Phylogenetic and Palaeobiogeographical Analysis of Tylosaurinae (Squamata: Mosasauroidea)

by

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ABSTRACT

Mosasaurs were a successful and diverse group of marine lizard that existed during the Cretaceous Period, spanning a period of geologic time from the Turonian to Maastrichtian. Their fossils are found around the world, although most records are known from the Northern Hemisphere. The Southern Hemisphere record of mosasaurs is poor and incomplete. The mosasaur clade/subfamily Tylosaurinae is characterized by an elongated rostrum, which does not bear teeth. While the genus *Tylosaurus* is known from hundreds of specimens collected from the Niobrara Formation in Kansas, and now from dozens of specimens from other localities around North America, the alpha taxonomy of the genus has remained confused and poorly diagnosed. This means that very little was understood about the classification and phylogenetic relationships of North American tylosaurine mosasaurs, not to mention global tylosaurine mosasaurs. This problem originated with the historical rivalry between E.D. Cope and O.C. Marsh during the 1800s, and hopefully, in part, it is resolved in the research reported in this thesis. This thesis reports on a reassessment and re-description of specimens both assigned to the Tylosaurinae, and thus that were newly discovered during this research project. The goal was to refine and improve the understanding of the evolution and palaeogeography of the clade. The clade Tylosaurinae was proved as monophyletic, as well as one of the genus: *Tylosaurus*. The concept of ‘tylosaurine’ changed from a diverse group with three genera and eleven species, to a more limited concept of the group, consisting in two genera and seven species. The geographic and temporal distribution of the two genera, and the subfamily, where established as upper Turonian to lower Maastrichtian of the North

Atlantic Basin for the genus *Tylosaurus*, while a cosmopolitan distribution, between the middle Santonian and lower Maastrichtian was determined for *Taniwhasaurus*.

The thesis is divided in seven chapters, starting with a general introduction, followed by reassessments and re-descriptions of specific taxa, with a phylogenetic and paleobiological analysis of the Tylosaurinae, and final conclusions regarding the results of the project.

PREFACE

This thesis project was designed by me and my thesis supervisor, Dr. M. Caldwell. Chapter Two of this thesis has been published as P. Jiménez-Huidobro and M. Caldwell. "Reassessment and reassignment of the early Maastrichtian mosasaur *Hainosaurus bernardi* Dollo, 1885, to *Tylosaurus* Marsh, 1872," Journal of Vertebrate Paleontology vol. 36, issue 3, e1096275-12. I was responsible for the data collection, analysis and manuscript composition. M. Caldwell was the supervisory author and was involved with edits, concept formation, manuscript composition, and financial support.

Chapter Three has also been published, as P. Jiménez-Huidobro, T. Simões, and M. Caldwell. "Re-characterization of *Tylosaurus nepaeolicus* (Cope, 1874) and *Tylosaurus kansasensis* Everhart, 2005: Ontogeny or sympatry?" Cretaceous Research vol. 65, 68–81. I was responsible for data collection and analysis, as well as the manuscript composition. T. Simões assisted with the data collection and contributed to manuscript edits. M. Caldwell was the supervisory author and was involved with concept formation, manuscript composition, edits and financial support.

Chapter Four has not been published, although ready for submission. The co-authors include P. Jiménez-Huidobro, M. Caldwell1, I. Paparella, and T. Bullard. T. Bullard and I were responsible for the data collection. The original idea was initiated by T. Bullard. New data were collected by me, I. Paparella and M. Caldwell. I was responsible for the manuscript composition. M. Caldwell was the supervisory author and was involved with concept formation, manuscript composition, edits, and financial support.

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ANATOMICAL ABBREVIATIONS

a	angular
ac	atlas centrum
ai	atlas intercentrum
ana	atlas neural arch
ar	articular
as	astragalus
ax	axis
bs	basisphenoid
c	coronoid
cl	cervical
co	coracoid
ccd	cephalic condyle
d	dentary
dr	dorsal rim of the quadrate
ecf	ectepicondylar foramen
ect	ectepicondyle
ent	entepicondyle
f	frontal
fe	femur
fi	fibula
fmc	frontal midline crest

fps	frontoparietal suture
gc	glenoid condyle
h	humerus
ha	haemal arch
il	ilium
is	ischium
isp	infrastapedial process
j	jugal
m	maxilla
mcd	mandibular condyle
mpms	maxillopremaxillary suture
nf	nuchal fossa
oc	occipital condyle
op	olecranon process
p	parietal
pc	pectoral crest of the humerus
pgp	postglenoid process of the humerus
pm	premaxilla
po	parietal opening
pof	postorbitofrontal
pt	pterygoid
q	quadrate
r	radius

sa	surangular
sc	scapula
sn	stapedial notch
sp	splenial
spt	stapedial pit
sq	squamosal
sqa	articulation site for squamosal
sr	sclerotic ring
srp	suspensorial ramus of parietal
ssp	suprastapedial process
t	tibia
ta	tympanic ala
vaj	vertical arm of the jugal
vpj	ventroposterior process of the jugal

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, U.S.A.
ANSP	Academy of Natural Sciences of Drexler University, Philadelphia, U.S.A.
CMNZ	Canterbury Museum, Christchurch, New Zealand.
FHSM	Fort Hays Sternberg Museum, Hays, Kansas, U.S.A.
IAA	Instituto Antártico Argentino, Buenos Aires, Argentina.
IPB	Goldfuss Museum im Institut für Pala€ontologie, Bonn, Germany.
IRScNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
KU	University of Kansas, Museum of Natural History, Lawrence, Kansas, U.S.A.
MCM	Mikasa City Museum, Hokkaido, Japan.
MDM	Canadian Fossil Discovery Center, Morden, Manitoba, Canada.
MCZ	Museum of Comparative Zoology, Harvard University, Massachusetts, U.S.A.
MNHN	Muséum Nationald'Histoire Naturelle, Paris, France.
MT	Miami Museum, Municipality of Thompson, Miami, Manitoba, Canada.
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.
NHMUK	Natural History Museum, London, U.K.
RMM	McWane Sciences Center, Birmingham, Alabama, U.S.A.
RSM	Royal Saskatchewan Museum, *T.rex* Discovery Centre, Eastend, Saskatchewan, Canada.
SAMK	Iziko South African Museum, Cape Town, South Africa

SDSM	South Dakota School of Mines, Rapid City, South Dakota, U.S.A.
YPM	Yale University Peabody Museum, New Haven, Connecticut, U.S.A.

CHAPTER ONE

GENERAL INTRODUCTION

Mosasauroidea (sensu Bell, 1997) is a diverse group of squamates that modified their pelvic girdle and limbs and radiated into aquatic environments around the world during the Late Cretaceous Period (Caldwell, 2012), including North America (Harlan, 1834; Cope, 1869, 1874, 1875; Marsh, 1872a; Williston, 1898, 1910; Wiman, 1920; Camp, 1942; Russell, 1967; Nicholls, 1988; Nicholls and Russell, 1990; Holmes and Sues, 2000; Gallagher, 2005; Konishi and Caldwell, 2011), South America (Caldwell and Bell, 1995; Carvalho and Azevedo, 1998; Paramó-Fonseca, 2011; Fernández and Gasparini, 2012; Jiménez-Huidobro et al., 2015), Europe (Lingham-Soliar, 1992, 1994, 1996; Lindgren and Siverson, 2002; Lindgren, 2004; Lindgren, 2005; Jagt, 2005; Jagt et al., 2005), Asia (Bardet et al., 2000; Mustafa and Zalmout, 2001; Christiansen and Bonde, 2002; Caldwell et al., 2008; Konishi et al., 2012; Sato et al., 2012; Konishi et al., 2015), Africa (Broom, 1912; Zdansky, 1935; Arambourg, 1952; Antunes, 1964; Soliar, 1988; Lingham-Soliar, 1991; 1994b; Bardet et al., 2004; Bardet et al., 2005; Schulp et al., 2006; Kear et al., 2008; Schulp et al., 2008; Schulp et al., 2009; Schulp et al., 2009b; Polcyn et al., 2010; Leblanc et al., 2012; Schulp et al., 2013; Bardet et al., 2015), Australia (Kear, 2003; Lundelius and Warne, 1960), New Zealand (Welles and Gregg, 1971; Wiffen, 1980; 1990; Caldwell et al., 2005; Wilson et al., 2005; Consoli and Stilwell, 2009), and Antarctica (Martin, 2002, 2006; Novas et al., 2002; Fernández and Gasparini, 2012). The known record of mosasaurs spans a temporal range from the late Cenomanian, beginning approximately 95 million years ago (Mya), to the late Maastrichtian, at 66 Mya (Russell, 1967; Bell, 1997; Grigoriev et al., 2009; Caldwell, 2012), becoming extinct during the Cretaceous/Palaeogene (K/Pg) mass extinction.

Mosasaurs were no doubt crown predators in the Late Cretaceous oceans. Their large to gigantic body sizes, tooth morphology and stomach contents, are ample evidence upon which to draw such conclusions. Broadly speaking, the large bodied mosasaur diet included ammonites, turtles, bony fishes, sharks, plesiosaurs and even smaller mosasaurs (Martin and Fox, 2007; Konishi et al., 2014). There is no data for smaller bodied mosasauroids, though they likely ate almost anything they encountered that could be swallowed whole, or rendered into smaller pieces for swallowing.

Mosasauroids were highly adapted for life in aquatic environments, demonstrating a number of morphological features indicative of an obligatory aquatic habit (e.g., loss of sacrum via the modification of the ilium, the development of flipper-like limbs, etc.). Recent research indicates viviparity as a reproductive strategy of fully aquatic mosasaurs (Field et al., 2015), an idea previously suggested by Caldwell and Lee (2001) and Houssaye and Bardet (2013). It has also been suggested that mosasaurs were likely endothermic lizards (Bernard et al., 2010). This hypothesis was further supported by the research of Harrell et al. (2016), who suggested, based on isotopic studies, that mosasaurs were indeed endothermic; this trait would allow the transition from ambush predation over short distance, to pursuit predation, with rapid changes of direction over longer distances, as well as to colonize colder waters (Martin, 2002; Polcyn et al., 2014).

In short, mosasaurs were highly evolved squamate reptiles, perhaps one of the most highly evolved and specialized group of lizards in the history of the clade. They radiated rapidly into the oceans of the world, achieving gigantic body sizes and highly specialized body size in a very short period of time during the Late Cretaceous (~15 million years; Caldwell, 2012). They likely gave live birth to their young, and were possibly even "endothermic", moving well beyond mass homeothermy.

HISTORY OF THE FIRST MOSASAUR DISCOVERY

The first reported discovery of what would become known as a "mosasaur" was of at least two partial skulls collected in 1764-1766, from the limestone quarries of Mount Saint Pierre, near the Meuse River, Maastricht, Holland. Speculation on the identity of the fossil materials created a substantial myth about the "grande animal de Maastricht" (Cuvier, 1808), such that during the French occupation of Maastricht in 1794, the fossil was confiscated by Napoleon's army and transferred to Paris (Caldwell, 2012). The specimen was misidentified as a fish, a crocodile, and even a whale, until Camper (1790) identified the specimen as a lizard. Cuvier (1808) confirmed Campers conclusion in his lengthy description of the specimen, although it was not named until 1822, when Conybeare proposed the generic name *Mosasaurus*, after the Meuse River (=mosa in Latin) where it was found, near to Maastricht. Seven years later, Mantell (1829) provided a specific epithet, as *Mosasaurus hoffmannii*, after Dr. Hoffmann. Thus birth of the term "mosasaur" is rooted in the name of the river running through Maastricht even though the Dutch and the French never created a name for the animal or the group, leaving it instead to the English in a patchwork quilt kind of creation.

PURPOSE OF THIS STUDY: REVISION OF THE CLADE TYLOSAURINAE

The modern conception of Mosasauroidea, sensu Caldwell (2012), essentially treats mosasauroids as a synyonym of Aigialosauridae plus Mosasauridae, as the latter is essentially a polyphyletic taxon. Several clades retain their distinction within Mosasauroidea as considered by Caldwell (2012), including the well-recognized Mosasaurinae Gervais, 1852, Halisaurinae Bardet et al., 2005, Plioplatecarpinae Dollo, 1884, Tylosaurinae Williston, 1897, Tethysaurinae Makádi et al., 2012, and Yaguarasaurinae Palci et al., 2013.

The purpose of this study is to revise and reassess the palaeontology and systematics of all of the taxa and as many specimens as possible, that have been attributed to the clade Tylosaurinae since Cope's (1869) description of *Tylosaurus proriger*. The genus *Tylosaurus* had a complicated history during the nineteenth century. When Cope (1869) described the holotype of *T. proriger*, he assigned the specimen to the genus *Macrosaurus* Owen, 1849, as *Macrosaurus proriger.* In 1870, he re-assigned the specimen to *Leiodon*; however, a fish preoccupied the genus, obligating him to rename the genus to *Liodon.* Marsh (1872), using a more complete specimen, renamed the genus to *Rhinosaurus*, which was also preoccupied by another animal. Cope (1872) suggested that *Rhinosaurus* and *Leiodon* were the same taxon, and suggested a new name, *Rhamphosaurus*. Later, Marsh proved that the name suggested by Cope was preoccupied as well, and proposed the genus *Tylosaurus* (Marsh, 1872), although Cope never accepted this name. It remained for Leidy (1873) to formally place *Macrosaurus proriger* Cope 1869 into *Tylosaurus*.

The type species, *Tylosaurus proriger* was described by Cope (1869), based on a partial snout and thirteen associated vertebrae (Fig. 1.1A), from the lower Campanian of the Upper Smoky Hill Chalk, Niobrara Group, found near Monument Rocks in Gove County, Kansas, U.S.A. The current temporal range of the species is from the upper

Santonian to the lower Campanian of the Mooreville Chalk of Alabama (Russell and Applegate, 1970; Kiernan, 2002), the Taylor Group of Texas (Bell, 1993), and the Pierre Shale of Kansas, Nebraska and South Dakota (Russell, 1967). The type species *T. proriger* is the best known tylosaurine mosasaur, in part due to the great number of specimens preserved from the Niobrara Chalk (in the thousands of partial skeletons, and hundreds of nearly complete to perfectly complete skeletons [pers. obs.]).

Tylosaurus nepaeolicus (junior synonym =*T. kansasensis*) was described by Cope (1874), based on a partial skull and a single vertebra (Fig. 1.1B; 1.2A) recovered from the upper Coniacian of the Lower Smoky Hill Chalk of Kansas, along the banks of the Solomon River (Russell, 1967; Sheldon, 1996). The current range of the species is from the upper Coniacian to the lower Santonian of the Lower Smoky Hill of Kansas (Russell, 1967) and the Boquillas Formation of Texas (Bell et al., 2012). When Russell (1967) re-diagnosed *T. nepaeolicus*, he noted that it was smaller than *T. proriger*. No more than 30 specimens are known in different collections, although none of them is complete.

Tylosaurus pembinensis (Nicholls, 1988), was described from the lower-middle Campanian of the Pierre Shale, based on a poorly preserved skull and postcranial material (Fig. 1.2B), found in the Miami-Morden area, southern Manitoba, Canada. The specimen was first described as *Hainosaurus pembinensis*, however, it was later synonymized to *Tylosaurus pembinensis* by Bullard and Caldwell (2010). There are twelve referred specimens.

Tylosaurus capensis Broom, 1912, considered here to be an indeterminate species of *Taniwhasaurus*, was described based on a partial frontal, a fragment of jaw and an isolated vertebra (Fig. 1.3A) from the Santonian of Pondoland, South Africa.

Tylosaurus gaudryi (Thevenin, 1896), was described based on an incomplete anterior portion of the skull (Fig. 1.3B), from the upper Santonian to lower Campanian of Eclusier Vaux near Péronne, France. The only specimen was originally assigned to *Mosasaurus gaudryi*, later re-assigned to *Hainosaurus gaudryi* (Bardet, 1990), and finally synonymized to *Tylosaurus gaudryi* (Lindgren, 2005).

Tylosaurus ivoensis (Persson, 1963), was described based on a marginal tooth crown from the lower Campanian of the Kristianstad Basin, Southern Sweden. It was first described as *Mosasaurus ivoensis*, and then moved to *Tylosaurus ivoensis* by Lindgren and Siverson, 2002, based on dental characters. Referred material consists of isolated teeth and 14 vertebrae from different localities of the Kristianstad Basin. It is considered here as a nomen dubium.

Tylosaurus iembeensis Antunes, 1964, from the upper Turonian of Iembe of Angola, was described based on a badly preserved partial skull. The specimen was lost in a fire in Lisbon, Portugal (Jacobs et al., 2006), and no more specimens have been described or figured, although there is a new but undescribed specimen mentioned by Jacobs et al. (2006) and Mateus et al. (2012).

Tylosaurus bernardi (Dollo, 1885) was described as *Hainosaurus bernardi* based on a nearly complete but badly preserved skull and skeleton (Fig. 1.4A) from the early Maastrichtian of the Ciply Phosphatic Chalks, Mons Basin, Belgium. A referred specimen consists of a badly preserved skull (Lingham-Soliar, 1992), and an isolated parietal from Belgium (Mulder and Mai, 1999).

Tylosaurus neumilleri (Martin, 2007), was described as *Hainosaurus neumilleri* from the upper Campanian of the Pierre Shale of Gregory County, South Dakota. The only specimen consists of a block with the parietal, a coronoid and an angular, an isolated quadrate and a fragment of premaxilla attached to both maxillae (Fig. 1.4B). This material is not diagnosable as a new species, and in this thesis is referred to *Tylosaurus* sp.

Taniwhasaurus oweni Hector, 1874, was described based on a holotype, and later on a lectotype that includes both left and right dentaries, a partial frontal, an isolated vertebra and a paddle (Fig. 1.5A). The specimen comes from the lower Haumurian (lower-middle Campanian) at Haumuri Bluff, South Island, New Zealand. A second taxon from the same locality was originally assigned to *Liodon haumuriensis* Hector, 1874, later re-assigned to *Tylosaurus haumuriensis* by Welles and Gregg (1971), and finally synonymized to *Taniwhasaurus oweni* by Caldwell et al. (2005). There are two paralectotypes and seven referred specimens (Welles and Gregg, 1971).

Taniwhasaurus antarcticus (Novas et al., 2002), was described based on a partial skull and vertebral elements (Fig. 1.5B) from the upper Campanian to lower Maastrichtian of the Santa Marta Formation, James Ross Island, Antarctica. The specimen was originally named *Lakumasaurus antarcticus*, and synonymized to *Taniwhasaurus antarcticus* by Martin and Fernández, 2007. An isolated vertebrae and a tooth crown from the Snow Hill Formation of Vega Island has also been referred to *Ta. antarcticus* (Fernández and Gasparini, 2012).

Taniwhasaurus mikasaensis Caldwell et al., 2008, was described based on a partial skull (Fig. 1.5C) from the upper Santonian to lower Campanian, near Mikasa city, Hokkaido Province, Japan. The specimen was originally assigned to a theropod dinosaur.

Three more specimens have been referred to *Ta. mikasaensis*; in this study, this material is also considered to be *Taniwhasaurus* indeterminate.

While the genus *Tylosaurus*, and especially the species *T. proriger*, are known from many specimens collected from the Niobrara Formation in Kansas, and specimens from other localities around North America, the alpha taxonomy of the genus is still confused and poorly diagnosed. This means that very little is currently understood about the classification and phylogenetic relationships of North American tylosaurine mosasaurs, not to mention the lack of understanding relating to tylosaurines on a global scale.

Therefore, the principle goal of this dissertation is a phylogenetic and palaeobiological analysis of the group, involving a re-assessment of the validity of taxa from the subfamily Tylosaurinae at the alpha taxonomic level, and from there, establishing the phylogenetic relationships between the different valid and well understood species within Tylosaurinae, in order to understand their temporal and geographic patterns of distribution.

ORGANIZATION OF CHAPTERS

Chapter Two

A reassessment of the genus *Hainosaurus* and its type species *Hainosaurus bernardi* from Belgium is presented. The principal problem regarding the diagnosis for *Hainosaurus bernardi* is that its characters are either not preserved or do not differentiate it from *Tylosaurus*. The aim of this chapter is to assess if *Hainosaurus* can be diagnosed independently from *Tylosaurus*. A reassignment of the taxon is suggested.

Chapter Three

This chapter provides an anatomical comparison between the North American *Tylosaurus nepaeolicus* and *Tylosaurus kansasensis* from the Western Interior Seaway; both species share geographic and temporal ranges. An emended diagnosis is provided for *T. nepaeolicus* considering the referred specimens. A discussion about the validity of the species *T. kansasensis* is presented, with comments on ontogenetically variable characters, and a possible synonym of the two taxa.

Chapter Four

A potential new species from the Bearpaw Formation of Saskatchewan is presented herein. This chapter provides anatomical comparisons between a well preserved and nearly complete specimen from Saskatchewan and the type species *Tylosaurus proriger* and other species of the group. A formal diagnosis is provided, and the relationship of the potentially new species with other known tylosaurines is discussed.

Chapter Five

In this chapter a reassessment of *Tylosaurus neumilleri* from the Pierre Shale of South Dakota is presented. Preliminary opinions are presented regarding the validity of the taxon. Comparisons of the species with other tylosaurines are provided. Discussion about affinities regarding this species and the potentially new species suggested in Chapter Four is provided.

Chapter Six

This chapter presents a phylogenetic analysis, using reassessed taxa from Chapters Two, Three, Four and Five, and a modified version of a previously existing data matrix. Emended diagnoses of all tylosaurine terminal taxa are provided, as well as generic diagnoses, based on anatomical features personally observed for all taxa from numerous specimens. In this chapter a discussion is presented regarding the geographic and temporal patterns of distribution of the Tylosaurinae.

Chapter Seven

This chapter presents a final discussion and conclusion of the thesis, including the results from all chapters. A new taxonomic classification of the Tylosaurinae and discussion of the new concept of ‘tylosaurine mosasaur’ are provided.

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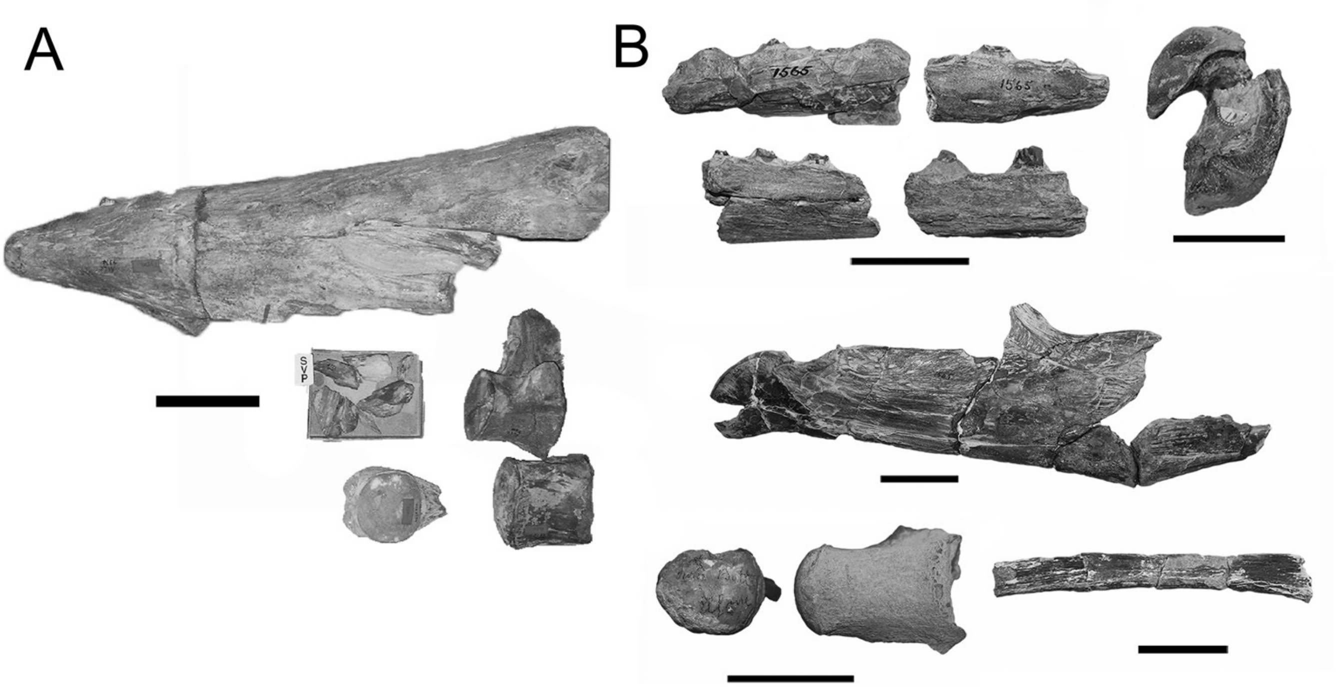

FIGURE 1.1: Holotypes of tylosaurines. **A**, holotype of *Tylosaurus proriger* MCZ 4374; scale bar equal to 10 cm. Photo courtesy of T. Ikejiri. **B**, holotype of *Tylosaurus nepaeolicus* AMNH 1565; all scale bars equal to 5 cm.

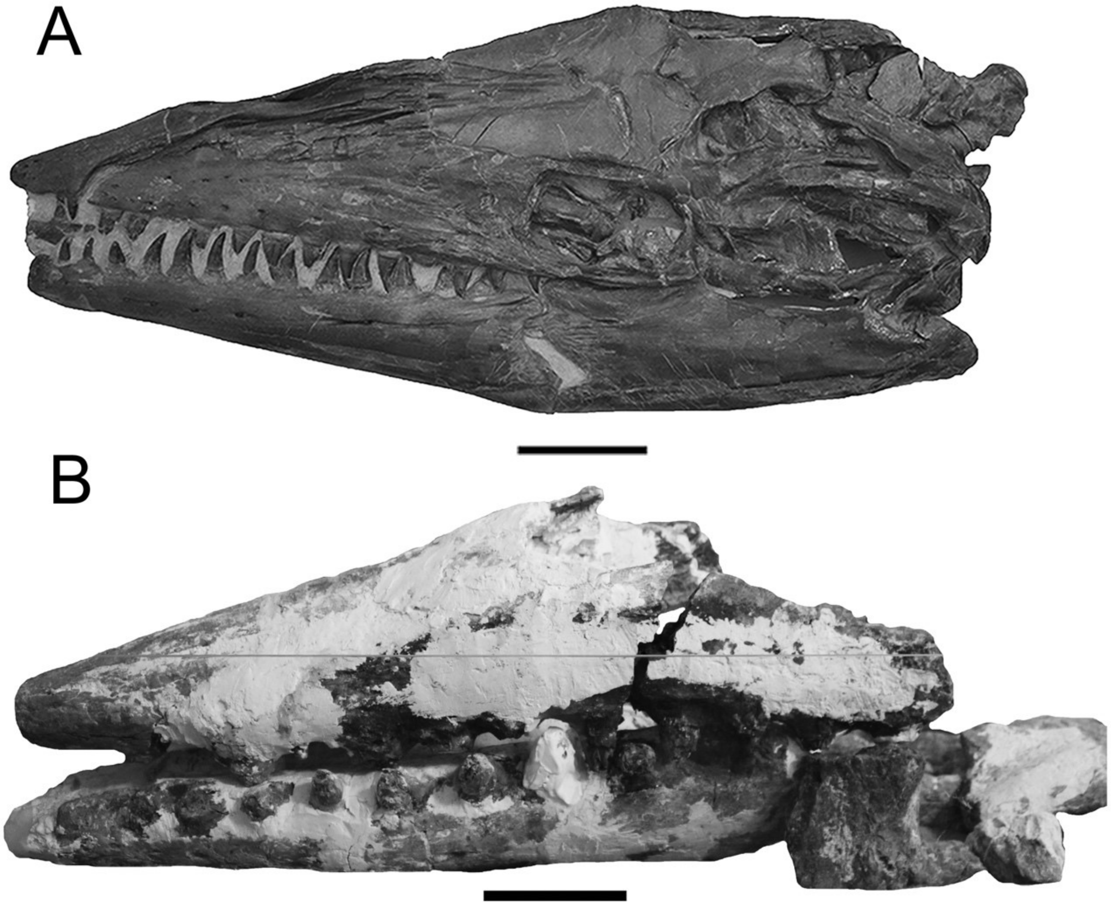

FIGURE 1.2: Holotypes of tylosaurines. **A**, holotype of *Tylosaurus kansasensis* FHSM VP-2295; scale bar equal to 10 cm. **B**, holotype of *Tylosaurus pembinensis* MT 2; scale bar equal to 10 cm.

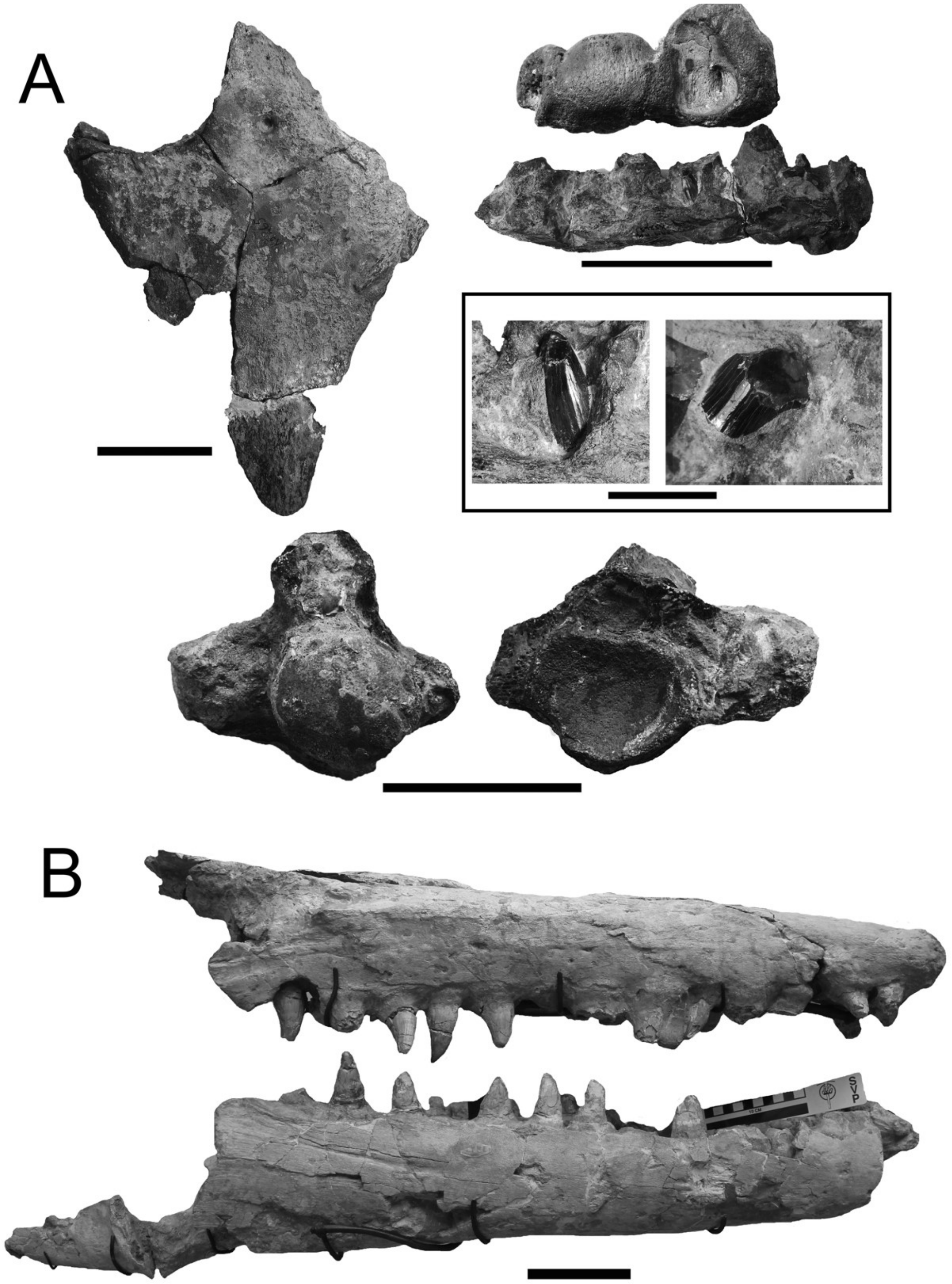

FIGURE 1.3: Holotypes of tylosaurines. **A**, holotype of *Tylosaurus capensis* SAM-PK-5265; scale bar of frontal equal to 10 cm, scale bars of jaw elements and vertebra equal to 5 cm, scale bar of teeth equal to 1 cm. **B**, holotype of *Tylosaurus gaudryi* MNHN 1896-15; scale bar equal to 10 cm.

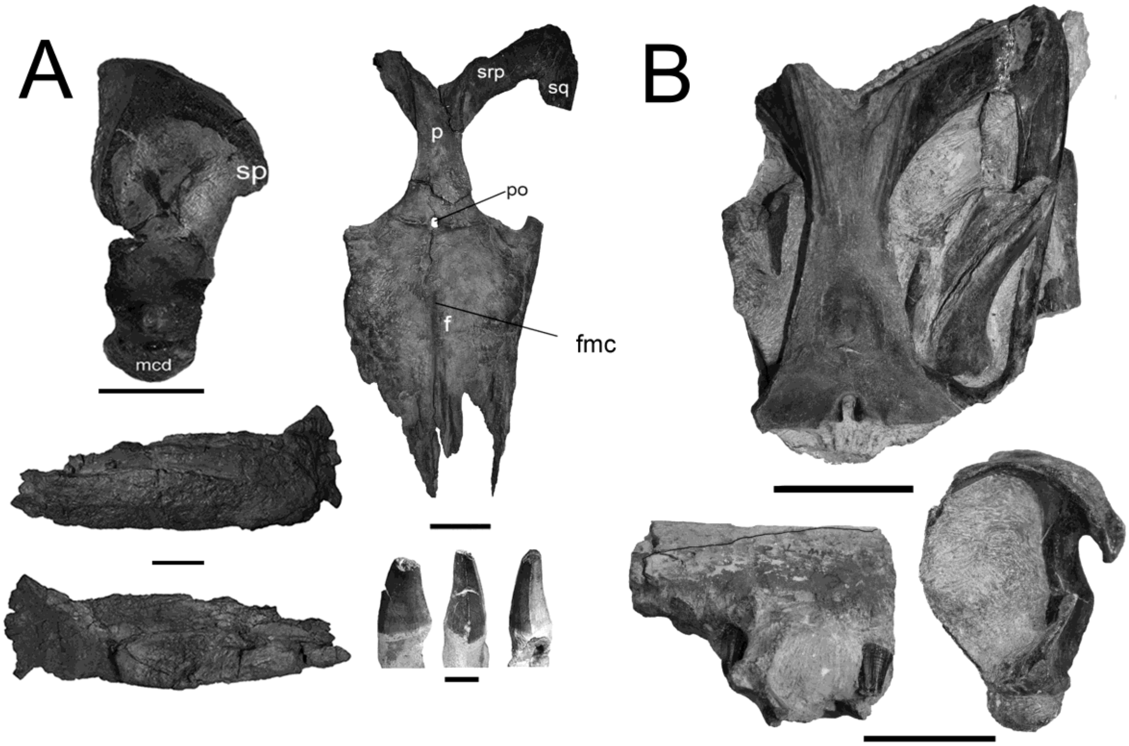

FIGURE 1.4: Holotypes of tylosaurines. **A**, holotype of *Hainosasurus bernardi* IRScNB R23; scale bars equal to 10 cm, except the quadrate scale bar (5 cm) and teeth scale bar (1 cm). **B**, Holotype of *Hainosaurus neumilleri* SDSM 75705; scale bars equal to 10 cm.

