
pop-vr
pmvk
dpp

FIGURE 5-8. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. parietal-postorbitofrontal articulation. **Abbreviations**: **pp**, parietal process of postorbitofrontal; **pt**, parietal table. All the other abbreviations as in Figure 4-13.

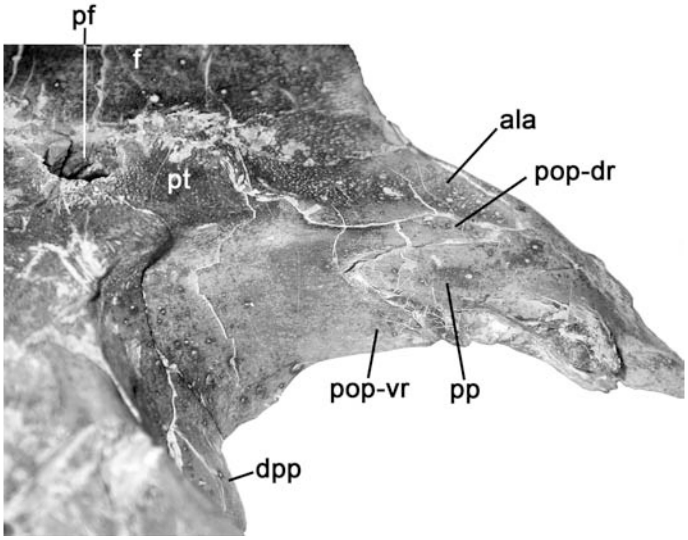

pf
f
ala
pop-dr
pt
pop-vr
pp
dpp

FIGURE 5-9. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. left upper temporal bar. **Abbreviations**: **avp**, anteroventral process of squamosal; **pap**, parietal process of squamosal; **pof-pr**, postorbitofrontal process of squamosal; **sq-pr**, squamosal process of postorbitofrontal. Arrowhead indicates posterior extremity of postorbitofrontal squamosal process, far behind the andterior border of main squamosal body (= quadrate process). Scale bar equals 5 cm.

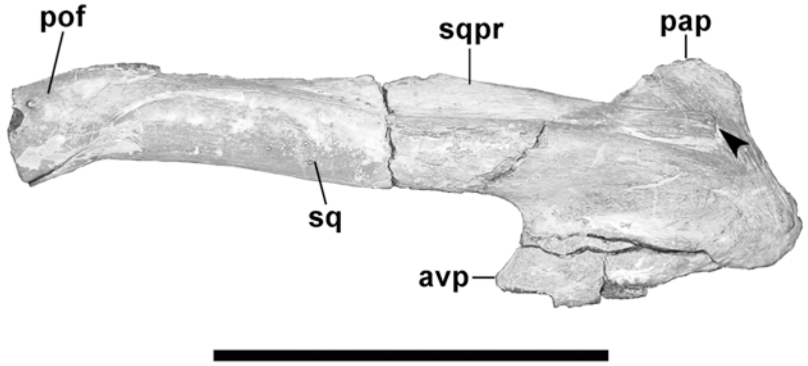

pof
sqpr
pap
sq
avp

FIGURE 5-10. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. palatal view showing a pair of orbitosphenoids. **A**, photograph of palate region; **B**, photograph of orbitosphenoids; **C**, diagram of **B**. **Abbreviations**: **dpp**, descensus processus parietalis; **ecpp**, ectopterygoid process; **epp**, epipterygoid; **f**, frontal; **iv**, interpterygoidal vacuity; **los**, left orbitosphenoid; **po**, prootic; **pof**, postorbitofrontal; **pop**, postorbital process of parietal; **ros**, right orbitosphenoid. Scale bar in **A** equals 8 cm.

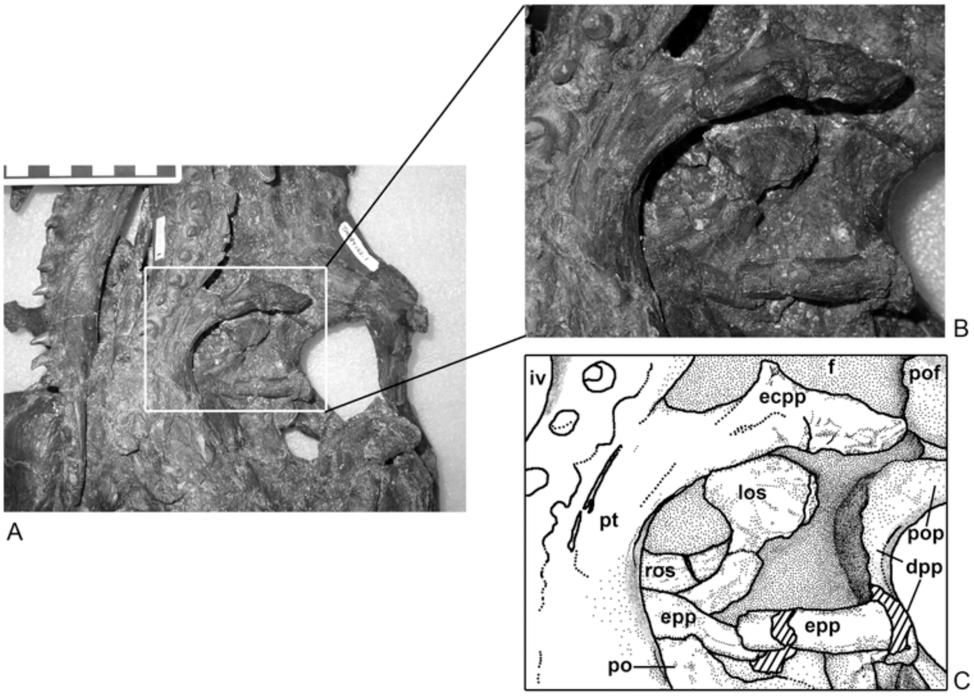

A
B
iv
f
pof
ecpp
pt
los
ros
pop
dpp
epp
epp
po
C

FIGURE 5-11. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. pterygoids in ventral view. **Abbreviations**: **ectp**, ectopterygoid process; **qr**, quadrate ramus. Scale bar equals 5 cm.

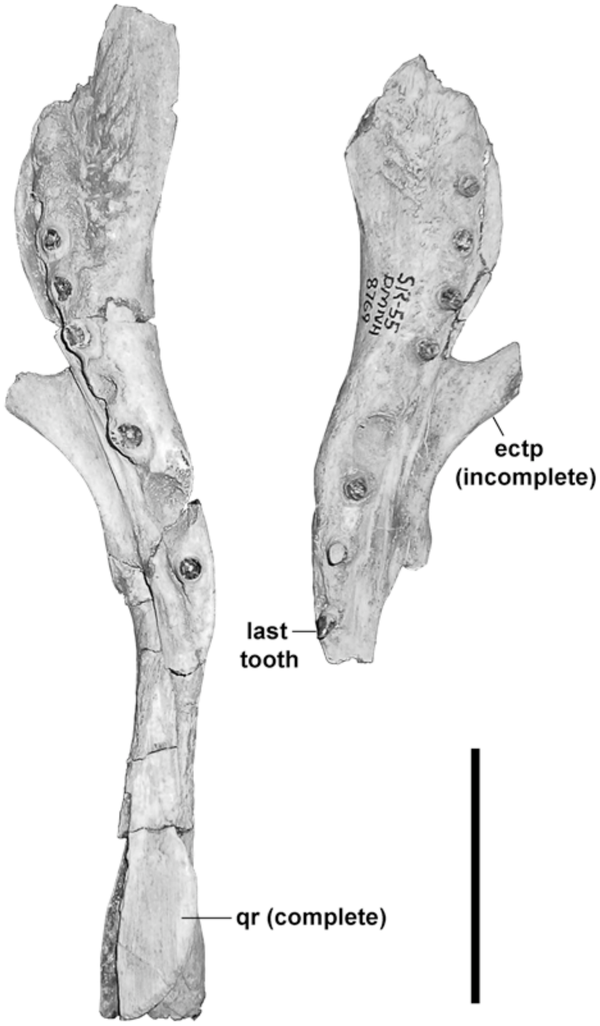

SR-55
DMNH
8769
ectp
(incomplete)
last
tooth
qr (complete)

FIGURE 5-12. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. left quadrate and suspensorial elements. **A**, photograph; **B**, diagram. **Abbreviations**: **ala**, tympanic ala; **ctl**, cartilage mass; **ecl**, extracolumella; **ip**, infrastapedial process; **mcd**, mandibular condyle; **pof**, postorbitofrontal portion of superior temporal bar; **popr**, paroccipital process; **qr**, quadrate ramus of pterygoid; **sp**, suprastapedial process; **sq**, squamosal; **st-pp**, supratemporal parietal process; **st-vp**, supratemporal ventral process. Scale bar equals 5 cm.

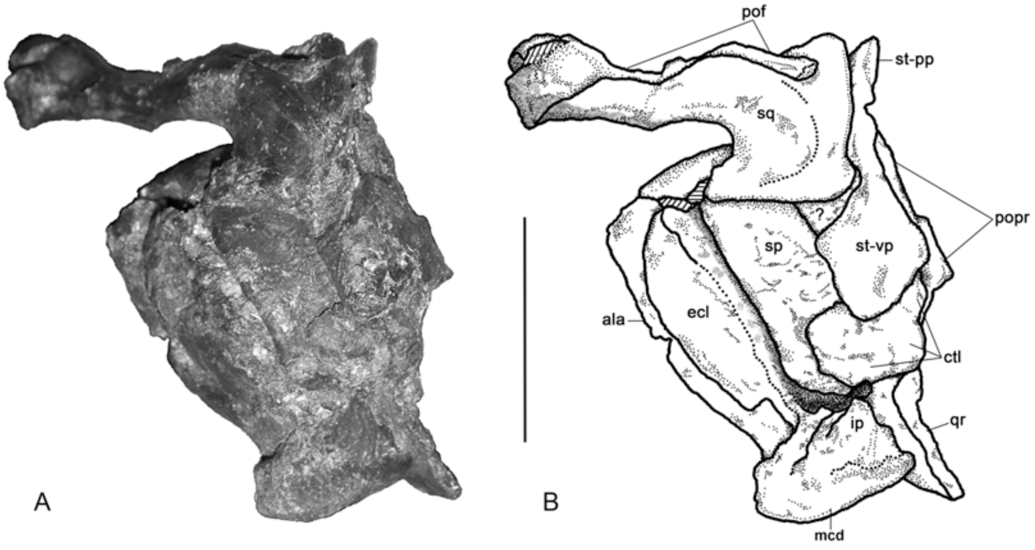

pof
st-pp
sq
popr
?
sp
st-vp
ala
ecl
ctl
ip
qr
mcd
A
B

FIGURE 5-13. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. quadrates. **A**, posterior view, left side; **B**, same view, right side; **C**, medial view, left side; **D**, same view, right side; **E**, lateral view, left side; **F**, same view, right side. **Abbreviations**: **ip**, infrastapedial process; **mcd**, mandibular condyle; **popr**, paroccipital process; **sp**, suprastapedial process; **spt**, stapedial pit; **sqa**, articulation site for squamosal; **sq-qp**, squamosal quadrate process; **st**, supratemporal main body; **sta**, articulation site for supratemporal; **st-vp**, supratemporal ventral process; **utb**, upper temporal bar. Arrows indicate lateral borders of suprastapedial process. Scale bars equal 5 cm.