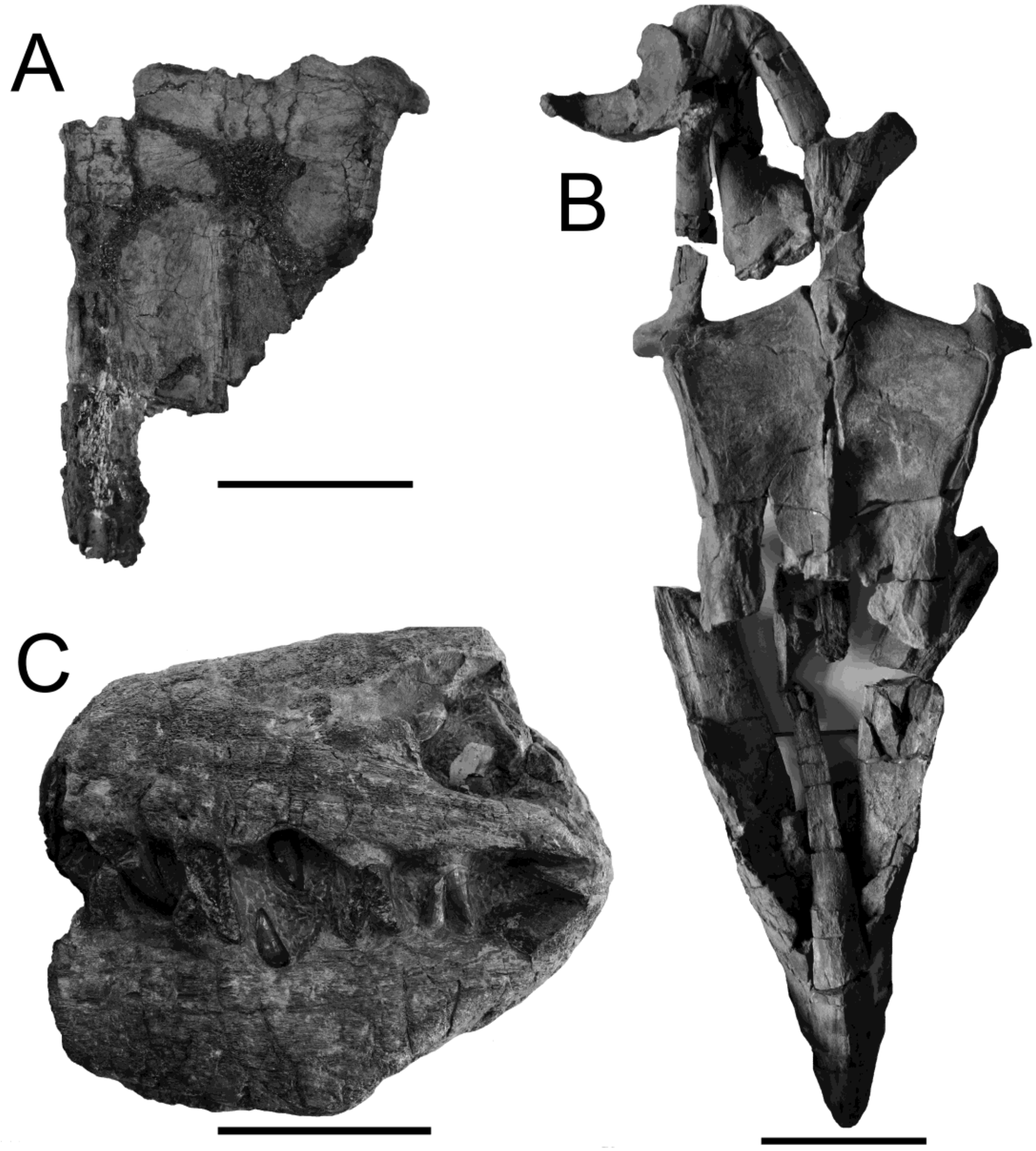

FIGURE 1.5: Holotypes of tylosaurines. **A**, skull element of *Taniwhasaurus oweni* lectotype NMNZ R 1536; scale bar equal to 10 cm. **B**, skull of the holotype of *Taniwhasaurus antarcticus* IAA 2000-JR-FSM-1; scale bar equal to 10 cm. **C**, holotype of *Taniwhasaurus mikasaensis* MCM.M0009; scale bar equal to 10 cm.

CHAPTER TWO

REASSESSMENT AND REASSIGNMENT OF THE EARLY MAASTRICHTIAN MOSASAUR *HAINOSAURUS BERNARDI* DOLLO, 1885 TO *TYLOSAURUS* MARSH, 1872

ABSTRACT

Redescription of *Hainosaurus bernardi* Dollo, 1885a, from the early Maastrichtian of the Ciply Phosphatic Chalk of Belgium, results in a reassignment of the taxon to the genus *Tylosaurus* Marsh, 1872, because the genus *Hainosaurus* cannot be diagnosed independent of *Tylosaurus*. The diagnosis of *Hainosaurus bernardi* by Dollo, 1885, is reviewed, and the two incomplete and poorly preserved specimens assigned to the taxon are compared with recognized species of *Tylosaurus. Hainosaurus* was originally diagnosed from characters of the jugal, quadrate, maxilla, premaxilla, frontal, parietal, and teeth. Here, I show that most of the characters of these elements are shared with the genus *Tylosaurus*, and that those that are not shared, but that are purported key diagnostic characters for *Hainosaurus*, are simply not preserved, or are too poorly preserved to support a differential diagnosis of *H. bernardi* at the generic level. The available data support the conclusion that *Hainosaurus* is a junior synonym of *Tylosaurus* because no anatomical features distinguish the former from the latter. The genus *Tylosaurus* occupied a wider geographic and temporal distribution than has been previously suggested, inhabiting the North Atlantic Circle Basin from the Turonian to the Maastrichtian. There are species-level features that support *T. bernardi* as distinct from other described species of *Tylosaurus*.

INTRODUCTION

Mosasaurs were a diverse and long-lived group of lizards that evolved paddle-like limbs and radiated into aquatic environments around the globe during the Late Cretaceous (Russell, 1967; Caldwell, 2012). They colonized a wide range of marine habitats of varying water depths, including shorelines, estuaries, shallow epicontinental seas, and, most likely, deep water open pelagic zones. Most recently, it has been recognized that they also invaded freshwater environments as more than occasional migrants (Holmes et al., 1999), also residents of rivers and streams (Makádi et al., 2012). In less than 10 million years, mosasaurs underwent a major adaptative radiation, evolving from terrestrial and/or semiaquatic ancestral forms to obligatorily aquatic, giant-bodied sea-going lizards with a global distribution.

Within this wide variety of mosasaurs, the clade Tylosaurinae, a marine group of large-bodied to gigantic mosasaurs, is principally distinguished by the possession of an elongated and cylindrical anterior portion of the premaxilla (the rostrum) that does not bear teeth (Russell, 1967; Bell, 1997). Specimens assigned to this group of mosasaurs are known from North America (Cope, 1869, 1869a, 1874; Everhart, 2005), Europe (Dollo, 1885, 1885a; Thévenin, 1896; Bardet, 1990; Lindgren, 2005; Hornung and Reich, 2014), New Zealand (Hector, 1874; Caldwell et al., 2005), Japan (Caldwell et al., 2008), South Africa (Broom, 1912), South America (Jiménez-Huidobro et al., 2015), and Antarctica (Novas et al., 2002; Martin and Fernández, 2007).

The first tylosaurines were recognized from fossils found in the Western Interior Seaway deposits of Kansas in the 19th century. The type species, *Tylosaurus proriger*

(Cope, 1869a) from the mid-Santonian to early Campanian of North America, is known from thousands of partial to complete specimens. Two other species of tylosaurine are also known from slightly older deposits of the Coniacian-Santonian portions of the Kansas Chalk: *T. nepaeolicus* (Cope, 1874), and *T. kansasensis* Everhart, 2005. The youngest known North American species is *T. pembinensis* (Nicholls, 1988) (middle Campanian, North America). Non-North American *Tylosaurus* includes *T. capensis* Broom, 1912 (Santonian, South Africa), and *T. gaudryi* (Thévenin, 1896) (Santonian, Europe).

The global fauna of non-*Tylosaurus* mosasaurs is known from a much smaller sample than has been recovered from Kansas, and these more global mosasaurs are also far less well preserved and complete. They are currently recognized from two genera: *Taniwhasaurus* and *Hainosaurus*. *Taniwhasaurus oweni* Hector, 1874, was described from a number of specimens (Caldwell et al., 2005) from New Zealand (lower Campanian). Two additional species, *Taniwhasaurus mikasaensis* Caldwell et al., 2008, from the Santonian of Japan and *Taniwhasaurus antarcticus* Novas et al., 2002, from the Campanian of Antarctica, have been described more recently. The second genus, the giant Maastrichtian tylosaurine, *Hainosaurus bernardi* Dollo, 1885, the subject of this study, was described from a single (holotype) specimen from the early Maastrichtian, Ciply Phosphatic Chalks, Mons Basin, Belgium (Robaszynski and Martin, 1988). Unfortunately, *H. bernardi* remains poorly understood because it is known from only two specimens, neither of which is well preserved, nor complete (Fig. 2.1A–C).

Hainosaurus bernardi was diagnosed by Dollo (1885), and later by Lingham-Soliar (1992), on the basis of cranial characters that include such features as the position of the pineal foramen, the shape of the suture between the maxilla and premaxilla, and features of quadrate, jugal, postorbitofrontal, and teeth, as well as vertebral count. The principal problem regarding the diagnosis for *Hainosaurus bernardi* (Dollo, 1885; Lingham-Soliar, 1992) is that these features are either not preserved or do not differentiate *Hainosaurus* from *Tylosaurus* (summarized in Table 1). This problem was first raised by Williston (1898), and seconded by Russell (1967), both of whom concluded that if valid, the only character diagnosing *Hainosaurus* from *Tylosaurus* was the substantially greater number of pygal vertebrae in *Hainosaurus*.

In light of this empirical problem (features not preserved, or not present), two species previously assigned to *Hainosaurus* have recently undergone rediagnosis and reassignment to *Tylosaurus*. Lindgren (2005) described a collection of teeth from Denmark that he assigned to *Hainosaurus*, but did not attribute them to a species. However, in revisiting the concept of *Hainosaurus* as delineated by Dollo (1885), and followed by Lingham-Soliar (1992), Lindgren (2005) found that the diagnosis of *Hainosaurus* was inclusive and reassigned *Hainosaurus gaudryi* (Thévenin, 1896) (Santonian, Vaux-Eclusier, Picardie, northern France), to *Tylosaurus gaudryi*. Another species, *Hainosaurus pembinensis* Nicholls, 1988, from the middle Campanian, Pembina Member, Pierre Shale, Manitoba, was reassigned to *Tylosaurus pembinensis* by Bullard and Caldwell (2010) in their restudy of the original specimens. Two other nominal species have been assigned to *Hainosaurus*, the status of which remains uncertain in light of the problematic generic diagnosis plaguing *H. bernardi*: *H. lonzeensis* (Dollo, 1904) (Coniacian-Santonian, Europe), and *H. neumilleri* Martin, 2007 (Campanian, North America).

It is therefore quite clear that *Hainosaurus* is a problematic taxon at the generic level and is hard to distinguish from *Tylosaurus*. Whereas reassigning various species to the appropriate genus is essential, the core problem remains the diagnosis of *Hainosaurus* as distinct from *Tylosaurus*. I thus present here the results of my investigation of the type and referred specimens of *Hainosaurus bernardi*, and present my conclusion that *Hainosaurus* (Dollo, 1885) is a junior synonym of *Tylosaurus* (Marsh, 1872) because the putatively diagnostic characters for *Hainosaurus* are shared with *Tylosaurus*.

MATERIALS AND METHODS

In order to attempt a new diagnosis and description of *Hainosaurus bernardi*, all known specimens of *H. bernardi*, and numerous specimens of the species assigned to *Tylosaurus*, were personally examined. Detailed photographs were taken using Canon EOS t2i camera and edited in Photoshop CS6 for Mac. Measurements in mm were taken using calipers and tape measures. Drawings were made using camera lucida attachments where possible, with finished drawings completed in Photoshop using drawing tablet software and hardware. To run the cladistics analysis, I used Mesquite 3.03 for Mac to edit the matrix; the cladograms were recovered using TNT 1.1 (Goloboff et al., 2008) and the official guide by Simões (2012). The tree was analyzed using Mesquite 3.03 and edited using Photoshop CS6 for Mac. Assessment of the phylogenetic relationships of tylosaurine mosasaurs was conducted using the data matrix of Palci et al. (2013), which itself was derived in sequence from Le Blanc et al. (2012), Caldwell and Palci (2007), Polcyn and Bell (2005), and Bell (1997). The matrix was modified by the inclusion of additional terminal taxa of tylosaurines: *Tylosaurus bernardi*, *Tylosaurus kansasensis*, *Taniwhasaurus oweni*, and *Taniwhasaurus antarcticus*. The species *Mosasaurus maximus* was replaced, because it has been synonymized with *Mosasaurus hoffmannii* (Mulder, 1999), and the extant monitor lizard *Varanus* was used as the outgroup for rooting and establishing character polarity. The scoring of character 32 was changed by reducing six character states down to only four; this character refers to the maxillary tooth number, previously scored as 20–24[0]; 17–19[1]; 15 or 16 [2]; 14[3]; 13[4]; 12[5]. Due to observed intraspecific variation in maxillary tooth counts in the type species *Tylosaurus proriger*, which possesses 12 or 13 teeth in the maxilla (Russell, 1967), I rescored this character as follow: 20–24[0]; 17–19[1]; 15[2] or 16 [2]; 12–14[3]. The final matrix includes 42 terminal taxa and 131 characters (see Appendix 1). Traditional search (heuristic search algorithm) was used in TNT 1.1, with 1000 replicates.

SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA Oppel, 1811

Family MOSASAURIDAE Gervais, 1852

Subfamily TYLOSAURINAE Williston, 1897

Genus TYLOSAURUS Marsh, 1872

Type Species—*Tylosaurus proriger* (Cope, 1869a) from the Niobrara Formation, western Kansas, U.S.A.

Range—Turonian to lower Maastrichtian.

Generic Diagnosis—(1) twelve or thirteen maxillary teeth; (2) prefrontal does not contribute to external nares (only maxilla, premaxilla, and frontal); (3) frontal overlaps supraorbital portion of prefrontal; (4) frontal does not contribute to orbit; (5) ventroposterior process on jugal present; (6) ten or eleven pterygoid teeth; (7) thirteen teeth on dentary; (8) broad projection of dentary anterior to first dentary tooth; (9) vertebral formula: 29 or 30 presacral vertebrae, six or seven pygals, 33 or 34 caudal chevron-bearing and 56–58 terminal caudals; (10) scapula smaller than coracoid, convex superior border of scapula; (11) radial process absent in humerus; (12) elongated radius, same length of metacarpals I and II; (13) ischium well expanded medially at symphysis; distal end of femur more expanded than proximal; (14) astragalus circular in shape; (15) phalangeal formula of pes 5-8-8-8- (Russell, 1967).

TYLOSAURUS BERNARDI (Dollo, 1885)

Holotype—IRScNB R23 (former IRScNB 1564?). Skull moderately complete; pectoral girdle fairly complete; dissociated limb bones and incomplete vertebral series, not well preserved.

Emended Diagnosis—(1) Vertical ramus of the jugal thick; (2) vertical ramus of the jugal presents a visible suture to articulate with the postorbitofrontal, instead of a deep excavation; (3) tympanic ala of the quadrate thin; (4) frontal midline dorsal eminence moderately developed; (5) parietal table rectangular in shape, wider in the anterior than posterior end; (6) ventromedial process of postorbitofrontal projects laterally.

Locality and Age—Upper Lower Maastrichtian Ciply Phosphatic Chalk, in La Malogne, near the town of Mesvin, Mons Basin, southwestern Belgium (Robaszynski and Martin, 1988; Robaszynski, 1989; Robaszynski and Christensen, 1989).

Referred Material—IRScNB 3672, consisting of a partial skull (upper and lower jaws, left postorbitofrontal, left quadrate), 17 vertebrae, and a few podial elements.

DESCRIPTION

Skull

The premaxilla of IRScNB R23 (holotype) is robust and bears an edentulous rostrum that is approximately 74 mm in length, describing a rectangular shape. The complete bone is 726 mm long. Specimen IRScNB 3672 bears two pairs of teeth, whereas in IRScNB R23 there are three tooth sockets and one poorly preserved tooth. This bone also preserves a moderately developed crest. The maxilla-premaxillary suture bears a sinusoidal shape in both specimens, a feature commonly observed in numerous specimens of *Tylosaurus proriger* (Fig. 2.2A, B, D); the midline of the suture ends after the fourth maxillary tooth, as in *T. proriger*. The internarial bar is formed almost entirely by the premaxilla, as seen in IRScNB 23. In IRScNB 3672, this section is broken and lost.

The maxilla is a long and slender tooth-bearing element. In the holotype (IRScNB R23), the left maxilla is 767 mm in length (Fig. 2.2E), and the right is 682 mm, although the latter is not complete (Fig. 2.2F). The holotype left and right maxillae bear 12 teeth each, whereas IRScNB 3672 bears 12 teeth in the right maxilla and 13 in the left. In the holotype, the external nares begin at the posterior margin of the fourth maxillary tooth. Above the 11th tooth, the maxilla carries a posterodorsal process that overlaps with the prefrontal. The posterodorsal process is nearly triangular in shape, projecting dorsally and finishing in a smooth tip, as in *T. proriger*. Given the poor preservation of the specimens, it is not possible to assess if the maxilla excludes the prefrontal from the narial opening.

The frontal of the holotype (IRScNB R23) includes articulated fragments of the prefrontal and parietal. The frontal is nearly triangular in shape; the anterior portion is slightly wider by comparison with that of *T. proriger*, but is not diagnostically different. The length of the bone is approximately twice the width. The shape of the alar wings is sharper in this species than in *T. proriger*. The frontal midline dorsal eminence is low and poorly developed; in this species, it is intermediate between *T. proriger*, which presents a well-developed ridge, and *T. nepaeolicus*, which does not (Fig. 2.3A–C). The posteroventral midline is present, but it is not well developed as in *T. proriger*, a feature that may well be due to taphonomic processes. The pineal foramen is at the frontoparietal suture, as in many specimens of *T. proriger* (Fig. 2.3D, E). The position of the foramen is inter- and intraspecifically plastic in tylosaurines. The internarial bar invades the anterior portion of the frontal extensively. In the holotype, the frontal is 451 mm in length, whereas in specimen IRScNB 3672 this bone is severely fragmented.

The parietal is a ‘Y’-shaped bone (cf. Bullard, 2006) with a visible fracture at its mid-length in the holotype, although both parts are complete. This bone is broad anteriorly and narrow posteriorly. The parietal defines the medial and posterior borders of the supratemporal fenestra. In dorsal view, the parietal table is rectangular in shape, not with a rounded border, as in *T. proriger*, or slightly rounded as in *T. nepaeolicus* (Fig.

2.3A–C). In both specimens, IRScNB R23 and IRScNB 3672, the parietal contains the parietal foramen right at the frontoparietal suture, although the latter specimen has a very fragmented parietal, it is still possible to see the anterior portion with the suture. This character (parietal foramen position) is shared with many specimens of *T. proriger* (Fig. 2.3D, E). In the holotype IRScNB R23, the parietal is 327 mm long; in IRScNB 3672, it is not possible to take measurements due to the fragmentary and poorly preserved condition of the bone.

The left prefrontal in IRScNB R23 is incomplete. It contributes to the anterodorsal border of the orbit and has a posterior process that contacts the postorbitofrontal, but because it is not complete, it is not possible to see if they overlap, as in *T. proriger*. The prefrontal is laterally slightly convex, and the orbital border, although not well preserved, seems to be concave and smooth. The descending border of the anterior portion is ventrally rounded. The anterior tip of the prefrontal is fragmented (Fig. 2.4A).

Only the badly fragmented left postorbitofrontal is preserved in IRScNB 3672, and neither postorbitofrontal is preserved in the holotype IRScNB R23. This bone is narrow, with the central portion of the bone robust and smooth. The portion facing the orbit is gently rounded. The anterior process to articulate with the prefrontal is not clearly preserved, because the bone is broken. The posterior process is attached to a portion of the squamosal (Fig. 2.4B); this process is slightly longer than in *T. proriger* (Fig. 2.4C). The ventromedial process to articulate with the vertical arm of the jugal projects laterally and not anteriorly, as in *T. proriger*, even though the border of this portion of the bone is not well preserved. The wings of the frontal and parietal overlap with the postorbitofrontal to the same degree as in *T. proriger*.

In the holotype (IRScNB R23), only the left squamosal is attached to a fragment of the left suspensorial ramus of the parietal (Fig. 2.4D). The posterior face of the squamosal is expanded dorsoventrally, as in *Tylosaurus proriger*, and it has a concave posteroventral horizontal facet to articulate with the suprastapedial process of the quadrate. The anterior shaft of the squamosal that articulates with the postorbitofrontal is missing. The squamosal does not contact the parietal because the supratemporal intervenes between the two elements. The right squamosal of the holotype and both squamosals of the referred specimen IRScNB 3672 are lost.

The right jugal of IRScNB R23 is a robust element, especially the vertical ramus (Fig. 2.4F), which is thicker than in *T. proriger* (Fig. 2.4E). In lateral view, it is possible to see a suture for the articulation with the postorbitofrontal, but this does not form a deep excavation as in *T. proriger*. The posteroventral process at the joint between the horizontal and vertical rami has the same shape and degree of development as that of *T. proriger*, contra Lingham-Soliar (1992). In both species, this bone has a posteroventral angle of approximately 90º. The horizontal ramus is thin, in comparison with the much thicker vertical ramus. The posterior portion bordering the orbit is gently rounded. In medial view, this bone is thick and smooth.

Quadrates of both specimens (Fig. 2.5A, B) show differences and similarities to those of *T. proriger* (Fig. 2.5D) and *T. nepaeolicus* (Fig. 2.5C). Only the left quadrate of the holotype, IRScNB R23 (Fig. 2.5E), is well enough preserved to permit some characterization and description. Although nearly complete, there is a fracture in the middle of the quadrate shaft. The infrastapedial process is very poorly developed and is barely recognizable. The suprastapedial process is not well preserved, although it looks small, descending ventrally less than one third of the length of the complete bone. The stapedial pit is rectangular in shape and elongated with a constricted middle (cf. Bell, 1997) as in *T. proriger* and *T. nepaeolicus*. The stapedial notch seems to be wide and broadly open. The cephalic condyle has a dorsal rim that is concave laterally and is saddle-shaped where it articulates with the squamosal. The median ridge is not present. The mandibular condyle is crushed anteroposteriorly, probably due to taphonomic processes, making it impossible to identify the anterior deflection of the mandibular condylar surface. The tympanic ala is missing. In IRScNB 3672 (Fig. 2.5F), only the left quadrate is preserved. Suprastapedial and infrastapedial processes are broken and lost, but their preserved bases indicate that both were poorly developed. The tympanic ala is very thin, and the tympanic rim is thin and slender. The cephalic condyle is saddle-shaped with a concave dorsal rim, as in the holotype. The median ridge is flat and smooth, even slightly concave. The stapedial pit is rectangular in shape and elongated; the stapedial notch is not visible as the suprastapedial process is missing. The mandibular condyle is convex, but it is not possible to identify its anterior deflection due to the displacement of the bone.

The dentary is long, robust, and strong. Both dentaries are present in the holotype IRScNB R23, and each bears 13 teeth. The left dentary (Fig. 2.6A) is 859 mm in length, whereas the right (Fig. 2.6B) is 881 mm, although the former is incomplete. The dentaries of the holotype present an anterior projection that is rectangular in shape, as is observed in *T. proriger*. The left dentary has anterior teeth with anterior carinae, whereas the posterior teeth present both anterior and posterior carinae.

The marginal dentition is moderately well preserved, especially in the maxillae. All teeth are large and robust (Fig. 2.6F), labiolingually compressed (dentary tooth of IRScNB 3672, ratio equal to 0.66; this ratio was measured as the difference between the width in labial view and the width in anterior view, at the base of the crown), and the crowns are mediodistally curved. Carinae are sharp and bear small denticles forming finely serrated edges. The first six maxillary teeth have only anterior carinae, whereas the seventh and more posterior teeth are bicarinate; in the dentary, the posterior teeth are bicarinate as well. In both bones, the teeth are tightly spaced, with less than 10 mm between each pair. They do not show any visible differences with respect to the teeth observed for *T. proriger* (Fig. 2.6G).

The angular is located along the ventrolateral border of the posterior portion of the lower jaw. This bone, although incomplete and poorly preserved, is present only in the left lower jaw of IRScNB R23 (Fig. 2.6D), and in both lower jaws of IRScNB 3672. The anterior portion is laterally compressed, describing an oval shape in anterior view. As the angular expands posteriorly, it narrows, although due to preservation, it cannot be stated just where the angular terminates along its articulation with the surangular.

The surangular is an elongated bone that contributes to the posterior portion of the lower jaw. In specimen IRScNB R23, this bone is very robust, more so even than in *T. proriger*. The left surangular (Fig. 2.6D) is 532 mm in length, whereas the right (Fig. 2.6E) is 539 mm. They are present in IRScNB 3672 as well, although fragmentary. The surangular coronoid buttress is low and thick, almost parallel to the lower edge of the mandible, with a rounded dorsal border, as in *T. proriger*. The glenoid fossa for articulation with the quadrate is markedly concave. The suture between the surangular and articular is posterior to the glenoid fossa. The articular is nearly rectangular, and it connects the surangular posteriorly. The articular contribution to the fossa is nearly triangular and dorsally convex. The retroarticular process is dorsally rounded and ventrally flat. The articular/retroarticular process has an inflection of about 60º and possesses a single large foramen.

The coronoids are not present in the holotype, and only the left coronoid is present in IRScNB 3672 (Fig. 2.6C). The fragmentary left coronoid, preserved in articulation with the surangular, is heavily reconstructed. It is a large, saddle-shaped element (cf. Russell, 1967:53), broken at the posterior tip. Anteriorly, its nearly horizontal dorsal edge terminates immediately posterior to the last dentary tooth. The angle described by the two processes of the coronoid bone is approximately 140º, similar to that in *T. proriger* and *T. nepaeolicus*. The posteromedial process is absent.

The curved pterygoids are fragmentary in both specimens. In IRScNB R23, both the left and right pterygoids bear eight teeth; in IRScNB 3672, the left bone bears seven broken and poorly preserved teeth, whereas the right bears ten. They are sharp and strongly recurved (especially the more posterior teeth) and smaller than the marginal teeth. The tooth row is curved, and all pterygoid teeth are smaller teeth than marginal teeth. In IRScNB R23, the right pterygoid preserves the ectopterygoid process (Fig. 2.4G, J); this process is anteriorly convex and straight along the posterior face. The palatine process is broken, and the basisphenoid process is absent.

The basisphenoid is an elongate rectangular block of bone, with an incomplete parasphenoid process that extends forward ventromedially. The process seems to be laterally compressed, but it is not possible to measure its full length (Fig. 2.7A). The basioccipital is a stout and triradiate bone. In IRScNB R23, the basal tubera are moderately developed, as in *T. proriger*. The occipital condyle is big and is wider than long (Fig. 2.7B).

Axial Skeleton

In the holotype specimen (IRScNB R23), the left and right atlas neural arches and the atlas intercentrum are preserved (Fig. 2.7C); the atlas centrum (odontoid) is absent. Both atlas neural arches are complete, but broken into two pieces. The spinal processes of the atlas neural arches are widely separated and do not appear to have been in contact with each other in life. The neural arch lateral process appears as an ill-defined rectangular bump with a rounded border; its anterior edge rises up immediately above the condylar articulation. The anterior concavity is virtually vertical, and the articulation surface with the atlas centrum is gently concave. The atlas intercentrum is very well preserved in the holotype, IRScNB R23. This is a prism-shaped bowed shaped bone (Russell, 1967), ventrally convex and dorsally slightly concave to articulate with the atlas centrum. It presents two parallel anterodorsal and posterodorsal faces, both flat and smooth.

The cervical vertebrae have a horizontally ellipsoid centrum, wider than tall (Fig. 2.7D). The transverse processes arise from the lateral face of the centrum and face up. The neural arches are not well preserved. The hypapophysis is represented in all cervicals by a well-developed and rounded peduncle. Pre- and postzygapophyses are large and well developed, and there are no apparent zygosphenes and zygantra on any of the cervical vertebrae.

The anterior dorsal vertebrae possess large pre- and postzygapophyses. The centrum is ellipsoid, but less horizontal than the cervicals, and they have tall condylar and cotylar surfaces (Fig. 2.7E). These surfaces in the posterior dorsal vertebrae (Fig. 2.7F) are more rounded in outline, although they are wider ventrally. The transverse processes project from the lateral surface of the centrum and present a robust surface for rib attachment. Few vertebrae have preserved any remnants of the neural arches, although it is clear that they are inclined posteriorly. The ventral face of the dorsal vertebrae is gently convex and smooth. The zygantra and zygosphenes are absent in dorsal vertebrae.

The pygal vertebrae have nearly triangular centra that are wider ventrally (Fig. 2.7G). The transverse processes are elongated, more inclined ventrolaterally than in the precaudal vertebrae, and have a short synapophysis. They do not possess pre- and postzygapophyses. Their flat and smooth ventral surfaces lack haemal arches.

Intermediate caudal vertebrae have vertically ellipsoid centra that are taller than wide (Fig. 2.7H). The transverse processes are inclined ventrolaterally from the lateral wall of the centrum. They have vertical condylar and cotylar surfaces. The neural arches are inclined posteriorly with the same inclination observed for the haemal arches. The latter are slender and long. Only a few neural and haemal arches are preserved attached to the vertebral body. Pre- and postzygapophyses are absent.

The terminal caudal vertebrae have vertically ellipsoid centra that are taller than wide, a feature that is more pronounced than in the intermediate vertebrae (Fig. 2.7I). The terminal vertebrae lack transverse processes, and the lateral sides of the centrum are slightly convex and smooth. The preservation of these vertebrae is not good; therefore, only a few of them have haemal arches attached. However, it is still possible to infer from the haemal peduncles that the chevrons are inclined posteriorly. The neural arches are more vertical than in anterior vertebrae. They do not have pre- and postzygapophyses.

This anteroposterior variation in the shape of vertebrae is observed in other species belonging to the genus *Tylosaurus*, as well.

Appendicular Skeleton

Only the left scapula is present in IRScNB R23. As in *Tylosaurus*, it is approximately half the size of the left coracoid (Fig. 2.8D, E). The scapula is wide anteroposteriorly, with width being about 1.5 times length (Fig. 2.8C). The anterior portion is not well preserved, but it is possible to see that the anterior portion is ventrally recurved. The medial face is flat and smooth, whereas the lateral surface is slightly concave. The superior border of this bone is convex. The scapula contributes to about half of the glenoid fossa, which is moderately concave. As in *Tylosaurus*, the suture between the scapula and coracoid appears to lack any interdigitations.

The coracoid is a large, fan-shaped bone. In IRScNB R23, the left coracoid seems to have a flat medial surface and the lateral face is moderately concave (Fig. 2.8B). There is a foramen in the anterior face of the bone, corresponding to the nerve of the supracoracoideus muscle. The coracoid is ventrally convex; the anterior border is straight, and the posterior border is gently concave. This character seems to be shared with all Tylosaurinae species. It forms the ventral half of the glenoid fossa. The right coracoid in the holotype is poorly preserved (Fig. 2.8A).

In the holotype, IRScNB R23, the left humerus is well preserved (Fig. 2.9A), and the right one is fragmented near the post- glenoid process (Fig. 9B). The left bone is elongated and slender and is 207 mm in length, whereas the right one is 210 mm. The length of the humerus is about 1.5 times greater than the distal width. The proximal articular surface for the glenoid is gently convex. The humerus presents a pronounced pectoral crest on the internal surface, and a foramen distally for the ectepicondylar nerve (radial nerve). The postglenoid process is distinctly elongated. The distally positioned entepicondylar or ulnar tuberosity is very small, almost indistinguishable. The ectepicondylar or radial tuberosity is absent. The humerus is virtually identical to that of *T. proriger* and *T. nepaeolicus*.

The ulna is a long and slender bone. In IRScNB R23, the well-preserved right ulna is 159 mm in length (Fig. 2.9C). The proximal end is expanded to articulate with the humerus. It shows a depression in the internal face and a weakly developed olecranon process in the proximal portion along the posterior edge. This bone is very similar to other *Tylosaurus*, such as *T. proriger* and *T. nepaeolicus*.

Only the left femur of IRScNB R23 is present (Fig. 2.9D). It is an elongated and slender element, with its distal end more expanded than the proximal. The tibial articulation is thicker than the fibular one. The distal end is slightly wider than the proximal portion of the bone. The left femur is 221 mm in length, almost as long as the left humerus, a character present in *T. proriger* as well.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis of tylosaurines produced 52 most parsimonious trees, with a tree length of 442 steps, a consistency index [CI] of 0.36, and a retention index [RI] of 0.71. The strict consensus tree is shown in Figure 2.10, and bootstrap values over 50% are reported. *Tylosaurus bernardi* is consistently nested within the clade *Tylosaurus*, specifically as the sister taxon of the type species *T. proriger* (bootstrap value: 58%). The species *T. nepaeolicus* and *T. kansasensis* form a polytomy with *T. proriger* and *T. bernardi*. The genus *Tylosaurus* is recovered as the sister group of the genus *Taniwhasaurus* (including only the species *Taniwhasaurus oweni* and *Taniwhasaurus antarcticus*; I excluded *Taniwhasaurus mikasaensis* due to limited material available), all of which form the well-supported clade, Tylosaurinae (bootstrap value: 99%).

Character 33[1] (maxillo-premaxillary suture ends above a point between the fourth and ninth maxillary teeth) is a synapomorphy of *Tylosaurus bernardi* and *T. proriger*. The genus *Tylosaurus* is diagnosed by character 46[1] (possession of a high quadrate posteroventral ascending tympanic rim, with an elongate triangular crest). The clade Tylosaurinae (Tylosaurus + Taniwhasaurus) is well supported, sharing 12 character states: premaxilla predental rostrum very large and inflated (character 2[2]), premaxilla internarial bar barely narrower than the rostrum (character 4[1]), premaxilla internarial bar base rectangular in shape (character 5[1]), premaxilla internarial bar dorsal keel present (character 6[1]), frontal olfactory canal not embraced ventrally by descending processes (character 13[0]), frontoparietal suture overlaps with all three ridges almost horizontally (character 16[1]), parietal foramen position close to or barely touching suture (character 22[1]), prefrontal and postorbitofrontal in contact (character 28[1]), prefrontal and postorbitofrontal overlap laterally (character 29[1]), quadrate suprastapedial process ends very near the mid-height (character 41[1]), dentary projection of bone anterior to first tooth present (character 58 [0]), and dentary anterior projection long (character 59[1]).

The clade Tylosaurinae is the sister group of the Plioplatecarpinae, and this clade is sister to the clade composed of *Yaguarasaurus, Romeosaurus, Russellosaurus, Pannoniasaurus,* and *Tethysaurus*, consistent with Palci et al. (2013). Within the Mosasaurinae, resolved relationships, and unresolved basal polytomies, are consistent with the results of LeBlanc et al. (2012). The Halisaurinae are the sister group to the Mosasaurinae inclusive of *Dallasaurus*, consistent with the results of Polcyn and Bell (2005) and Palci et al. (2013).

DISCUSSION

Analysis of the holotype and referred specimen of *'Hainosaurus' bernardi* indicates an absence of diagnostic characters supporting a generic distinction of *'Hainosaurus'* from *Tylosaurus*, as shown in Table 2.1. The purportedly diagnostic sinusoidal shape of the maxilla- premaxillary suture (Fig. 2.2A–F) is observed in numerous specimens and species of tylosaurine, including *Tylosaurus proriger, Taniwhasaurus oweni, and Taniwhasaurus antarcticus* (Fernández and Martin, 2009). This feature is also observed in *Tylosaurus gaudryi*, previously referred to *'Hainosaurus' gaudryi* (Lindgren 2005), from the Santonian of France (Fig. 2.2C). '*Hainosaurus'* and

Tylosaurus possess similar teeth in terms of curvature, striations, and carinae, although there are few complete teeth for *'H.' bernardi*. The position of the pineal foramen is variable between the various specimens assigned to *T. proriger*, showing similar states to that observed in the holotype and referred specimen of *'H.' bernardi*; this character therefore does not differentially diagnose *'Hainosaurus'* as distinct from *Tylosaurus*.

The quadrate is considered to be a key element for diagnosing mosasaurid lizards, including tylosaurines. However, when considering the purported diagnostic quadrate characters of *'H.' bernardi*, it becomes clear that the variation within and between species of *Tylosaurus* (e.g., *T. proriger* and *T. nepaeolicus*; Fig. 2.5C, D) encapsulates the variation observed for *'H.' bernardi*. For example, in the latter taxon, the quadrate possesses a thin tympanic ala, a feature shared with some specimens assigned to different species of *Tylosaurus*; however, all species present the same rectangular shape of the stapedial pit. Due to the fragmentary condition of the quadrate in *'H.' bernardi*, it is impossible, due to breakage and loss, to assess the morphology of the suprastapedial and infrastapedial processes, and so this set of diagnostic characters is not diagnostic because they are not preserved.

With respect to the jugal, both '*Hainosaurus' bernardi* and *Tylosaurus proriger* possess a ventroposterior process, with a similar degree of development and similar angle between the horizontal and vertical arms of this bone, contra Lingham-Soliar (1992). The ventromedial process of the postorbitofrontal forms a deep excavation in the vertical arm of the jugal of *T. proriger*, which is absent in *'H.' bernardi*. Thus, on the one preserved point of comparison, the two taxa are the same, and on the other, they cannot be compared because the feature is not preserved in *'H.' bernardi*.

Vertebral counts have been considered as a good diagnostic character ever since the proposal of the genus *'Hainosaurus'* (see Russell, 1967). *'Hainosaurus' bernardi* was diagnosed as possessing about 40 presacrals, whereas *Tylosaurus* possesses about 30 presacrals (Table 2.2). However, the available material of *'H.' bernardi* does not support the vertebral count used to diagnose the genus, due to the incompleteness of the vertebral series, and no articulated specimens have ever been found. Therefore, diagnosis of the genus using vertebral number is not possible because the actual number of precaudal and caudal vertebrae is unknown.

Although this study is the first to detail the type species of the genus *'Hainosaurus'* and to rediagnosis the species, it is not the first to address the utility of the diagnosis of *'Hainosaurus'*. Lindgren and Siverson (2002) discussed the characters proposed by Lingham-Soliar (1992) as diagnostic of *'Hainosaurus'* and concluded that some of Lingham-Soliar's (1992) characters were not diagnostic, such as the shape of the maxillopremaxillary suture (present in *Tylosaurus*) and the length of the external nares (*'Hainosaurus'* is insignificantly larger). From this review, Lindgren and Siverson (2002) proposed a diagnosis for the genus *'Hainosaurus'* (i.e., '*H'. bernardi*) that included new features: (1) marginal tooth crowns more buccolingually compressed in *'Hainosaurus'* than in *Tylosaurus*; (2) more developed carinae in *'Hainosaurus'* than in *Tylosaurus*; (3) serrated pterygoid teeth in *'Hainosaurus',* whereas the carinae lack serrations in *Tylosaurus*; (4) infrastapedial process on the quadrate is smaller in *'Hainosaurus'* than in *Tylosaurus*; (5) suprastapedial process on the quadrate virtually absent in *'Hainosaurus',* but well developed in *Tylosaurus*; (6) in lateral view, the quadrate has a rectangular shape in *'Hainosaurus',* whereas in *Tylosaurus* it is more circular; (7) femur longer than humerus in *'Hainosaurus',* whereas in *Tylosaurus* they are virtually equal; (8) vertebral counts between cervicals and chevron-bearing caudals greater in *'Hainosaurus'* than in *Tylosaurus*; and (9) anteriorly positioned intermediate caudal with vertebral centra wider and shorter in *'Hainosaurus'* than in *Tylosaurus*.

However, based on my observations, I find contrary observations to those of Lindgren and Siverson (2002) regarding their diagnostic features for '*Hainosaurus',* To begin: (1) in *Tylosaurus*, the marginal tooth crowns are buccolingually compressed, similar to *'Hainosaurus'*; (2) as the type and referred specimens of *'H'. bernardi* have so few complete teeth, I consider it impossible to diagnose the genus by such a qualitative measure as 'more developed carinae' and conclude that if there is accuracy in this observation, it is perhaps, at best, a species-level distinction, not a generic one; (3) with regard to serrated pterygoid teeth, I observed no such feature in the type and referred specimens of '*H'. bernardi*; (4, 5, and 6) the quadrates of *'H'. bernardi* are so poorly preserved that the length of the suprastapedial process cannot be ascertained as 'short,' as in this case it is merely broken, and it is not clear if the infrastapedial process is absent because it is broken away at that point on the shaft; likewise, the only remaining bony tissues are those of the quadrate shaft, and I note that the quadrate shaft of all mosasaurids is straight when the conch is broken away; (7) the femur and humerus of *'H.' bernardi* are virtually equal in length, but the femur is longer than the humerus for both *T. pembinensis* (Bullard and Caldwell, 2010) and *'T. saskatchewanensis'* (Bullard, 2006), which means that it is not an exclusive trait of *'Hainosaurus'*; (8) because the vertebral columns of both *'H.' bernardi* specimens are incomplete, it is not possible to know the count and diagnose *'H.' bernardi* as having more vertebrae; and (9) with respect to the last character, "anteriorly positioned intermediate caudal with vertebral centra wider and shorter in *Hainosaurus*. . .," Lindgren (2005:1162) followed Lindgren and Siverson (2002) and added a new qualifier to the vertebral character to further diagnose *'Hainosaurus'* from *Tylosaurus*, arguing that the outline of the pygal centra and anterior intermediate caudals is 'markedly' triangular in *T. pembinensis* and 'roughly triangular' in *T. bernardi*. Although it is certainly true that such qualitative descriptors as 'markedly' versus 'roughly' are indeed problematic and hard to assess, because both are triangular, I also note that in all tylosaurine and plioplatecarpine mosasaurs, the shape of the centrum in pygals and anterior intermediate caudals is always nearly 'triangular' (Le Blanc et al., 2012; Konishi, pers. comm.). Therefore, I do not consider such qualitative terms as 'roughly' versus 'markedly' to be diagnostic.

Unequivocally, the original (Dollo, 1885) and emended diagnoses (Lingham-Soliar, 1992; Lindgren and Siverson, 2002; Lindgren, 2005) of *'Hainosaurus' bernardi* do not differentially diagnose this taxon as generically distinct. The available data suggest that *'Hainosaurus'* is a junior synonym of *Tylosaurus*, although there are characters that diagnose the species *Tylosaurus bernardi* (Dollo, 1885) as distinct within *Tylosaurus*. These characteristics include (1) vertical ramus of the jugal thick; (2) vertical ramus of the jugal presents a visible suture to articulate with the postorbitofrontal, instead of a deep excavation; (3) tympanic ala of the quadrate thin; (4) frontal midline dorsal eminence moderately developed; (5) parietal table rectangular in shape, wider in the anterior than posterior end; and (6) ventromedial process of postorbitofrontal projects laterally.

The phylogenetic analysis also supports the conclusions that there are no diagnostic characters that distinguish between *Tylosaurus* and *'Hainosaurus'*, because the Belgian species is nested within the genus *Tylosaurus*. The strict consensus tree shows the phylogenetic relationships of tylosaurine mosasaurs, as well as other mosasauroid squamates, where *Tylosaurus bernardi* is sister to *T. proriger*, rather than to either *T. nepaeolicus* and *T. kansasensis*.

The long-held view was that *Tylosaurus* was endemic to North America, known from the Turonian to Campanian (Russell, 1967; Flores, 2013), and present in both northern and southern subprovinces of the Western Interior Seaway (Sohl, 1971; Nicholls and Russell, 1990). However, Lindgren's (2005) reassignment of the French Santonian-aged species to *Tylosaurus gaudryi* (Lindgren, 2005), and the assignment here of *'bernardi'* to *Tylosaurus bernardi* (Dollo, 1885), recognizes a much broader temporal and spatial distribution of *Tylosaurus* than was previously thought (Bardet, 1990). This implies that the temporal range of tylosaurines extended to the early Maastrichtian and not just the Campanian (contra Russell, 1967). This wider distribution suggests that the subfamily Tylosaurinae (with the exception of the genus *Taniwhasaurus*) occupied the North Atlantic Circle Basin, not just the North American epicontinental seas.

CONCLUSIONS

The two specimens referred to '*Hainosaurus bernardi',* from the Maastrichtian of Belgium, cannot be differentially diagnosed from *Tylosaurus*. The shape of the maxillopremaxillary suture, the position of the pineal opening, characters of the jugal, quadrate, postorbitofrontal, and teeth, and the vertebral count have traditionally been considered key characters to diagnosing '*Hainosaurus'* from *Tylosaurus* (Dollo, 1885; Lingham-Soliar, 1992). However, as shown in this study, the shape of the maxillopremaxillary suture is shared with numerous other tylosasaur specimens assigned to several species of *Tylosaurus* and *Taniwhasaurus*, the jugal and postorbitofrontals are the same as those of *Tylosaurus*, the quadrates are poorly preserved in '*Hainosaurus'* and are merely broken (and thus do not demonstrate morphological differences representing evolutionary divergence), the teeth are the same as those present in *Tylosaurus*, and the purported high vertebral count cannot be verified because no specimen of '*H'. bernardi* is complete enough to permit a precise vertebral count (Williston, 1898; Russell, 1967; Lindgren and Siverson, 2002; Lindgren, 2005). Contrary to a long tradition of recognizing two separate genera, the empirical observations presented here support the conclusion that *'Hainosaurus'* is a junior synonym of *Tylosaurus*, because no anatomical features distinguish the former from the latter. Based on these observations and data, I justify my recognition of *'Hainosaurus'* as a junior synonym of *Tylosaurus*. This reassignment precipitates a new understanding of the temporal and spatial distribution of the genus *Tylosaurus*, previously known only from North American epicontinental seas (Russell, 1967). The fossil record shows that the genus occupied a wider geographic and stratigraphic distribution than has been previously observed, inhabiting the North Atlantic Circle Basin. Temporally, *Tylosaurus* spans a significant portion of the Upper Cretaceous, being recognized in rocks from the Turonian through to the Maastrichtian.

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TABLE 2.1. Summary of characters that have been used to distinguish the genus *"Hainosaurus"* from *Tylosaurus*. The comparison was made between the species *Tylosaurus bernardi*, *Tylosaurus proriger* and *Tylosaurus nepaeolicus*. Symbols: +, presence of the character; –, absence of the character; **np**, not preserved.

	T. bernardi	***T. proriger***	***T. nepaeolicus***
Sinusoidal maxillopremaxillary suture.	+	+	–
Twelve to thirteen teeth in maxilla.	+	+	+
Frontal midline dorsal eminence.	+	+	–
Pineal foramen onto the frontoparietal suture.	+	+	–
Rectangle parietal table.	+	–	+
Jugal angle virtually 90º.	+	+	+
Ventroposterior process of the jugal.	+	+	+
Deep excavation on jugal to articulate with postorbitofrontal.	+	–	np
Thin tympanic ala of the quadrate.	np	+	–
Rectangular stapedial pit.	+	+	+
Short suprastapedial process of the quadrate.	np	–	–
Presence of infrastapedial process of the quadrate.	np	+	+

TABLE 2.1. (Continued)

Rectangular anterior tip of the dentary.	+	+	+
Dentary bears 13 teeth.	+	+	+
Teeth labiolingually compressed, crown mediodistally curved.	+	+	+
Anterior and posterior carina extends full length of the teeth.	+	+	+
Number of vertebrae anterior to chevron-bearing caudals > 40.	**np**	–	**np**
Pygals and anterior intermediate caudals present nearly triangular centra.	+	+	+
Scapula half size of coracoid.	+	+	np
Femur length almost equal than humerus.	+	+	+
Distal end of humerus more expanded than proximal.	+	+	+

TABLE 2.2. Comparison of vertebral counts in *Tylosaurus* (*Hainosaurus) bernardi* and North American *Tylosaurus.* Precaudal vertebrae include pygals; caudal vertebrae include the chevron bearing caudals: intermedials and terminals, following Russell (1967).

	T. bernardi	*H. bernardi* Lingham-Soliar, 1992	*H. bernardi* Lindgren, 2005	*H. bernardi* Dollo, 1885	*Tylosaurus* Russell, 1967
Cervical	6-7	7-8	-	10	7
Dorsal	26	32-33	-	19	-
Pygal	7	>9	-	>9	-
Precaudal	>39	>49	41 excluding pygals	49	36-37
Caudal	>45	>68	47 including pygals	49	89-112
Total	>84	>117	88	>98	125-149

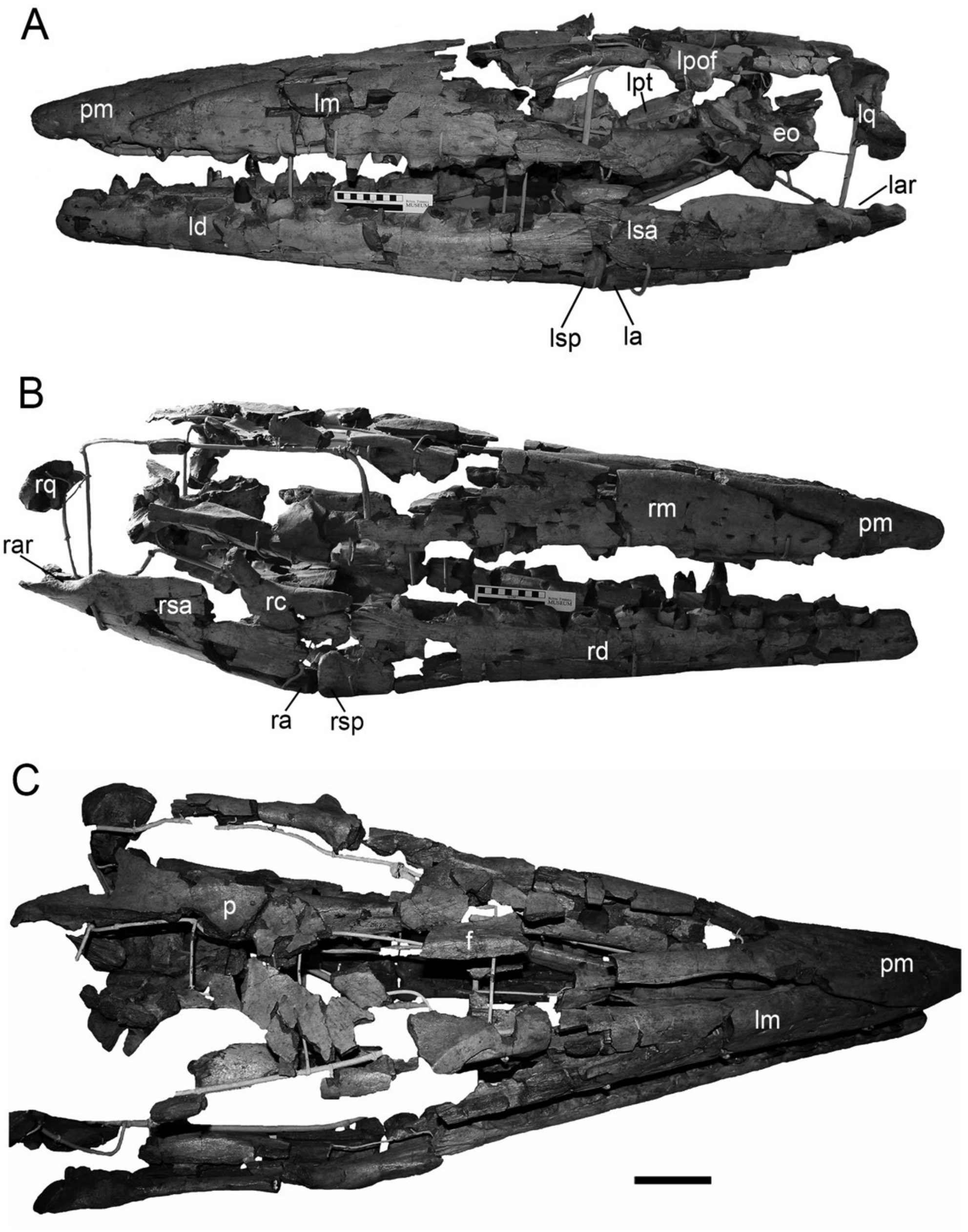

FIGURE 2.1. IRScNB 3672 *Tylosaurus bernardi* skull. **A**, left lateral view; **B**, right lateral view; **C**, dorsal view. Scale bar equals 10 cm.

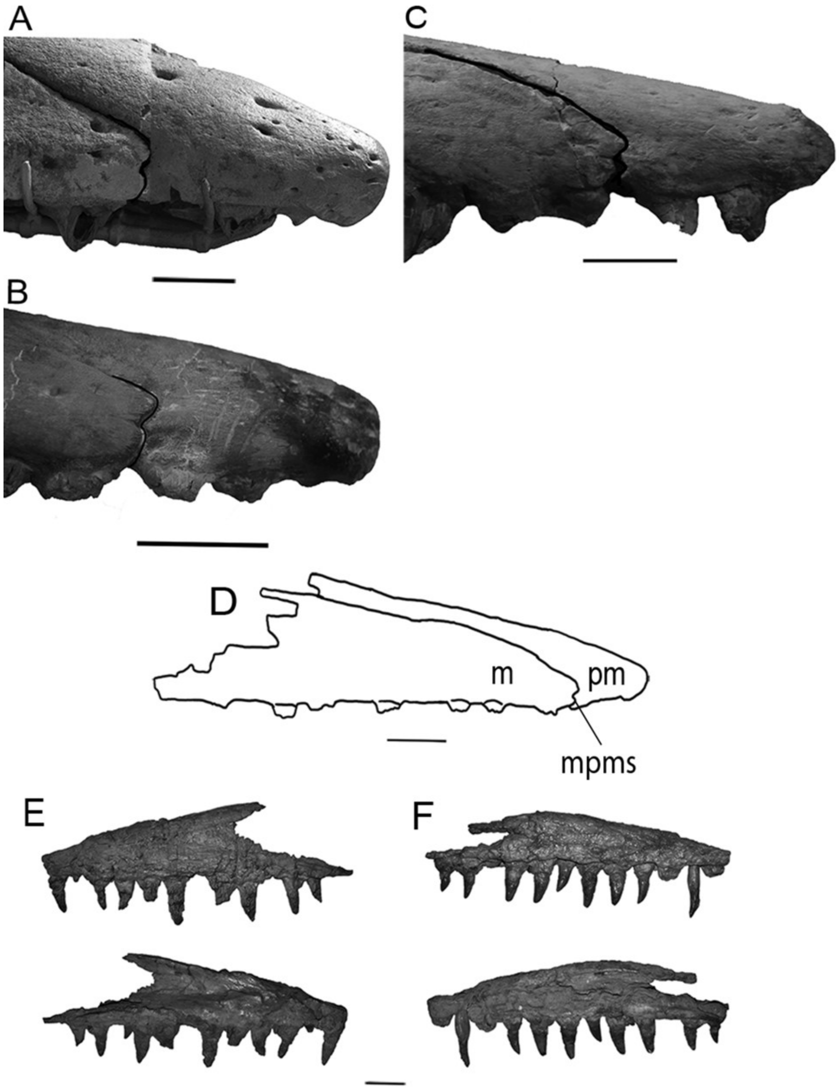

FIGURE 2.2. **A**, maxillopremaxillary suture, *Tylosaurus bernardi* IRScNB 3672; **B**, maxillopremaxillary suture, *Tylosaurus* sp. KU1129; **C**, maxillopremaxillary suture, *Tylosaurus gaudryi* MNHN 1896-15; **D**, line drawing of the maxillopremaxillary suture of IRScNB 3672; **E**, left maxilla, lateral (above) and medial (below) views, *Tylosaurus bernardi* IRScNB R23; **F**, right maxilla, lateral (above) and medial (below) views, *Tylosaurus bernardi* IRScNB R23. Scale bars equal 5 cm (A–C) and 10 cm (D–F).

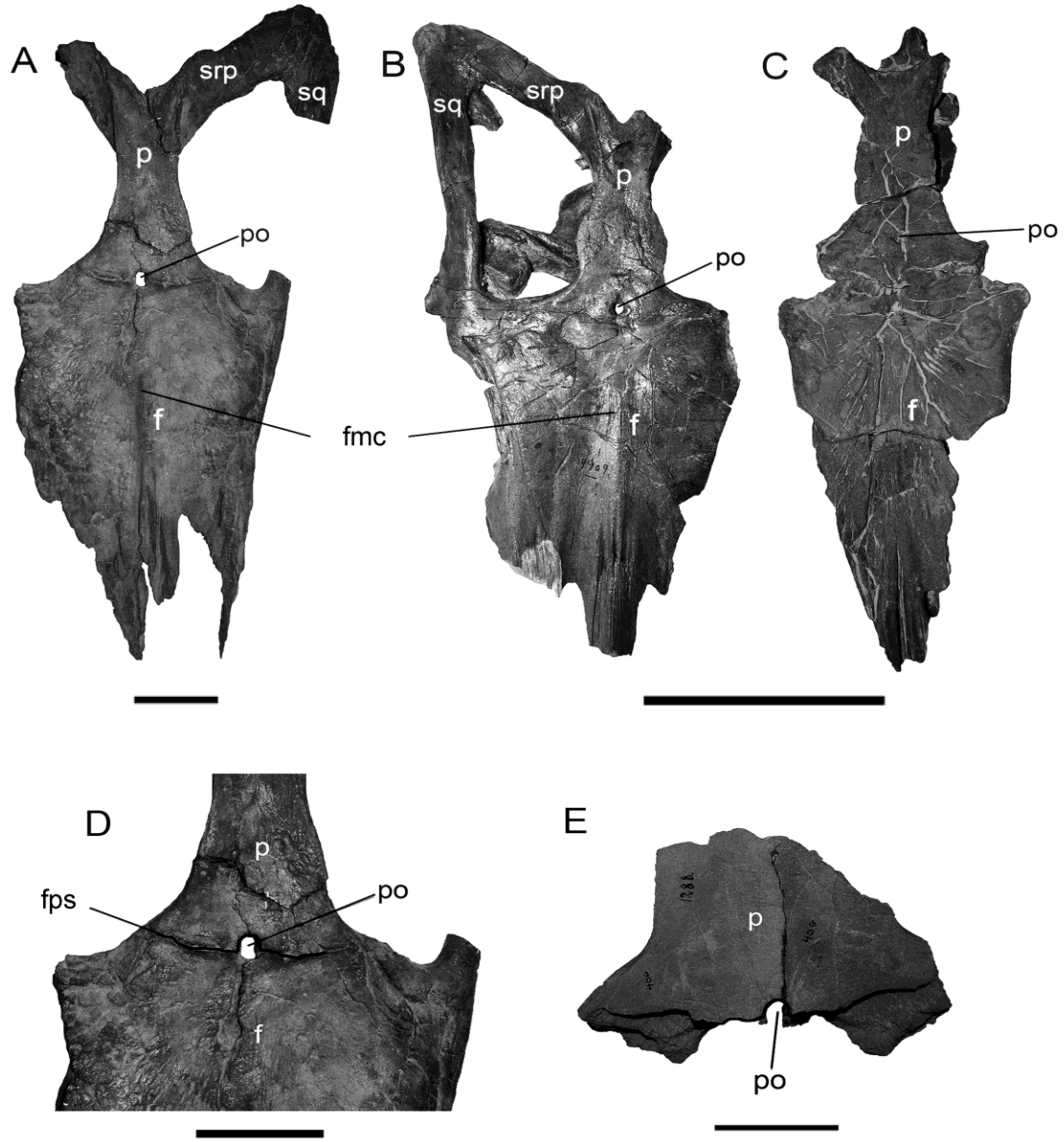

FIGURE 2.3. Frontal and parietal. **A**, *Tylosaurus bernardi* IRScNB R23; **B**, *Tylosaurus proriger* AMNH 4909; **C**, *Tylosaurus nepaeolicus* YPM 3974; Frontoparietal suture. **D**, *Tylosaurus bernardi* IRScNB R23; **E**, *Tylosaurus proriger* YPM 1288. Scale bars equal 10 cm (A–C) and 5 cm (D, E).

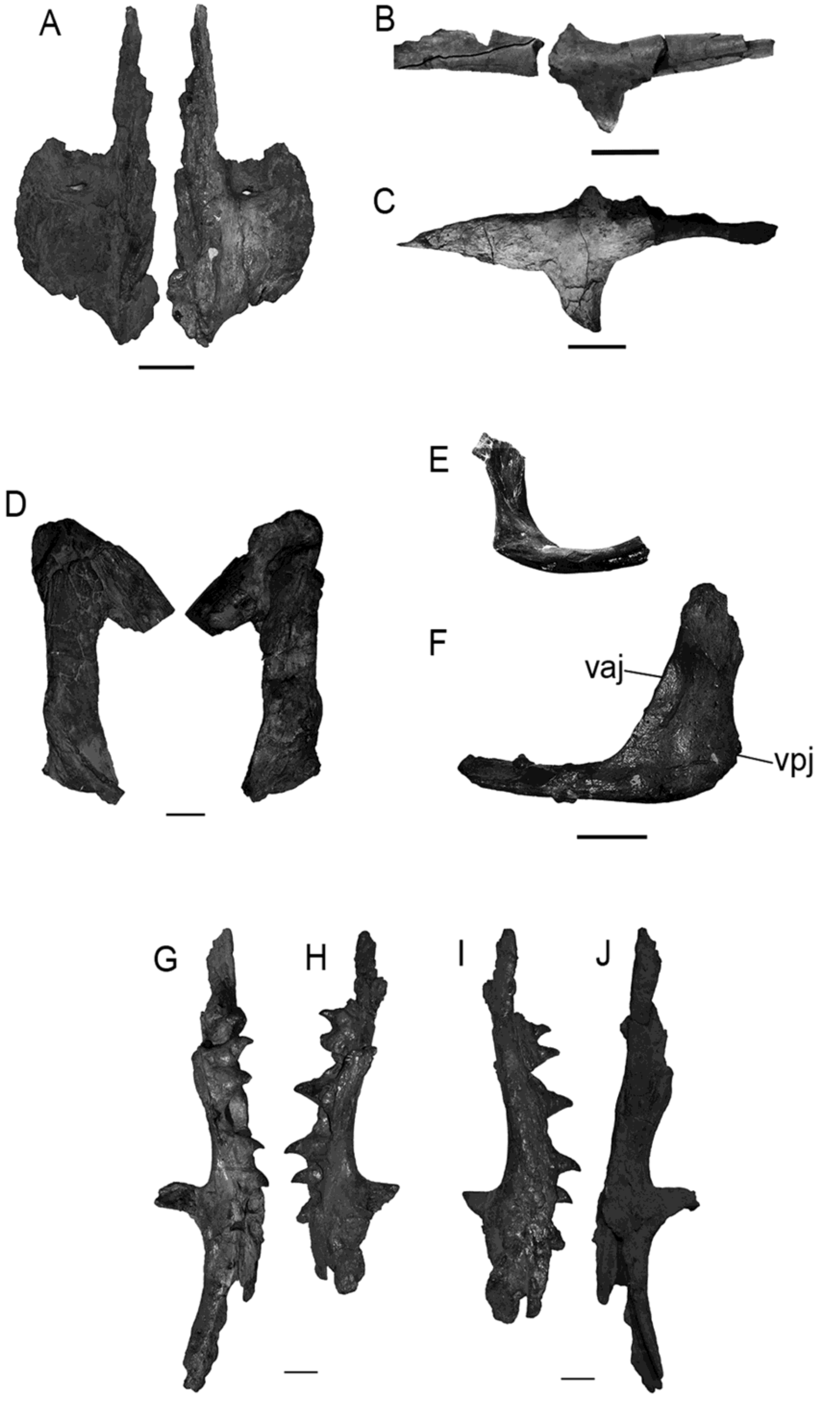

FIGURE 2.4. Skull bones. **A**, right prefrontal, dorsal and ventral views, *Tylosaurus bernardi* IRScNB R23; **B**, left postorbitofrontal, *Tylosaurus bernardi* IRScNB R23; **C**, left postorbitofrontal, *Tylosaurus proriger* RMM 3253; **D**, right squamosal, dorsal and

ventral views, *Tylosaurus bernardi* IRScNB R23; **E**, left jugal, lateral view, *Tylosaurus proriger* NHMUK 3624; **F**, right jugal, lateral view, *Tylosaurus bernardi* IRScNB R23; **G**, right pterygoid, ventral view, *Tylosaurus bernardi* IRScNB R23; **H**, left pterygoid, ventral view, *Tylosaurus bernardi* IRScNB R23; **I**, **J**, left and right pterygoids, dorsal view, *Tylosaurus bernardi* IRScNB R23. All scale bars equal 5 cm.

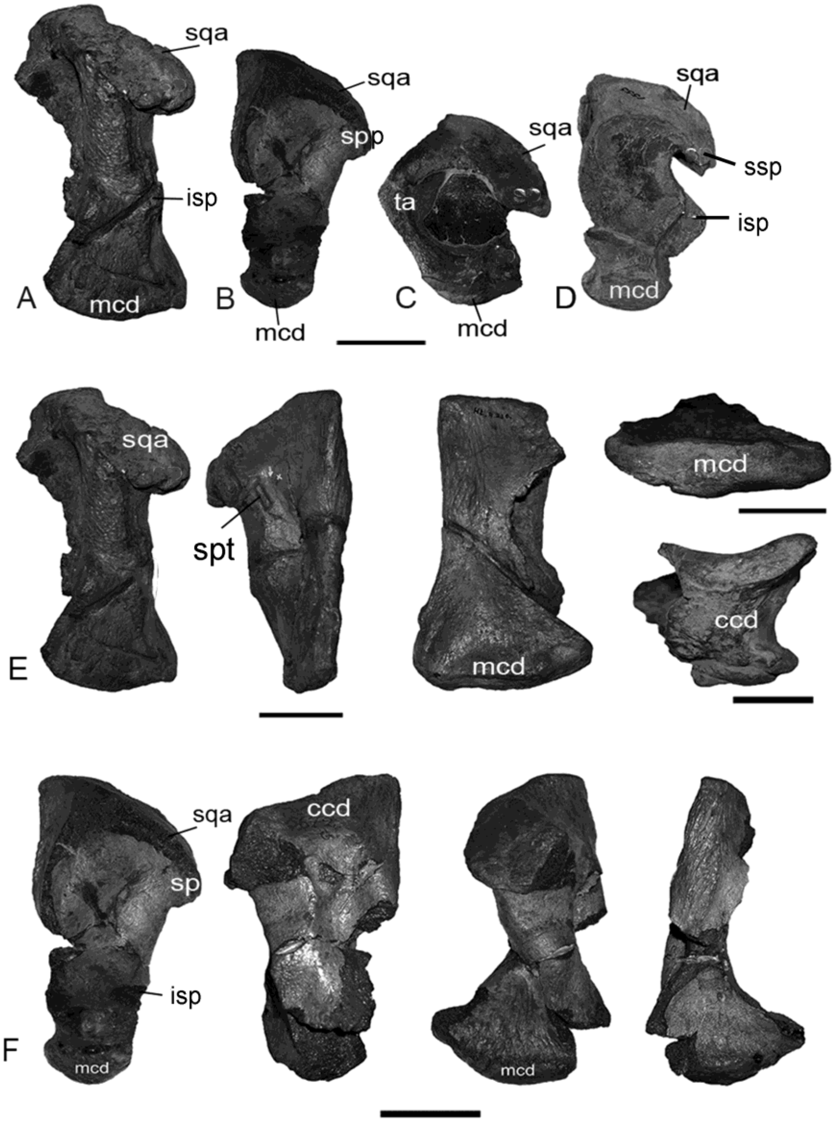

FIGURE 2.5. Left quadrate, lateral view (A–D). **A**, *Tylosaurus bernardi* IRScNB R23; **B**, *Tylosaurus bernardi* IRScNB 3672; **C**, *Tylosaurus nepaeolicus* YPM 3970; **D**, *Tylosaurus proriger* AMNH 1555; **E**, lateral, medial, anterior, mandibular, and cephalic views, *Tylosaurus bernardi* IRScNB R23; **F**, lateral, medial, posterior, and anterior views, *Tylosaurus bernardi* IRScNB 3672. All scale bars equal 5 cm.

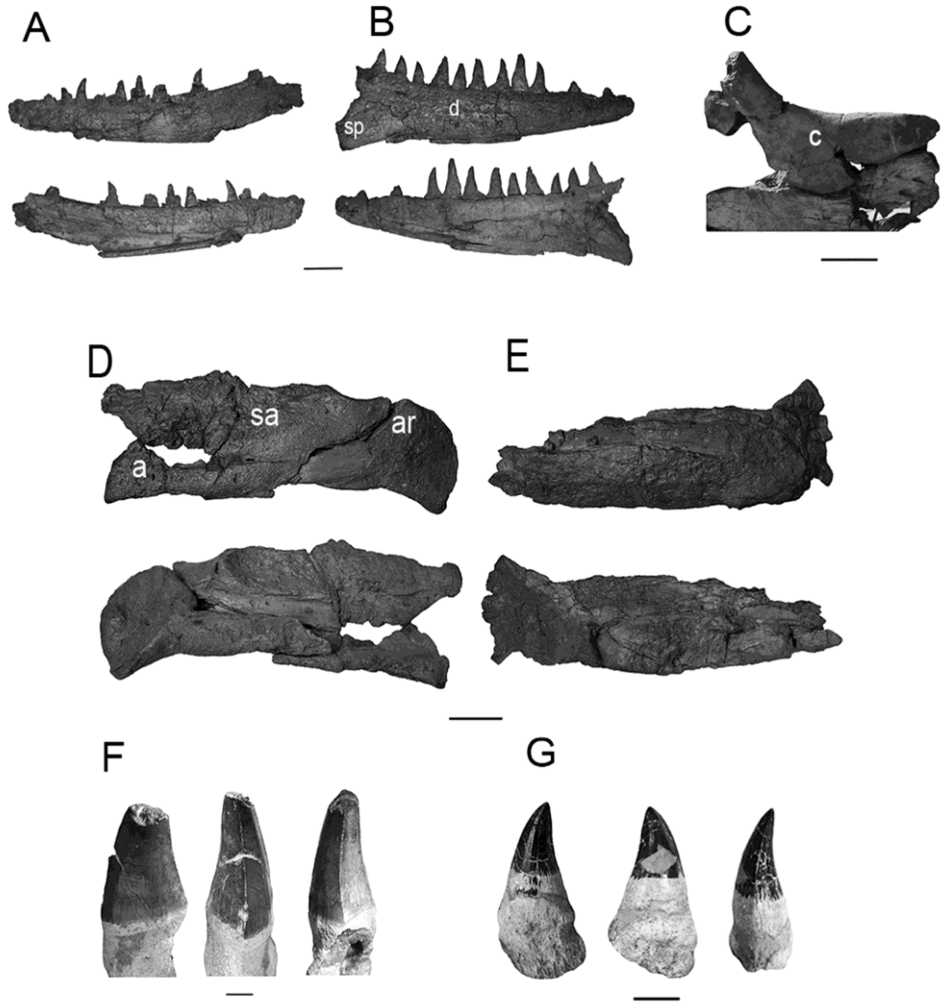

FIGURE 2.6. **A**, left dentary, lateral and medial views, *Tylosaurus bernardi* IRScNB R23; **B**, right dentary, lateral and medial views, *T. bernardi* IRScNB R23; **C**, right coronoid, lateral view, *Tylosaurus bernardi* IRScNB 3672; **D**, left surangular attached to angular and articular, lateral and medial views, *Tylosaurus bernardi* IRScNB R23; **E**, right surangular, lateral and medial views, *Tylosaurus bernardi* IRScNB R23; **F**, marginal tooth, lateral view, lingual, posterior, and anterior sides, *Tylosaurus bernardi* IRScNB 3672; **G**, marginal tooth, lateral view, lingual, labial, and anterior sides, *Tylosaurus proriger* RMM 1613. Scale bars equal 10 cm (A, B, D, E), 5 cm (C), and 1 cm (F, G).

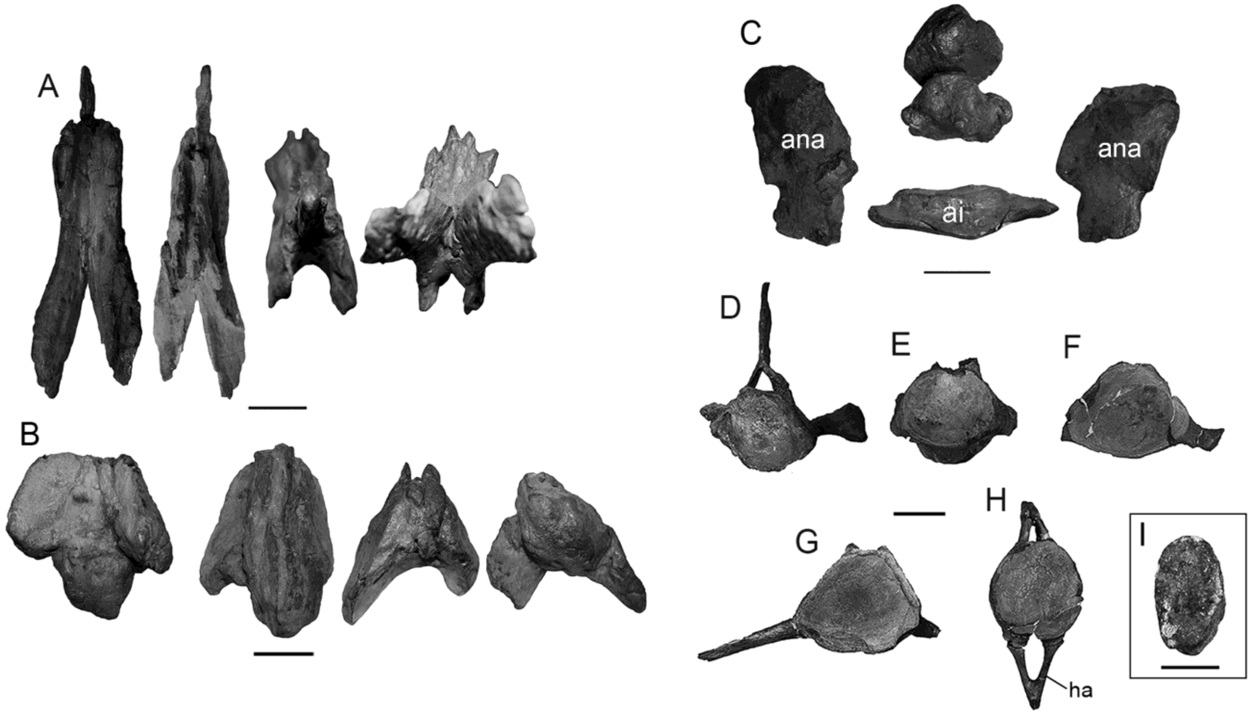

FIGURE 2.7: **A**, basisphenoid, ventral, dorsal, anterior and posterior views (left to right), *Tylosaurus bernardi* IRScNB R23; **B**, basioccipital, ventral, dorsal, anterior, and posterior views (left to right), *Tylosaurus bernardi* IRScNB R23; **C**, atlas intercentrum and both atlas neural arches, *Tylosaurus bernardi* IRScNB R23; **D**, cervical vertebra, *Tylosaurus bernardi* IRScNB R23; **E**, anterior dorsal vertebra, *Tylosaurus bernardi* IRScNB 3672; **F**, posterior dorsal vertebra, *Tylosaurus bernardi* IRScNB 3672; **G**, pygal vertebra, *Tylosaurus bernardi* IRScNB R23; **H**, intermedial vertebra, *Tylosaurus bernardi* IRScNB R23; **I**, terminal vertebra, *Tylosaurus bernardi* IRScNB R23. Scale bars equal 5 cm (A–H) and 1 cm (I).