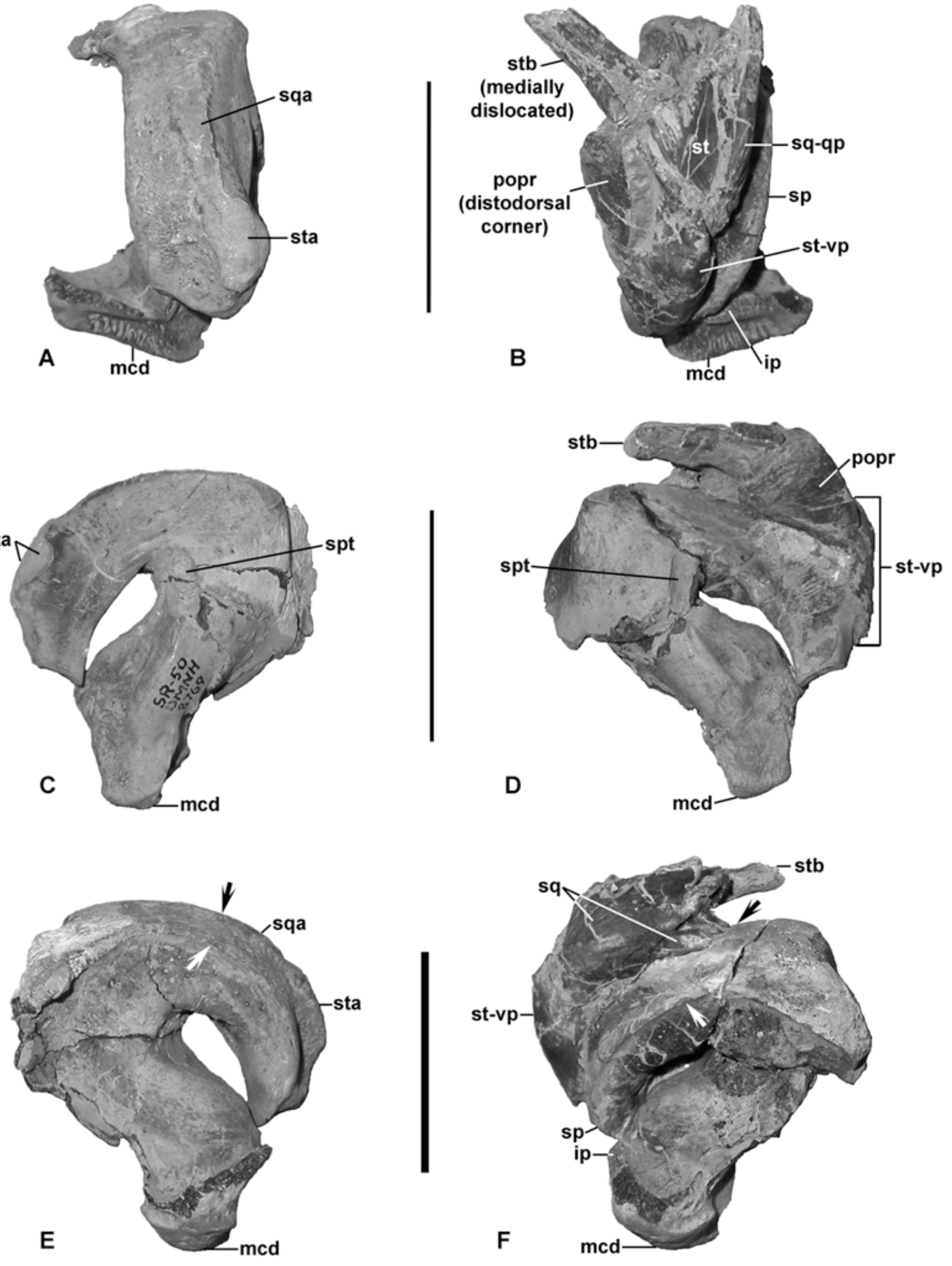

sqa
sta
A
mcd
stb (medially dislocated)
st
sq-qp
popr (distodorsal corner)
sp
st-vp
B
mcd
ip
sta
spt
SR-50
C
mcd
stb
popr
spt
st-vp
D
mcd
sqa
sta
E
mcd
sq
stb
st-vp
sp
ip
F
mcd

FIGURE 5-14. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. left jugal in lateral view. **Abbreviations**: **art-po**, articulation for postorbitofrontal jugal process. Note that horizontal ramus is nearly twice as long as vertical ramus. Scale bar equals 5 cm.


art-po
SR-I
DMNH
8769

FIGURE 5-15. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. braincase. **A**, lateroventral view; **B**, lateral view; **C**, posterodorsal view; **D**, ventral view. **Abbreviations**: **alp**, alar process of basisphenoid; **bac**, canal for basilar artery (exit); **bsp**, basisphenoidal process of prootic; **bt**, basal tuber; **eoc**, exoccipital; **fo**, fenestra ovalis; **fr**, fenestra rotunda; **ocd**, occipital condyle; **op**, opisthotic; **plw**, posterolateral wing of basisphenoid; **pp**, parietal process of prootic; **soc**, supraoccipital; **st**, supratemporal; **stp**, stapes; **st-ppr**, prootic process of supratemporal; **stpr**, supratemporal process of prootic; **st-qa**, supratemporal quadrate articulation surface; **st-vpr**, ventral process of supratemporal; **tn**, trochlear notch; **vii**, opening for seventh cranial nerve; **x-xii**, opening for cranial nerve 10–12. Arrows in C indicate sutural boundary between supraoccipital (soc) and opisthotic (op). Scale bars equal 5 cm.

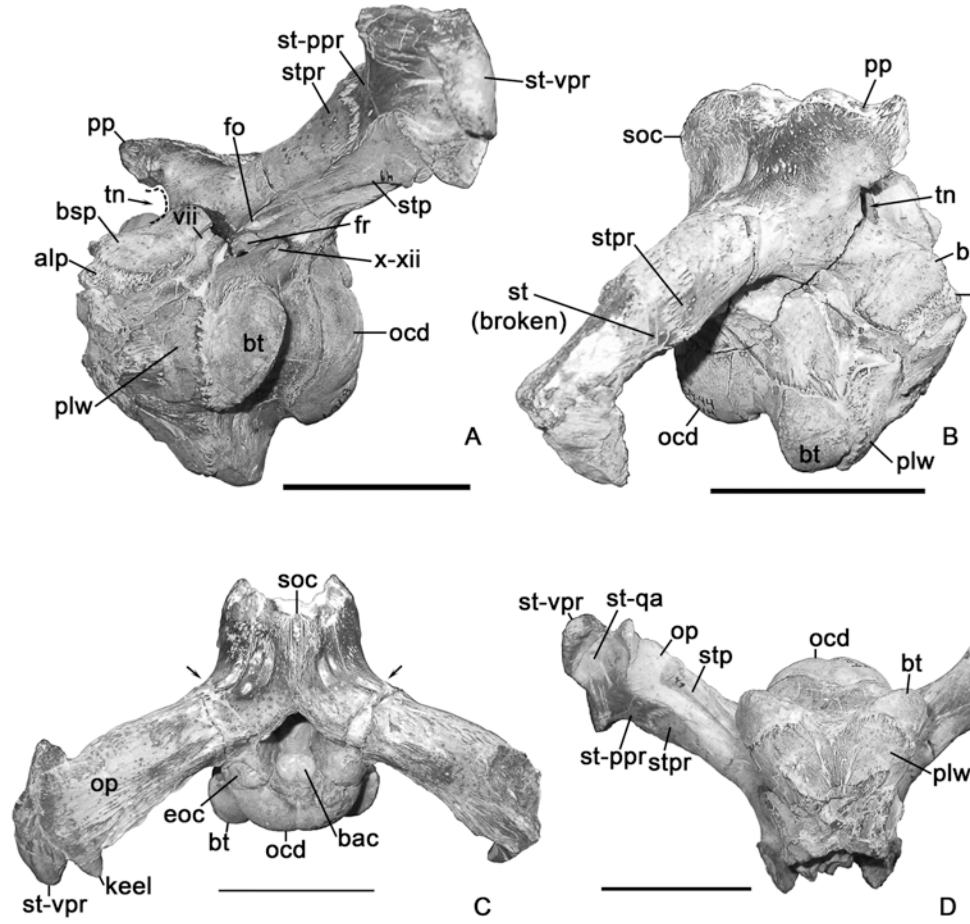

st-ppr
st-vpr
stpr
pp
fo
tn
bsp
vii
stp
fr
alp
x-xii
bt
ocd
plw
A
pp
soc
tn
stpr
bsp
alp
st
(broken)
ocd
bt
plw
B
soc
op
eoc
bt
ocd
bac
st-vpr
keel
C
st-vpr
st-qa
op
stp
ocd
bt
st-ppr
stpr
plw
D

FIGURE 5-16. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. mandibles. **A**, lateral view; **B**, medial view. Scale bar equals 5 cm.

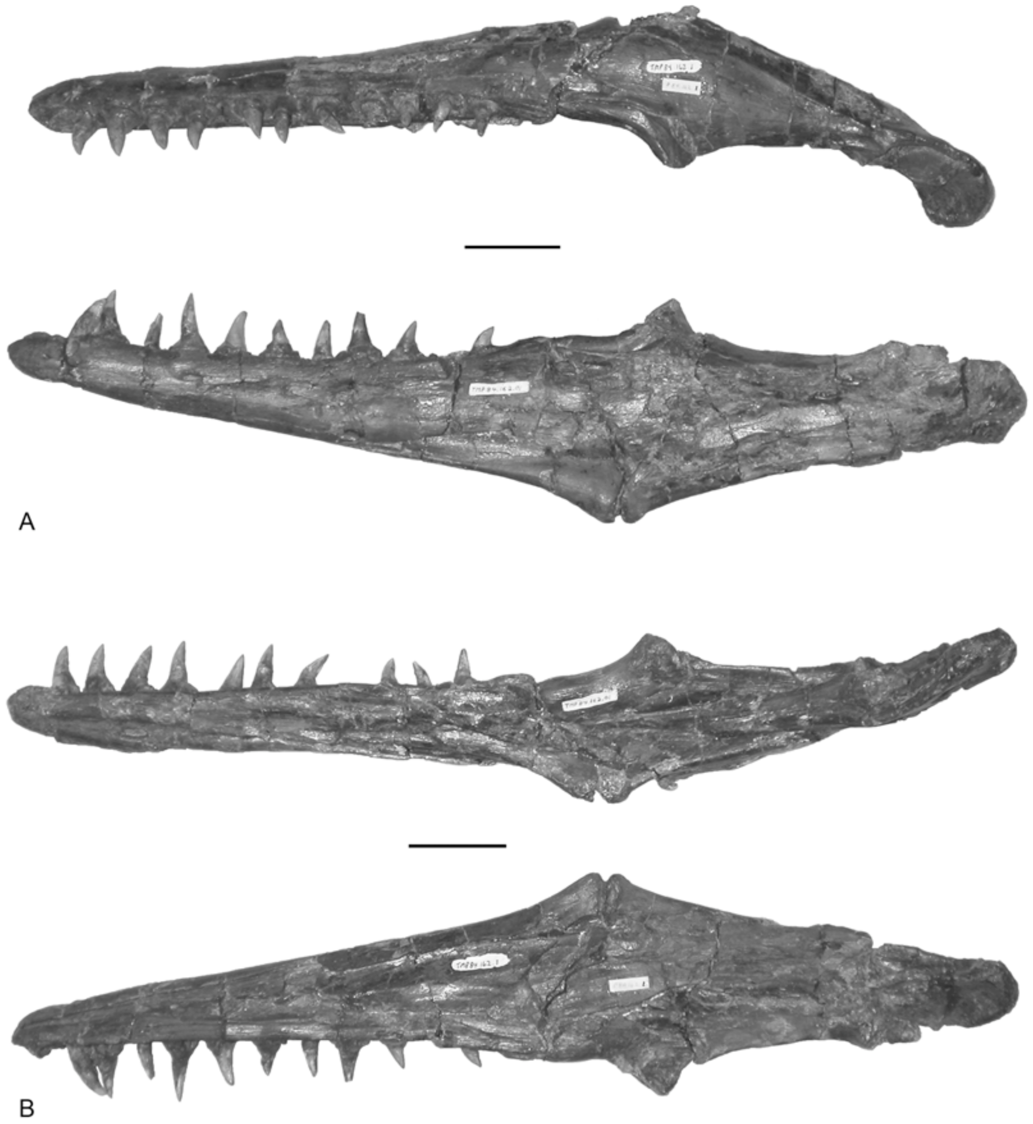

A
B

FIGURE 5-17. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. dentaries in lateral views. Scale bar equals 5 cm.

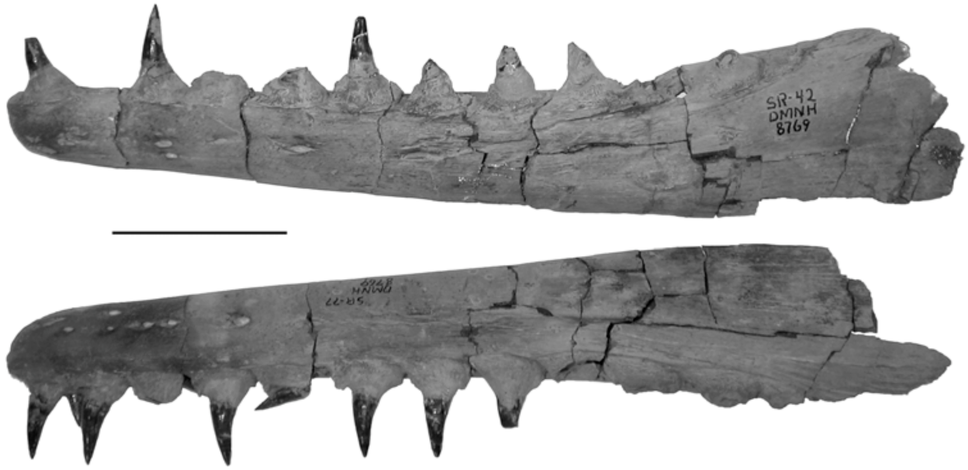

SR-42
DMNH
8769

FIGURE 5-18. DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov. mandibular elements. **A**, lateral view, left side; **B**, medial view, left side; **C**, lateral view, right side; **D**, left coronoid in lateral view. **Abbreviations**: **a**, angular; **asf**, anterior surangular foramen; **ca**, coronoid articulation; **gl-ar**, articular portion of glenoid fossa; **gl-sa**, surangular portion of glenoid fossa; **lw**, splenial lateral wing; **mw**, splenial medial wing; **par**, prearticular; **rar**, retroarticular process; **sa**, surangular; **spl**, splenial. Arrow in C indicates an abnormal bone growth forming a lump. Scale bars equal 5 cm.

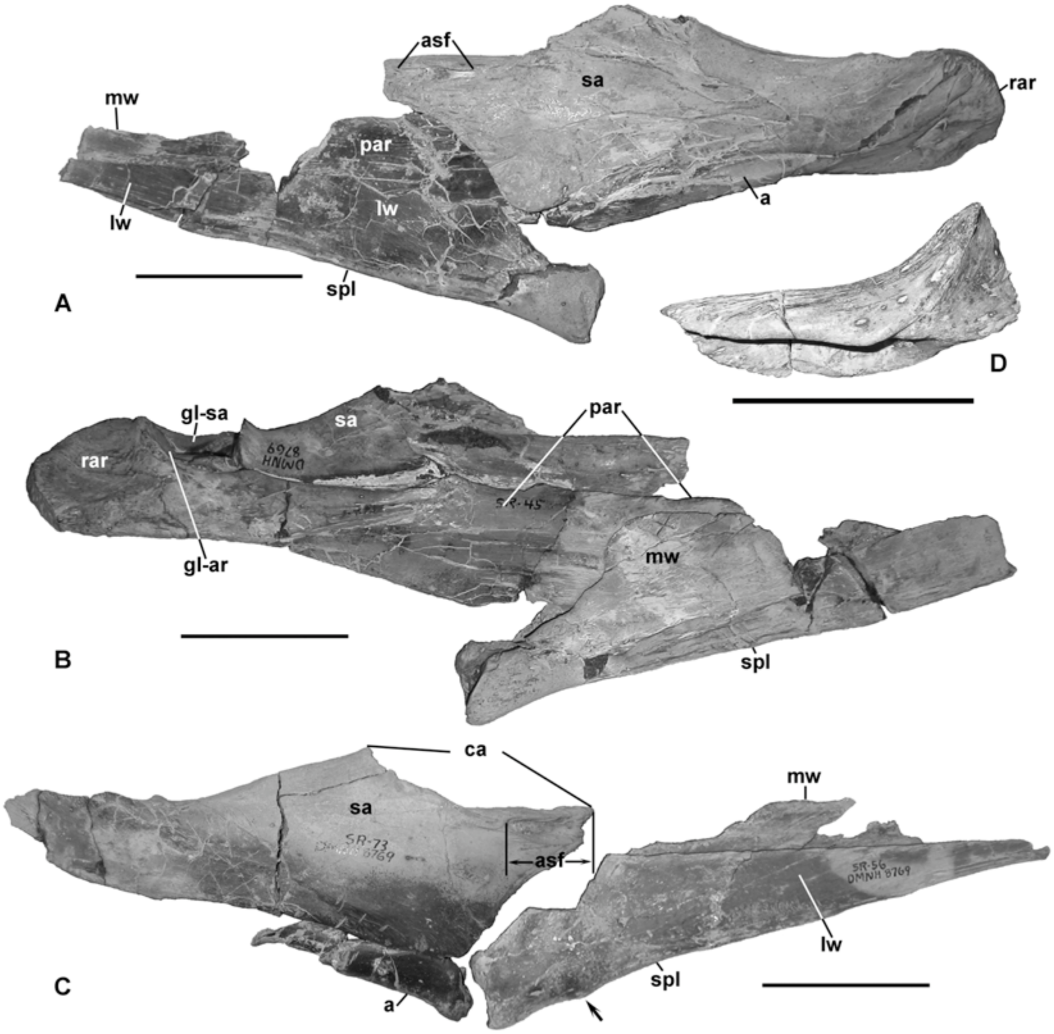

asf
sa
rar
mw
par
lw
lw
a
spl
A
D
gl-sa
sa
DMNH 8769
par
SR-45
rar
mw
gl-ar
B
spl
ca
sa
SR-73 DMNH 8769
asf
mw
SR-56 DMNH 8769
lw
C
a
spl

FIGURE 5-19. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. right coronoid region. **A**, lateral view; **B**, medial view. **Abbreviations**: **a**, angular; **c**, coronoid; **d**, dentary; **mj**, intramandibular joint; **par**, prearticular; **sa**, surangular; **spl**, splenial. Arrow indicates curved coronoid posterior margin. Note the reduced posterior coronoid process. Scale bar equals 5 cm.

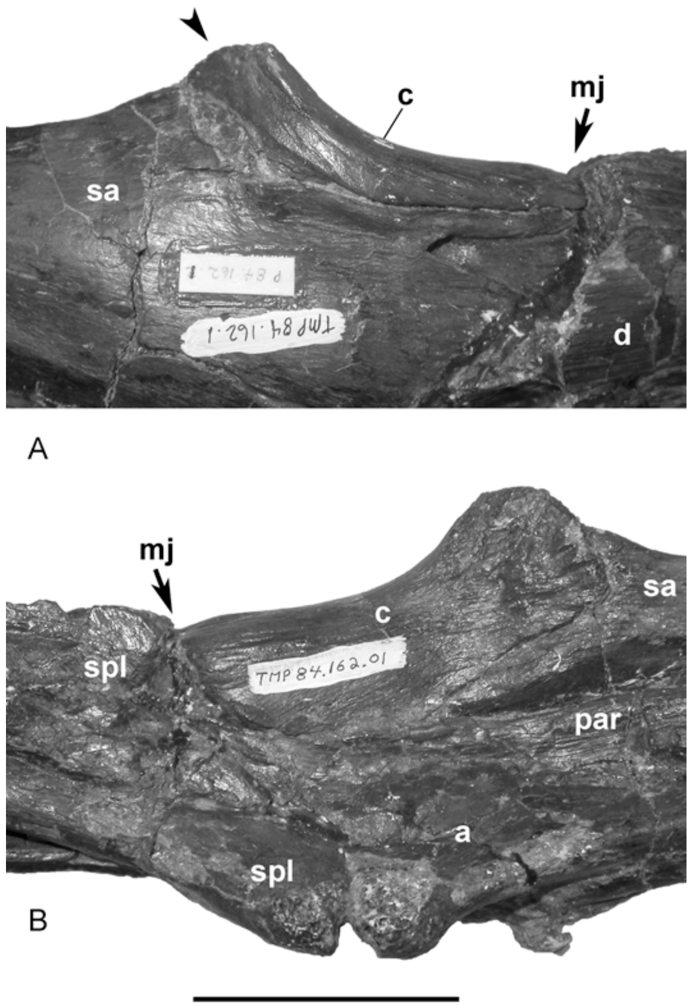

c
mj
sa
d
A
mj
c
sa
spl
par
a
spl
B
TMP 84.162.01

FIGURE 5-20. Comparisons of glenoid fossa among plioplatecarpines. **A**, TMP 84.162.01, *Latoplatecarpus willistoni* holotype; **B**, TMP 83.24.01, *Latoplatecarpus nichollsae*; **C**, AMNH 1821, *Platecarpus tympaniticus*; **D**, FHSM VP-13907, *Plesioplatecarpus planifrons*; **E**, DMNH 8769, *Latoplatecarpus willistoni*. **Abbreviations**: **ar**, articular; **gl**, glenoid fossa; **sa**, surangular. Broken lines indicate suture between articular and surangular on the glenoid surface. **B** after Konishi and Caldwell (2009:fig. 13). Scale bars equal 5 cm.