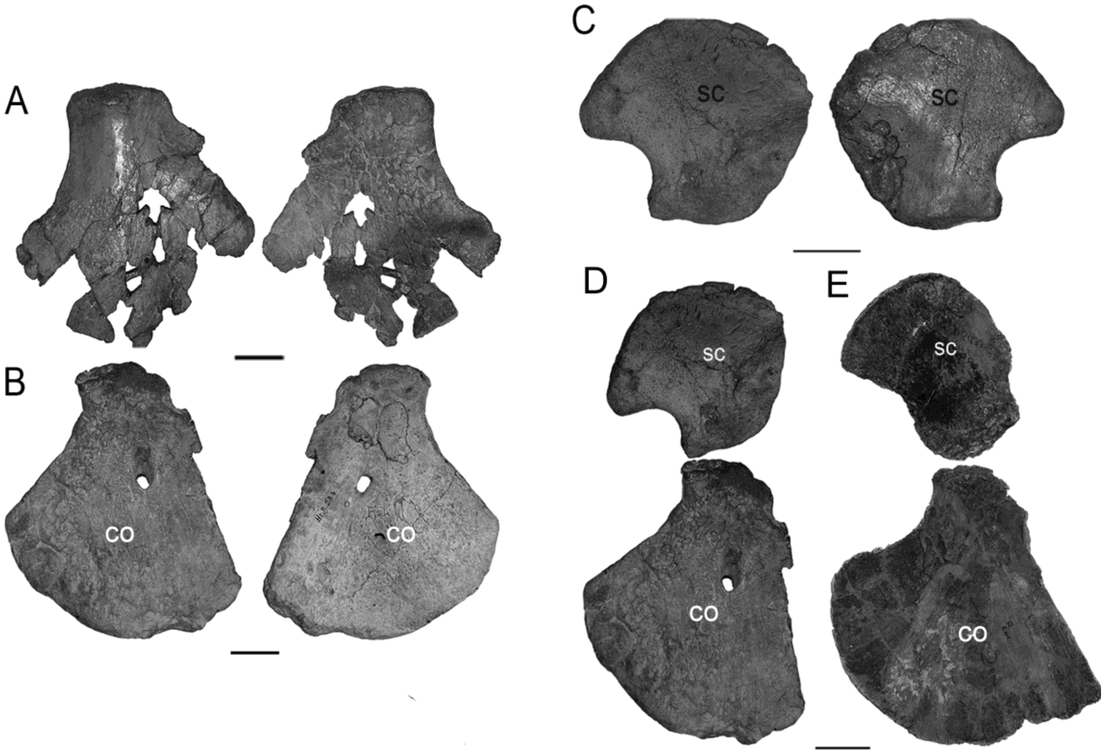

FIGURE 2.8. Pectoral girdle elements of *Tylosaurus bernardi*, IRScNB R23. **A**, right coracoid, extensor and flexor views; **B**, left coracoid, extensor and flexor views; **C**, left scapula, extensor and flexor views. **D**, **E**, comparison of coracoid-scapula size. **D**, *Tylosaurus bernardi* IRScNB R23; **E**, *Tylosaurus proriger* KU 5033. All scale bars equal 5 cm.

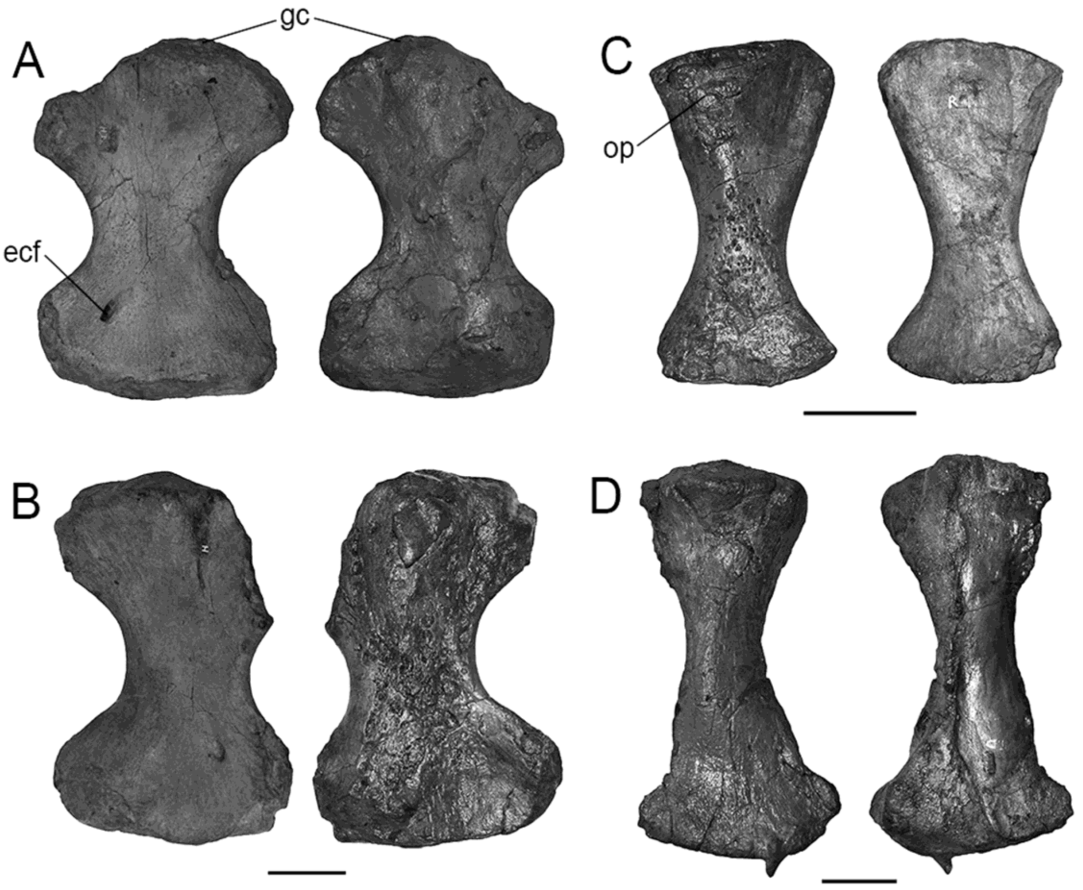

FIGURE 2.9. Podial elements of *Tylosaurus bernardi* IRScNB R23. **A**, left humerus, extensor and flexor views; **B**, right humerus, extensor and flexor views; **C**, right ulna, extensor and flexor views; **D**, left femur, extensor and flexor views. All scale bars equal 5 cm.

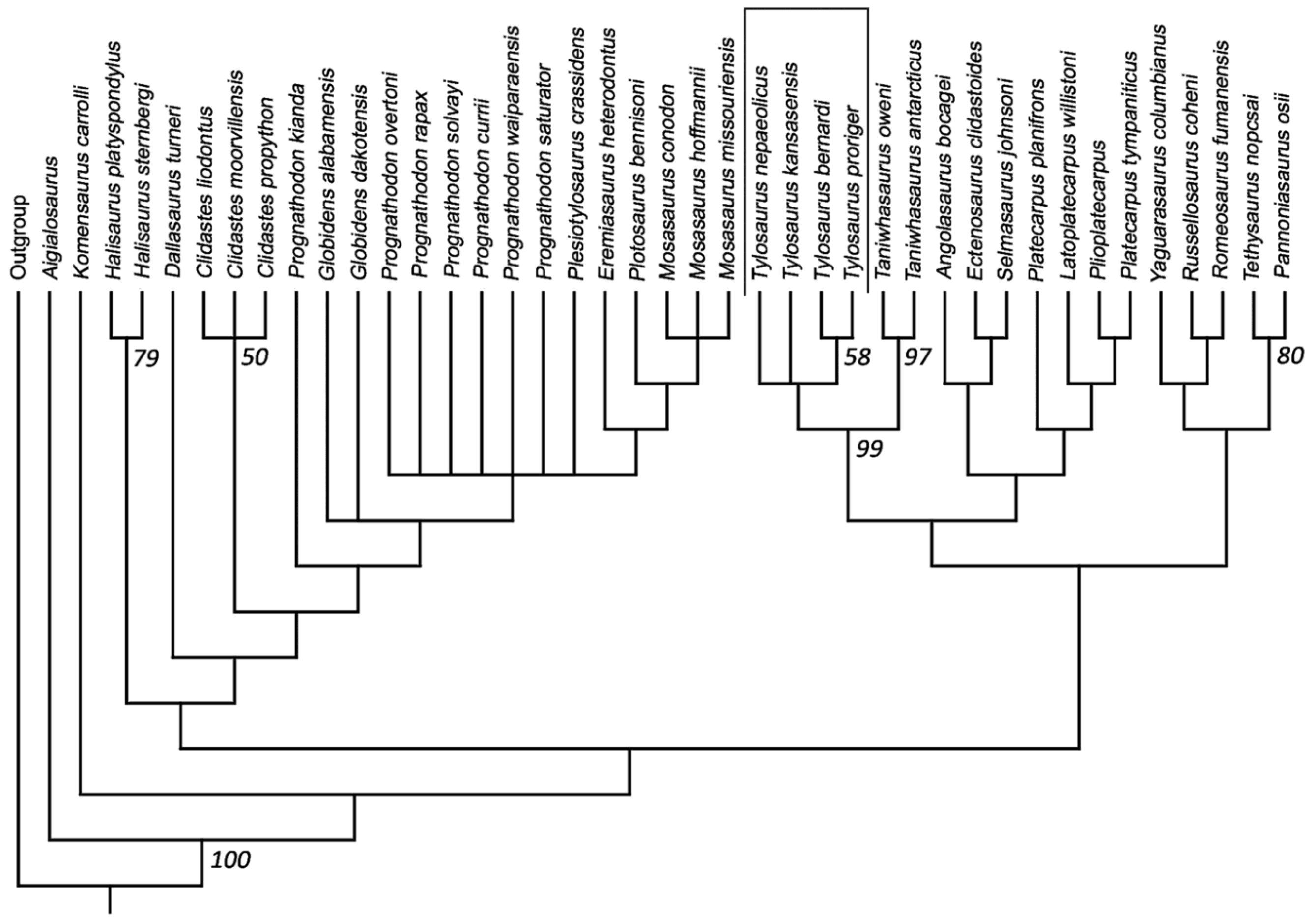

FIGURE 2.10. Phylogenetic relationships within Mosasauroidea, using *Varanus* as outgroup. Strict consensus tree of the 52 most parsimonious trees, length of 442 steps, consistency index (CI) D 0.36, and retention index (RI) D 0.71. Bootstrap branch support values equal or over 50% are shown.

CHAPTER THREE

RE-CHARACTERIZATION OF *TYLOSAURUS NEPAEOLICUS* (COPE, 1874) AND *TYLOSAURUS KANSASENSIS* EVERHART, 2005: ONTOGENY OR SYMPATRY?

ABSTRACT

Tylosaurus nepaeolicus (Cope, 1874), from the lower Smokey Hill Chalk upper Coniacian of Kansas is reassessed and compared to *T. kansasensis* Everhart, 2005, its sympatric contemporary from the same formation; both are compared to a later species from the upper Smoky Hill Chalk, *T. proriger* (Cope, 1869). *Tylosaurus nepaeolicus* (Cope, 1874) is virtually indistinguishable from *T. kansasensis* Everhart, 2005, and both show important similarities with *T. proriger*, particularly the smaller individuals of *T. kansasensis*. Many of the anatomical features of *T. kansasensis* are indicative of a juvenile stage based on comparisons to *T. proriger*. In addition to the aforementioned spatial and temporal sympatry between *T. nepaeolicus* and *T. kansasensis*, it is anatomically difficult to distinguish the two species from each other, with the few notable differences being ontogenetically variable, and possibly indicating allometric changes during post-embryonic development; in addition, *T. nepaeolicus* is known from fragmentary remains of very large individuals, while *T. kansasensis* is known from a small number of complete and recently collected skulls, though of much smaller size than the type materials of *T. nepaeolicus*. I suggest that *T. kansasensis* is a juvenile of *Tylosaurus nepaeolicus*, and is thus the junior synonym of the latter. Furthermore, I find ontogenetic evidence to suggest that *T. proriger* is likely a paedomorph of *T. nepaeolicus*, albeit, a gigantic one.

INTRODUCTION

Mosasauroid lizards were a diverse group of squamates that radiated into aquatic environments around the world during the later part of the Cretaceous (Russell, 1967; Bell and Polcyn, 2005; Caldwell and Palci, 2007; Caldwell, 2012). The fossil record of mosasaurs is present on all continents, mainly in marine strata, though there are some recent records of probable fresh water mosasaurs found in fluvial sediments from the Santonian of Hungary (Makádi et al., 2012). Mosasauroids and their kin range in age from the late Cenomanian (Russell, 1967; Grigoriev et al., 2009) to the late Maastrichtian, becoming extinct at the K/Pg boundary, at the end of the Mesozoic (Caldwell, 2012). Within the family Mosasauridae, the subfamily Tylosaurinae is a broadly distributed clade of gigantic mosasaurs, e.g., *Tylosaurus proriger*, characterized by a large rostrum anterior to the premaxillary teeth, 12 to 13 teeth in the dentary and maxilla, no canal for the basilar artery in the basioccipital or basisphenoid, 29 or more presacral vertebrae, articulating haemal arches, and poorly ossified appendicular elements that lack smoothly finished articular surfaces (Russell, 1967).

The type species, *Tylosaurus proriger* (Cope, 1869), was described based on a partial snout and thirteen associated vertebrae (MCZ 4374), found near Monument Rocks, Gove County, in the Upper Smoky Hill Chalk of Kansas, USA (upper Santonian-lower Campanian, Upper Cretaceous) (Russell, 1967; Sheldon, 1996). *Tylosaurus proriger* is currently known from several well preserved skulls and skeletons from Kansas and other localities in Alabama, Nebraska, Texas, and South Dakota (Bell, 1993).

The second taxon that was described, *Tylosaurus nepaeolicus* (Cope, 1874), was based on a partial skull and a single vertebra (AMNH 1565; Fig. 3.1A), found along the Solomon River, in the upper Coniacian of the Lower Smoky Hill Chalk of Kansas (Russell, 1967; Sheldon, 1996); the current known species range is from the upper Coniacian to the lower Santonian. When Russell (1967) diagnosed *T. nepaeolicus*, he noted that it "... seems generally to be a smaller species than *T. proriger*."

The third species, *Tylosaurus kansasensis* Everhart, 2005, was recently described from 13 specimens, including the holotype that comprises a nearly complete skull, FHSM VP 2295 (Fig. 3.2), found near Ellis County, in the upper Coniacian of the Lower Smoky Hill Chalk (Everhart, 2005), two specimens defined as the paratypes, and ten referred specimens.

Among North American tylosaurine mosasaurs, *Tylosaurus proriger* is the best known, with literally hundreds of specimens currently housed in various collections around the world. Cranial and postcranial materials are known from nearly complete specimens (Russell, 1967), including adults and juveniles (Sheldon, 1990; PJH pers. obs.), and thousands of isolated elements. On the other hand, the stratigraphically older taxon, *T. nepaeolicus*, is known from no more than 30 specimens (Everhart, 2002), none of which contain complete skulls. In addition, the postcranial skeleton of *T. nepaeolicus* remains poorly understood. In stark contrast, the newly recognized *T. kansasensis* Everhart, 2005 is known from new specimens, which include a large number of very complete though comparatively smaller skulls with some associated postcranial remains.

The problem is immediately obvious and can be posed around the following question e if *Tylosaurus nepaeolicus* is known from weakly diagnostic remains from the

Coniacian of the Lower Smoky Hill Chalk of Kansas, and *T. kansasensis* is known from the same beds but from complete specimens, then which differences, if any, separate these two taxa from each other (Fig. 3.3)? In Bell's (1993:188) study, the author recognized thirteen traits separating his *Tylosaurus* taxon novum, and which Everhart (2005) named *T. kansasensis*, as follows: "Diagnosis: Thirteen characters were assigned to this taxon by the analysis, however only three of those (1-3 below) are unequivocal and none are unique." Those three unequivocal characters are 1) Premaxilla rostral foramina large, 2) Infrastapedial process of quadrate absent, and 3) Quadrate median ridge diverging ventrally. As I will argue below, the size of premaxillary foramina is variable and not a reliable character; the infrastapedial process is also absent in *T. nepaeolicus*; and the divergence of the quadrate median ridge is also variably present in specimens from both *T. nepaeolicus* and *T. kansasensis*. Of the remaining ten characters, Bell (1993) noted that *Tylosaurus* taxon novum shares, in some form or another, seven of those characters with *T. nepaeolicus*, usually with a reversal in *T. proriger*. These issues raise the question if *T. kansasensis* Everhart, 2005, represents a valid taxon. The aim of this study is to present data and arguments in favor of a synonymy of *T. nepaeolicus* and *T. kansasensis*, with the latter being the junior synonym of the former. I also present a suite of characters that vary during ontogeny, providing the first comparison of such features across different mosasaur taxa, and a potentially useful way to assess the ontogenetic stage of other mosasauroid specimens in future research.

GEOLOGICAL SETTINGS

The localities where the first specimens of *T. 'kansasensis'* were found remain unknown; however, those found after 1968 were all recovered from Ellis County (Everhart, 2005), which corresponds to the Lower Smoky Hill Chalk of the Niobrara Formation, Kansas. The Niobrara Formation is located in western North America, occupying part of the area where the Western Interior Seaway was located during the Cretaceous. There are two members described for this formation: Fort Hays Limestone Member, which is overlain by the Smoky Hill Chalk Member. The latter includes outcrops in Kansas, Nebraska, Wyoming and South Dakota (Schumacher, 1997); Russell (1967) divided this chalk in Upper and Lower zones.

Lithologically, the Smoky Hill Chalk corresponds to olive-grey shaly chalk with white coccoliths, weathering orange-grey and yellow-grey, with thin seams of bentonite (Hattin and Siemers, 1987). The Lower Smoky Hill Chalk is hard, mainly composed by caprock with lichen spots, and it is recognized as a highly eroded area (Hattin and Cobban, 2011).

Stratigraphically, the Smoky Hill Chalk extends from the upper Coniacian to the lower Campanian (Obradovich, 1993), but the Lower Smoky Hill Chalk strings out from upper Coniacian to lower Santonian (Russell, 1967). The fossil localities in Ellis County, where the specimens were recovered, correspond to the lower layers of the Chalk, assigned to the upper Coniacian based on biostratigraphic zones of *Protosphyraena perniciosa* and *Spinaptychus* n. sp. (Stewart, 1990).

MATERIAL AND METHODS

Specimens of all three species of *Tylosaurus* were personally examined by me. Detailed photographs were taken using a Canon EOS t2i camera, and edited in Photoshop CS6 for Mac. Calipers and measurement tapes were used in order to take measurements. Drawings were made using Wacom tablet software and hardware, and using Photoshop CS6, as well. A phylogenetic analysis was performed using the dataset from Jiménez-Huidobro and Caldwell (2016). The dataset was analyzed using the software T.N.T (Goloboff et al., 2008), using TBR (1000 replicates/10 trees sampled per replicate), and using *Varanus* as outgroup (Palci et al., 2013). One tree was obtained using the data matrix that includes *T. kansasensis*, and a second tree was obtained as a result of the removal of *T. kansasensis*.

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1811

MOSASAURIDAE Gervais, 1852

TYLOSAURINAE Williston, 1897

TYLOSAURUS Marsh, 1872

Type species—*Tylosaurus proriger* (Cope, 1869)

Holotype—MCZ 4374.

Revised diagnosis—(1) twelve or thirteen maxillary teeth; (2) prefrontal does not contribute to external nares (only maxilla, premaxilla, and frontal); (3) frontal overlaps supraorbital portion of prefrontal; (4) frontal does not contribute to orbit; (5) ventroposterior process on jugal present; (6) ten or eleven pterygoid teeth; (7) thirteen teeth on dentary; (8) broad projection of dentary anterior to first dentary tooth; (9) unflutted and posteriorly curved teeth; (10) vertebral formula: 29 or 30 presacral vertebrae, six or seven pygals, 33 or 34 caudal chevron-bearing and 56–58 terminal caudals; (11) scapula smaller than coracoid, convex superior border of scapula; (12) radial process absent in humerus; (13) elongated radius, same length of metacarpals I and II; (14) ischium well expanded medially at symphysis; distal end of femur more expanded than proximal; (15) astragalus circular in shape; (16) phalangeal formula of pes 5-8-8-8- (Russell, 1967).

TYLOSAURUS NEPAEOLICUS (Cope, 1874)

Holotype—AMNH 1565.

Locality and horizon—Lower Smoky Hill Chalk Member, Niobrara Formation, Kansas, from the upper Coniacian to lower Santonian.

Synonymy—*Tylosaurus kansasensis* Everhart, 2005.

Emended diagnosis—*Tylosaurus nepaeolicus* differs from other species of *Tylosaurus* by the following combination of character-states: (1) premaxillomaxillary suture terminates posteriorly above midpoint between third and fourth maxillary tooth; (2) frontal with dorsal midline crest in juveniles, but poorly developed or absent in adults; (3) lateral borders of parietal table weakly convex; (4) infrastapedial process of quadrate poorly developed or absent; (5) suprastapedial process of quadrate long, reaching about half length of complete bone; (6) tympanic ala thick; (7) mandibular condyle of the quadrate broad lateromedially; (8) lateral crest of tympanic ala ends posteriorly near mandibular condyle.

DESCRIPTIONS

Skull

Premaxilla—the element constitutes a slender and cylindrical bone that consists of an edentulous rostrum, and the pre-dental process, followed by two pairs of teeth. A premaxilla for *Tylosaurus nepaeolicus* is not present in the holotype; however it is present in other specimens, such as AMNH 124, AMNH 1561, FHSM VP2209, and YPM 3969. The lengths of these bones are not available, since none of the premaxillae are complete. The anterior tip can be rectangular or rounded, and is certainly variable within specimens assigned to the taxon. The premaxilla does not have a dorsal crest. The maxillopremaxillary suture has either a U-shape or rectangular shape, a character that also seems to be variable in *T. proriger* (Fig. 3.4A, B). In *Tylosaurus 'kansasensis'* the premaxilla of the holotype, FHSM VP 2295, is 330 mm long, however, in the other referred specimens this bone is smaller, such as FHSM VP 15632, FHSM VP 17206 and FHSM VP 14840. The outline of the anterior portion in lateral view is either rectangular or rounded, contrary to Everhart (2005) who argued that a rounded shape of the rostrum is a feature to recognize *T. 'kansasensis'*. Observations of different specimens allow to recognize intraspecific variation in the shape of the rostrum, being 'rectangular' or 'rounded', as well as in the shape of the maxillopremaxillary suture (Fig. 3.4C, D, E).

The premaxilla does not have a dorsal crest. The internarial bar is formed almost entirely by the premaxilla. This bone contributes to the external naris.

Maxilla—in *Tylosaurus nepaeolicus* all the known maxillae bear twelve to thirteen teeth. The maxilla contributes to the lateral margin of the external naris where the latter begins above or anterior to the fourth maxillary tooth, and extends posteriorly to the eighth maxillary tooth. Above the tenth tooth the maxilla presents a posterodorsal process, triangular in shape, that projects dorsally, overlapping the prefrontal and contacting the frontal medially. The left maxilla of the specimen AMNH 124 is 365 mm in length, while the right is 371 mm long. In *T. 'kansasensis'* the maxilla bears twelve to thirteen teeth (twelve in IPB R322 and thirteen in FHSM VP 2295). The external naris, which begins above or anterior to the fourth maxillary tooth, are equivalent to that in adult specimens of *T. nepaeolicus*. The external naris extends posterior to the eighth maxillary tooth. The posterodorsal process is triangular in shape, projecting dorsally. In FHSM VP 2295 the left maxilla is 361 mm in length, while it is 348 mm long on the right.

Prefrontal—this laterally convex bone is trapezoid in shape, and wider at the posterior half. This bone is not significantly different in species of *Tylosaurus*. The prefrontal in *T. nepaeolicus* is preserved in AMNH 124 and is wider posteriorly, where it contributes to the anterior and part of dorsoanterior margin of the orbit. Anterolaterally, the prefrontal contacts the maxilla, while anteromedially it contacts the frontal, excluding the latter from the orbit. Posteriorly, this bone bears an elongated and rather thin posterior process that finishes in a clasp-shape, and participates in forming the dorsal rim of the orbit. The posterior process overlaps laterally with the anterior process of the postorbitofrontal, throughout the clasping artic- ulation surface. The prefrontal of *T. 'kansasensis'* is similar to that of *T. proriger* and *T. nepaeolicus* (Fig. 3.1B; 2; 3A, B). Dorsally, the prefrontal contacts the frontal, ventrally and anteriorly contacts the maxilla, and posteriorly has a process that contacts the postorbitofrontal, overlapping laterally as in *T. proriger* and adult *T. nepaeolicus*. The anterodorsal margin of the orbit is rounded and smooth. This bone participates in the anterodorsal margin of the orbit, excluding the frontal from that margin.

Frontal—part of the roof of the skull, this bone has a nearly triangular shape. The length of the bone is approximately twice the width. The anterior portion contributes to the posterior end of the external naris. In *Tylosaurus nepaeolicus* this bone overlaps anteriorly with the posterior process of the premaxilla, laterally with the prefrontal and the postorbitofrontal, anteroposteriorly and posteriorly the frontal contacts the parietal. The length of this bone in AMNH 124 is 179 mm, although it is broken anteriorly. This bone is dorsally flat (Fig. 3.1Bv; 3.5A) in *T. nepaeolicus*, while in *T. 'kansasensis'* it presents a well developed dorsal midline crest, a trait shared with juvenile and adult specimens of *T. proriger*, but not with adult specimens of *T. nepaeolicus* (Fig. 3.5). The internarial bar invades the anterior portion of the frontal, and the latter posteriorly invades the parietal. The frontal alae overlap with the postorbitofrontals (IPB R322, Fig. 3B). The frontal alae are broadly pointed and slightly sharper than in *T. proriger* and in adult specimens of *T. nepaeolicus*. In the specimen FHSM VP 2295 (Fig. 3.2) this bone is 170 mm in length.

Parietal—is a 'Y-shaped' bone (cf. Bullard, 2006) that participates in the posterior edge of the supratemporal fenestra. It is a narrow bone, wider in the anterior portion, than the posterior margin, and divided into two suspensorial rami of the parietal at the posterior end. In *Tylosaurus nepaeolicus* the parietal is preserved in AMNH 124 (Fig. 3.3A) and in other specimens as well. The parietal table is straighter than in *T. proriger* where the lateral margins are more convex in shape. In the latter species, the position of the parietal foramen is variable, from being completely within the parietal, to being on the posterior margin of the frontoparietal suture. Posteriorly, the nuchal fossa is less concave than in *T. 'kansasensis'* (Fig. 3.5A). In AMNH 124 the parietal is 129 mm in length. In *T. 'kansasensis'* the parietal is a slender bone, as well. The suspensorial rami are broken in specimens FHSM VP 2495 (Fig. 3.5B) and FHSM VP 15632, but they can be observed in FHSM VP 2295 (Fig. 3.2). The parietal table has slightly convex borders, as in *T. proriger*, and it is more pronounced than in adult specimens of *T. nepaeolicus* (Fig. 3.5). The parietal foramen is located close to the frontoparietal suture, although its position varies between and within species of the genus *Tylosaurus*. In FHSM VP 2495 the length of the parietal table is 112 mm.

Jugal—the jugal contributes to the posteroventral border of the orbit, which is gently rounded and smooth. There are not many jugals preserved in the various specimens of *Tylosaurus nepaeolicus*, although there is a partial one in FHSM VP 7262 (Fig. 3.6A). The latter is incomplete at the dorsal part of the vertical ramus, and at the anterior tip of the horizontal ramus. The posteroventral process is still visible and moderately well developed. The angle of the horizontal and vertical rami is close to 90º. The anterior tip of the horizontal ramus overlaps with the posteroventral margin of the prefrontal, while the vertical one is overlain by the ventral process of the postorbitofrontal. In *T. 'kansasensis'* both jugals are preserved in FHSM VP 2295 (Fig.

3.2) in articulation with the prefrontals and postorbitofrontals, and in FHSM VP 2495 the left jugal is a fragmented and isolated bone (Fig. 3.6B, C). This 'L-shaped' bone, with vertical and horizontal rami, describes an angle of approximately 90º. Between the two rami is the posteroventral process of the jugal, which is well preserved in FHSM VP 2295 and FHSM VP 2495, showing the same degree of development as the jugal in adult specimens of *T. nepaeolicus* and *T. proriger*. In the juvenile specimen of the *T. proriger* (RMM 5610) the process is located at the bottom of the vertical ramus, instead of at the intersection between the two rami (Fig. 3.6B, D).

Postorbitofrontal—this narrow bone contributes to the dorsoposterior margin of the orbit. In *Tylosaurus nepaeolicus* the postorbitofrontal is present in specimens, including both left and right elements in AMNH 124 (Fig. 3.6E). This bone has two processes, dorsal and ventral. These two processes are wider and shorter than the anterior or posterior and more elongate processes. The anterior process overlaps laterally with the prefrontal, above the orbit. Posteriorly, the longer process overlaps with the squamosal. Dorsally, the bone contacts the lateral process of the frontal, and ventrally the ascending ramus of the jugal. The left and right postorbitofrontals in AMNH 124 are 167 mm and 160 mm, respectively. In specimens of *T. 'kansasensis'*, this bone is present in FHSM VP 2295, FHSM VP 2495 and IPB R322. The postorbitofrontal contributes to the posterodorsal border of the orbit, which is smoothly rounded. In specimen IPB R322 there is a right postorbitofrontal, that is fragmented at the squamosal and prefrontal processes (Fig. 3.3B), while in FHSM VP 2495 the left bone is complete but isolated (Fig. 3.6F). In FHSM VP 2295 both postorbitofrontals are complete and in articulation with the other cranial bones (Fig. 3.2). The anterior process overlaps the prefrontal, the posterior process is longer and overlaps with the squamosal, the dorsal process articulates with the frontal to the level of the frontoparietal suture, and the ventromedial process articulates with the vertical ramus of the jugal. This bone does not show any differences with those of adult specimens of *T. nepaeolicus*, although the orbital face looks more rounded than the nearly rectangular surface of the juvenile *T. proriger* (RMM 5610).

Squamosal—in *Tylosaurus nepaeolicus* this bone is preserved in many specimens, including AMNH 124 (Fig. 3.1A; 3.3A), AMNH 2167, and FHSM VP 7262. The squamosal is narrow and anteroposteriorly elongated, curving downwards posteriorly. Anteriorly, the squamosal overlaps laterally with the posterior process of the postorbitofrontal. Posteriorly, the squamosal expands, forming an ovoid surface, dorsally convex and ventrally concave, to articulate with the quadrate; next to the quadrate articulation surface, there is a small ventromedial articulation surface to contact the suspensorial ramus of the parietal. In *T. 'kansasensis'*, FHSM VP 2295 preserved both left and right complete squamosals in articulation with postorbitofrontals (Fig. 3.2). The anterior portion continues until it contacts the jugal process of the postorbitofrontal. The posterior portion has a concave ventroposterior face to articulate with the suprastapedial process of the quadrate. This bone does not seem to vary among *T. proriger* and adult *T. nepaeolicus*.

Pterygoid—In *Tylosaurus nepaeolicus* there is at least one isolated pterygoid present in YPM 3974. The bone bears seven pterygoid teeth, although the bone is broken anteriorly and at the posterior tip. The curvature of the bone, where the teeth are inserted, shows no differences from that of *T. proriger*. All teeth are incomplete, missing the apex of the crown, with a protruding and crystallized calcite pulp cavity infilling. The bases of the teeth suggest they are mediolaterally compressed. The ectopterygoid process is broken. In *T. 'kansasensis'* this bone is present in FHSM VP 2295, FHSM VP 2495 and FHSM VP 13742, although none are well preserved. In FHSM VP 2295 these bones are not visible, only a row of three teeth on the left and four teeth of the right pterygoids are exposed, between the two mandibles. In FHSM VP 2295 and FHSM VP 2495 the pterygoids present a fragmented tooth row. The tooth row is curved in shape, and it preserves six teeth in FHSM VP 13742 and nine teeth in FHSM VP 2495, although incomplete, while the pterygoid bears 10 to 11 teeth in *T. proriger* (Russell, 1967). Pterygoidal teeth are significantly smaller than are those of the marginal dentition; they are posteriorly curved and sharp at the tip. Due to taphonomy, it is not possible to see if the ectopterygoid contacts the maxilla or not. This bone is morphologically similar to that of *T. proriger* and adult *T. nepaeolicus*.

Quadrate—there are several quadrates of *Tylosaurus nepaeolicus* in different collections, including the holotype specimen AMNH 1565. The quadrate is mediolaterally compressed, with a well developed suprastapedial process that reaches one-third to the mid height of the shaft; this process is robust and thick, with no deflection when descending ventrally, making the stapedial notch look smaller in comparison to those present on the various specimens of *T. 'kansasensis'*. The infrastapedial process, if present, is poorly developed, although it is absent in most of the specimens. The tympanic ala of the quadrate is thick, broader than in the quadrate of *T. proriger*, and it extends downward, nearly to the mandibular condyle, and the tympanic rim is thick. Medially, the stapedial notch is dorsoventrally elongated, while anteriorly, the shaft of the bone looks rectangular in shape. Dorsally, this bone is saddle-shaped, with a crest at the articulation surface with the squamosal. Ventrally, the mandibular condyle of the quadrate is ovoid in shape, and convex to where it contacts the concave fossa of the surangular/articular. The quadrate of the holotype AMNH 1565 is 81.1 mm in height, while in YPM 3970 is 121 mm and YPM 3974 (Fig. 3.7A) is 81.5 mm tall. There are ten quadrates preserved of *T. 'kansasensis'*, belonging to six different specimens in the FHSM collections (see Fig. 3.7B). Surprisingly, these quadrates show remarkable similarities with those of *Russellosaurus coheni* (Polcyn and Bell, 2005). The bigger quadrates are FHSM VP 3366 (D) and FHSM VP 2295 (Fig. 3.7B), being about 9 and 7.5 mm tall, respectively, while the other quadrates are much smaller. The suprastapedial process is well developed and longer, although thinner than the adult of *T. nepaeolicus*, same character found between juvenile and adult of *T. proriger* and *Clidastes propython* (Table 3.1), reaching from about a half of the length of the complete bone to about two thirds of it; this process shows a deflection medially when is descending ventrally (Fig. 3.7E). The suprastapedial process takes part of the cephalic condyle, with a saddle-shaped dorsal rim that articulates with the squamosal. The median ridge is quite prominent in the bigger specimens (FHSM VP 2295 and FHSM VP 3366), although absent in smaller specimens. The infrastapedial process is absent or very poorly developed. The mandibular condyle has a convex surface, to articulate with the articular, and it is displaced anteriorly. On medial view, the stapedial pit looks elongated, rectangular in shape with a constriction in the middle (cf. Bell, 1997), similar to that of *T. proriger* and adult specimens of *T. nepaeolicus*. The stapedial notch has a semi-elliptical shape, and is proportionally bigger than in adult specimens of *T. proriger* and *T. nepaeolicus*, although in the juvenile specimen of *T proriger*, RMM 5610, this notch is still bigger than in adults (Fig. 3.8B); the stapedial notch is also wide, except in the right quadrate of FHSM VP 78, and is probably due to taphonomy. The tympanic ala is thick and it goes down until the mandibular condyle, similar to that of adult *T. nepaeolicus*, and the tympanic rim is thick as well.