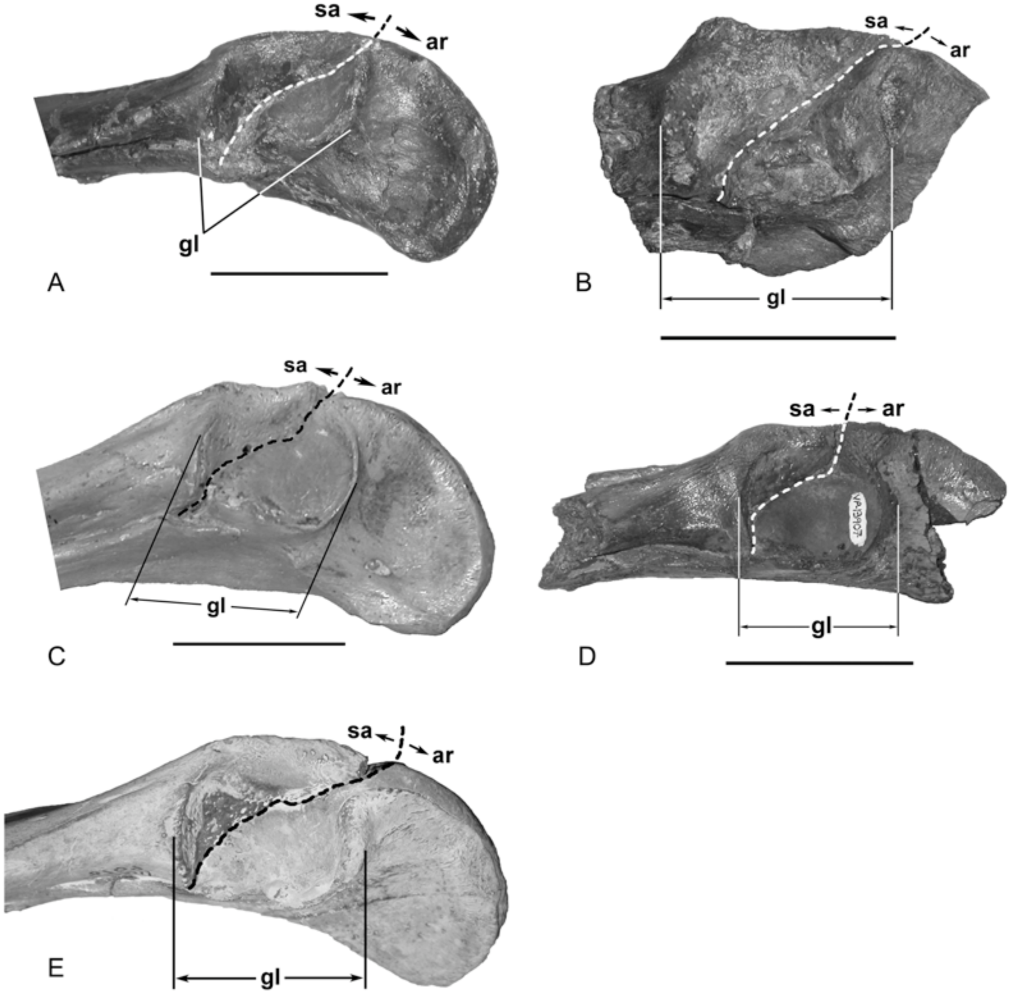

sa
ar
gl
A
sa
ar
gl
B
sa
ar
gl
C
sa
ar
gl
D
sa
ar
gl
E

FIGURE 5-21. Change in centrum width from axis to the seventh dorsal vertebra in DMNH 8769, *Latoplatecarpus willistoni* gen. et sp. nov., UNO 8611-2 (*Plioplatecarpus* sp.; after Burnham, 1991), and CMN 11835 (*Plio. primaevus*; after Holmes, 1996). Condylar surface is incomplete on sixth cervical on DMNH 8769. Note rapid increase in centrum size along this region of the column.

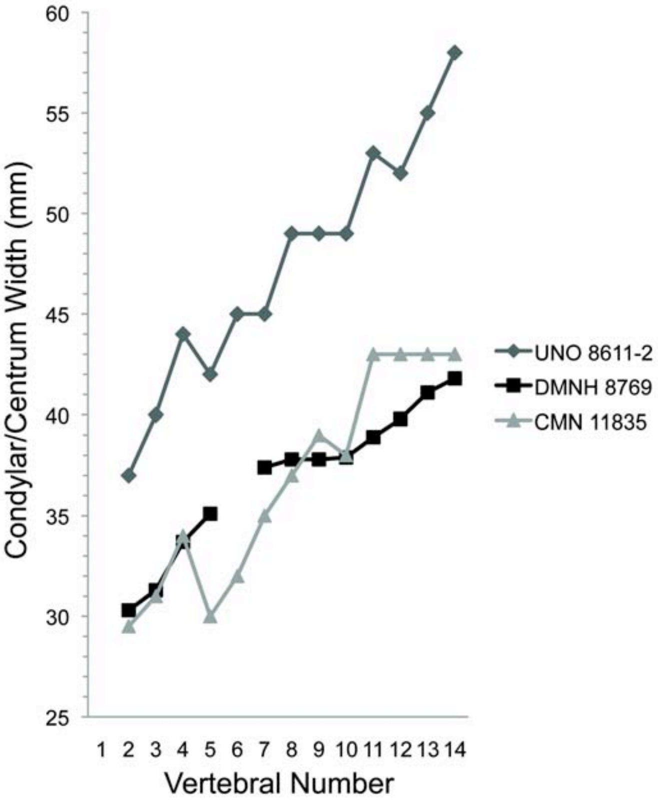

Condylar/Centrum Width (mm)
60
55
50
45
40
35
30
25
Vertebral Number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
UNO 8611-2
DMNH 8769
CMN 11835

FIGURE 5-22. TMP 84.162.01, holotype *Latoplatecarpus willistoni* gen. et sp. nov. left scapula. **A**, lateral view; **B**, medial view; **C**, articular view. **Abbreviations**: **art-cdl**, articulation condyle; **co**, coracoid articulation surface; **gl**, glenoid surface. Arrows indicate broad notch along ventral border of the blade immediately posterior to articulation condyle. Note the notch occupies more than half the entire ventral border posterior to the condyle. Scale bars equal 5 cm.