Splenial—it is a long and slender bone participating in the intramandibular joint. In *Tylosaurus nepaeolicus* both left and right splenials are complete and well preserved in AMNH 134 (Fig. 3.1Bii, Biv) and still in articulation with the dentaries and angulars. Both splenials are laterally exposed below the eleventh dentary tooth, and medially below the seventh tooth. This bone is mediolaterally compressed. Anteriorly, the splenial starts as a sharp and mediolaterally flattened bone, expanding dorsoventrally as it proceeds posteriorly. Posteriorly, this bone finishes as an ovoid surface, taller than wide and posteriorly concave, where it articulates with the angular. In *T. kansasensis*, the best preserved and isolated splenial is the left bone from FHSM VP 2495. It is lateromedially flattened, narrows anteriorly, overlapping with the dentary, and finishes in a sharp anterior tip. The posterior portion is ovoid in shape, with a concave surface to articulate with the angular. In lateral view, the splenial is exposed below the eleventh dentary tooth, while in medial view this bone overlaps the dentary, covering the mandibular channel medially to the seventh dentary tooth, as in adult specimens of *T. nepaeolicus*. Both left and right splenials can be seen in the holotype (Fig. 3.2). This bone does not show any difference with either *T. proriger* or adult specimens of *T. nepaeolicus*.

Dentary—this is elongated and robust in bigger specimens, but more slender in lateral view, in smaller specimens. In *Tylosaurus nepaeolicus* both left and right dentaries are very well preserved in specimen AMNH 134 (Fig. 3.1Bii, Biv). Anteriorly, this bone has a rectangular shape in outline, with a predental process anterior to the first dentary tooth. The dentary is mediolaterally flattened, with the Meckelian canal at the medial face and extending the complete length of the bone. The left and right dentaries bear 14 teeth. In AMNH 134 the left dentary is 421 mm in length while the right is 375.5 mm long. In *T. 'kansasensis'* this bone shows a rectangular anterior projection, same character seen in *T. proriger* and adult specimens of *T. nepaeolicus* (Fig. 3.3). The bigger dentaries at FHSM belong to FHSM VP 15632 and FHSM VP 2295; in FHSM VP 15632 the right bone is 527 mm and the left one is 540 mm long, while in FHSM VP 2295 the right dentary is 441 mm and the left bone is 452 mm in length. All the complete dentaries bear thirteen teeth.

Marginal dentition—the maxillary teeth in *Tylosaurus nepaeolicus* are posteriorly recurved and labiolingually compressed, defining a clear oval in cross section. The crown presents fine striations, and some teeth, usually anteriorly situated, present only anterior carinae, while other teeth are bicarinate, anterior and posteriorly; all carinae are serrated with small denticles. The dentary teeth are not different from that of the maxilla, and are labiolingually compressed, posteriorly recurved and finely striated. The maxillary teeth are sharp and labiolingually compressed in *T. 'kansasensis'*. In the right maxilla of the specimen FHSM VP 2295 anterior teeth present anterior carinae. The dentary teeth are slender, striated, labiolingually compressed and posteriorly curved. In FHSM VP 78 some posterior teeth present both anterior and posterior carinae, with serrations. The space between teeth is less than 6 mm in FHSM VP 2295 and FHSM VP 78. The teeth do not exhibit significant differences with respect to *T. proriger* or adult specimens of *T. nepaeolicus* (Fig 3.3A, B).

Coronoid—this bone is present in different specimens of *Tylosaurus nepaeolicus*, and they are especially well preserved in AMNH 134, where both coronoids are present in articulation with the lower jaw (Fig. 3.1Bii, Biv). It is located in the anterodorsal quadrant of the surangular. Anteriorly, this bone is almost horizontal, while posteriorly it projects upwards, forming an angle approaching 140º. The left coronoid of *T. 'kansasensis'* is complete and well preserved in FHSM VP 2495, attached to the surangular. Laterally, the coronoid invades a small area of the surangular, and the anterior tip of the coronoid extends the anterior border of the angular and surangular. Medially, the bone overlaps with the surangular, occupying the anterodorsal quadrant. The anterior process is almost horizontal, while the posterior process has a vertical inclination. The angle between the two processes of the coronoid bone is potentially 140º, similar to that in *T. proriger* and adult specimens of *T. nepaeolicus*.

Angular—this lateromedially compressed bone is situated along the ventral border of the surangular bone, in the posterior lower jaw. This bone is well preserved in many specimens of *T. nepaeolicus*, including AMNH 134 where it is preserved in both left and right lower jaws (Fig. 3.1Bii, Biv). Anteriorly, the angular is ovoid in shape, taller than wide, and with a convex articulation surface to contact the splenial. The angular is narrow and thin as it continues posteriorly. The anterior face of the angular of *T. 'kansasensis'* is ovoid in shape, taller than wide, with a convex surface to articulate with the splenial. This bone narrows posteriorly, diminishing about at the middle point of the total surangular/ articular length in lateral aspect, similar to those of adult *T. nepaeolicus*. In the specimens FHSM VP 78, FHSM VP 2295 (Fig. 3.2), FHSM VP

2495, FHSM VP 15632 and in IPB R322 (Fig. 3.3B), both left and right angulars are in articulation with the respective surangulars.

Surangular/articular—the surangular is an elongated bone that participates in the formation of the posterior lower jaw. For *Tylosaurus nepaeolicus* these two bones are preserved in AMNH 134 (Fig. 3.1Bii, Biv). The total length of the left surangular + articular is 338 mm, whereas the elements from the right jaw are 354 mm total length. This element is lateromedially flattened, with a slightly convex ventral margin. Dorsoanteriorly, the coronoid buttress of the surangular is concave, to receive the coronoid, while dorsoposteriorly this bone is almost straight. This bone contributes with the anterior area of the glenoid fossa, to articulate with the mandibular condyle of the quadrate. Posterior to the surangular, the articular bone contributes to the posterior surface of the fossa, which is concave. The retroarticular process is deflected downwards and the posterior margin of the bone is rounded. The surangulars considered to represent *T. 'kansasensis'* are both from FHSM VP 2295, where the left bone is 280 mm and the right is 291 mm in length (Fig. 3.2). This long bone is lateromedially flattened, with a surangular coronoid buttress lower and thinner than in adult specimens of *T. proriger* and *T. nepaeolicus*, but similar to that of juvenile *T. proriger* RMM 5610. The articulation surface with the quadrate is highly concave. The suture between the surangular and articular is posterior to the articulation surface. The articular has a recurved shape dorsally, is flat ventrally, and rounded at the posterior border.

Basioccipital/Basisphenoid—in *Tylosaurus nepaeolicus* both bones are preserved in YPM 3969, while YPM 3974 only preserves a fragment of the basisphenoid, and FHSM VP 2209 only preserves the basioccipital unit. The basisphenoid is nearly rectangular, anteroposteriorly elongated and posteriorly wider. The parasphenoid process is not preserved in any of the specimens. Ventrally, the basisphenoid has a foramen, where probably the jugular vein was hosted (Russell, 1967:33) that passes through the middle of the bone, dividing it in left and right. The basioccipital bone is stout and triradiate. Anteriorly, two basal tubera develop at both left and right sides. Posteriorly, the occipital condyle is ovoid in shape. In *T. 'kansasensis'* there are only two isolated and well-preserved basioccipitals, preserved in FHSM VP 9350 and FHSM VP 15632. These bones are very small as compared to any adult *Tylosaurus proriger* or *T. nepaeolicus*. The occipital condyle is ovoid, i.e., wider than tall. Both FHSM VP 9350 and FHSM VP 15632 are missing the exoccipitals. The basal tubera is distally wider and moderately developed, as in all tylosaurine mosasaurs. In FHSM VP 9350 there is a clear suture that divides the bone into a left and right sides, a feature seen in *T. proriger* as well.

Postcranial skeleton

Vertebrae—the atlas complex, or first cervical, includes left and right atlas neural arches, an atlas intercentrum and an atlas centrum (odontoid). There is an atlas intercentrum and neural arches for *Tylosaurus nepaeolicus* preserved in NHM R3624, and only the atlas intercentrum in YPM 3974 and in FHSM VP 2209. The atlas intercentrum exhibits a prism-like shape, i.e., lateromedially elongated with a convex ventral face and a slightly concave dorsal face that contacts the condyle of the axis. The neural arches of NHM R3624 are laterally convex and medially concave, to which the odontoid articulates. Ventrally the neural arches have an articulation surface for the atlas intercentrum, while dorsally they bear a spinous process that faces medially, almost touching the spinous process of the other neural arch. Anteriorly, the surface is concave to receive the occipital condyle, and posteriorly, is slightly concave to articulate with the atlas centrum. At the lateral face, very short transverse processes are oriented downwards. Although this complete and articulated complex is present in the holotype of *T. 'kansasensis'* in FHSM VP 2295, it is crushed and hidden behind the squamosal (Fig. 3.2). At the FHSM collections, the only bone of the atlas present is the intercentrum (FHSM VP 3366). This element has a bowed prism shape (cf. Russell, 1967), where the ventral face is convex and the dorsal is slightly concave, for articulation with the atlas centrum. The atlas intercentrum has anterodorsal and posterodorsal surfaces that are both smooth and flat.

The axis, or the second cervical vertebra, is not known in any of the previously defined specimens of *Tylosaurus nepaeolicus*. The axis is present in *T. 'kansasensis'* in FHSM VP 2295, but hidden by the squamosal in that specimen. The axis in FHSM VP 15632 is isolated, complete and well preserved, while in FHSM VP 78 and IPB R322 this bone is in articulation with the atlas anteriorly and the third cervical vertebra posteriorly. The axis has a nearly circular centrum outline of both the condyle and cotyle. The axis neural arches appear fused, but the suture is still visible at the distal tip; the neural arches are broad in lateral view, in comparison with the more narrow neural arches of other vertebrae. The transverse processes are horizontal, short and wide. In dorsal view, it presents zygapophyses that project anterodorsolaterally, and a ventral hypapophysis with an articulating peduncle.

In *Tylosaurus nepaeolicus* the third to seventh-eighth cervicals are present in many specimens, e.g., FHSM VP 2209 and NHM R3624. The centrum is wider than long and dorsoventrally compressed, with an ovoid articular surface. The transverse processes project from the middle of the lateral surface of the centrum, and face upwards. The neural arch is lateromedially flattened, and anteroposteriorly wide. The ventral surface of the vertebra bears a hypapophysis, a small tubercle that is rounded in shape. These cervicals also possess well developed pre and postzygapophyses. Cervical vertebrae are also present in specimens assigned to *T. 'kansasensis'*, such as IPB R322, FHSM VP 78, FHSM VP 2295, FHSM VP 2495 and FHSM VP 15632 (Everhart, 2005). They have a moderately ovoid centrum, wider than long, with transverse processes from the lateral surface of the centrum projecting upwards. Pre and postzygapophyses are well developed, and the hypapophysis is positioned ventrally, and is also well developed and rounded. Using specimen IPB R322, it is possible to count eight cervical vertebrae, including the atlas and axis (Fig. 3.3B).

Isolated elements corresponding to dorsal vertebrae of *Tylosaurus nepaeolicus* are present in several specimens including FHSM VP 2209 and NHM R3624. The dorsal vertebra has an ovoid centrum, slightly wider than long in anterior and posterior view, with well developed transverse processes situated horizontally. In ventral view, the centra are smooth and slightly convex, and dorsally possess a spinous process that is lateromedially flattened and anteroposteriorly wide, and quite posteriorly deflected; dorsal vertebrae of this kind are usually anterior dorsals in the vertebral series. Another dorsal vertebra presents a taller centrum, longer than wide in anterior and posterior view, and ventrally even wider. The transverse processes originate ventrally on the lateral face of the centra, and project downwards. The centrum itself is a ventrally smooth and nearly flat surface, and the dorsal spinous process is lateromedially flattened and posteriorly deflected; such morphs are typical of posterior dorsals. Dorsal vertebrae are also present in *T. 'kansasensis'* in IPB R322 and FHSM VP 2495. The centrum is quite rounded in IPB R322, but ovoid and wider than long in FHSM VP 2495. The transverse processes are horizontally oriented in IPB R322, and they face upwards in FHSM VP 2495. These two character states, plus the presence of pre- and post- zygapophyses, suggest that FHSM VP 2495 is an anteriorly positioned dorsal vertebra. These dorsal vertebrae present robust transverse processes for rib attachments, and a smooth and convex ventral surface. In lateral view, the neural arches have a posterior deflection.

Neither specimens of *Tylosaurus nepaeolicus* nor *T. 'kansasensis'* preserve pygal vertebrae, and further, there are no caudal vertebrae preserved in specimens assigned to *T. nepaeolicus*. Intermediate caudal vertebrae are present in FHSM VP 78 and FHSM VP 2495, in the former the centrum is hexahedral, wider at the bottom, and in the latter it is more ovoid, and is longer than wide. Although none of these vertebrae have complete transverse processes, it is still noticeable that they face downwards. In ventral view, they present haemal arches, slightly medially inclined, to attach to the chevrons. Finally, terminal caudals are present in *T. 'kansasensis'*, in specimens FHSM VP 2495 and FHSM VP 15632. They are much smaller, with no transverse processes; their centrum is vertically ovoid, longer than wide in anterior and posterior view, and they have haemal arches on the ventral surface to articulate with the chevrons. None of these materials have preserved neural arches. A count of the vertebrae is not possible as none of the specimens are complete and articulated. The vertebrae do not show any important differences with any other *Tylosaurus* species.

Humerus—this bone is preserved in *Tylosaurus nepaeolicus* in FHSM VP 2209 and in YPM 3974. The right humerus in FHSM VP 2209 is 165 mm in length, while the left one in YPM 3974 is 101 mm long. Laterally, the humerus has an ectepicondylar groove located in the anteroventral quadrant of the shaft that hosts the radial nerve. Medially, this bone has a pectoral crest that originated at the proximal margin and goes down until about half of the shaft. Anteroproximally, a poorly developed anterior tuberosity shows up, and the glenoid condyle at the proximal face appears slightly convex. Distally, the anteriorly located ectepicondyle is poorly developed, and the entepicondyle is very small. In T. *'kansasensis'*, only the specimen FHSM VP 15631 includes a complete and well preserved right humerus (Fig. 3.8H), which is 96 mm in length, and 64 mm wide at the distal end. The distal end of this bone is more expanded than the proximal tip. This appendicular element is elongated and slender. Proximally, it has a condyle that articulates with the glenoid fossa (formed by coracoid and scapula), while the distal surface articulates with the radius and ulna. On the internal surface, the humerus has a pronounced pectoral crest, and a distally located foramen for the ectepicondylar nerve (radial nerve). Externally, the humerus presents a distally positioned ectepicondylar groove. The humerus does not seem to be different from other specimens assigned to *Tylosaurus*. Unfortunately, this is the only existing humerus assigned to *T. 'kansasensis'*.

Radius—this bone is preserved in *Tylosaurus nepaeolicus* but only in YPM 3974 (both right and left radii). It is an elongate element: the left radius is 75 mm in length and the right bone is 72 mm long, and both are lateromedially flattened. Distally the tip is broader than the proximal face, expanding posteriorly and forming a semi-fan-shape. The proximal border is slightly convex and almost straight in outline, while the distal border is also convex but convex and rounded in outline. This element is also present in *T. ‘kansasensis’*, but only in FHSM VP 15631. The right radius is 87 mm long, slender and thin; the width of the distal end is less than the half of the total length. The proximal surface for articulation with the radial facet of the humerus is quite flat, while the distal end is rounded in outline, gently convex, fan shaped and wider than the proximal tip. This bone is virtually equal to that of *T. proriger*.

Ulna—both ulnae are preserved in *T. nepaeolicus* in the specimen YPM 3974; the right ulna is complete and well preserved, while the left one is broken, missing the distal half. The right ulna is 65 mm long. This element is lateromedially flattened, slender and dorsoventrally elongated. The proximal face is more expanded than the distal margin of the bone. The anterior and posterior margins of the bone are concave. At the proximoposterior quadrant of the medial face, there is a depression, also seen in other species of *Tylosaurus*. The olecranon process of the proximal surface is poorly developed. In *T. ‘kansasensis’* it is also a long, slender and thin bone that articulates proximally with the humerus. The right ulna belongs to the specimen FHSM VP 15631, which is a nicely preserved bone. This element shows a depression on the internal face and a poorly developed olecranon process on the proximal face, where the triceps muscle inserts. The proximal face is more expanded and thinner than the distal end, as shown in other specimens of *Tylosaurus*. The distal end has a facet to articulate with the ulnare.

Ulnare—this carpal element is present in *T. ‘kansasensis’* only in FHSM VP 15631, and is a very small bone, located between the ulna and the fourth distal carpal. It is rounded, almost circular, and laterally flat, and does not differ from that of *T. proriger*. No ulnare elements are preserved for *T. nepaeolicus*.

DISCUSSION

Distinguishing between ontogenetic stages and interspecific variation can be problematic for fossil taxa, particularly because there are often very few known specimens representative of juvenile stages. This is also true for mosasauroids, though there is some good ontogenetic data for limb development and ossification patterns (Caldwell, 2012), and such features as the retention of large amounts of juvenile cartilage in large bodied adults (Sheldon, 1987, 1990; Caldwell, 1995, 1996; Caldwell et al., 1995). There are, however, a few additional differences that can be observed through a broad survey of mosasauroids in terms of the ontogeny of the quadrates, frontals and humeri (Table 3.1). As these elements are preserved in the known specimens assigned to *Tylosaurus nepaeolicus, T. 'kansasensis',* and *T. proriger*, it is possible to assess whether or not the differences between the first two taxa are species level differences, or ontogenetic.

In the original description of *T. kansasensis*, Everhart (2005) identified a number of these potential ontogenetically variable features in his 'readily recognizable' list of characters supporting *T. kansasensis* as a diagnosable taxon. These include: premaxillary rostral foramina large; predental process of premaxilla short (abbreviated) and rounded; quadrate ala thick; the quadrate conch (alar cavity) shallow; quadrate lacking infrastapedial process; parietal foramen adjacent to or invading frontoparietal suture;

frontal medial sutural flanges extend onto parietal; keel on dorsal midline of frontal; posteroventral angle of jugal virtually 90º.

The number and position of the premaxillary foramina is variable amongst specimens, and within an individual premaxilla, varies from right to left, in both *T. 'kansasensis'* and *T. nepaeolicus* (see Fig. 3.3; 3.6); therefore, such a character does not distinguish two separate morphotypes as previously suggested (Everhart, 2005) and is consistent with similar conclusions drawn by Konishi and Caldwell (2007) for plioplatecarpine mosasaurs.

The predental process of the premaxilla seems to be shorter in *T. 'kansasensis'*, when compared to *T. nepaeolicus*. Although the ratio could not be measured for *T. nepaeolicus*, since none of the specimens have a complete premaxilla with the internarial bar; the rostrum seems to grow longer as the animal grows. The largest individuals have the longest predental processes of the premaxilla.

There is a tendency for some skeletal elements to become stouter throughout ontogeny, and this includes the quadrates of mosasaurs. The suprastapedial process of the quadrate is more slender in juvenile specimens of *T. proriger* and *Clidastes propython*, in comparison with adults of the respective species, which reduces the size of the stapedial notch in the adults (Fig. 3.8A, B, C). The suprastapedial process is also more strongly curved in juveniles, being ventrally directed, whereas in adults the curvature angle is less pronounced, and the suprastapedial process is medially deflected. The exact same changes are also observed among specimens attributed to *T. 'kansasensis'* and *T. nepaeolicus* (Fig. 3.8A).

The position of the parietal foramen, the frontal medial sutural flanges, as well as the frontal midline crest are features that also change during ontogeny in other mosasauroids (see Table 3.1). A high degree of variation in some of these features is also observed in the post-embryonic development of extant terrestrial lizards. For instance, the position of the parietal foramen and the shape of the frontoparietal suture can be quite plastic throughout ontogeny, such as in the lacertid *Gallotia galloti* (Barahona and Barbadillo, 1998), the gymnophthalmid *Neusticurus ecpleopus* (Bell et al., 2003), as well as in *Iguana iguana* and the fossil lizard *Polyglyphanodon sternbergi* (T. Simões, pers. obs.); the position of the pineal foramen is also plastic intraspecifically within *T. proriger*, in which some specimens have the parietal (or pineal) foramen on the frontoparietal suture, and others within the parietal table far from the suture. The widespread variation of such ontogenetic plasticity for these features within squamates indicates they are not suitable as diagnostic characters.

The frontal midline crest is more strongly developed in adults as compared to juveniles in *Clidastes propython* (Fig. 3.8D); contrary to that, in *T. proriger* it remains well developed in juvenile and adult stages (Fig. 3.8E). However, the midline crest is more developed in *T. 'kansasensis'* in comparison to *T. nepaeolicus* (Fig. 3.8F), thus differing from the ontogenetic pattern observed in *C. propython*. The nuchal fossa, positioned posteriorly on the parietals for the reception of the cervical epaxial musculature, is open anteriorly in juveniles of *T. proriger*, whereas in adults there is a distinct anterior border for that fossa (this region of the parietal is unknown in *C. propython*). Such a pattern is also observed between *T. 'kansasensis'* and *T. nepaeolicus* (Fig. 3.8F).

Comparing the parietal tables of the various species of *Tylosaurus* reveals that the sides of the table in juveniles of *T. nepaeolicus* (previous *T. 'kansasensis'*) are more convex in comparison with adults of *T. nepaeolicus*. In the latter, the parietal table is slightly convex to straight laterally (Fig. 3.8F); this shows a tendency for elongation of the bone during the growth. When the frontal and parietal of *T. proriger* are compared to those of *T. nepaeolicus*, it is observed that the lateral borders of the parietals are convex (the juvenile condition in *T. nepaeolicus*) in both juveniles and adults. The same phenomenon is observed when the dorsal midline of the frontal is examined in *T. proriger*, where the eminence remains well developed from juvenile to adult stages, resembling the juvenile condition of *T. nepaeolicus*.

Humeri of juveniles of *Tylosaurus proriger* are currently unknown. However, in *Clidastes propython* (Fig. 3.8G) it is possible to observe a large number of changes throughout ontogeny with special regard to the development of the humeral processes. The pectoral and postglenoid processes become more robust in adults, as well as the entepicondyle. Furthermore, the humeral shaft is also larger in the adults. The humerus in *T. nepaeolicus* and *T. 'kansasensis'* has processes less pronounced than *C. propython*. However, some of the changes observed in *C. propython* are also observed in *T. 'kansasensis'* and *T. nepaeolicus*. For instance, the pectoral process in *T. nepaeolicus* is proportionally stouter than in *T. 'kansasensis'*, and the entepicondyle in *T. nepaeolicus* is also proportionally larger than in *T. 'kansasensis'*.

Since *T. 'kansasensis'* and *T. nepaeolicus* overlap stratigraphically, geographically (upper Coniacian of the Lower Smoky Hill Chalk, Niobrara Formation, Kansas), as well as morphologically, and considering the smaller overall size of *T.*

'kansasensis' relative to *T. nepaeolicus*, the position taken here is that they represent distinct semaphoronts of the same species: *Tylosaurus nepaeolicus*. Invoking sympatric speciation to explain the presence of virtually identical species is a far more complex hypothesis to support, than the one I propose here, that *T. kansasensis* cannot be distinguished from *T. nepaeolicus*, and that the minor character differences reflect ontogenetic variation within a very small sample size of less than forty individual specimens.

PHYLOGENETIC ANALYSIS

In order to compare the effects of the removal of *T. 'kansasensis'* upon the sister group relationships of tylosaurine mosasaurs, I re-analyzed the dataset of Jiménez-Huidobro and Caldwell (2016; Chapter 2), deleting *T. 'kansasensis'* as an OTU, thus utilizing only comparable semaphoronts. Furthermore, the paucity of information on post-embryonic morphological variation in mosasauroid squamates (which I tried to shed some light on in the present paper) makes the inclusion of juvenile specimens in cladistic analyses even more problematic, as it is difficult to determine which features observed in juveniles will be most prone to modification when the skeletally mature condition is attained. Therefore, I kept only information obtained from adult specimens (previously referred to *T. nepaeolicus*) in the dataset. The resulting trees are shown in Fig. 3.9.

There are two groups that appear clearly separated on both phylogenetic trees: the first one includes the clades Tethysaurinae + Yaguarasaurinae, Tylosaurinae, and Plioplatecarpinae, and the second group is formed by Halisaurinae and Mosasaurinae, in agreement with Palci et al. (2013). The clade Tylosaurinae is separated in two groups: *Taniwhasaurus* and *Tylosaurus*. In the clade *Taniwhasaurus, T. oweni* appears as sister group of *T. antarcticus*. The clade *Tylosaurus* shows *T. proriger* as sister group of *T. bernardi* (Jiménez-Huidobro and Caldwell, 2016), and both as sister group of *T. nepaeolicus* and *T. 'kansasensis'*. The first tree (Fig. 3.9A) shows a polytomy of *T. nepaeolicus, T. 'kansasensis', T. proriger* and *T. bernardi*, where the relationship between the two taxa at the base of the branch is unresolved. When *T. 'kansasensis'* is removed, the general topology of the tree does not change, although *T. nepaeolicus* appears alone at the base of the *Tylosaurus* clade, as a sister group of the *Tylosaurus proriger* + *Tylosaurus bernardi* branch (Fig. 3.9B). The clade Tylosaurinae and the clade *Taniwhasaurus* are well supported by Bremer indices ≥ 10. However, the clade *T. proriger* + *T. bernardi* only presents Bremer = 3 when *T. 'kansasensis'* is included, and the relationship between *T. nepaeolicus + T. bernardi, T. nepaeolicus,* and *T. 'kansasensis'* is weakly supported only by Bremer = 1. When *T. 'kansasensis'* is removed, the relationship between *T. proriger* and *T. bernardi* improves to Bremer = 8, although their relationship with *T. nepaeolicus* is still poorly supported (Bremer = 1).

The autapomorphic character state that defines *T. nepaeolicus* in the phylogenetic tree including *T. 'kansasensis'* is character 38 [1], ectopterygoid contacts the maxilla, whereas the autapomorphy for *T. 'kansasensis'* is 84 [1], last hypapophysis occurs on eight or more posterior cervical vertebra. When *T. 'kansasensis'* is excluded from the analysis, *T. nepaeolicus* is defined by the same autapomorphy (38[1]) and also by character state 47 [1], quadrate ala thick. The first character (38[1]) did not appear when synapomorphies were mapped onto the tree including *T. 'kansasensis'* as it was considered ambiguous as a consequence of the polytomy formed by this species and *T. nepaeolicus*. When *T. 'kansasensis'* was excluded from the analysis, the character (38[1]) appeared as an unambiguous autapomorphy, not seen in any other tylosaurine or russellosaurine mosasaur (Polcyn and Bell, 2005), except in *Romeosaurus fumanensis*.

CONCLUSIONS

The type species *Tylosaurus proriger* occupied the Western Interior Seaway between the late Santonian to the early Campanian, while the older species, *T. nepaeolicus*, occupied the same region between the late Coniacian to the early Santonian (Russell, 1967; Sheldon, 1996). Close comparison of the anatomical features of *T. nepaeolicus* with those of the sympatric species erected by Everhart (2005), i.e., *T. 'kansasensis'* Everhart, 2005, have revealed no differences between the two nominal species that cannot be attributed to size and thus ontogenetic stage. My observations indicate that the diagnostic characters argued to distinguish *T. 'kansasensis'* are shared with *T. nepaeolicus*, and in some cases even with *T. proriger*, and therefore are not sufficient enough to warrant the erection of a new species. There are no juvenile specimens reported for *T. nepaeolicus*, while at the same time, all the specimens assigned to *T. 'kansasensis'* present juvenile characters such as the longer and more slender and medially deflected suprastapedial process of the quadrate, the nuchal fossa of the parietal is open anteriorly, the humeral pectoral process is more slender, and there is a smaller entepicondyle. Importantly, those same features are present in juvenile specimens of *T. proriger*, leading me to propose that they can be considered as ontogenetic markers, and that the later occurring *T. proriger* is perhaps paedomorphic for a number of characters possessed in earlier ontogenetic stages of *T. nepaeolicus*. The differences between *T. nepaeolicus* and *T. 'kansasensis'* are argued here to be the product of ontogenetic variation, not sympatric speciation. Such a possibility describes the data using far fewer ad hoc explanations than does the difficult model proposed by postulating sympatric species of *Tylosaurus*.

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Table 3.1. Comparisons between juveniles and adults of three species of mosasaurs: *Tylosaurus nepaeolicus* (*Tylosaurus 'kansasensis'* as juvenile of *Tylosaurus nepaeolicus*), *Tylosaurus proriger* and *Clidastes propython*. **X** and **Y** show different character states; **?** shows that the character was not preserved to asses; **NP** means the character is not present in the taxon.

	Tylosaurus 'kansasensis'	*Tylosaurus nepaeolicus*	*Tylosaurus proriger (juvenile)*	*Tylosaurus proriger (adult)*	*Clidastes propython (juvenile)*	*Clidastes propython (adult)*
Parietal nuchal fossa with anterior border indistinct (X)/ distinct (Y).	X	Y	X	Y	?	?
Degree of curvature of suprastapedial process of the quadrate more (X)/ less (Y) pronounced.	X	Y	X	Y	X	Y
Suprastapedial process of the quadrate is more slender (X)/ robust (Y)	X	Y	X	Y	X	Y
Posterolateral processes of the frontal more slender (X)/ robust (Y).	X	Y	X	Y	?	?
Frontal midline crest present (X)/ weak or absent (Y).	X	Y	X	X	?	Y

Humeral shaft slender (X)/ stouter (Y).	X	X	?	?	X	Y
Humerus entepicondyle less (X)/ more (Y) robust.	X	Y	?	?	X	Y
Humerus postglenoid process less (X)/ more (Y) robust.	NP	NP	?	?	X	Y
Humerus pectoral process less (X)/ more (Y) robust.	X	Y	?	?	X	Y

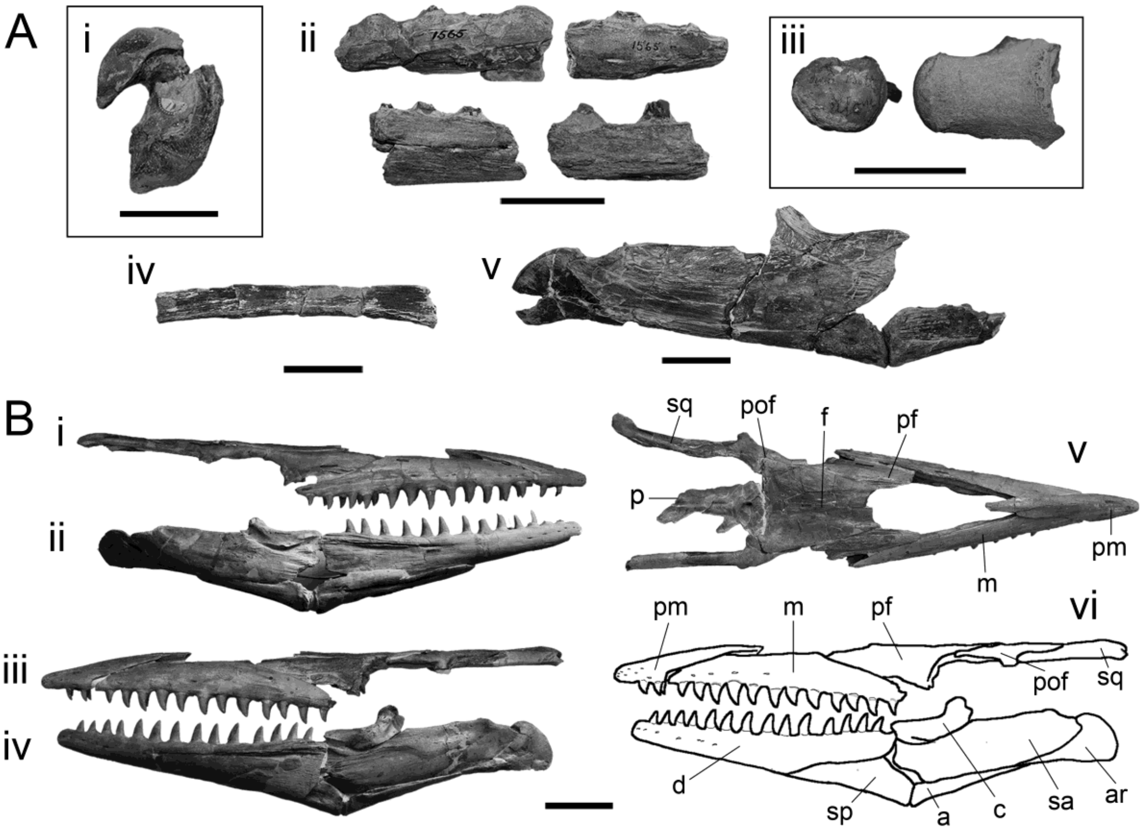

FIGURE 3.1: **A**, holotype of *Tylosaurus nepaeolicus* AMNH 1565: **i**, right quadrate, scale bar 5 cm; **ii**, fragments of maxillae and premaxilla, scale bar 5 cm; **iii**, partial isolated dorsal vertebra, scale bar 5 cm; **iv**, fragmented rib, scale bar 5 cm; **v**, right post-dentary elements, including the surangular, angular, coronoid, articular and a fragment of the splenial in articulation with the angular. **B**, The best preserved skull of *Tylosaurus nepaeolicus* AMNH 124, with the associated lower jaw AMNH 134: **i**, right side of the skull roof AMNH 124; **ii**, complete right lower AMNH 134; **iii**, left side of the skull AMNH 124; **iv**, complete left lower jaw; **v**, dorsal view of the skull AMNH 124; **vi**, drawn outline of the left side of the skull and lower jaw, based on 1Biii and 1Biv. Scale bar equal to 10 cm.

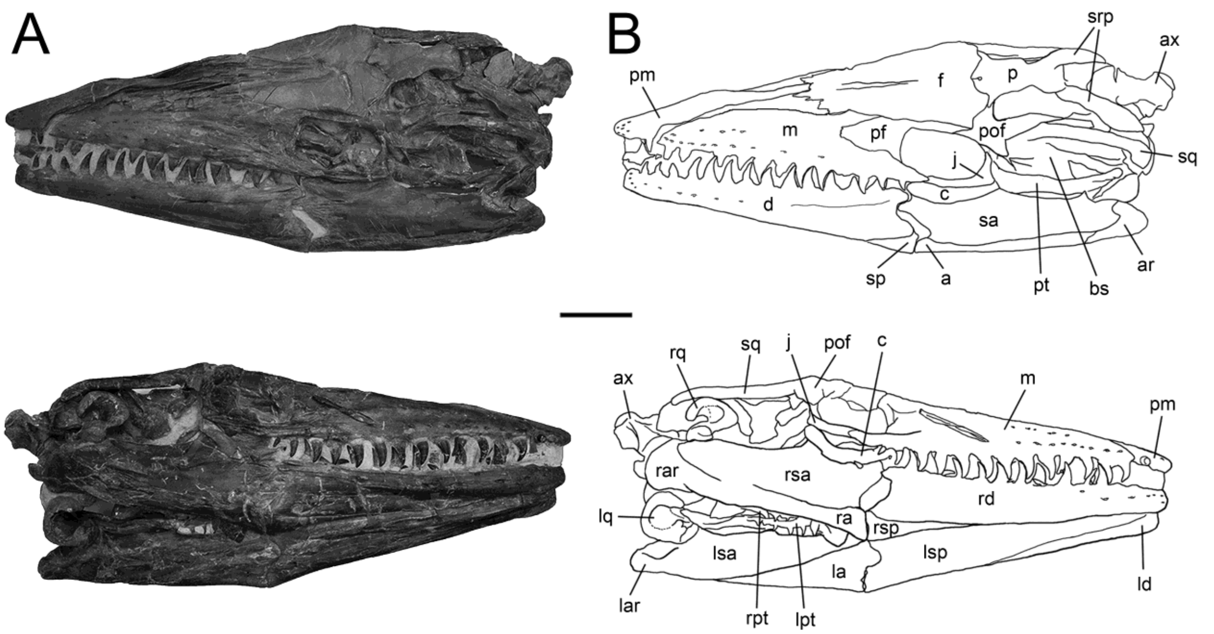

FIGURE 3.2. Right and left lateral views of the holotype skull of *Tylosaurus 'kansasensis'* FHSM VP 2295. **A**, Photograph; **B**, Diagram. Scale bar equal to 10 cm.