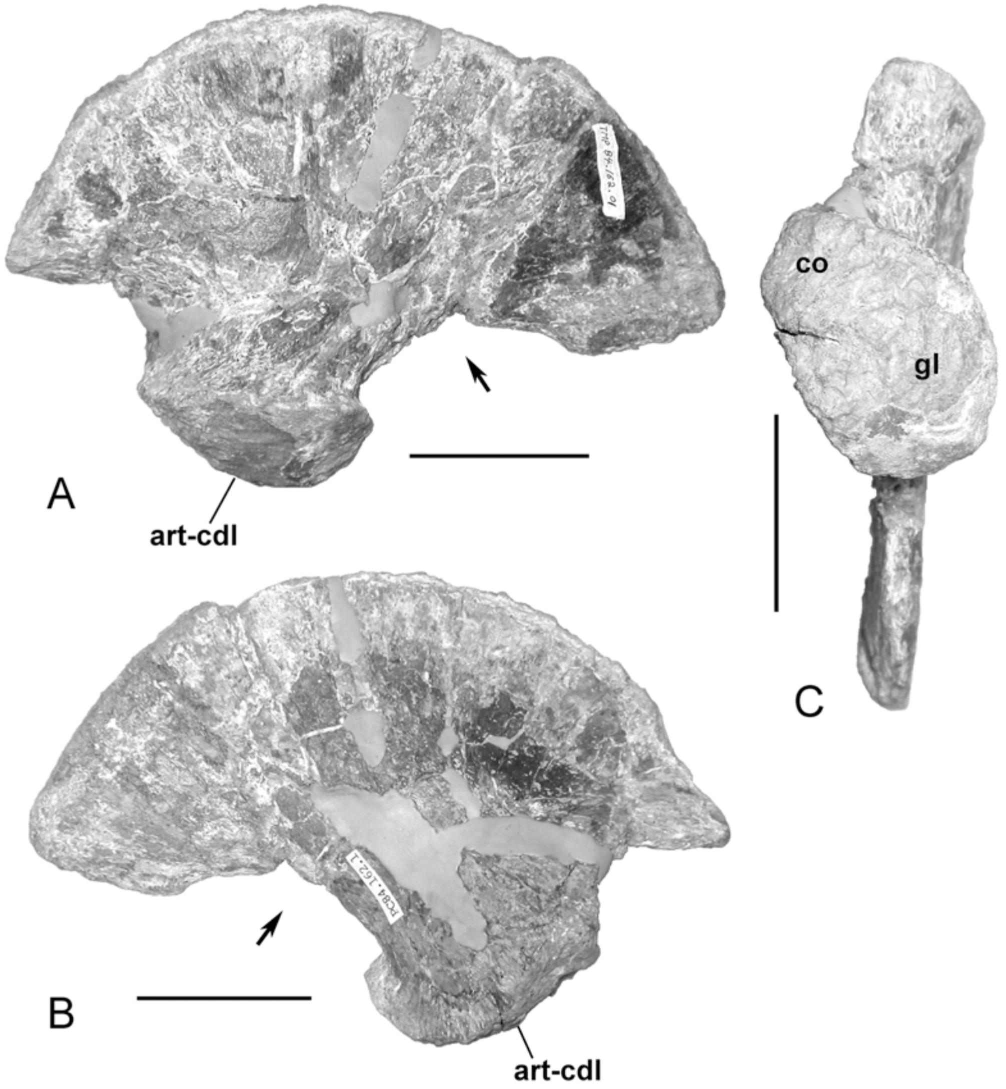

A
art-cdl
B
art-cdl
C
co
gl

FIGURE 5-23. Phylogeny of Plioplatecarpinae. **A**, 50% majority rule consensus tree of nine most parsimonious trees (MPTs) each of 243 steps, consistency index (CI) of 0.7160, retention index (RI) of 0.7723, and rescaled consistency index (RC) of 0.5530. Numbers at nodes indicate percentage of the nine MPTs in which these nodes were recovered, and those without numbers were recovered in all MPTs; **B**, preferred ingroup relationship among all derived plioplatecarpine taxa represented at the node marked with an asterisk (*) in **A**. Under each branch, the number of unambiguous character changes is indicated; **C**, ingroup relationship depicted in **B** with biostratigraphic and biogeographic data superimposed. Thick branches indicate the ones with more than five unambiguous character changes. **Abbreviations**: **a**, Russellosaurina; **b**, primitive 'tethysaur' clade; **c**, Tylosaurinae; **d**, Plioplatecarpinae; **E**, Western Europe; **G**, northern Gulf of Mexico; **I**, Western Interior Basin; **W**, North Atlantic western margin (New Jersey). Biostratigraphic data compiled from the following sources and references therein: Gill and Cobban, 1965, 1966; Hattin, 1982; Jarvis, 1992; Cobban and Kennedy, 1993; Holmes, 1996; Everhart, 2001; Ogg et al., 2004; Jagt, 2005; Mancini and Puckett, 2005; Cobban et al., 2006; Konishi, 2008b. Paleobiogeographic data compiled from personal observations and the following sources: Russell, 1965; Shannon, 1975; Lingham-Soliar, 1994a; Mulder, 1999; Cuthbertson et al., 2007; Konishi and Caldwell, 2007; Konishi, 2008b; Konishi and Caldwell, 2009.

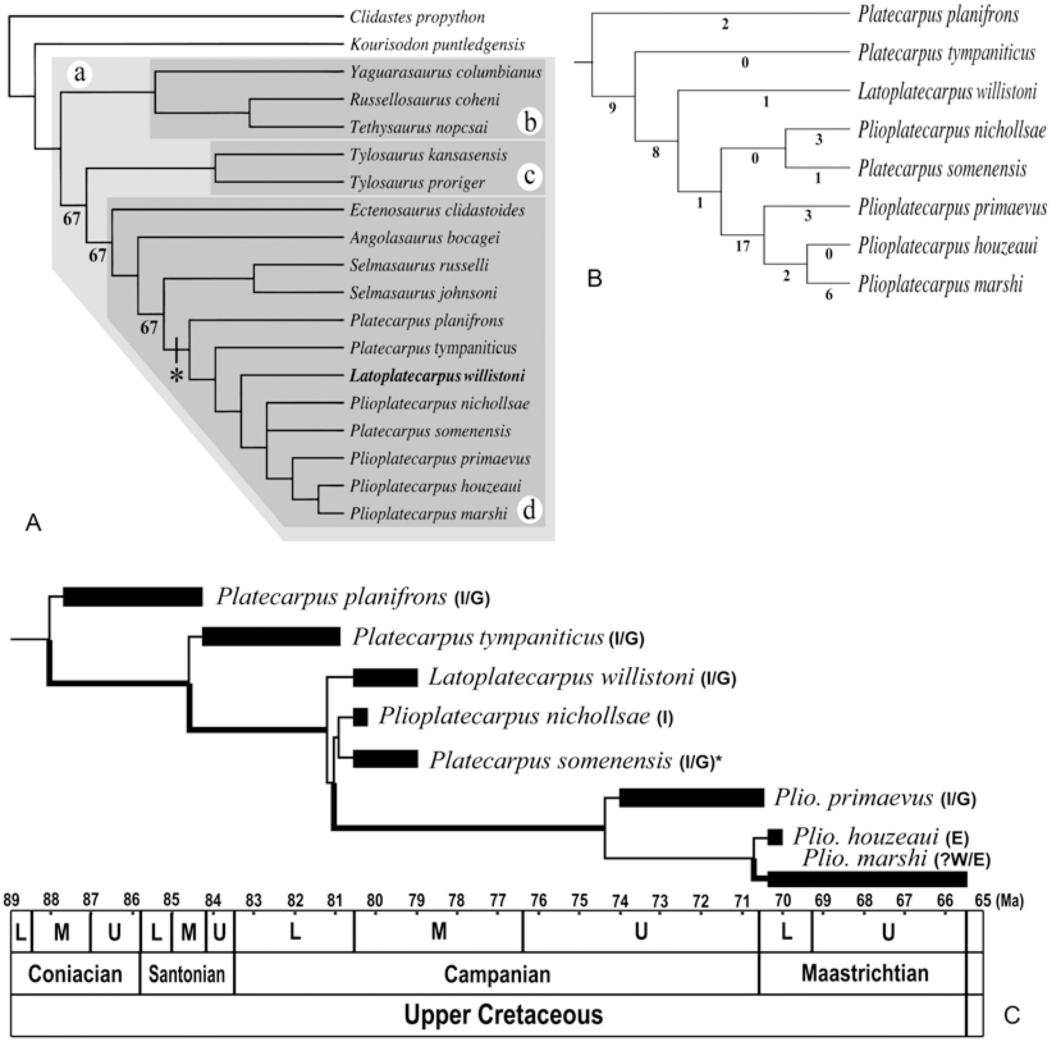
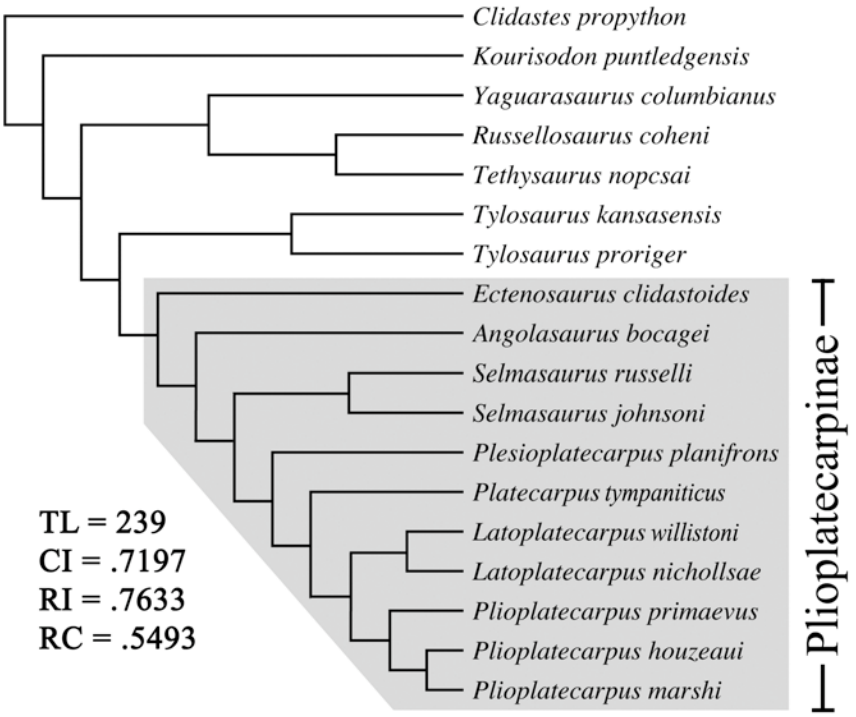

Clidastes propython
Kourisodon puntledgensis
a
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
b
Tylosaurus kansasensis
Tylosaurus proriger
c
67
Ectenosaurus clidastoides
67
Angolasaurus bocagei
Selmasaurus russelli
Selmasaurus johnsoni
67
Platecarpus planifrons
Platecarpus tympaniticus
*
Latoplatecarpus willistoni
Plioplatecarpus nichollsae
Platecarpus somenensis
Plioplatecarpus primaevus
Plioplatecarpus houzeaui
Plioplatecarpus marshi
d
A
Platecarpus planifrons
2
Platecarpus tympaniticus
0
9
Latoplatecarpus willistoni
1
8
Plioplatecarpus nichollsae
3
0
Platecarpus somenensis
1
1
Plioplatecarpus primaevus
3
17
Plioplatecarpus houzeaui
0
2
Plioplatecarpus marshi
6
B
Platecarpus planifrons (I/G)
Platecarpus tympaniticus (I/G)
Latoplatecarpus willistoni (I/G)
Plioplatecarpus nichollsae (I)
Platecarpus somenensis (I/G)*
Plio. primaevus (I/G)
Plio. houzeaui (E)
Plio. marshi (?W/E)
89 88 87 86 85 84 83 82 81 80 79 78 77 76 75 74 73 72 71 70 69 68 67 66 65 (Ma)
L M U L M U L M U L U
Coniacian
Santonian
Campanian
Maastrichtian
Upper Cretaceous
C

FIGURE 5-24. New, preferred ingroup relationships among Plioplatecarpinae, based on a slightly modified character matrix with 16 ingroup taxa with newly proposed taxon names indicated. In this analysis, initial character codings for *Platecarpus* cf. *P. somenensis* and *Plioplatecarpus nichollsae* were combined, based on phylogenetic, biogeographic, biostratigraphic, and ontogenetic considerations, but the characters scored against the taxa remained identical to the first set of analyses. **Abbreviations**: **CI**, consistency index; **RC**, rescaled consistency index; **RI**, retention index; **TL**, tree length.


Clidastes propython
Kourisodon puntledgensis
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
Tylosaurus kansasensis
Tylosaurus proriger
Ectenosaurus clidastoides
Angolasaurus bocagei
Selmasaurus russelli
Selmasaurus johnsoni
Plesioplatecarpus planifrons
Platecarpus tympaniticus
Latoplatecarpus willistoni
Latoplatecarpus nichollsae
Plioplatecarpus primaevus
Plioplatecarpus houzeaui
Plioplatecarpus marshi
Plioplatecarpinae
TL = 239
CI = .7197
RI = .7633
RC = .5493

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# APPENDIX 1

Description of characters for phylogenetic analyses. Characters were polarized using *Clidastes propython* and *Kourisodon puntledgensis* as outgroup taxa. All characters were unordered and not weighted. Where applicable, reference to a character number from previous work is provided in parentheses at the end of each character.