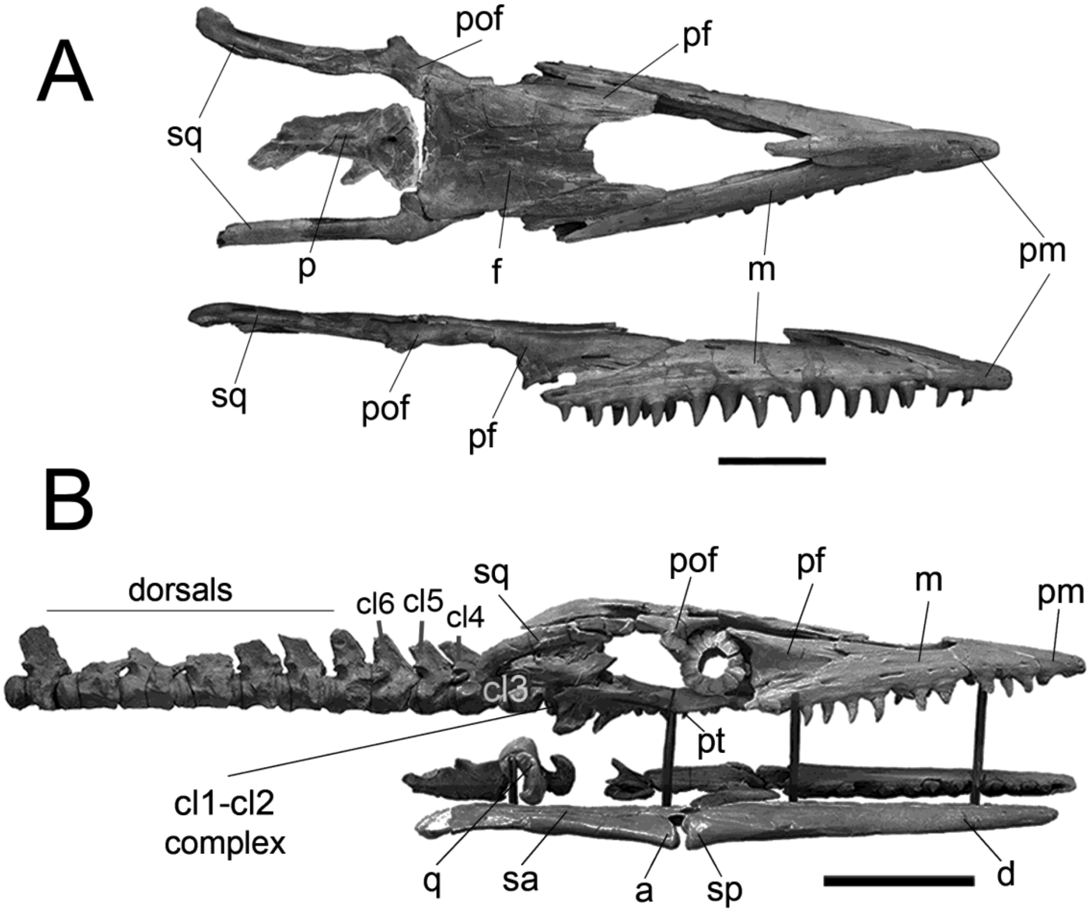

FIGURE 3.3. Comparison between partial skulls of **A**, *Tylosaurus nepaeolicus* AMNH 124; and **B**, *Tylosaurus 'kansasensis'* IPB R322, previously assigned to *Clidastes tortor* (=*propython*). Scale bar equal to 10 cm.

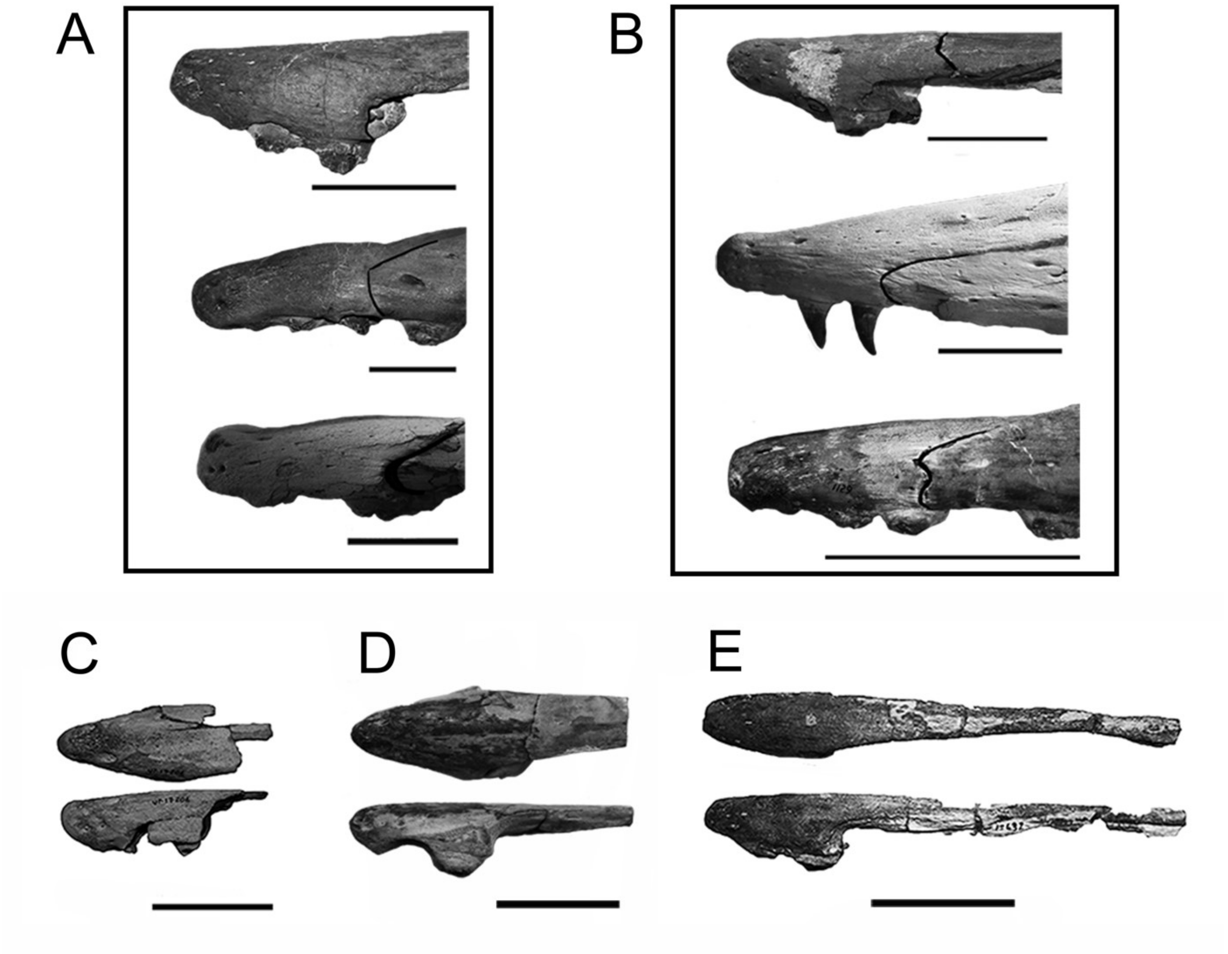

FIGURE 3.4. Dorsal and lateral views of premaxillae. **A**, *Tylosaurus nepaeolicus* from top to bottom YPM 3969, FHSM VP 2209, and AMNH 1561, scale bars equal to 5 cm; **B**, *Tylosaurus proriger*, from top to bottom AMNH 1543, FHSM VP 3, and KU 1129, scale bar equal to 10 cm; **C**, *Tylosaurus 'kansasensis'* FHSM VP 17206, scale bar 5 cm; **D**, *Tylosaurus 'kansasensis'* FHSM VP 14840, scale bar 3 cm; **E**, *Tylosaurus 'kansasensis'* FHSM VP 15632, scale bar 5 cm.

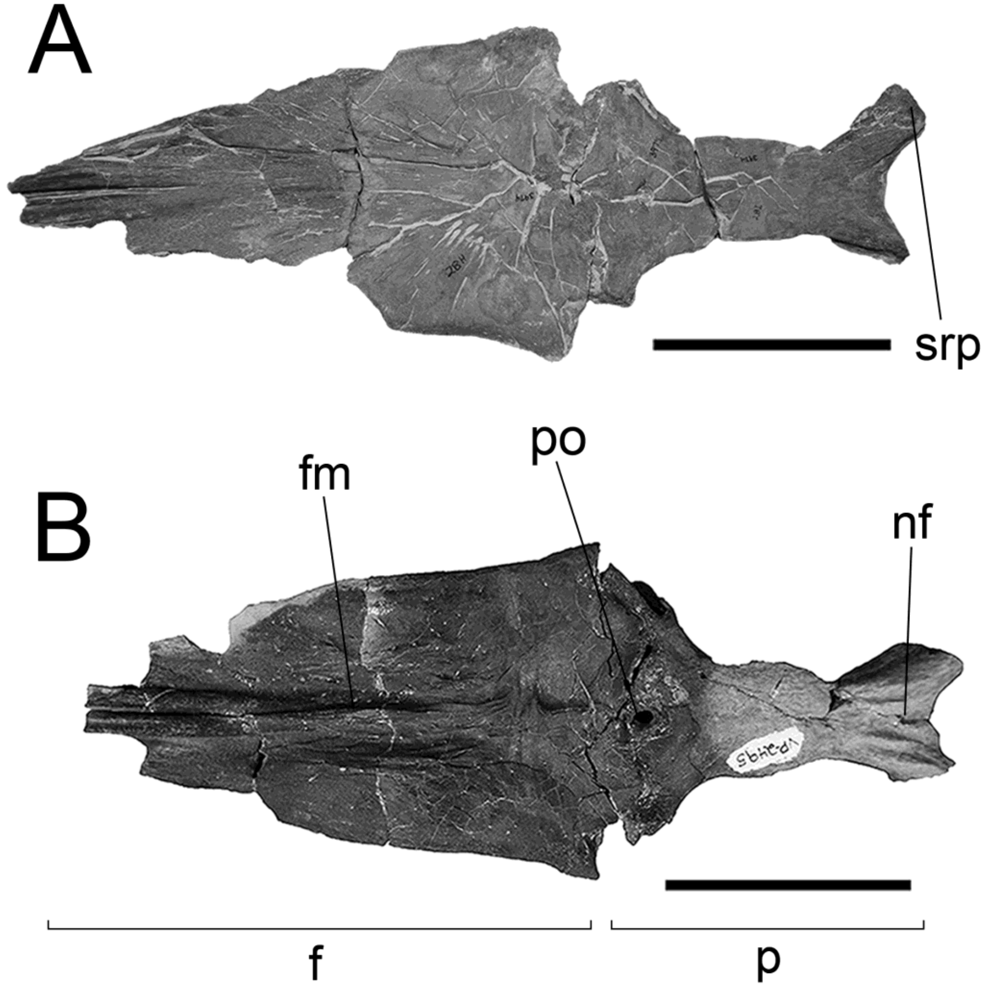

FIGURE 3.5. Frontal and parietal of: **A**, *Tylosaurus nepaeolicus* YPM 3974, scale bar equal to 10 cm; **B**, *Tylosaurus 'kansasensis'* FHSM VP 2495, scale bar equal to 5 cm.

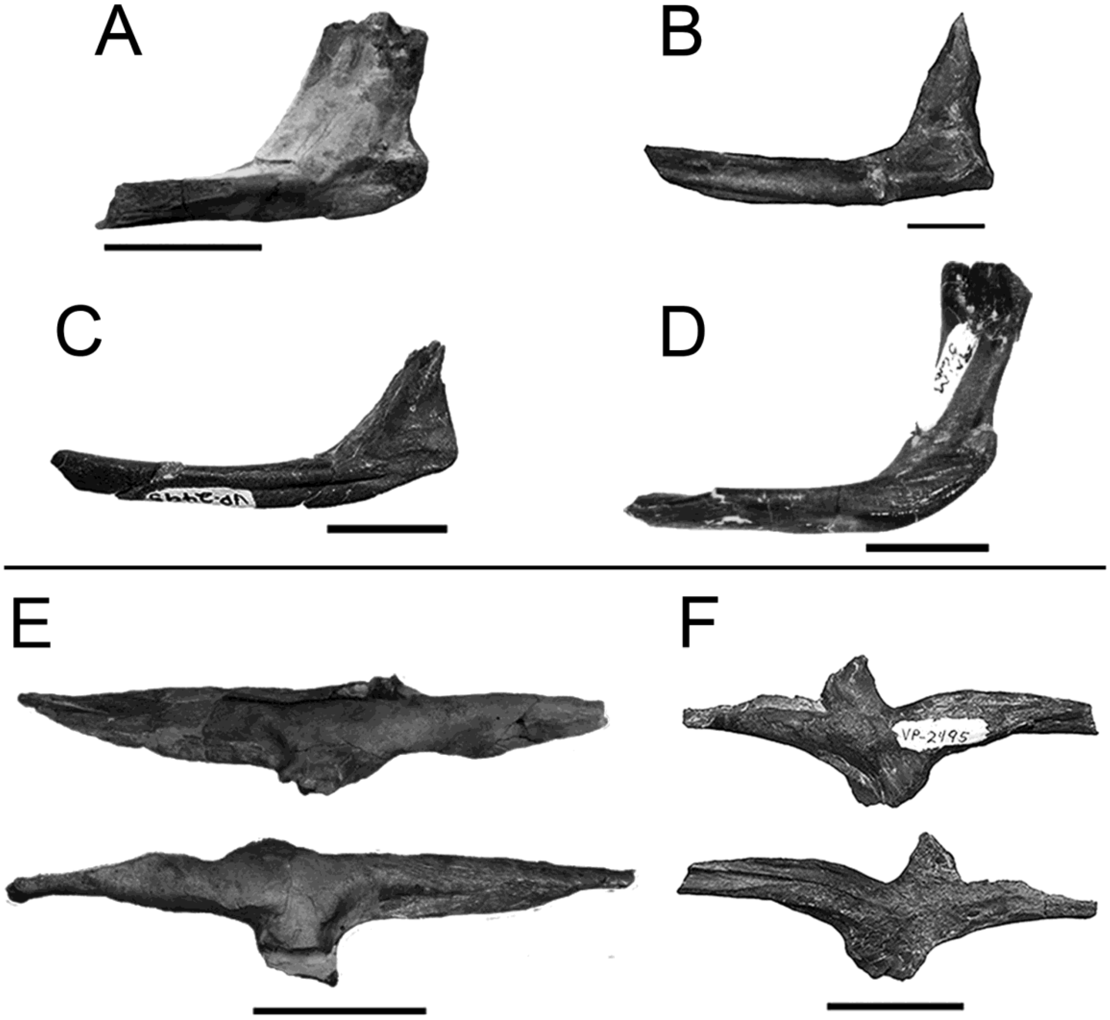

FIGURE 3.6. Comparisons of jugal and postorbitofrontal elements of various species of *Tylosaurus*. **A**, Left jugal of *Tylosaurus 'kansasensis'* FHSM VP 2495, scale bar equal to 2 cm; **B**, Left jugal of *Tylosaurus 'kansasensis'* FHSM VP 2295, scale bar equal to 2 cm; **C**, Right jugal of *Tylosaurus nepaeolicus* FHSM VP 7262, scale bar equal to 5 cm; **D**, Right jugal of juvenile *Tylosaurus proriger* RMM 5610, scale bar 2 cm; **E**, Left and right postorbitofrontal of *Tylosaurus 'kansasensis'* FHSM VP 2495, scale bar 3 cm; **F**, Right and left postorbitofrontal of *Tylosaurus nepaeolicus* AMNH 124, scale bar 5 cm.

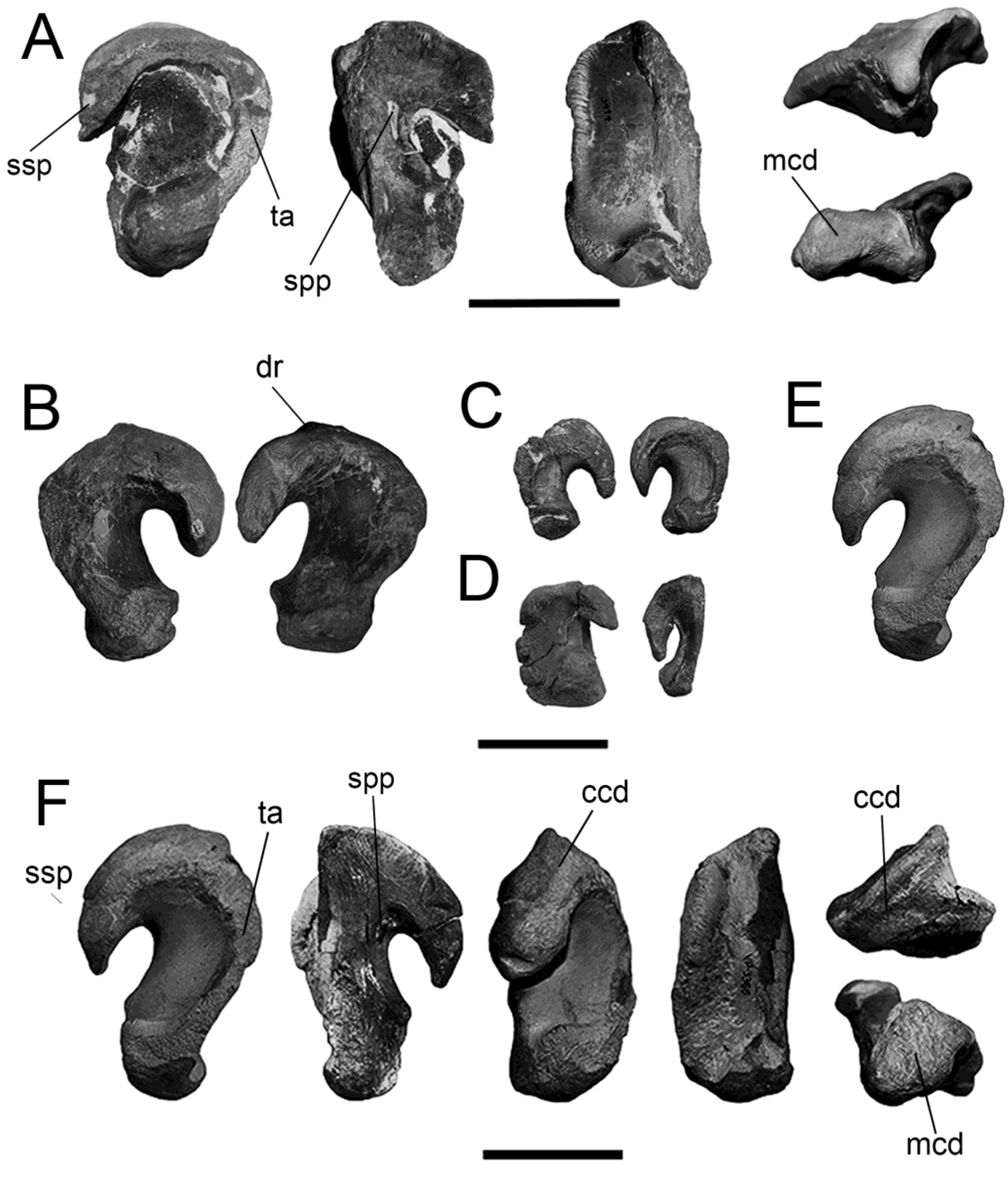

FIGURA 3.7. Quadrate of *Tylosaurus nepaeolicus* **A**, YPM 3974. Quadrates of *Tylosaurus 'kansasensis'*. **B**, FHSM VP 2295; **C**, FHSM VP 15632; **D**, FHSM VP 78; **E**, FHSM VP 3366, scale bar equal to 5 cm; **F**, Different views of FHSM VP 3366 quadrate: lateral, medial, posterior, anterior, dorsal and ventral; scale bar equal to 5 cm.

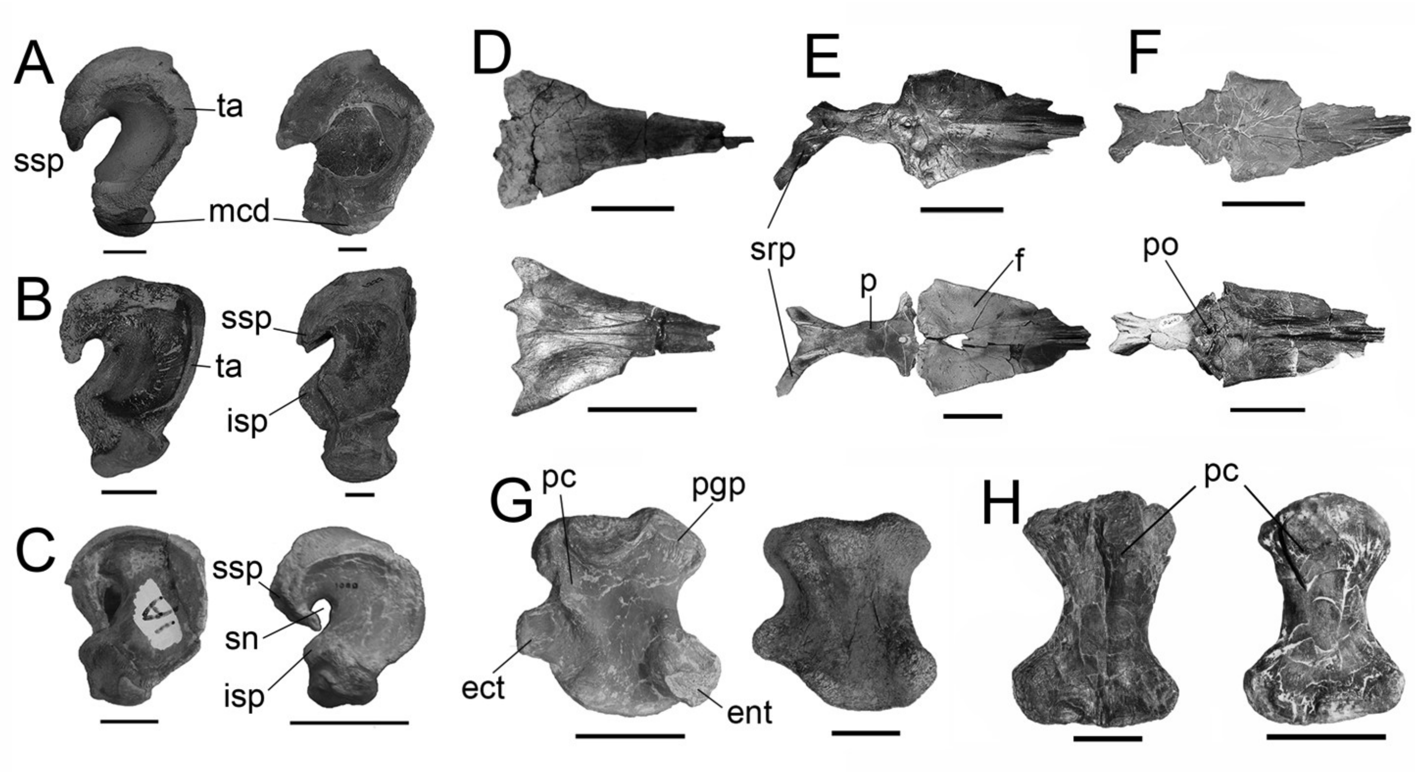

FIGURE 3.8. Comparisons between juveniles and adults: **A**, left, quadrate of *Tylosaurus 'kansasensis'* FHSM VP 3366; right, quadrate of *Tylosaurus nepaeolicus* YPM 3970, scale bars equal to 2 cm; **B**, left, quadrate of juvenile *Tylosaurus proriger* RMM 5610; right, adult of the same species AMNH 1555, scale bars equal to 2 cm; **C**, left, quadrate of *Clidastes propython* juvenile RMM 2473, scale bar equal to 1 cm; right, adult of the same species KU 1000, scale bar 5 cm, photos courtesy of V. Zavaleta; **D**, top, frontal of adult *Clidastes propython* FHSM VP 985.0012, photo courtesy of T. Konishi; bottom, juvenile of the same species ANSP 10193, photo courtesy of H. Street, both scale bar 5 cm; **E**, top, frontal and parietal of *Tylosaurus proriger* adult AMNH 4909, scale bar 10 cm; bottom, frontal and parietal of *Tylosaurus proriger* juvenile RMM 5610, scale bar 5

cm; **F**, top, frontal and parietal of *Tylosaurus* nepaeolicus YPM 3974, scale bar 10 cm; bottom, frontal and parietal of *Tylosaurus 'kansasensis'* FHSM VP 2495, scale bar 5 cm; **G**, left, adult humerus of *Clidastes propython* KU 1000, scale bar 5 cm, photo courtesy of H. Street; right, juvenile specimen of the same species RMM 2550, scale bar 5 cm, photo courtesy of H. Street; **H**, left, humerus of *Tylosaurus nepaeolicus* FHSM VP 2209; right, humerus of *Tylosaurus 'kansasensis'* FHSM VP 15631, both scale bars equal to 5 cm.

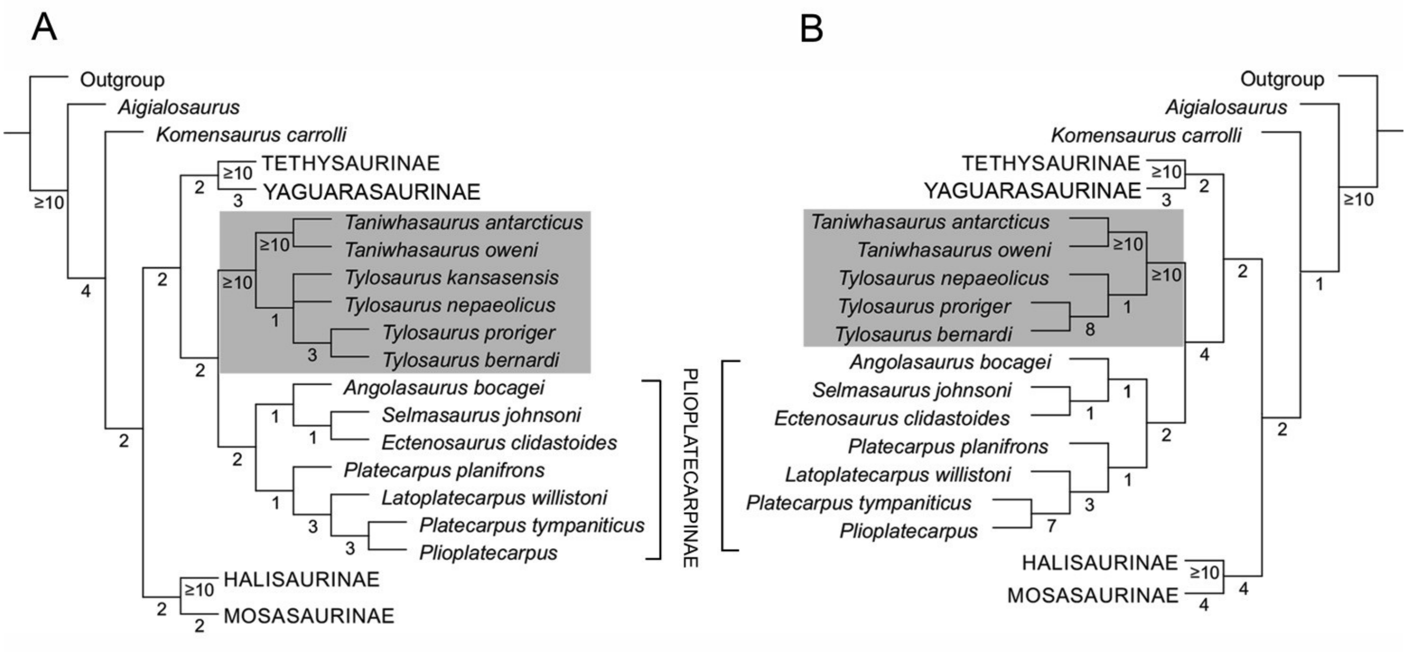

FIGURE 3.9. Abbreviated view of strict consensus trees depicting all major mosasauroid lineages. To the left, strict consensus tree (442 steps) obtained from 52 most parsimonious trees (MPTs) of 424 steps each (consistency index = 0.377; retention index = 0.724) with *Tylosaurus 'kansasensis'* in the analysis. To the right, strict consensus tree (439 steps) obtained from 26 MPTs of 422 steps each (consistency index = 0.379; retention index = 0.718) with *Tylosaurus 'kansasensis'* excluded from the analysis. Values beneath branches indicate Bremer (decay) indices, and the box highlights the clade Tylosaurinae.

CHAPTER FOUR

A NEW SPECIES OF TYLOSAURINE MOSASAUR FROM THE UPPER CAMPANIAN BEARPAW FORMATION OF SASKATCHEWAN, CANADA.

ABSTRACT

Mosasaurs assigned to the genus *Tylosaurus* have been reported from the North Atlantic Circle Basin in North America and Europe, from the Turonian of Chihuahua, Mexico, to the early Maastrichtian of Belgium. The youngest record of *Tylosaurus* in North America is from the middle Campanian of the Pierre Shale, South Dakota. Data obtained by examination of an almost complete skull and associated postcranial elements of a large tylosaurine mosasaur from the upper Campanian of Saskatchewan supports the recognition of this specimen as a new species. The specimen, collected from the Bearpaw Formation, southern Saskatchewan, Canada, presents unique features and combinations of features. It is recognized as a tylosaurine based on: edentulous rostrum, relatively long suprastapedial process of quadrate not reaching infrastapedial process, predental anterior extension of dentaries, twelve to thirteen maxillary and dentary teeth. Characters that support recognition of the new species include: exclusion of prefrontal from dorsal rim of orbit by anterior process of postorbitofrontal, frontal extends anteriorly well into narial openings, well developed dorsal medial crest of frontal, straight margins of parietal table, small infrastapedial process of quadrate located high on quadrate shaft almost touching suprastapedial process, thick tympanic ala of quadrate, 55 vertebrae anterior to chevron bearing caudals, rounded astragalus with big semicircular crural emargination. This new species extends the stratigraphic distribution of the genus *Tylosaurus* into the late Campanian, and the geographic distribution into the northern part of the Western Interior Seaway of North America.

INTRODUCTION

The fossil record of tylosaurinae mosasaurs in North America extends from the Turonian (Loera-Flores, 2013) to the middle Campanian (Nicholls, 1988; Martin, 2007; Bullard and Caldwell, 2010). In North America, *Tylosaurus proriger* Cope, 1869, described from the upper Santonian - lower Campanian of the Kansas Chalk, Niobrara Formation, is also known from the upper Santonian - lower Campanian of the Mooreville Chalk of Alabama (Russell and Applegate, 1970; Kiernan, 2002), the middle Campanian of the Taylor Group of Texas, and the middle Campanian of the Pierre Shale of Kansas and South Dakota (Russell, 1967). *Tylosaurus nepaeolicus* was described from the upper Coniacian - lower Santonian of the Kansas Chalk (Russell, 1967) and some referred specimens were recovered from the upper Coniacian of the Boquillas Formation, Texas (Bell et al., 2012). And finally, *Tylosaurus neumilleri* and *Tylosaurus pembinensis* were both described from the middle Campanian of the Pierre Shale of South Dakota and Manitoba, respectively (Martin, 2007; Nicholls, 1988, Bullard and Caldwell, 2010).

The Bearpaw Formation in both outcrop and subcrop, is located in Montana (USA) and southern Alberta and southern Saskatchewan (Canada) (Hatcher and Stanton, 1903). It is considered to be a Campanian-aged marine deposited shale, rich in marine reptiles, such as elasmosaurid and polycotylid plesiosaurs (Sato, 2003; 2005), chelonioid turtles (Brinkman et al., 2006) and a diverse assemblage of mosasaurs: Holmes (1996) recognized the plioplatecarpine *Plioplatecarpus primaevus* from Saskatchewan; Konishi et al. (2014) described an extraordinarily well preserved

Mosasaurus missouriensis and Konishi et al. (2011) described exceptional specimens of *Prognathodon* both from southern Alberta.

Bullard (2006) described the right side of a skull belonging to a tylosaurine mosasaur from the Bearpaw Formation of Saskatchewan in his dissertation, but this was never published. More recently, the preparation of the other half of the skull, together with the analysis of the postcranial material of the same specimen, allowed the collection of more data and supports the recognition of a new species (Fig. 4.1). The specimen indeed shows a set of unique characters that distinguish it from all the other *Tylosaurus* species. The aim of this research is to present the new taxon from the upper Campanian of the Bearpaw Formation of Saskatchewan (Canada), highlighting its differences in comparison to all the other tylosaurine mosasaurs.

GEOLOGICAL SETTINGS

Bullard (2006) described Royal Saskatchewan Museum specimen RSM P2588.1, which was found in deposits belonging to the Snakebite Member, one of eleven members of the Bearpaw Formation, near Herbert Ferry, Southern Saskatchewan (Fig. 4.1). The Bearpaw Formation consists of silty clays and subordinate sands deposited in shallow-water, marine conditions during the last part of the Late Cretaceous in the Western Interior Seaway (Caldwell, 1968); the Snakebite Member is dominated by dark grey silty clays, including numerous bentonite seams, and limestone concretions (Caldwell, 1968). Based on ammonites, the Bearpaw Formation ranges from the upper Campanian to the lower Maastrichtian. The deposits of the Snakebite Member cropping out near Herbert

Ferry, where RSM P2588.1 was found, are included in the *Baculites reesidei* Zone, suggesting an upper Campanian age (71-72 Ma) (cf. Caldwell, 1968; Kauffman et al., 1993).

MATERIALS AND METHODS

The specimen RSM P2588.1 was collected in 1995 from the Snakebite Member of the Bearpaw Formation, near Herbert Ferry on the shore of the lake Diefenbaker in Southern Saskatchewan. The right side of the skull was studied by Bullard (2006), while the left side of the skull was only recently prepared; both sides of the now prepared skull were studied. Detailed photographs were taken using a Canon EOS t2i camera, and edited in Photoshop CS6 for Macintosh computer. Drawings were made in Photoshop using a drawing tablet software and hardware. Measurements (in mm) were made using calipers and a measuring tape.

To run the phylogenetic analysis, the matrix was edited using Mesquite 3.03 for Mac; traditional search (heuristic algorithm) with 1000 replicates was performed in TNT 1.1 (Goloboff et al., 2008); cladograms were recovered using TNT 1.1. The trees were analyzed in Mesquite 3.03, and edited using Photoshop CS6 for Mac. Assessment of the phylogenetic relationships of tylosaurine mosasaurs was conducted using the data matrix of Jiménez-Huidobro et al. (2016; chapter 3), which itself was derived from Palci et al. (2013). The matrix was modified by the inclusion of the new species. Character 7 was deleted as most taxa were coded as a “?”. Characters 93 and 94 were summarized in a single character, as follows: Character (92): presacral vertebrae number: 32 or less (0);

33-38 (1); 39 or more (2). Character 95 was deleted because the sacral vertebral number does not apply to hydropelvic mosasauroids, and a new character (129) was added, addressing the condition of the sacrum - Sacrum: present (0); absent (1). The final data matrix consists of 42 terminal taxa and 129 characters.

SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA Oppel, 1811
Family MOSASAUROIDEA Gervais, 1853
Subfamily TYLOSAURINAE Williston, 1897
Genus *TYLOSAURUS* Marsh, 1872

Type Species—*Tylosaurus proriger* (Cope, 1869a) from the upper Smoky Hill Chalk member, Niobrara Formation, western Kansas, USA.

Range—upper Turonian? to lower Maastrichtian (Loera-Flores, 2013; Jiménez-Huidobro and Caldwell, 2016; Chapter 2)

Generic Diagnosis—twelve to thirteen maxillary teeth; prefrontal does not contribute to external nares; frontal overlaps supraorbital portion of prefrontal; frontal does not contribute to the orbit; ventroposterior process on jugal present; ten to eleven pterygoid teeth; broad projection of dentary anterior to first dentary tooth; thirteen teeth on dentary; six to seven pygals, 33 to 34 caudal chevron-bearing and 56 to 58 terminal caudals; scapula smaller than coracoid, convex superior border of scapula; radial process absent in the humerus; elongated radius, same length of metacarpal one and two; ischium well expanded medially at symphysis; distal end of femur more expanded than proximal; phalangeal formula of pes 5-8-8-8- (modified from Russell, 1967).

TYLOSAURUS SASKATCHEWANENSIS n.sp.

Holotype—RSM P2588.1. Moderately complete and articulated skull (Fig. 4.2), associated with a quite complete and disarticulated postcranium. The vertebral column is almost complete, except missing a few vertebrae in the caudal series; among the appendicular elements only the phalanges are missing.

Locality/Horizon—near Herbert Ferry on the shore of lake Diefenbaker, Snakebite Member, Bearpaw Fm., Saskatchewan, Canada, upper Campanian (Kauffman and Caldwell, 1993).

Etymology—named after the Canadian province of Saskatchewan, where the holotype and only known specimen was found.

Diagnosis—(1) extensive overlap of premaxilla onto the frontal; (2) anterior process of the frontal extending anteriorly up to half of the length of the external naris; (3) frontal with a well-developed dorsal midline crest; (4) exclusion of the prefrontal from the dorsal rim of the orbit, by a long anterior process of the postorbitofrontal; (5) suprastapedial process of the quadrate moderate in size; (6) infrastapedial process of the quadrate rounded, and located high on the quadrate shaft, almost touching the suprastapedial process; (7) tympanic ala of the quadrate thick; (8) femur longer than the humerus; (9) 55 vertebrae anterior to chevron bearing caudals; (10) rounded astragalus with big semicircular crural foramen.

DESCRIPTIONS

Cranium (Fig. 4.3)

Premaxilla—In RSM P2588.1 the premaxilla is complete, and appears long and slender. Its anterior tip is cylindrical in cross section, while in lateral view it has a rectangular shape. An edentulous rostrum, 74 mm in length, is present anterior to the premaxillary teeth. The predental process is characterized by a bump, visible on the ventral surface, anterior to the premaxillary teeth. Laterally, the suture with the right maxilla is sinusoidal in shape, while the maxillo-premaxillary suture is rectangular on the left side; both shapes are usually observed in *T. proriger*. The dorsal crest is moderately developed. The premaxilla bears two pairs of teeth, all actually preserved in the bone. The teeth are sharp, striated, posteriorly recurved, and labiolingually compressed, with only anterior carina. The premaxilla contributes to the anterior half of the medial margin of the narial openings. The internarial bar invades deeply into the frontal.

Maxilla—Both maxillae are present. The left maxilla is 654 mm long, while the right is 616 mm. Both left and right elements bear twelve teeth. The maxilla contributes to the lateral rim of the narial openings, which starts above the posterior border of the fourth maxillary tooth and ends at the posterior border of the ninth tooth; the external narial opening is five teeth long. The posterodorsal process is located above the tenth tooth, where it projects dorsally and contacts the anterior border of the prefrontal, and a small portion of the frontal; this process is subtriangular in shape, as in *T. proriger* (Russell, 1967). The contact between the right maxilla and the prefrontal is crushed and badly preserved.

Prefrontal—both prefrontals are present in the specimen, although the right one is crushed at the contact with the maxilla. The bone is trapezoidal in shape, slightly convex laterally, and bears a posterior process that overlaps the postorbitofrontal above the orbit. However, in RSM P2588.1 the prefrontal is excluded from the dorsal rim of the orbit by the anterior process of the postorbitofrontal, unlike in any other species of *Tylosaurus*. Therefore, the contribution of the prefrontal is limited to the anterior margin of the orbit; this contact surface appears smoothly rounded. Anteriorly and ventrally, the prefrontal contacts the maxilla, while dorsally it is in contact with the frontal, excluding the participation of the latter to the orbital rim.

Frontal—The frontal is a shield-shaped bone that is nearly triangular and is longer than wide (~304 mm in length). Its posterior portion is broad, while it becomes narrower anteriorly. In dorsal view, it is characterized by a well-developed median dorsal keel-shaped crest that is even sharper than the one present in *T. proriger*. It runs from the posterior half of the bone to the point where the frontal overlaps the posterior end of the premaxilla. The anterior processes extend up to half of the length into the narial openings, a feature not observed in other species of *Tylosaurus*. Anterolaterally, the frontal contacts the prefrontal, whereas posterolaterally it contacts the postorbitofrontal. Posteriorly, the lateral and medial frontal alae are rounded in outline.

Parietal—the parietal is incomplete and badly preserved, with the main fragment having been removed from the matrix during preparation. The bone is dorsoventrally compressed, and anteroposteriorly elongated. The dorsal surface is well preserved, but the ventral face is broken. A small fragment of the anterior parietal is still attached to the frontal. The incompletely preserved suture between the two bones shows that the parietal foramen is close to the suture with frontal. The outline of the parietal table is straight instead of curved, a character more pronounced in *T. saskatchewanensis*, than in *T. nepaeolicus*, and differing in both from *T. proriger* where the parietal table is dorsally convex. The suspensorial rami are dorsoventrally flattened, and diverge posterolaterally from the parietal table, forming an angle of about 30º with the mediolateral axis. Only a fragment of the right suspensorial ramus is preserved, and the left ramus is only preserved at the base. The total length of the parietal table is 236 mm. However, due to the incompleteness of the suspensorial rami, it is not possible to take measurements of the complete bone.

Postorbitofrontal—both left and right postorbitofrontal are present. This bone has a rhomboid shape with two long processes, one extending anteriorly and the other posteriorly, and two short and broad processes, one extending dorsally and the other ventrally. The postorbitofrontal contributes to the posterodorsal margin of the orbit, which is rounded and smooth. The long anterior process overlaps the posterior process of the prefrontal, excluding the latter from the dorsal margin of the orbit, feature unique for RSM P2588.1. Laterally, the long posterior process overlaps the squamosal; dorsally, the dorsomedial process articulates with the frontal and parietal, whereas laterally, the ventrolateral process extends down to half of the orbit with a concave surface, to finally overlap the jugal; this is visible only on the right side of the skull.

Jugal—only the right jugal is preserved in the holotype. This ‘L-shaped’ bone contributes to the posteroventral margin of the orbital notch. The ascending ramus is wide and laterally compressed, thicker than in *T. proriger*; it overlaps dorsally with the ventral process of the postorbitofrontal, but it is not possible to see that articulation surface as the process is hidden by the postorbitofrontal. The horizontal ramus is thin in comparison to the ascending one and the process articulates anteriorly with the prefrontal first, and then with the maxilla. The angle between the vertical ascending and horizontal rami is about 95º, similar to that in other species of the genus like in other *Tylosaurus* species. There is a very reduced posteroventral process of the jugal that looks like a short extension of the horizontal arm, less developed than that of *T. proriger*.

Sclerotic ring—The sclerotic ring, visible in lateral view, is only preserved on the right side of the skull, is composed of at least eight complete ossicles, unlike the fourteen ossicles described for *Tylosaurus proriger* (specimen FFHM 1997–10, Yamashita et al., 2015). The overall shape of the sclerotic ring is nearly circular, as it usually is in mosasauroids. The ossicles are slightly convex and finely striated.

Quadrate—both quadrates are present: the right one is almost complete but not well preserved, and is still in articulation with the skull; the left quadrate is disarticulated and anteroposteriorly crushed, missing the suprastapedial process. The quadrate is an ovoid bone, lateromedially compressed and longer than wide. The suprastapedial process is moderately long, extending downwards to the mid-length of the bone. The infrastapedial process is located high on the quadrate shaft, in contrast with other tylosaurines, such as *T. proriger* and *T. bernardi*, in which it is usually lower on the shaft, closer to the mandibular condyle. The tympanic ala is quite thick in comparison to that of *T. proriger*, and similar to that of *T. nepaeolicus*; it extends ventrally to almost contact the mandibular condyle. The tympanic rim is thin and sharp. Unfortunately, the stapedial notch is not recognizable, as the right quadrate is partially covered by sediment, and in the left one is missing. The stapedial pit, visible in the left quadrate, is rectangular and elongated dorsoventrally, as is typical in the genus *Tylosaurus*. The dorsal rim is saddle-shaped, and characterized by the presence of a crest similar to that of *T. proriger*. The right quadrate is in articulation with the rest of the skull and is anteriorly inclined. The posterodorsal surface of the suprastapedial process of the quadrate (cephalic condyle) articulates with the ventral face of the squamosal. The ventral condyle is convex and contacts the concave glenoid formed mostly by the surangular. The right quadrate is 183 mm high, while the left bone is 181 mm.

Squamosal—The right squamosal is complete in RSM P2588.1, while the left one is fragmented, missing the posterior portion. Its morphology is essentially the same as in *T. proriger*. Anteriorly, the bone overlaps the postorbitofrontal on a long articular surface. It curves downwards along an anteroposterior axis. The posterior portion of the bone is nearly ovoid in shape, with a convex dorsal surface and a concave ventral surface. Its anteroposterior length is 257 mm. The posteroventral surface of the squamosal articulates ventrally with the quadrate, medially with the suspensorial ramus of the parietal, and with a small portion of the supratemporal.

Marginal dentition—the marginal dentition is moderately well preserved. All of the teeth are relatively large and robust, labiolingually compressed, finely striated, and gently curved posteriorly, as in *T. proriger*. The fifth, sixth, and seventh maxillary teeth preserved on the right maxilla, measured from the base of the crown to the apex are 54, 55 and 54 mm, respectively. The first four maxillary teeth have only the anterior carina, while on the fifth tooth both anterior and posterior carinae are present. In the posterior portion of the dentary, all the teeth are bicarinate. The carinae of the dentary and maxillary teeth are serrated, with small and slender denticles that contribute to the cutting effectiveness of the teeth. The interdental space on both maxillae and the dentaries is quiet small, being about 9 mm between each tooth.

Dentary— both left and right dentaries are present, and moderately well preserved. Posteroventrally, the dentary contacts the splenial, and posteriorly the surangular. Both left and right dentaries have thirteen tooth positions. In lateral view, the anterior tip of the bone is rectangular in outline, with a projection that departs anteriorly to the first tooth; the same process is also present in *T. proriger* and all other species of *Tylosaurus*. The left predental process is 64 mm long, while the right process is 61 mm before the first tooth. The total length of the left dentary is 818 mm, and the right dentary is 766 mm, though the latter is posteriorly fragmented.

Splenial—both splenials are preserved. The left splenial is 450 mm in length, while the right bone is 426 mm. The anterior portion is mediolaterally flattened and becomes thicker posteriorly, elliptical in cross section, and higher than wide. Posteriorly, the articulation surface with the angular is slightly concave, similar to that of *T. proriger*. Dorsally, it articulates with the dentary, and contributes to the intramandibular joint. No significant differences were found with *T. proriger*.

Angular— both angulars are preserved, although the right one is broken posteriorly. The right angular is 316 mm in length, and the left one is not well preserved enough to take measurements. The anterior portion of the bone is elliptical in cross section, being higher than wide, while posteriorly it narrows and is mediolaterally flattened. Anteriorly, the articulation surface with the splenial is slightly convex. It articulates dorsally with the surangular and posteriorly with the anterior border of the articular. It also contributes to the intramandibular joint. It does not show differences with *T. proriger*.

Surangular—both surangulars are preserved in the specimen. The right surangular is well preserved, while the left one is incomplete and crushed. The surangular is elongated, mediolaterally flattened, that articulates anterodorsally with the coronoid, posteriorly with the articular, ventrally with the angular, and anteriorly with the posterior margin of the dentary. The coronoid buttress is low and thick with a dorsal border slightly rounded, as in *T. proriger*. The right surangular is 438 mm in length, whereas the left one is 391 mm long, although incomplete. The posterodorsal portion of the surangular contributes to most of the glenoid fossa, which articulates with the mandibular condyle of the quadrate. The glenoid fossa appears strongly concave.

Articular— The right articular is moderately well preserved and in articulation with the rest of the skull, whereas the poorly preserved left angular is still covered in matrix. Anteriorly, it contacts with a small portion of the angular, anterodorsally articulates with the surangular, and dorsally with the quadrate. It is rectangular in outline, with its long horizontal dimension following the same horizontal axis as the surangular; this feature differs from the condition in *T. proriger* where the articular curves downwards at the posterior end of the bone. Dorsoanteriorly, the articular contributes to the most posterior portion of the glenoid fossa to articulate with the quadrate. Posteriorly, the retroarticular process twists about 90º, and it possesses a present but poorly preserved foramen.

Axial skeleton (Fig. 4.4)

Vertebrae—The atlas complex is completely preserved: left and right neural arches, atlas intercentrum, and atlas centrum (i.e., odontoid). Ventrally, the two halves neural arches contact the atlas intercentrum, forming a ring, although the spinal processes of the atlas neural arches do not contact each other. The lateral processes of the neural arch appear as small, approximately rectangular protuberance. Posteriorly, the articular surface for the atlas centrum is concave. The atlas intercentrum is prism-shaped and is wider than tall; this bone is dorsally concave to receive the ventral surface of the centrum. The atlas centrum, or odontoid, has a dorsoventrally compressed cone shape (cf. Russell, 1967), and is wider than tall. The anterior surface of the centrum, or cotyle, is concave to articulate with the occipital condyle, while the posterior face (or condyle) is convex.

The axis attaches posteriorly to the atlas and is a robust vertebra. The centrum of the axis is rounded, almost circular. Laterally, two transverse processes extend, both are short, wide and extend horizontally, to occupy the whole lateral face of the centrum. The neural arches are fused to the centrum and are anteroposteriorly wide and lateromedially flattened. Ventrally, a posteriorly pointing tubercle (the hypapophysis) contacts the third cervical vertebra.

There are seven robust, moderately well preserved cervicals, all of which have an ovoid centrum that is wider than tall. Transverse process arises from the lateral face of the centrum and extends upwards. The neural arch is almost complete in all cervicals, although they are laterally deflected to the left side. The hypapophyses are not preserved, although the rounded base of the posteriorly facing peduncle is visible on the ventral surface of each centrum. Pre- and postzygaphophyses are only present in a few of the cervicals, and there are no zygosphenes and zygantra.

There are 39 dorsal vertebrae. The anterior dorsals resemble the cervicals, with a horizontally ovoid centrum shape. More posteriorly, the condyles become more rounded, and in the posterior trunk region, nearly triangular, with a wide ventral surface. The anterior dorsals have transverse processes that arise from the lateral face of the centrum and project dorsolaterally; in the mid-region of the trunk, these processes become more horizontal, and posteriorly, they incline ventrolaterally with robust surfaces for rib attachment. The ventral faces of the centra are smooth and slightly convex, and the dorsal face hosts the long and wide posteriorly inclined neural arches.

Posterior to the dorsal vertebrae, nine or ten pygals form the base of the tail. They are robust and large, with a centrum shape that is nearly triangular. The transverse processes arise from the ventrolateral face of the centra and are inclined downwards thus creating a large space between the neural arch and each transverse process, presumably for epaxial musculature attachments. The elongate transverse processes thin towards their tips, and do not have a surface for rib attachment. The neural arches are long, anteroposteriorly wide and posteriorly inclined. The ventral face of the centrum is smooth and convex.

Posterior to the pygals, there are 18 intermediate caudal vertebrae preserved; the complete number is not known. The centra range in shape from triangular to ovoid in shape, taller than wide, opposite to that of cervicals, following an anteroposterior trend. The transverse processes are still facing downwards. The dorsal face of the centra hosts the neural arches, posteriorly inclined, while the ventral face exposes the articulation surface for haemal arches, although there are no haemal arches preserved.

Only 13 terminals were found, although the posterior portion of the tail is missing. The size of these vertebrae decreases posteriorly. Condyles and cotyles are ovoid, and are taller than wide. As in the intermediate caudals, nearual spines are posteriorly inclined, but transverse processes are lacking. All bear articulation facets for the haemal arches, though none are preserved.

Appendicular skeleton (Fig. 4.5)

Scapula—both left and right scapulae are quite well preserved. The lateral face of the scapula is slightly convex, while the medial face is flat. The posterior margin of the scapula is gently concave. It forms about half of the glenoid surface. Anteroposteriorly, the scapula is wider, about 1.3 times the height. The left scapula is 90 mm in length and 115 mm in width, while the right one is 88 mm long and 118 mm wide. The suture between scapula and coracoid does not show any interdigitation. The lateral and medial faces of the scapula are covered by radial striations.

Coracoid—both coracoids are present and moderately well preserved. It is fan-shaped, dorsoventrally flattened, and much larger than the scapula, about twice the size of the latter, which is a character of *Tylosaurus*. The left scapula is 176 mm in length and 177 mm in width, whereas the right scapula is 179 mm long and 180 mm wide.

Anteriorly, the coracoid possesses a foramen for the insertion of the *M. supracoracoideus* (Russell, 1976). A gently concave facet forms about half of the glenoid fossa for the articulation of the humerus. The lateral face of the coracoid is gently concave. The ventral margin of the coracoid looks convex, while the anterior border is straight, and the posterior margin is strongly concave. At the dorsoanterior face, this bone shows a gently concave depression.

Humerus—The left humerus is complete, whereas the right one is missing the posterior margin of both the glenoid and distal condyles. They are slender, elongated, and longer than the maximum width, similar to that of *T. proriger*. The left humerus is 188 mm long, while the right is 197 mm length. Medially, the humerus bears a pectoral crest that extends down half the length of the bone. Laterally, each humerus bears a distal foramen (or ectepicondylar groove) that hosts the ectepicondylar nerve. The glenoid condyle is gently convex. Anterior to the glenoid condyle the humerus presents an anterior tuberosity, and posterior to the condyle, a poorly developed postglenoid process is preserved on the left humerus. The distal condyle is lateromedially compressed and is divided into two condyles: anteriorly, the ectepicondyle to articulate with the radius, and posteriorly, the entepicondyle, to contact the ulna. The midlength of the humeral shaft is compressed similar to the humerus of *T. proriger*.

Radius—both left and right radii are present. The right radius is well preserved, while the left is crushed and broken from the middle of the bone to the distal end. The radius is slender and thin, and spreads out anterodistally into a wide fan (cf. Russell, 1967). The left and right humeri are 135 mm and 137 mm length respectively. The ectepicondylar condyle is dorsoventrally thicker than the distal condyle. The shaft constricts at the midpoint of the bone.

Ulna—both ulnae are complete and well preserved. It is a slender bone, lateromedially flattened and elongated. The proximal and distal condyles are slightly anteroposteriorly expanded. Laterally, the ulna is flat and smooth. Anteroproximal on the medial face, the ulna presents a moderately well developed olecranon process, where the M. triceps muscle inserted. Posterior to the olecranon process, there is a depression at the proximal section of the medial face. The left ulna is 124 mm long while the right is 122 mm long.

Ilium—both ilia are well preserved: the left ilium is 301 mm in length, whereas the right bone is 299 mm long, including the acetabular region. The ilium is characterized by a slender and elongated anterior supracetabular process, dorsoanteriorly oriented, as in typical hydropelvic mosasaurs (cf. Caldwell & Palci, 2007). The anterior process is mediolaterally compressed and ovoid in cross section, especially at the mid-point, and more distally where it departs from the iliac shaft; the tip of the anterior process instead becomes slightly more rounded in section and on the lateral edge bears a dorsoventrally oriented facet, likely for attachment of the iliopubic ligament). The acetabular facet on the iliac shaft for articulation of femur appears slightly convex and quite roughened, suggesting the attachment of soft tissue. Both pubic and ischial facets on the ilium are quite straight in lateral/medial view, and about equal in length.

Ischium— both ischia are present and well preserved. The left ischium is 173 mm in length, while the right ischium is 168 mm long. The proximal head of the ischium bears two distinct facets: a dorsoposterior one for articulation with the ilium, and an anterior one to articulate with the pubis (cf. Russell, 1967). The iliac facet is large and slightly convex, while the pubic facet is quite small and convex. The distal end of the bone becomes mediolaterally flattened and anteroposteriorly expanded. The ischiadic tubercle is present as a wide triangular projection facing posteriorly and arising from above the mid-length of the shaft. The anterior margin is deeply concave, while the posterodorsal one is straight.

Pubis—both pubes are present and complete. The left pubis is 216 mm in length and the right is 209 mm long. The dorsal head is characterized by a gently convex articular surface that bears a small facet for articulation with the ilium, and a posteriorly oriented facet to articulate with the ischium. The proximal head of the pubis is dorsoventrally expanded while the rest of the shaft is basically rod-like and broadly ovoid in cross section. The distal end is slightly convex and about as large as the mid-shaft, with no terminal expansion, similar to that of mosasaurines. There is no evidence of a pubic tubercle along the anterior margin of the shaft, although a preservation bias cannot be excluded in this case. The obturator foramen is visible on the anterolateral surface of the bone, located very high on its proximal head. The obturator foramen hosts the obturator nerve, which innervates the ventral musculature of the thigh (Romer, 1942; Russell, 1967).

Femur—both femora are present but fragmented; the right femur is slightly twisted. It is a slender and elongated bone, distally broader than it is proximally. The femur presents a trochanter at the anteroproximal surface of the medial face; the trochanter looks similar to the crest that extends downwards to a point just above the midlength of the shaft. Proximally, the condylar head is thick and slightly convex. Distally, the bone becomes dorsoventrally convex, and expands to articulate with the carpals. The left and right femora are 201 mm and 193 mm in length respectively. The femur is only slightly longer than the humerus, similar to *Prognathodon* (Russell, 1967) and unlike *T. proriger* and *T. bernardi* (Russell, 1967; Jiménez-Huidobro and Caldwell, 2016).

Tibia—both tibiae are present; the left tibia is well preserved, but the right one is fragmented and reconstructed at the midpoint of the shaft. This bone is slightly longer than wide, considerably broader that the fibula. The shaft is anterodorsally constricted at the midpoint of the shaft. Anteriorly, the margin of the tibia is convex in proximal and distal sections and concave at the middle. Posteriorly, this bone is concave at the border of the crural foramen. Anteriorly in the medial face of the bone, there is a depression, where the tibia becomes thinner mediolaterally, although it remains thick at the posterior surface of the medial face. The proximal margin of the tibia is thicker than the distal border. The left and right tibiae are 132 mm and 136 mm length, respectively.

Fibula—both fibulae are preserved in good condition. It is a slender and elongated element, with a constriction at the mid-height of the shaft, and is slightly expanded at the proximal and distal margins. Proximally, this bone has a slightly flat articulation surface to contact the femur, oval in shape, and lateromedially thicker than the distal margin. Distally, the fibula is thick and convex at the border. The posterior border of the shaft is more convex than that of the anterior border. The left fibula is 112 mm and the right bone is 110 mm in length, respectively. No significant differences with respect to that of *T. proriger* were found.

Autopodium—the well preserved astragalus is mediolaterally flattened, discoidal in shape, and with a proximal emargination for the crural foramen facing the tibia. The crural emargination is quite regular in shape, with a semicircular outline, making the crural space larger. The maximum diameter of this bone is 53 mm. Some phalanges are also preserved. They are elongated and cylindrical elements that are mediolaterally compressed. They are slightly expanded anteroposteriorly, at the proximal and distal margins.

PHYLOGENETIC ANALYSIS

In order to assess the phylogenetic position of *T. saskatchewanensis*, a traditional search (TBR algorithm) was performed. A total of 26 MPTs were retained, with a consistency index [CI] of 0.37 and retention index [RI] of 0.72, and with a tree length of 447 steps. The resulting strict consensus tree is shown in Figure 4.6 including both Bremer support indices and bootstrap values >50%. *Tylosaurus saskatchewanensis* appears nested within the clade Tylosaurinae (Bremer = 6; Bootstrap = 96%), as sister group of the upper Coniacian-lower Santonian mosasaur *T. nepaeolicus* (weakly supported by Bremer = 1), and both emerge as the sister group of the clade *T. proriger* + *T. bernardi* (Bremer = 2; Bootstrap = 67%). The clade *Tylosaurus* is weakly supported (Bremer = 1). The relationship between species of *Taniwhasaurus* improves with a Bremer value equal to 4, and Bootstrap values = 88%. There is a clear separation of the group Tylosaurinae (Bootstrap value 96%, Bremer value equal to 6), related to the other mosasauroid clades. The clade Plioplatecarpinae appears differentially separated by a Bremer value equal to 3. The clade Tethysaurinae + Yaguarasaurinae are well defined, supported by Bremer = 2, the subfamily Mosasaurinae is supported by Bremer = 3, and the subfamily Halisaurinae is supported by Bootstrap value of 85%.

When the synapomorphies were mapped, the characters that define *T. saskatchewanensis* include: character 69[1], articular retroarticular process with extreme inflection, almost 90º; character 88[1], condyle of anterior-most trunk vertebrae essentially equidimensional. The clade *T. saskatchewanensis* + *T. nepaeolicus* is defined by character 45[1], quadrate posteroventral ascending tympanic rim high, with and elongate triangular crest; and by character 46[1], quadrate tympanic ala thick. The genus *Tylosaurus* is defined by character 91[1], centrum of cervical vertebrae almost as long as in other vertebrae. The clade Tylosaurinae is the sister group of Plioplatecarpinae, in accordance with previous phylogenies (e.g., LeBlanc et al., 2012; Palci et al., 2013).

DISCUSSION

The type specimen of *Tylosaurus saskatchewanensis,* RSM P2588.1, represents a large tylosaurine mosasaur with a skull length of 132 cm. The specimen is characterized by a unique suite of features that distinguish it from all the other species of *Tylosaurus*. Usually, the cervical vertebrae are somewhat dorsoventrally compressed in tylosaurines, however, in *T. saskatchewanensis* the condyle/cotyle faces of the cervicals are quite rounded, essentially equidimensional. The articular in tylosaurines is usually slightly laterally turned, such as in *T. proriger* and *T. nepaeolicus*, however, in *T. saskatchewanensis,* this lateral deflection is more pronounced from vertical position to horizontal, about 90º compared to the axis of the surangular. The frontal of *T. saskatchewanensis* has a very well developed dorsal midline crest, sharper than in *T. proriger* and *T. bernardi*, and more similar to that of *Taniwhasaurus oweni* and *Ta.*

antarcticus (Novas et al., 2002; Caldwell et al., 2005; Martin and Fernández, 2007); the frontal dorsal midline crest is absent in *T. nepaeolicus.*

Russell (1967) described the vertebral formula of *Tylosaurus* as 36-37 precaudals (cervicals + dorsals + pygals), probably based only on *T. proriger* as there are no known complete vertebral series for any specimens of *T. nepaeolicus*. For the European *T. bernardi*, Lingham-Soliar (1992) described >49 precaudals, Lindgren (2005) counted 47, while Jiménez-Huidobro and Caldwell (2016; chapter 2) noted >39 vertebrae anterior to the chevron bearing caudals. However, *T. saskatchewanensis* represents a bigger specimen with a higher vertebral count of 55 vertebrae anterior to the chevron bearing caudals. The femur of *T. saskatchewanensis* is slightly longer than the humerus, differing from that of *T. proriger* and *T. bernardi*, where the humerus and femur are virtually the same length. The astragalus possesses a semicircular emargination on the distal face, contributing to the crural space. This emargination is quite large in comparison to the astragalus of other tylosaurines, such as *Tylosaurus proriger* (Russell, 1967; Caldwell, 1996), and different from other mosasauroids, where the astragalus does not show a large emargination (Caldwell, 1996).

One character not accounted for in the data matrix is the elongated anterior process of the postorbitofrontal, only diagnostic for this specimen, which excludes the prefrontal from the dorsal margin of the orbit. In all other tylosaurines, both the prefrontal and postorbitofrontal contribute to the dorsal edge of the orbit, overlapping at about the midpoint of the dorsal margin, a character that was described by Russell (1967). Another unique character of *Tylosaurus saskatchewanensis* is the greater contribution of the frontal to the narial opening in comparison to other tylosaurines: in *T. proriger* and *T.*

bernardi the frontal contributes to a third, or less, of the posteromedial border of the narial openings (Russell, 1967; Jiménez-Huidobro and Caldwell, 2016; chapter 2), while in *T. saskatchewanensis* the anterior processes of the frontal extend half-length of the narial openings, and the internarial bar of the premaxilla extends far posteriorly, overlapping the frontal midline. This overlapping is however unknown in *Ta. oweni* and *Ta. antarcticus*. In the phylogeny, *T. saskatchewanensis* is the sister group of *T. nepaeolicus*, based on the morphology of the quadrate (i.e., the similar thickness of the tympanic ala, and the tall quadrate posteroventral ascending tympanic rim). The length of the suprastapedial process of the quadrate is similar to that of *T. proriger* and *T. nepaeolicus*. However, the infrastapedial process is located higher up on the quadrate shaft than the other North American tylosaurine mosasaurs, where the process is closer to the mandibular condyle, near to the ventral end of the suprastapedial process, and forms a small stapedial notch, although the processes do not contact each other, as in *Platecarpus* (Russell, 1967).

The stratigraphic range for the genus *Tylosaurus* in North America now ranges from the upper Turonian of Chihuahua, Mexico (Loera-Flores, 2013), to the upper Campanian of the Pierre Shale of South Dakota and Manitoba, and the Bearpaw of Saskatchewan, based on this chapter (Nicholls, 1988; Martin, 2007; Bullard and Caldwell, 2010). *Tylosaurus bernardi* (formerly *Hainosaurus bernardi* Dollo, 1885) from the Ciply Phosphatic Chalk of Belgium extends the temporal range of *Tylosaurus* to the lower Maastrichtian, showing a North Atlantic Circle Basin pattern of distribution for the genus (Jiménez-Huidobro and Caldwell, 2016).

CONCLUSIONS

The tylosaurine specimen RSM P2588.1 from the upper Campanian of the Bearpaw Formation, southern Saskatchewan, presents a unique set of characters that allows assignment to a new species: *Tylosaurus saskatchewanensis*. The new taxon represents a large tylosaurine mosasaur characterized by the exclusion of the prefrontal from the dorsal rim of the orbit by a long anterior process of the postorbitofrontal, the frontal extends anteriorly well into the narial openings, the dorsal medial crest of the frontal is well developed, the parietal table is straight in shape, the tympanic ala is thick, there are 55 vertebrae anterior to the chevron-bearing-caudals, and there is a rounded astragalus with a big semicircular crural emargination.

In terms of phylogenetic relationships, *T. saskatchewanensis* is nested within the monophyletic genus *Tylosaurus*, as the sister group of *T. nepaeolicus*. In comparison to all the other tylosaurines, the two species share the presence of a thick tympanic ala, and a high posteroventral ascending tympanic rim of the quadrate. The clade formed by *T. saskatchewanensis* and *T. nepaeolicus* appears as the sister group of the clade including *T. proriger* and *T. bernardi*. The *Tylosaurus* group is the sister group of the monophyletic genus *Taniwhasaurus*, forming the clade Tylosaurinae.

The Campanian corresponds to the longest age of the Late Cretaceous, from 70.6 to 83.5 Ma (Gradstein et al., 2004). The new species *T. saskatchewanensis* represents the latest North American tylosaurine that occupied the Western Interior Seaway during the late Campanian; indeed, before its discovery, the genus *Tylosaurus* in North America was known only until the middle Campanian (Nicholls, 1988; Bullard and Caldwell, 2010;

Martin, 2007). Although the new tylosaurine taxon is not the youngest species of *Tylosaurus*, as *T. bernardi* has been recognized from the early Maastrichtian of Belgium (Dollo, 1885), *T. saskatchewanensis* extends the stratigraphic range of the genus in the Western Interior Seaway.

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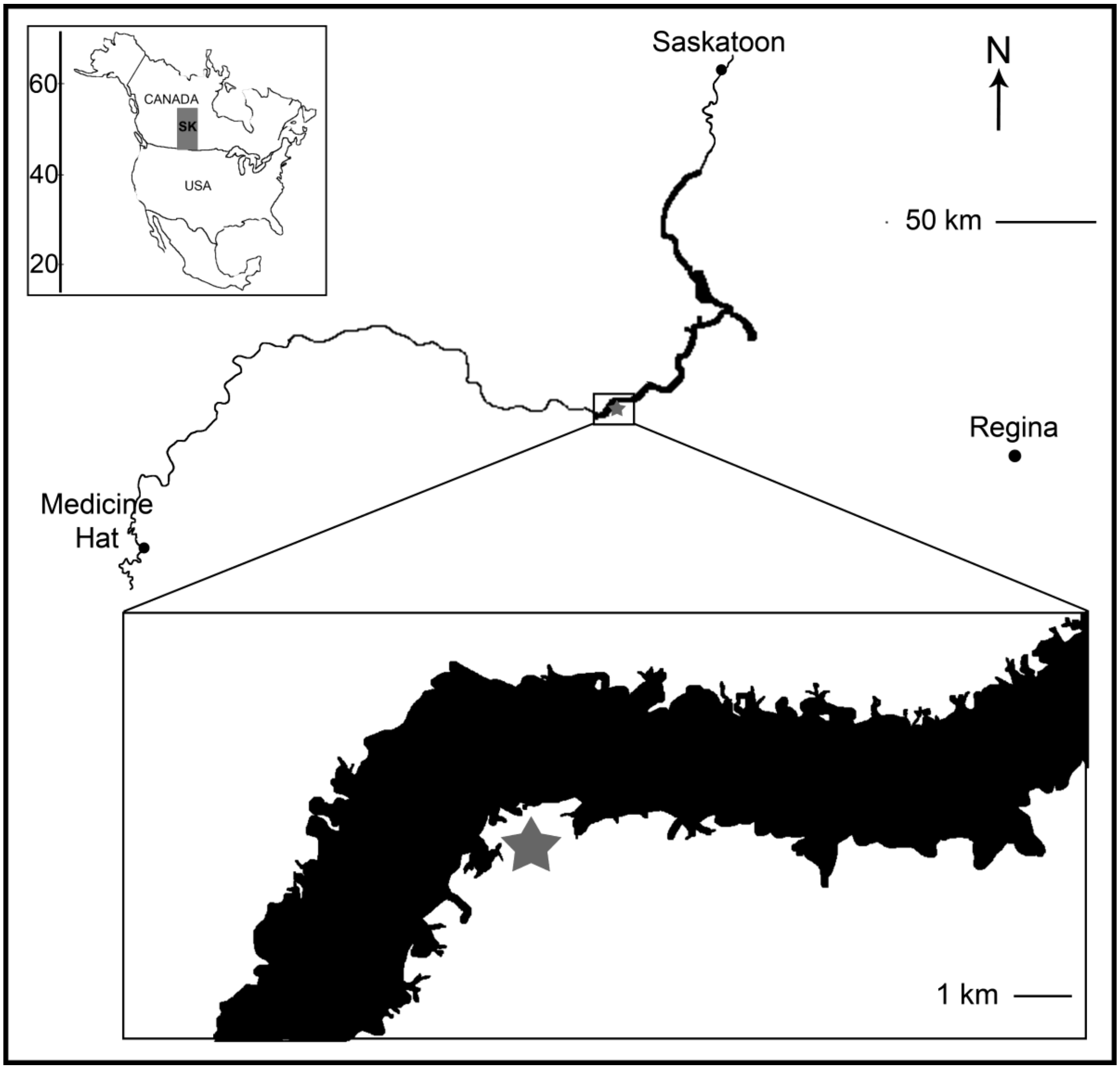

FIGURE 4.1. Map of Southern Saskatchewan. The star indicates the locality where the specimen RSM P2588.1 was recovered. Stratigraphically, the locality corresponds to the Snakebite Member of the Bearpaw Formation.

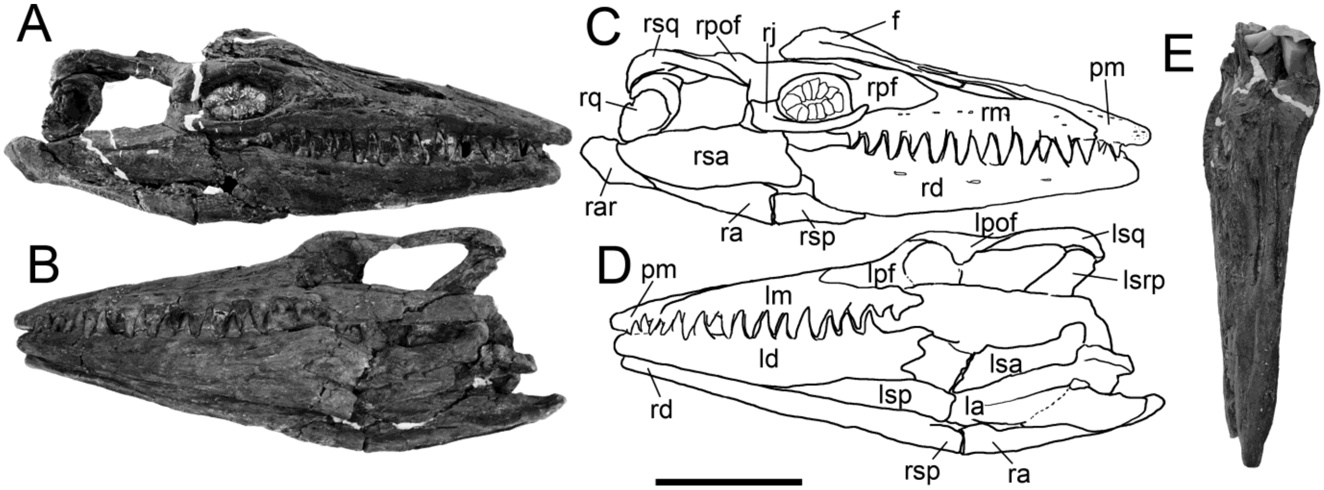

FIGURE 4.2. Skull of RSM P2588.1 *Tylosaurus saskatchewanensis* n. sp.: **A**, right side of the skull in lateral view; **B**, left side of the skull in lateral view; **C**, schematic drawing of the right side of the skull; **D**, schematic drawing of the left side of the skull; E, dorsal view of the skull of RSM P2588.1. Scale bar equal to 30 cm.