1. Premaxilla predental rostrum: absent (0); present, short and obtuse in lateral view (1); present, distinctly pointed in lateral view (2); present, large and rectangular in lateral view (3).
2. Median dorsal ridge on premaxilla: absent (0); present, only on broad dentigerous portion (1); present, on both dentigerous portion and narrow internarial ramus (2).
3. Premaxilla rostrum end in dorsal aspect: semicircular/broadly parabolic (0); sub-trapezoid (1); scalloped (2); 'U'-shaped (3); conical/narrowly parabolic (4); 'V'-shaped (5).
4. Premaxillo-maxillary suture length: short, suture posteriorly terminating anywhere between first and third maxillary teeth inclusive (0); long, suture posteriorly terminating anywhere above or posterior to the fourth maxillary tooth (1).
5. Posterior terminus of premaxillo-maxillary suture: confluent with anteriorly deepest portion of maxilla (0); precedes anteriorly deepest portion of maxilla (1).

6. Maxillary tooth count: 12 (0); between 13 and 15 (1); more than 15 (2). These states roughly correspond to low, intermediate, and high tooth count in mosasaurs, respectively.

7. Prefrontal participation in forming posterolateral border of external naris: absent (0); present (1) (cf., Bell, 1997: character 38).

8. Prefrontal supraorbital process: process absent, or present as very small rounded knob (0); distinct to large, triangular or rounded, overhanging wing (1) (cf., Bell, 1997: character 29).

9. Frontal width: element broad and short (0); long and narrow (1). The maximum length to maximum width ratio of 1.5 : 1 or smaller characterizes the state (0), that of about 2 : 1 characterizes the state (1) (Bell, 1997: character 10).

10. Frontal narial emargination: frontal not embayed anteriorly on each side by posterior end of naris, lacking anterolateral process (0); narrow embayment present, resulting in forming closely spaced anterolateral processes (1); broad embayment present, resulting in widely separated anterolateral processes (2) (cf., Bell, 1997: character 11). In the state (2), the distance between two anterolateral processes is greater than 50% of interorbital distance. In *Tylosaurus kansasensis*, while appearing to possess broad anterior narial embayment of the frontal, the distance between the two processes is less than half the interorbital width and hence here scored for the state 1.

11. Frontal median dorsal eminence: absent or present as anteriorly confined weak bulge (0); long and acute crest moderately well developed (1); long and acute crest highly developed, accompanied by strong parasagittal excavations on both

sides (2).

12. Frontal table in lateral view: straight (0); arched, as a result of sloping anterior to parietal foramen (1).

13. Frontal interorbital constriction: absent (0); present (1).

14. Shape of frontal preorbital margins: converge anteriorly to form triangular anterior frontal outline (0); distinctly diverge immediately anterior to orbits but re-converge anteriorly (1); straight and remain sub-parallel with each other leading to widely separated anterolateral processes (2); sinusoidal in outline, ending in widely separated anterolateral processes (3).

15. Frontal ventral separation ridge: absent (0); present, preventing prefrontal from contacting postorbitofrontal posteriorly (1) (cf., Bell, 1997: character 30).

16. Frontal ala shape: sharply acuminate (0); more broadly pointed or rounded (1) (Bell, 1997: character 13).

17. Frontal ala posterior border: posteromedially inclined (0); transversely oriented (1); anteromedially inclined (2).

18. Dorsal posteromedian border of frontal and parietal foramen contact: frontal does not participate in forming anterior border of parietal foramen, foramen well separated from frontal by at least one foramen length (0); frontal approaches or touches anterior extremity of parietal foramen but without or minimally forming indentation (1); frontal touches anterior extremity of parietal foramen and is distinctly indented to surround or directly border anterior-half of parietal foramen (2).

19. Parietal table outline: nearly equilateral triangle (0); longer than wide, anterior

border gently convex (1); longer than wide, anterior border bilobate (2); as wide as long and pentagonal (3); vaguely bell-shaped, with lateral borders posteriorly converging but without meeting (4); lateral borders remain semi-parallel with each other without meeting posteriorly (5); highly elongate with lateral borders slowly converging posteriorly but never meeting (6).

20. Parietal foramen relative size on dorsal surface: small (0); intermediate (1); large (2). In state (0), the maximum dimension of the foramen is typically 25% or less than the maximum parietal table width, while in state (1), it ranges between 25% and one-third the parietal table width. In state (2), the maximum (= longitudinal) dimension of foramen clearly exceeds one-third the maximum parietal table width.

21. Parietal foramen morphology in dorsal aspect: nearly circular (0); short oval with curved sides, with length : width ratio less than 1.5 (1); elongate oval with curved sides, with length : width ratio greater than 1.5 (2); elongate oval with straight sides, with length : width ratio greater than 1.5 (3); teardrop-shaped with apex pointing anteriorly (4); broadly teardrop-shaped with apex pointing posteriorly (5). In states (2) and (3), the ratio is typically greater than 1.6.

22. Parietal foramen ventral opening: opening is level with main ventral surface (0); opening surrounded by rounded, elongate ridge (1) (cf., Bell, 1997: character 25).

23. Length of postorbital process of parietal: forms anteromedial border of supratemporal fenestra, visible in dorsal aspect (0); forms anteromedial border of supratemporal fenestra, concealed in dorsal aspect (1); forms entire anterior

border of supratemporal fenestra with its broad, posteriorly sloping surface dorsally exposed (2); forms entire anterior border of supratemporal fenestra with its narrow dorsal plateau forming small portion of horizontal skull table posterior to frontal ala (3); same as (3), except process much more dorsally exposed, so much that parietal and frontal ala divide skull table corner sub-equally (4). In state (3), the degree of dorsal exposure ranges from very thin to approximately half the longitudinal dimension of the adjacent frontal ala.

24. Descensus processus parietalis posterior border: originates anterior to parietal fossa (0); originates at level of parietal fossa and process posteriorly extends well beyond it (1) (Bahl, 1937:142).

25. Postorbitofrontal frontal-parietal wing dorsal surface: bears broad, single facet for receiving frontal ala (0); bears distinct anterior and posterior facets for frontal ala and parietal postorbital process, respectively (1). In state (0), a small, wedge-shaped concavity may exist at the posteromedial corner of the wing for receiving a short parietal postorbital process.

26. Postorbitofrontal jugal process: ventrally projecting with well-developed anteroventral projection (0); ventrally projecting with small anteroventral projection (1); ventrally projecting, short and cup shaped (2); ventrally projecting, clasping distal end of jugal in form of ‘U’ (3); laterally projecting, broadly rounded and wing-like (4).

27. Postorbitofrontal squamosal process: reaches end of supratemporal fenestra (0); does not reach end of supratemporal fenestra (1) (cf., Bell, 1997: character 34).

28. Jugal posteroventral process: absent (0); present forming rounded or obtuse corner (1); present forming acute, posteriorly projecting keel (2) (cf., Bell, 1997: character 40).

29. Jugal ascending ramus: distally ending in broad and concave articulation with postorbitofrontal (0); distally attenuating to end as slender rod (1).

30. Jugal ascending ramus length: clearly less than 50% horizontal ramus length (0); approximately 50% horizontal ramus length (1); clearly more than 50% horizontal ramus length (2).

31. Ectopterygoid process: long, comprising expanded distal articulation process with ectopterygoid and stalk-like proximal shaft (0); long, without or with little distal expansion (1); short, without distal expansion (2).

32. Ectopterygoid process orientation: projects anterolaterally from dentigerous body (0); projects laterally at right angle (1).

33. Anterior border of quadrate cephalic condyle: excavated posteriorly (0); straight, forming right angle with long axis of suprastapedial process (1); straight or nearly straight, forming obtuse angle with long axis of suprastapedial process (2).

34. Thickness of quadrate ala: thin (0); thick (1) (cf., Bell, 1997: character 51). This character based on Bell’s (1997) definition in general differentiates derived russellosaurines from mosasaurines.

35. Quadrate ala anterior surface: concave (0); relatively planar (1); bulges anterolaterally (2).

36. Suprastapedial process length: clearly longer than two-thirds quadrate height

(0); about two-thirds quadrate height (1); clearly shorter than two-thirds quadrate height (2) (cf., Bell, 1997: character 44).

37. Infrastapedial process: absent (0); present, not contacting suprastapedial process (1); present, contacting but not fusing with suprastapedial process (2); present, distal end fusing with suprastapedial process (3); dorsally sends tongue-like lamina to fuse with and overlap suprastapedial process posterodistally (4). State (4) is unique to *Ectenosaurus*.

38. Quadrate shaft posteroventral bulging: virtually absent, border straight (0); small with convex posterior border (1); moderate in size with straight posterior border (2); large with convex posterior border (3).

39. Quadrate mandibular condyle outline: transversely elongate saddle-shaped (0); transversely elongate, roughly spindle-shaped (1); transversely elongate, curved teardrop-shaped (2); transversely narrow triangle with its vertex pointing medially (3).

40. Quadrate mandibular condyle main surface: concave (0); planar (1); convex (2) (cf., Bell, 1997: character 61).

41. Quadrate stapedial pit morphology: sub-reniform (0) elongate, slit-like (1); rectangular (2); sub-hexagon (3); narrow, keyhole-shaped (4); broad oval with straight lateral borders (5); broad oval with curved lateral borders (6); inverted teardrop-shaped (7).

42. Quadrate ala posteroventral extension: ascends posterodorsally at more than 60 degrees from horizontal (0); ascends posterodorsally about 45 degrees from horizontal (1); extends posteriorly around lateral rim of mandibular condyle with

very subtle ascent towards posterior end (2); diminishes ventrally, forming low, roughened area on lateral face of mandibular condyle (3) (cf., Bell, 1997: character 50).

43. Quadrate dorsal median ridge: relatively thin and elevated crest (0); low, broadly inflated dome (1) (cf., Bell, 1997: character 58).

44. Quadrate vertical median ridge: sharp, crest-like (0); broadly rounded (1).

45. Medial flange along vertical median ridge of quadrate: absent (0); present (1).

46. Basisphenoid basipterygoid process shape: relatively narrow with articular surface facing mostly anterolaterally (0); somewhat thinner, more fan-shaped with posterior extension of articular surface causing more lateral orientation (1) (cf., Bell, 1997: character 64).

47. Basal tubera: short and low, laterally projecting and widely separated from each other (0); short, more ventrally projecting but remain widely separated (1); short, ventrally projecting, closely spaced but not inflated, with distinct ventral migration of pitted lateral surface (2); short, ventrally projecting, closely spaced and highly inflated, with clear ventral migration of pitted lateral surface (3); longitudinally elongate, projecting ventrolaterally at about 45 degrees from sagittal plane (4). In *Plioplatecarpus primaevus*, the tubera exhibit less inflation than in the other taxa scored for the state (3).

48. Otosphenoidal crest on prootic: absent (0); present, laterally covering seventh cranial nerve exit on prootic (1); present, laterally covering both seventh and ninth cranial nerve exits on prootic and opisthotic, respectively (2). (Bahl, 1937; Russell, 1967) (crista prootica of Rieppel and Zaher, 2000).

49. Jugular and condylar (= hypoglossal) foramina: externally separate on braincase (0); externally fused (1).

50. Squamosal parietal process outline: very low (0); modest in development and roughly triangular (1); well developed and rectangular/parallelogram in outline (2).

51. Anteroventral projection of squamosal quadrate process: absent (0); short, less than half quadrate process length (1); highly elongate, greater than half quadrate process length (2). State (2) is unique to *Plioplatecarpus houzeaui*, based on IRSNB R36 reported by Lingham-Soliar (1994a).

52. Squamosal quadrate process posterior notch: absent (0); present (1).

53. Posterior edentulous ramus on dentary: small, no more than 15% marginal border length present (0); large, about 20% marginal border length present (1).

54. Dentary medial parapet height: lower than lateral dentary wall (0); same height as lateral wall (1); deeper than lateral wall (2).

55. Anterior edentulous prow on dentary: absent (0); present, projection small and squared in lateral view (1); present, projection small and round in lateral view (2); present, projection broad and rectangular in lateral view (3).

56. Dentary tooth count: 12 or fewer (0); between 13 and 15 (1); more than 15 (2). As in the maxillary tooth count, these states roughly correspond to low, intermediate, and high dentary tooth count in mosasaurs, respectively.

57. Splenial-angular articulation surface: smooth, single vertical ridge-and-groove articulation surface (0); obliquely oriented numerous ridge-and-groove

articulation surface (1); smooth articulation surface in outline of pear (2) (cf., Bell, 1997: character 73).

58. Coronoid posterodorsal process angle: acute (0); 90 degrees (1); obtuse (2).

59. Coronoid posterodorsal process development: well developed (0); moderate (1); significantly reduced (2). A very low coronoid profile results from state (2).

60. Surangular lateral profile: post-coronoid portion longer, deepening anteriorly with straight dorsal and ventral borders (0); post-coronoid portion longer, deepening anteriorly with slight dorsal curvature (1); post-coronoid portion longer, dorsal and ventral borders running sub-parallel with each other, curving dorsally (2); post-coronoid and coronoid portion sub-equal in length, with anteriorly diverging post-coronoid part preceded by attenuated coronoid region (3).

61. Anterior surangular foramen: short, less than one-third coronoid suture length (0); moderately long, greater than one-third but clearly less than half coronoid suture length (1); extremely long, approaching or exceeding half coronoid suture length (2).

62. Portion of coronoid suture that occurs anterior to splenio-angular (= intramandibular) joint: does not exist, coronoid suture terminating posterior to this joint (0); only 20% or less portion of suture extending beyond joint (1); greater than 20% and up to 30% extending beyond joint (2); greater than 30 % extending beyond joint (3).

63. Retroarticular process ventral foramina: no large foramina on ventral (or lateral) face (0); one to three large foramina present (1) (cf., Bell, 1997: character 82).

64. Participation of articular in forming glenoid fossa: clearly greater than 50% (0); 50% or less than 50% total area (1).

65. Surangular-articular suture on glenoid surface: terminating anterior to posterior border (0); terminating at posterior border (1).

66. Atlas neural arch: notch present in anterior border (0); no notch in anterior border (1) (Bell, 1997: character 91).

67. Zygapophyses: present throughout prepygal vertebrae (0); absent posterior to fifth dorsal vertebra (1).

68. Zygosphenes and zygantra in post-axis cervical vertebrae: well developed (0); incompletely developed/vestigial (1); completely absent (2).

69. Vertebral condyle shape: condyles of anteriormost trunk (= dorsal) vertebrae extremely dorsoventrally depressed (0); slightly depressed (1); essentially equidimensional (2) (Bell, 1997: character 101).

70. Prepygal vertebrae number: 32 or fewer (0); 39 or more (1) (cf., Bell, 1997: character 105).

71. Pygal vertebrae count: lower than 10 (0); 10 or more (1). In state (0), there are seldom nine pygal vertebrae.

72. Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0); several spines dorsally elongated behind middle of tail (1) (Bell, 1997: character 108).

73. Haemal arch and spine complex: fused to caudal centra (0): articulates with haemapophyses (1).

74. Scapular neck constriction: absent (0); present (1).

75. Scapular condylar surface length: greater than 30% blade length (0); about 30% blade length (1); less than 30% blade length (2).

76. Length ratio between anteroventral border and posteroventral border of scapular blade: 1 : 2.5 or less (0) about 1 : 2 (1); about 1 : 1.5 (2); about 1 : 1 (3).

77. Scapula and coracoid size: scapula smaller than coracoid (0); two elements sub-equal in size (1); scapula larger than coracoid (2) (cf., Bell, 1997: character 113).

78. Humerus length: humerus distinctly elongate, about three or more times longer than distal width (0); greatly shortened, about 1.5 to two times longer than distal (antero-posterior) width (1); length and distal width virtually equal (2); distal width slightly greater than length (3) (Bell, 1997: character 121).

79. Surface of humeral head: deltoid, pectoral, and postglenoid processes widely separated from head (0); processes not clearly separated from articular surface of head (1).

80. Shape of humeral head: relatively planar (0); conspicuously domed (1).

81. Humerus pectoral crest position: anteroproximal corner of humerus (0); middle of proximal region of humerus (1) (cf., Bell, 1997: character 125).

82. Humerus pectoral crest thickness: thin (0); thickened and enlarged, but proximal humeral surface antero-posteriorly longer than dorso-ventrally thick (1);

thickened and inflated, making proximal humeral surface nearly as thick as long (2).

83. Humerus ectepicondyle: short and bulbous (0); present as flange (1); present as tubular prominence (2) (cf., Bell, 1997: character 127).

84. Radiale: absent (0); present, radiale larger than intermedium/centrale (1); present, radiale smaller than intermedium/centrale (2). The preceding statements on absence/presence and size comparison of these carpal elements are based on large and presumably fully matured specimens of representative taxa, and thought to preclude any ontogenetic considerations.

85. Ulnare: enters posteroventral margin of antebrachial foramen (0); excluded from foramen (1) (cf., Bell, 1997: character 130).

86. Distal carpal I: absent (0); present (1). As above, the data come from large (mature) specimens.

87. Metacarpal I expansion: spindle-shaped, elongate (0); broadly expanded (1) (Bell, 1997: character 134).

88. Number of phalanges in first manal digit: 3–4 (0); 5 (1); 6 (2); more than 6 (3). These values approximate the degree of hyperphalangy in mosasaurs.

89. Ischiadic tubercle size: elongate (0); short (1) (Bell, 1997: character 139).

90. Degree of marginal tooth root exposure: little exposed, tooth root constituting less than 25% tooth height above dental margin (0); moderately exposed, tooth root constituting between 25% and 30% tooth height above dental margin (1); highly exposed, tooth root constituting nearly one-third tooth height exposed above dental margin and inflated (2). Measurements were taken using fully

erupted teeth in a given individual specimen.

91. Marginal tooth crown cross-section at base: laterally highly compressed, ellipsoid (0); sub-circular (1). In *Plioplatecarpus marshi* and *P. houzeaui*, both morphs seem to occur on the same individual or intraspecifically.

92. Marginal tooth surface: finely striate medially (0); not medially striate (1) (Bell, 1997: character 83).

93. Premaxillary teeth: not procumbent (0); procumbent, main long axis of teeth forming about 110 to 120 degree angle with dental margin of premaxilla (1). These angles were measured along the long axis of the tooth base (i.e., exposed root portion) and basal portion of the crown, not the posteriorly recurved distal portion of the latter.

94. Pterygoid tooth base: large, occupying nearly entire width of pterygoid body (0); small, occurring on narrow ridge along lateral margin of ventral pterygoid surface (1) (cf., Bell, 1997: character 42).

95. Quadrate mid-shaft medial bending: absent (0); present (1).

96. Scapular blade: elongate along axis perpendicular to condylar surface (0); elongate along axis parallel with condylar surface (1).

97. Basioccipital canal: no canal (0); a small pair separated by median septum (1); a large pair separated by median septum (2); a single bilobate canal (Bell and Polcyn, 2005: character 67). Some specimens of cf. *Platecarpus tympaniticus* (e.g., YPM 4025; 40671) show that the canal is anteriorly separated by median septum while it is bilobate at its posterior exit on medullary floor. Therefore, the

scoring of this character is based on morphology of the canal at its posterior exit when such a fact is known.

# APPENDIX 2

List of taxa analyzed, and sources of information for character scoring, i.e., specimens and/or published work. Asterisks (*) indicate principal data sources. **Abbreviations**: **HT**, holotype. For institutional abbreviations refer to the main text.

## Outgroup

***Clidastes propython***—ANSP 10193* (HT); UALVP 43*; Russell (1967); Bell (1997).

***Kourisodon puntledgensis***—CDM 022* (HT); Nicholls and Meckert (2002).

## Ingroup

***Yaguarasaurus columbianus***—Páramo (1991)*; Páramo (1994)*.

***Russellosaurus coheni***—SMU 73056* (HT); Polcyn and Bell (2005).

***Tethysaurus nopcsai***—Bardet et al. (2003)*; UALVP 48850*.

***Tylosaurus kansasensis***—FHSM VP-2295* (HT); VP-2495* (PT); Bell (1997); Everhart (2005).

***Tylosaurus proriger***—AMNH FR 221*; FHSM VP-3*; RMM 5610*; KU 28705; Osborn (1899); Russell (1967); Caldwell (1996); Bell (1997).

***Ectenosaurus clidastoides***—FHSM VP-401* (PT); TMP 2008.013.0001*; Russell (1967); Caldwell (1996).

***Angolasaurus bocagei***—Telles-Antunes (1964)*.

***Selmasaurus russelli***—GSATC 221* (HT); Wright and Shannon (1988).

***Selmasaurus johnsoni***—FHSM VP-13910* (HT); Polcyn and Everhart (2008).

***Platecarpus planifrons***—AMNH 1491* (HT); FHSM VP-2116*; 2296*; UALVP 24240*; 40402*; YPM 40508*.

***Platecarpus tympaniticus***—AMNH 1820*; 1821*; 2005*; 2006*; 1488; ALMNH PV 985.0021*; FHSM VP-322*; FMNH UC-600*; LACM 128319*.

***Latoplatecarpus willistoni***—DMNH 8769*; SDSMT 30139*; TMP 84.162.01* (HT); AMNH 2182.

***Plioplatecarpus nichollsae***—CMN 52261* (HT); TMP 83.24.01*; M 83.10.18; Cuthbertson et al. (2007).

**'*Platecarpus*' *somenensis***—FMNH PR 465*; 467*; GSATC 220; Russell (1967).

***Plioplatecarpus primaevus***—USNM 18254* (HT); CMN 11835*; 11840*; P 1756*; Holmes (1996); Holmes et al. (1999).

***Plioplatecarpus houzeaui***—IRSNB R35* (HT); R36*; IRSNB 3101*; 3108*; 3130*; Lingham-Soliar (1994a).

***Plioplatecarpus marshi***—IRSNB R38* (HT); R37*; Lingham-Soliar (1994a).

# APPENDIX 3

Character-taxon data matrix used for the initial set of phylogenetic analyses that yielded phylogenetic hypotheses presented in Figure 4-23.

## Outgroup

***Clidastes propython***:

`20510 21110 10101 10050 012?? 4???? ??010 (12)(12)011 (34)1000 0?10? ??012 2??03 13000 0002? ?10?? ??200 002?1 ????? 0?010 10`

***Kourisodon puntledgensis***:

`?051? ?110? 101?1 12050 0120? 401?? 10?10 110?1 01000 00??? ?0?12 ??003 01??? ?0021 0?010 01200 002-1 -1??0 010?0 10`

## Ingroup

***Yaguarasaurus columbianus***:

`10000 11?10 00111 12000 1?0?? 1110? 0?0?1 11?01 ?1001 10?10 00??0 ??00? ????? ??0?? ????? ????? ????? ????0 100?0 ?1`

***Russellosaurus coheni***:

`00000 21010 00101 01000 00000 10200 00010 10000 03001 101?0 00000 20001 0?100 ????? ????? ????? ????? ????0 10?10 ?1`

***Tethysaurus nopcsai***:

0000? 21011 00101 01000 (03)00?0 ?120? 0001? 21101
7?001 1?110 ?0?00 20000 ???0? ?000? ??100 00??? ??0??
????0 00010 01

***Tylosaurus kansasensis***:

32310 10001 10100 11150 4130? 1?1?? ??010 210?1 2?000
?4??? 00013 1?000 ?1100 0?11? ????? ?01?? 1???? ????0
10000 ?0

***Tylosaurus proriger***:

32310 10001 10100 1?050 11100 10101 20010 21021 21000
1421? 00013 10000 11100 10?10 01110 00101 10100 00100
10000 10

***Ectenosaurus clidastoides***:

(12)0410 20010 10111 10010 1?0?? 00200 ??00? 24-?2
10000 10??0 ?0011 2?000 011?0 ?001? ???10 0?2?0 ??120
100?0 10010 1?

***Angolasaurus bocagei***:

????? 0??0? 00101 11010 0?0?0 ????? ??001 211?1 41000
??01? ???1? ??000 02100 ??0?? ??1?? ????? ????? ????0
10?10 ?2

***Selmasaurus russelli***:

????? ???0? 00100 12062 51000 3020? ??(02)0?
(12)2(01)12 70000 10??1 10??? ????? ????? 1???? ?????
????? ????? ????? ????1 ?3

***Selmasaurus johnsoni***:

10000 ?1000 00100 10060 51000 10?0? ?000? 22012 71000
10011 10010 00000 0?111 1001? ????? ????? ????? ????1
10011 ?1

***Platecarpus planifrons***:

00000 01001 00111 11020 1?100 ?0200 00001 02012 41000
10??1 10010 00000 01100 ?01?? ???00 002?0 ??1?0 ?0??0
10010 12

***Platecarpus tympaniticus***:

00100 01001 10100 1(01)131 10100 00200 00101 02(02)22
51110 11111 10010 00110 03100 10?10 00110 01210 10100
00011 10110 13

***Latoplatecarpus willistoni***:

00201 01002 20130 0123(12) 1030? 00100 00101 01022
51110 ?3111 10010 00(12)10 13111 1011? ??110 01???
????? ????2 10?10 13

***Plioplatecarpus nichollsae***:

00201 01002 20020 11232 20301 00??? ?0101 01222 51110
?3??1 10??0 0?21? ???11 10110 1?110 01310 111?? ?0?12
10?10 1?

**'*Platecarpus*' *somenensis***:

00201 01002 20130 11232 20301 ?0101 (01)0101 01022
?1110 132?2 10010 01(12)11 23111 1?1?? ??110 01???
????? ????2 10110 13

***Plioplatecarpus primaevus***:

00201 ??002 21130 12242 30411 2?0?? ??202 21332 52110

13010 11010 0?222 23111 10210 1?11(12) (12)2311 12101

00212 1??10 13

***Plioplatecarpus houzeaui***:

???01 0??02 21130 12242 3041? 0001? 21202 21332 62110

?1011 20?(01)? ?1222 13?11 ?121? ??112 32??? ?????

????2 (01)?110 13

***Plioplatecarpus marshi***:

0120? 1??02 2?020 10??? ?0?1? ???1? 21202 ??3?? 6?11?

1201? ??120 02222 ????? 11210 1?112 3??11 121?? ????2

(01)01?? 13

# CHAPTER SIX

# GENERAL CONCLUSIONS

In this thesis, a comprehensive revision to the systematics of plioplatecarpine mosasaurs was undertaken based on direct examination of nearly 500 plioplatecarpine specimens that were collected in North America and Western Europe over the last 140 years. All the nominal plioplatecarpine species known from these continents were studied. Some material that had been referred to plioplatecarpines were also examined, notably the specimens of *Platecarpus* sp., cf. *P. somenensis* from the Western Interior Basin of North America. Excellent plates provided by Antunes (1964) on *Angolasaurus bocagei* from Angola, Africa, constituted a sole source of anatomical information on the species.

This large-scale survey of plioplatecarpine specimens yielded the following major systematic findings: (1) *Platecarpus planifrons* (Cope, 1874) is valid, and is readily distinguishable from the other congener *Platecarpus tympaniticus* by its dermal skull roof (frontal and parietal) and quadrate morphology. While *P. planifrons* and *P. tympaniticus* commonly occurred in the Smoky Hill Chalk Member of west-central Kansas, they were stratigraphically separate except a possible brief overlap in the middle Santonian, *P. planifrons* occurring in the lower horizons (Konishi and Caldwell, 2007a; Konishi, 2008); (2) *Plioplatecarpus nichollsae* Cuthbertson et al., 2007, and specimens referred to as *Platecarpus* sp., cf. *P. somenensis*, both from the lower Pierre Shale Formation (lower middle Campanian) in the Western Interior Basin, are morphologically most similar to each other, and here concluded to represent the same species. Generally known from large size (lower jaw up to 1 m long), assignment of the specimens previously referred to *P. somenensis* in North America to

*Plioplatecarpus nichollsae* provides a great insight into ontogeny of plioplatecarpine mosasaurs in general, and hints at a major heterochronic event in the lower middle Campanian in this lineage since no stratigraphically older species of plioplatecarpines exceeded 0.7 m in their maximum mandible length; (3) recognition of *Latoplatecarpus willistoni*, gen. et sp. nov. from lower middle Campanian strata in the Western Interior Basin, and subsequent global phylogenetic analysis of plioplatecarpine mosasaurs indicate high taxonomic diversity of the group, comprising as many as 11 species within seven genera found both inside and outside North America. Characterization of *L. willistoni* and comparisons with other closely-related members indicate that *Plioplatecarpus nichollsae* best be considered as pertaining to this new genus, which was also independently supported by the phylogenetic, biostratigraphic, and biogeographic points of view. By recognizing two species of *Latoplatecarpus*, the genus *Plioplatecarpus* consistently becomes a monophyletic group.

Several novel anatomical features were also recognized among plioplatecarpines. In particular, the quadrate of *Platecarpus*, *Latoplatecarpus*, and by inference *Plioplatecarpus* articulated with the squamosal and supratemporal along the distomedial border of its elongate suprastapedial process, rather than at the broadly convex cephalic condyle proximal to the process (cf. Fernandez and Martin, 2009). This configuration of suspensorial articulation necessitates the quadrate shaft to rotate forward, so as to maintain the horizontal orientation of the supratemporal bar, formed by the squamosal and postorbitofrontal. As there is very little space left between the suprastapedial process of the quadrate and the supratemporal process under the proposed orientation of the quadrate, it seems highly improbable that the quadrate could swing forward to facilitate any streptostylic movement (cf. Fernandez and Martin, 2009). The rather tight, ball-and-socket mode of quadrate-suspensorium articulation is also in accordance with the immobile nature of the quadrate in the skull of these mosasaurs, particularly those with a long suprastapedial process.

Recognizing generally large-sized plioplatecarpine specimens thus far commonly referred to as *Platecarpus somenensis* from North America as large individuals of *Latoplatecarpus nichollsae* has provided some new insights into ontogenetic changes in certain anatomical features of plioplatecarpine taxa. In *L. nichollsae*, for instance, not only the number of the marginal dentition remained constant, the overall proportion of the teeth and jaws underwent little or no change according to the individual ontogeny. This is in some stark contrast with *Tylosaurus proriger*, where marginal teeth became increasingly conical and more tightly spaced along the length of the jaw ramus as an individual animal grew (Konishi and Caldwell, 2007b). Although the largest mandible of *L. nichollsae* reached 1 m in length, such ontogeny-related changes in their tooth morphology were apparently absent when compared to the specimens half as large.

Konishi and Caldwell (2007b) hypothesized that the change in the tooth morphology in *Tylosaurus proriger* reflected changes in their dietary habits, which is a known phenomenon in some extant carnivorous monitor lizards such as *Varanus niloticus* (Martins, 1942; Lenz, 2004). The apparent lack of morphological change in the marginal dentition during ontogeny of *L. nichollsae* may reflect more limited dietary habits in plioplatecarpines in general when compared to the generalist mosasaurs, such as adult *Tylosaurus proriger* (Martin and Bjork, 1987), a poorly investigated aspect of plioplatecarpine biology.

From the late Turonian *Angolasaurus bocagei* from western Africa to the latest Maastrichtian *Plioplatecarpus marshi* from Western Europe, plioplatecarpine mosasaurs exhibited high taxonomic diversification in the course of their long evolutionary history, which nearly matched that of the entire group Mosasauridae (e.g., Antunes, 1964; Jagt, 2005; Polcyn and Bell, 2005; Jacobs et al., 2006). In this long evolutionary history of the group, however, all the known plioplatecarpines except *Ectenosaurus clidastoides* retained the minimum marginal tooth count known to mosasaurs, ca. 12 maxillary and 12 dentary teeth. With the strong tendency toward retention of homodonty and slender jaws (e.g., Russell, 1967), such high evolutionary conservatism in particular relationship to their feeding apparatus only seems to underscore the magnitude of ecological and evolutionary success that this basic anatomical bauplan brought to these mosasaurs, the plioplatecarpines.

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