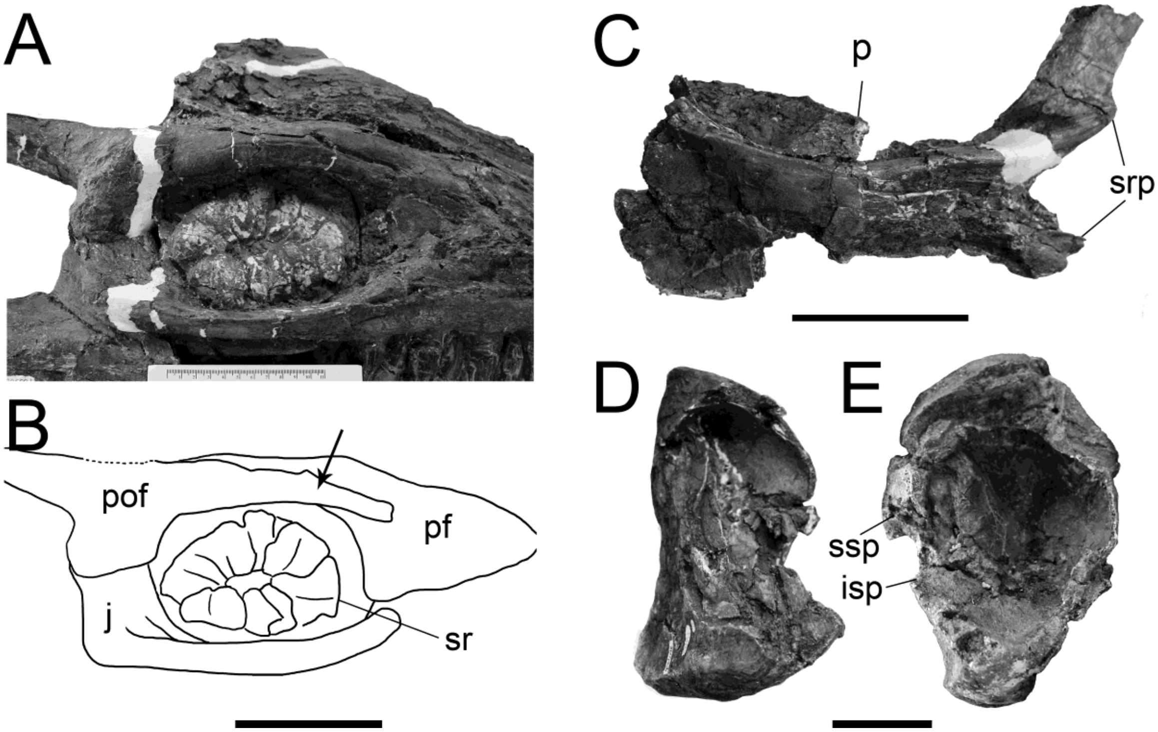

FIGURE 4.3. Detailed characters of RSM P2588.1 *Tylosaurus saskatchewanensis*: **A**, right orbit showing the jugal at the posteroventral margin of the orbit, and prefrontal and postorbitofrontal overlapping over the dorsal margin; **B**, schematic drawing of the orbit, note the arrow indicating the long prefrontal process of the postorbitofrontal, at the dorsal margin of the orbit, scale bar equal to 5 cm; **C**, parietal bone in dorsal view, disarticulated from the skull, scale bar equal to 10 cm; **D**, left quadrate in lateral view; **E**, right quadrate in lateral view. **D** and **E** scale bar equal to 5 cm.

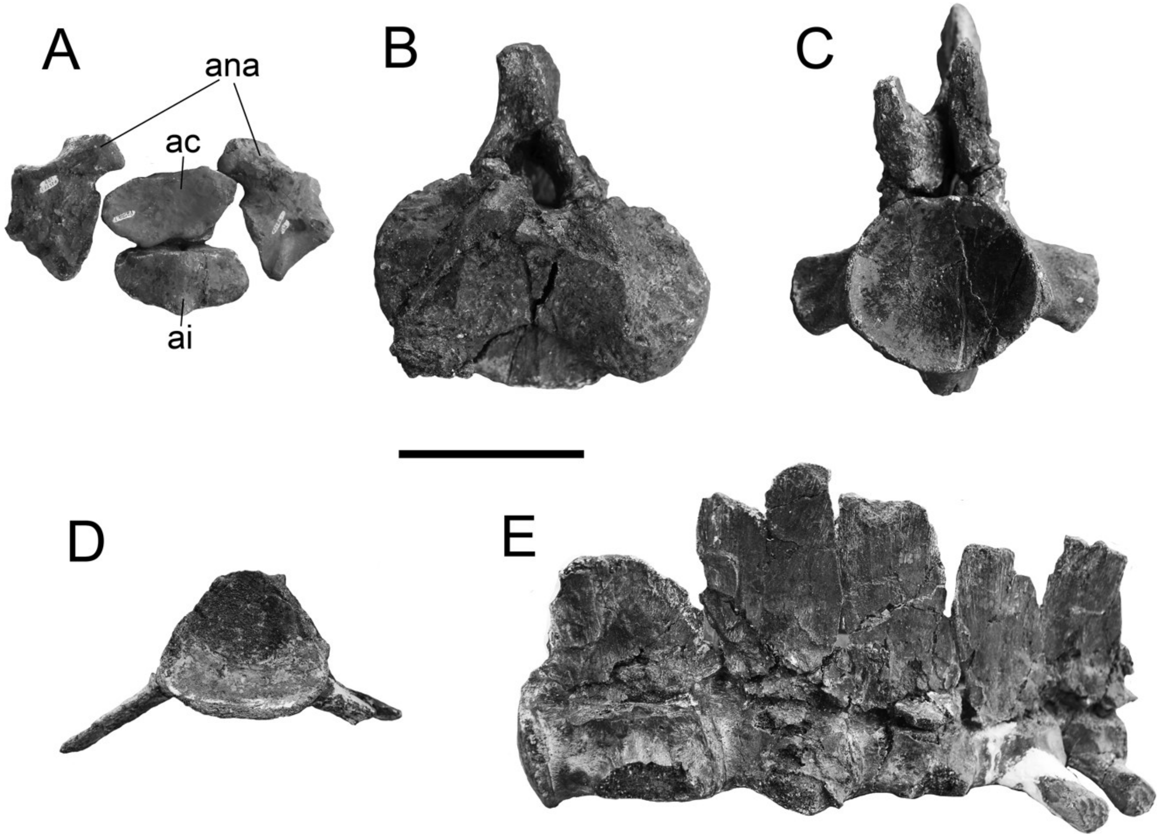

FIGURE 4.4. Vertebral morphology of RSM P2588.1 *Tylosaurus saskatchewanensis*. **A**, atlas elements, including both left and right neural arches, atlas intercentrum, and atlas centrum or odontoid. **B**, anterior view of the axis. **C**, cervical vertebrae in anterior view. **D**, posterior dorsal vertebra in anterior view. **E**, lateral view of dorsal vertebrae series in articulation. Scale bar equal to 10 cm.

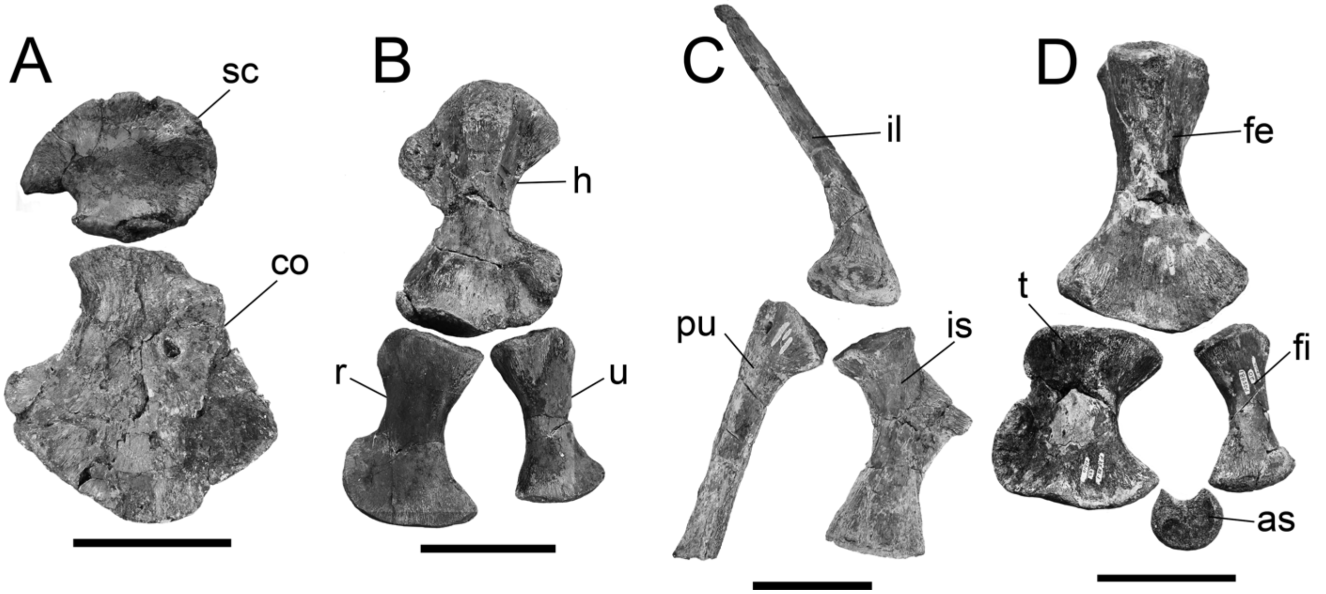

FIGURE 4.5. RSM P2588.1 *Tylosaurus saskatchewanensis*: **A**, right pectoral girdle consisting in scapula and coracoid, scale bar equal to 10 cm. **B**, left forelimb in medial view, showing humerus, radius and ulna, scale bar equal to 10 cm. **C**, right pelvic girdle with ischium, ilium and pubis, scale bar equal to 10 cm. **D**, right hindlimb in medial view, showing femur, tibia, fibula and astragalus, scale bar equal to 10 cm.

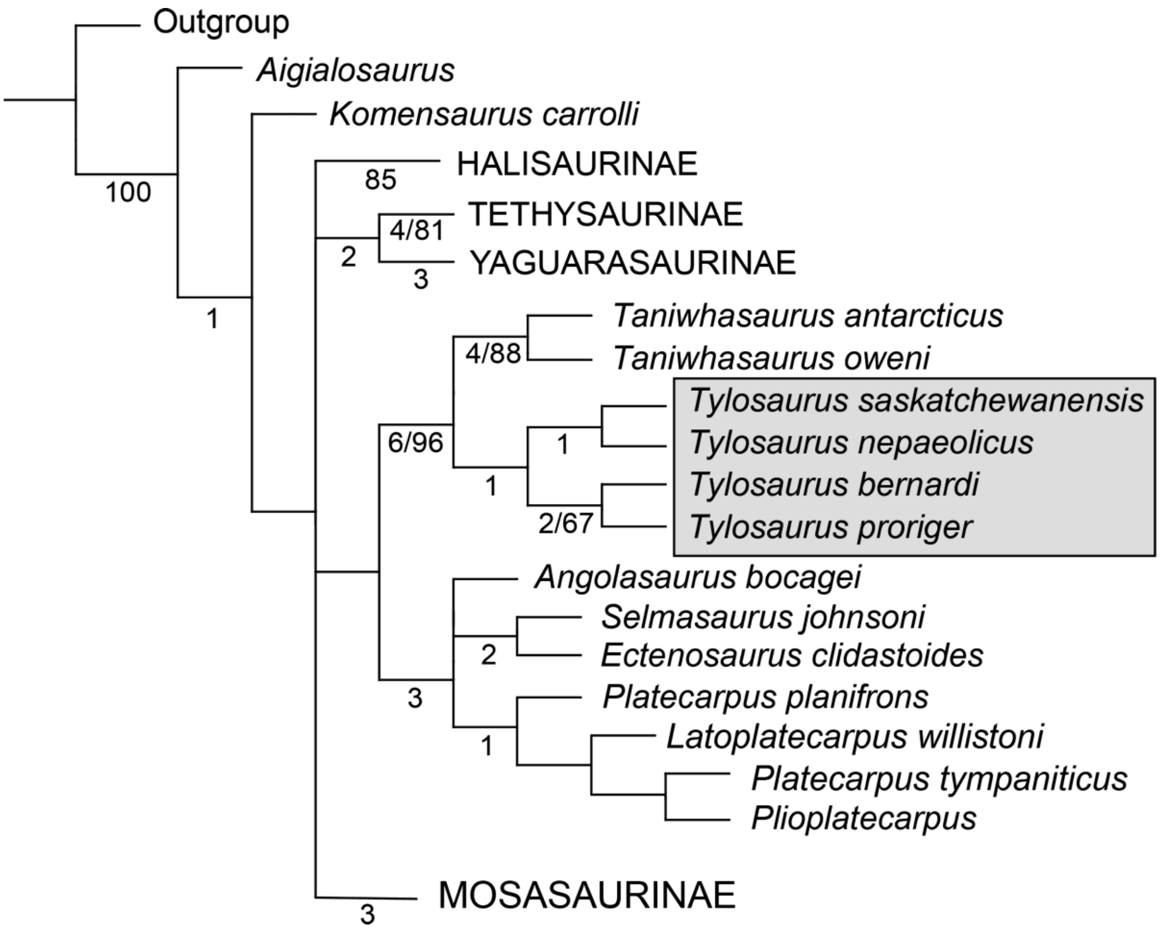

FIGURE 4.6. Strict consensus tree (CI: 0.37; RI: 0.72) of 26 most parsimonious trees of 447 steps, for a data matrix of 41 taxa and 129 characters. Bremer support values of greater than 1 and bootstrap support values of greater than 50% are reported below the branches (Bremer/Bootstrap). The coloured box highlights *Tylosaurus saskatchewanensis* and its relationship with the other species of *Tylosaurus.*

CHAPTER FIVE

THE STATUS OF *TYLOSAURUS NEUMILLERI* AND A REASSESSMENT OF TYLOSAURINE MOSASAURS FROM THE LATE CAMPANIAN OF NORTH AMERICA

ABSTRACT

A specimen recovered from the DeGrey Formation of the lower Pierre Shale of South Dakota was described as *Hainosaurus neumilleri* Martin, 2007. However, *Hainosaurus* was synonymized with *Tylosaurus* when its type species from Belgium was re-assessed as *Tylosaurus bernardi* Dollo, 1885. The specimen of *T. neumilleri* from South Dakota, catalogued in the South Dakota School of Minds (SDSM) as SDSM 75705, includes a fragment of premaxilla attached to both left and right maxillae, a left quadrate, and a block with cranial elements, including the parietal, left coronoid and angular, and right articular. Reanalysis of this material, and comparisons with other tylosaurines, indicates that this material is not diagnostic at the species level, and thus must be considered a nomen dubium. The materials included in the original holotype, parietal block, left quadrate, and premaxilla/maxillary fragment, are not diagnostic on their own of a new species, though the preserved elements show strong similarities to *T. saskatchewanensis* from similarly aged rocks (upper Campanian) in the Bearpaw Shale, Saskatchewan. Morphological characters shared between them include the shape of the parietal, the morphology of the quadrate and articular, and the shape and ornamentation of the marginal dentition.

INTRODUCTION

The genus *Hainosaurus* Dollo, 1885, was described based on the former type species *Hainosaurus bernardi*, from the lower Maastrichtian of Belgium, and re-described by Lingham-Soliar (1992). However, the characters considered diagnostic for the genus, such as the position of the pineal foramen, the shape of the suture between the maxilla and premaxilla, and features of the quadrate, jugal, postorbitofrontal, and teeth, as well as vertebral count, are either not preserved or do not differentiate *Hainosaurus* from *Tylosaurus*. For these reasons, *Hainosaurus* was synonymized with *Tylosaurus* in Chapter 2, and the species was recognized as *Tylosaurus bernardi.* The absence of clearly diagnostic characters for *Hainosaurus* was addressed first by Williston (1898) and later by Russell (1967), though neither author formally synonymized the two taxa.

Tylosaurus saskatchewanensis (Chapter 4) was described based on a single well preserved and almost complete specimen, from the late Campanian of the Bearpaw Formation, southern Saskatchewan (Fig. 1A). The species was first recognized by Bullard (2006), although it was never formally published.

Tylosaurus pembinensis (Nicholls, 1988), is a tylosaurinae mosasaur, described from a poorly preserved skull and postcranial material (MT 2; Fig. 1B) from the Campanian of the Pembina Member of the Pierre Shale in southern Manitoba, Canada. The specimen was first recognized as *Hainosaurus pembinensis* by Nicholls (1988), based on characters mentioned above. However, it was later suggested that it should be reassigned to *Tylosaurus,* as *T. pembinensis,* by Lindgren (2005), and was formally synonymized by Bullard and Caldwell (2010).

Martin (2007) described a new species of tylosaurine mosasaur *Hainosaurus neumilleri*, based on a block with a few skull elements, a quadrate, a fragment of upper jaw, and a number of poorly preserved vertebrae. The specimen was recovered from the Campanian of the DeGrey Formation of the Pierre Shale Group, in Gregory County, South Dakota, U.S.A. The specimen was diagnosed as *Hainosaurus* based on characters such as the position of the parietal foramen and the shape of the maxillopremaxillary suture; both of these features were recognized as highly variable within species of tylosaurine mosasaurs, and even with a single individual regarding the maxillopremaxillary suture (Jiménez-Huidobro and Caldwell, 2016; Chapter 2).

The aim of this thesis chapter is to examine the materials assigned to *T. neumilleri*, and compare them to the slightly older *T. pembinensis*, but most importantly to the coeval and stratigraphically equivalent *T. saskatchewanensis* to determine species affinities.

GEOLOGICAL SETTINGS

The Pierre Shale is a geological formation that extends in outcrop and subsurface from the Pembina Valley of Manitoba, Canada, to New Mexico, U.S.A., east of the Rocky Mountains in the prairies. Stratigraphically, the Pierre Shale ranges in time from the early Campanian to the early Maastrichtian (Parris et al., 2007). The Pierre Shale Group has a marine origin, deposited in the Western Interior Seaway, and overlies the Niobrara Formation and is itself overlain by the Fox Hills Sandstone (Gill and Cobban, 1966).

The holotype and specimens referred to *T. pembinensis* have been found in the Morden-Miami area, Pembina Member of the Pierre Shale, southwestern Manitoba, Canada (Fig. 2). The Pembina Member extends from southern Manitoba to southern North Dakota, U.S.A., and consists of black carbonaceous shale with numerous bentonite seams. This formation is contained in the *Baculites obtusus* zone (McNeil and Caldwell, 1981) and is assigned to early-middle Campanian (Gill and Cobban, 1966).

The specimen assigned to *T. neumilleri* was found in a concretion along the bank of the Missouri River in the DeGrey Formation of South Dakota (Martin, 2007) (Fig. 2). The DeGrey Formation is exposed along the Missouri River in North and South Dakota, and crops out as gray non-calcareous bentonite beds, with fossiliferous iron-magnesium carbonate concretions (Crandall, 1950). The DeGrey Formation is within the *Baculites compressus* ammonite range zone, and is thus late Campanian (Fox, 2007; Hanczaryk and Gallagher, 2007).

Tylosaurus saskatchewanensis was recovered from the Snakebite Member, one of eleven members of the Bearpaw Formation, Southern Saskatchewan (Fig. 2). The Bearpaw Formation consists of silty clays and subordinate sands deposited in shallow-water, marine conditions during the Late Cretaceous in the Western Interior Seaway (Caldwell, 1968); the Snakebite Member is characterized by dark grey silty clays, including limestone concretions. The Snakebite Member outcrops near Herbert Ferry, are included in the *Baculites reesidei* Zone, suggesting an upper Campanian age for the rocks and thus for the species (Caldwell, 1968).

MATERIAL AND METHODS

All the specimens were personally examined by me. Photographs were taken using camera a Canon EOS 2ti and edited in Photoshop CS6 for Macintosh computer. Drawings were made using a Wacom tablet software and hardware.

SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA Oppel, 1811
Family MOSASAURIDAE Gervais, 1852
Subfamily TYLOSAURINAE Williston, 1897
Genus *TYLOSAURUS* Marsh, 1872

Type Species—*Tylosaurus proriger* (Cope, 1869).

Range—upper Santonian to lower Campanian.

TYLOSAURUS NEUMILLERI Martin, 2007

nomen dubium

Holotype—SDSM 75705.

Locality and Horizon—V2005-20 Gregory County, from the upper Campanian of the DeGrey Formation, lower Pierre Shale, South Dakota (Martin, 2007).

Original Diagnosis—(1) medium-sized tylosaurine mosasaur with parietal foramen in the frontoparietal suture; (2) premaxillary-maxillary suture sinusoidal in shape; (3)

relatively wide snout; (4) quadrate with large, deep, bowl-shaped excavation incorporating the stapedial pit and covering much of the medial quadrate; (5) suprastapedial with relatively long internal process; (6) suprastapedial deflected laterally compared with axis perpendicular to distal condyle; (7) teeth relatively well faceted and symmetrically flattened.

Comments—characters such as the shape of the maxillopremaxillary suture and the position of the parietal foramen have been found to be variable among *Tylosaurus* (Jiménez-Huidobro and Caldwell, 2016); the deflected suprastapedial process of the quadrate has been considered ontogenetically variable (Jiménez-Huidobro et al., 2016). All characters considered diagnostic for *Hainosaurus/Tylosaurus neumilleri* (Martin, 2007) are likely shared with other tylosaurs. The material is not diagnostic on their own species, although the specimen shows strong similarities to *T. saskatchewanensis.*

TYLOSAURUS SP.

Locality/Horizon—Western interior seaway of North America and Western Europe. Turonian to lower Maastrichtian.

DESCRIPTION OF SDSM 75705

Fragments of both the left and right maxillae are in articulation with the premaxilla (Fig 5.4A). The premaxilla is robust and shows numerous foramina. Unfortunately, the bone does not preserve the anterior part of the rostrum or the internarial bar. The left side preserves the suture between the premaxilla and maxilla, which is sinusoidal in shape, while the right side does not preserve the suture. Both maxillae are robust, although they do not present characters such as the position of the narial openings or whether or not they contact the frontal, or not. On the left side, two teeth are preserved, while on the right side only a badly preserved and fragmented tooth is present.

The parietal is an elongated bone, 23 cm long (Fig. 5.5A). The parietal table is straight, almost concave in lateral outline. Anteriorly, the bone is almost straight, where the parietal contacts the frontal. The parietal foramen is on the frontal/parietal suture and the foramen is anteroposteriorly elongated. Posteriorly, a nuchal fossa is present, and the left suspensorial ramus of the parietal is preserved and is dorsoventrally flattened. The parietal table presents a constriction at the level where the suspensorial ramus originates. Anteriorly on the table, and posterior to the foramen, there is a depression, although it is not possible to know if this is a post mortem artifact or not.

The left coronoid is preserved in the block with other cranial elements (Fig. 5.5D). The bone is 16.6 cm in length. The ventromedial process of the bone where it attaches to the surangular seems to be broken. It is a saddle-shaped element (cf. Russell, 1967:53) dorsally concave, demonstrating an angle close to 135º. Although the bone is not in articulation, is still possible to see that the anterior portion is almost horizontally situated into the surangular, and the posterior arm of the bone project upwards, looking more vertical.

The right articular is present, although broken at the ventroposterior margin, with a fragment of the bone projecting outwards (Fig. 5.5F). The anterodorsal portion of the bone contributes to the posterior half of the glenoid fossa, which is concave to receive the quadrate. The lateral outline of the bone is dorsally convex, and ventrally slightly convex, bending ventrally at the posterior portion. Only the anterior portion of the angular is preserved and it is lateromedially compressed.

The left quadrate is well preserved although there is sediment remaining on the quadrate shaft (Fig. 5.6A). The bone is 15.2 cm tall and quite massive, and the shaft is wide, being 10 cm in maximum wide at midheight. The cephalic condyle, where it articulates with the squamosal, has a marked notch typical of tylosaurines. Medially, there is a visible concavity from the stapedial pit to the level of the infrastapedial process. The suprastapedial process is long, reaching to the midheight of the shaft and deflects medially. The infrastapedial process is moderately well-developed and is rounded in shape, located near to the midheight of the shaft. The stapedial pit is rectangular and narrow, and completely included into the medial concavity. Dorsally, the quadrate is a triradiate bone, splitting posteriorly into the suprastapedial process, and anteriorly into the ala and anteromedial process. Posteriorly, the quadrate looks nearly rectangular in shape, with a depression in the middle that arises from the dorsal notch of the quadrate. The alar cavity is deep and wide, and the tympanic ala looks thin, although it extends completely to the rounded ventral condyle. The posteroventrally ascending tympanic rim is triangular in shape.

Only two maxillary teeth are preserved. The teeth are large and robust; they are 4.3 cm and 2.8 cm in length, although the second one is not complete. They are posteriorly recurved and labiolingually compressed. The tip of the crown is sharp, and they both present small denticles, forming a serrated carina. The enamel of these teeth is ornamented with prismatic facets and fine striations (Fig. 5.4B).

COMPARISONS

Characters such as the shape of the parietal, the long suprastapedial process of the quadrate, and the rectangular stapedial pit of the quadrate support the assignation of specimen SDSM 75705 to the Tylosaurinae.

The sinusoidal shape of the suture between the premaxilla and maxilla of SDSM 75705 has been considered diagnostic of the genus *Hainosaurus* (Lingham-Soliar, 1992). However, when the Belgian species was synonymized to *T. bernardi*, it was shown that the shape of the maxillopremaxillary suture is variable amongst species of *Tylosaurus*. As an example, in *T. proriger* some specimens have a rectangular shaped suture, while other specimens show the sinusoidal shape (Jiménez-Huidobro and Caldwell, 2016; Chapter 4). Another example is the holotype of *T. saskatchewanensis*, in which the suture is rectangular on the left side, while the right side shows a sinusoidal suture between the maxilla and premaxilla. *Tylosaurus gaudryi*, formerly *Hainosaurus gaudryi*, as synonymized by Lindgren (2005), presents the sinusoidal shape of the suture, as does *T. pembinensis* (Bullard and Caldwell, 2010).

The parietal of SDSM 75705 is an elongated element, as in all tylosaurines, unlike the parietals of mosasaurines and halisaurines. The lateral outline of the parietal table is almost straight, similar to that of *T. nepaeolicus*, *T. bernardi*, *T. saskatchewanensis* (Fig. 5.5B), and *T. pembinensis* (Fig. 5.5C), but differs from that of *T. proriger* which is convex. The size of the parietal foramen and its ovoid shape are characters similar to other tylosaurines.

The position of the parietal foramen has been considered a diagnostic character for the genus *Hainosaurus* (Lingham-Soliar, 1992); however, this character seems to be intraspecifically variable in *T. proriger* (Jiménez-Huidobro and Caldwell, 2016; Chapter 2), and other squamates such as *Gallotia galloti* (Barahona and Barbadillo, 1998) and *Neusticurus ecpleopus* (Bell et al., 2003). The frontoparietal suture is straight, as in *T. pembinensis* (Bullard and Caldwell, 2010), differing from that seen in *T. proriger*, where the frontal posssesses posterior median alae to invade the parietal. Due to the poor preservation of the anterior border of the parietal in *T. saskatchewanensis*, it is not clear whether or not the suture with the frontal is straight. The dorsoventrally flatted suspensorial rami of the parietal are similar to other tylosaurines.

The quadrate of SDSM 75705 has a long suprastapedial process, almost reaching the midheight of the shaft, a character also seen in *T. proriger*, *T. nepaeolicus, T. saskatchewanensis* (Fig 5.6B) and *T. pembinensis* (Russell, 1967; Bullard and Caldwell, 2010; Fig. 5.6C), and different from that of *T. bernardi* (Lingham-Soliar, 1992; Jiménez-Huidobro and Caldwell, 2016; Chapter 2). The position of the infrastapedial process varies within different species of *Tylosaurus*; in SDSM 75705 it is located high on the shaft, as in *T. saskatchewanensis* (Bullard, 2006; Chapter 4; Fig. 5.6B) and *T. pembinensis* (Bullard and Caldwell, 2010; Fig. 5.6C), The position of the infrastapedial process of SDSM 75705 is not similar to that of *T. proriger*, where the process is located lower into the shaft (Russell, 1967). And it is also different to that of *T. bernardi* and *T. nepaeolicus*, where such a process is poorly developed or altogether absent (Russell, 1967; Lingham-Soliar, 1992; Jiménez-Huidobro and Caldwell, 2016; Jiménez-Huidobro et al., 2016; Chapter 2; Chapter 3). The quadrate conch of SDSM 75705 is deep and wide, as in *T. saskatchewanensis* (Fig. 5.6A, B), and unlike *T. pembinensis*, where the conch is almost equally wide and tall, also different to *T. proriger* and *T. bernardi*, where the bone looks more elongated (Russell, 1967; Ligham-Soliar, 1992; Jiménez-Huidobro and Caldwell, 2016; Chapter 2). The stapedial pit of SDSM 75705 is an elongated rectangle, as in all tylosaurines. The tympanic ala is quite thin, and it extends ventrally, almost to the mandibular condyle, as in *T. saskatchewanensis* (Chapter 4), different to *T. proriger*, *T. bernardi* and *T. saskatchewanensis*, where it finishes before the mandibular condyle (Russell, 1967; this thesis, Chapter 4), and also different from that of *T. pembinensis* and *T. nepaeolicus*, where although the ala extends ventrally, it is thick instead of thin (Russell, 1967; Bullard and Caldwell, 2010; Jiménez-Huidobro et al., 2016; Chapter 3). The mandibular condyle is very rounded, as in *T. saskatchewanensis* (Fig. 5.6A, B). The cephalic condyle, at the dorsoposterior portion of the bone presents a rim as in all tylosaurines.

The marginal dentition of SDSM 75705 differs from the teeth of *T. proriger*, *T. nepaeolicus*, and *T. bernardi*, where the teeth have relatively smooth enamel, bearing only weak striations, but lacking flutes and facets. *Tylosaurus pembinensis* and *T. saskatchewanensis* have preserved teeth where it is possible to observe that the crown has faceted enamel, forming a prismatic shape (Bullard and Caldwell, 2010; Fig. 5.4B, C, D), character seen in SDSM 75705 (Fig. 5.4B, C). The lack of flutes is also shared among SDSM 75705 and *T. saskatchewanensis* and *T. pembinensis*. The serrated carina is a character shared among different species of *Tylosaurus*, but differs with that of *Taniwhasaurus* where the carinae lack serrations (PJH, pers. obs.).

The articular of SDSM 75705 is fan-shaped as in all tylosaurines. This bone exhibits the same articular retroarticular process inflection of more than 60º, similar to that of *T. pembinensis* and *T. saskatchewanensis* (Fig. 5.5F, G, H). The coronoid presents a similar dorsal angle of ~135º, and a similar position of the horizontal and vertical arms as seen in *T. proriger*, *T. nepaeolicus, T. pembinensis* (Fig. 5.5D) and *T. bernardi.* The coronoid of *T. saskatchewanensis* is unknown (Chapter 4). The angular of SDSM 75705 does not show differences to other *Tylosaurus*.

DISCUSSION AND CONCLUSIONS

Morphological characters such as the overall shape of the parietal, the long suprastapedial process of the quadrate, the rectangular and elongated stapedial pit of the quadrate, and the labiolingually compressed and posteriorly curved teeth support the assignation of SDSM 75705 to Tylosaurinae. More specific features of SDSM 75705 indicate strong similarities to both *T. saskatchewanensis* (Chapter 4) and *T. pembinensis* (Bullard, 2006; Bullard and Caldwell, 2010). SDSM 75705 shares with both taxa the elongated parietal with the parietal table straight in lateral outline, quadrate with long suprastapedial process that reaches the midheight of the shaft, a well developed infrastapedial process located high on the shaft, posteriorly curved and labiolingually compressed teeth, ornamented with facets and fine striations, although unflutted, and teeth that bear serrated carinae with small denticles. The overall shape of the quadrate of SDSM 75705 resembles more that of *T. saskatchewanensis*, especially the shape of the quadrate conch, the thin tympanic ala that extends ventrally to the mandibular condyle, and the rounded shape of the mandibular condyle, different from that of *T. pembinensis*.

The "suprastapedial process of the quadrate medially deflected" has been suggested to be an ontogenetic character (Chapter 3). Observations of three species of mosasaurids show that the process is deflected in adult specimens but not necessarily in subadults (Jiménez-Huidobro et al., 2016). The position of the parietal foramen was previously considered diagnostic to the species-level (Lingham-Soliar, 1992), though more recent research has shown that this character can vary intraspecifically among squamates, affected by many factors, including ontogeny (Barahona and Barbadillo, 1998; Bell et al., 2003; Jiménez-Huidobro et al., 2016; Chapter 3). For instance, in some specimens of *T. proriger,* the parietal opening invades the frontoparietal suture, while in others the foramen is only in the parietal, located some distance from the suture (Jiménez-Huidobro and Caldwell, 2016; Chapter 2). In addition, the shape of the frontoparietal suture is another plastic character amongst squamates, where the shape is intraspecifically variable, linked to allometric growth through ontogeny, and/or sexual dimorphism (Barahona and Barbadillo, 1998; Bell et al., 2003; Simões et al., 2016), although no confirmed evidence of sexual dimorphism has been found in mosasauroid lizards.

Recognition of the nomen dubium status of *Hainosaurus/Tylosaurus neumilleri*, and the likely assignment of SDSM 75705 to T*ylosaurus* sp., since there is not clear diagnosis of the specimen. The results suggest a far more restricted concept of North American tylosaurines, in the following stratigraphic succession: *T. nepaeolicus* from the upper Coniacian to lower Santonian of the Niobrara and Boquillas Formation, *T. proriger* from the upper Santonian to lower Campanian of Niobrara, Mooreville Chalk and Taylor Group, *T. pembinensis* from the lower-middle Campanian of Pembina Formation of the lower Pierre Shale, and *T. saskatchewanensis* from the upper Campanian of the Bearpaw Formation. This result does not affect the previously suggested North Atlantic Circle Basin distribution of the genus in North America and Europe (Jiménez-Huidobro and Caldwell, 2016; Chapter 2).

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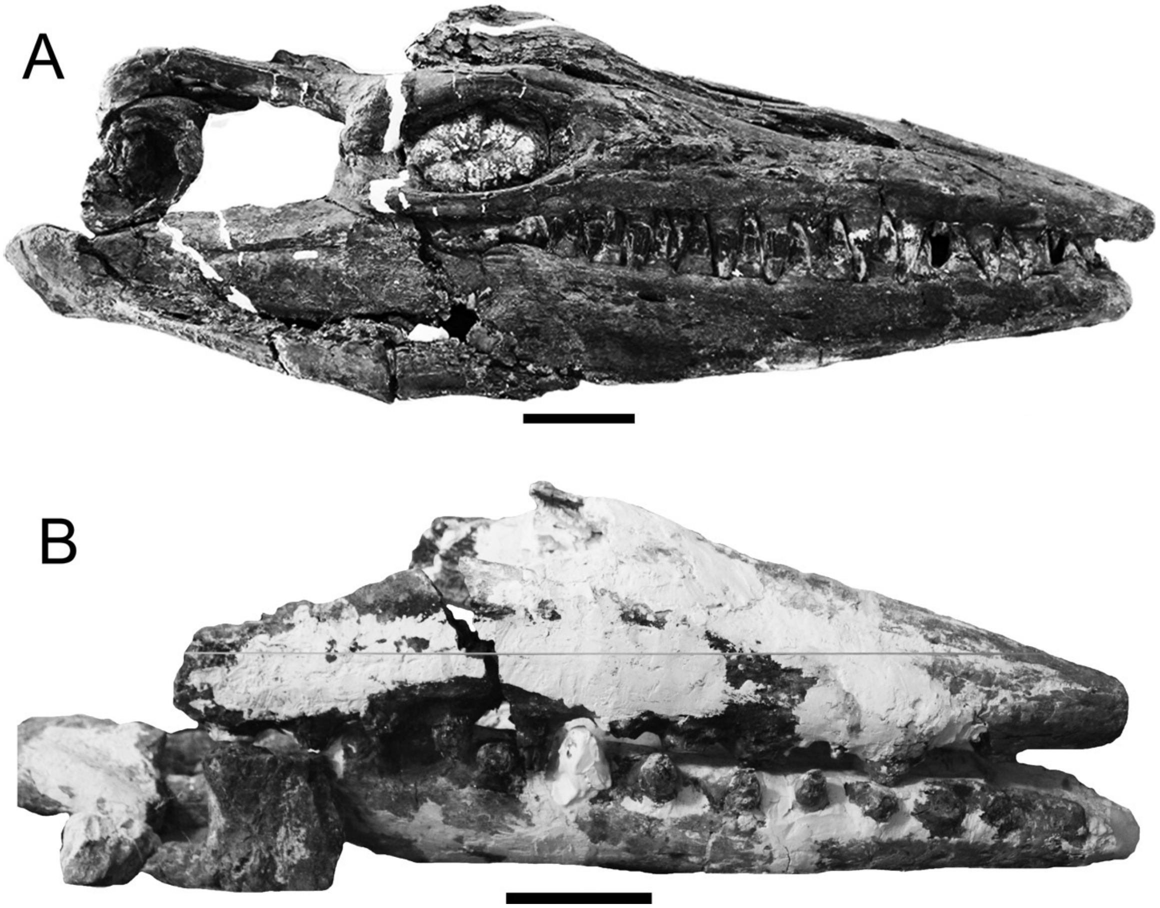

FIGURE 5.1. **A**, skull of the holotype of *Tylosaurus saskatchewanensis* RSM P2588.1 from the Bearpaw Formation of Saskatchewan; scale bar equal to 10 cm. **B**, skull of the holotype of *Tylosaurus pembinensis* MT 2 from the Pembina Formation of Manitoba; scale bar equal to 10 cm.

FIGURE 5.2. Map of North America showing the localities where the specimens were recovered. Stars indicate upper Campanian localities: top, Bearpaw Formation of Saskatchewan; bottom, DeGrey Formation of the Pierre Shale of South Dakota. The triangle indicates the lower-middle Campanian, Pembina Formation of the Pierre Shale, Manitoba.

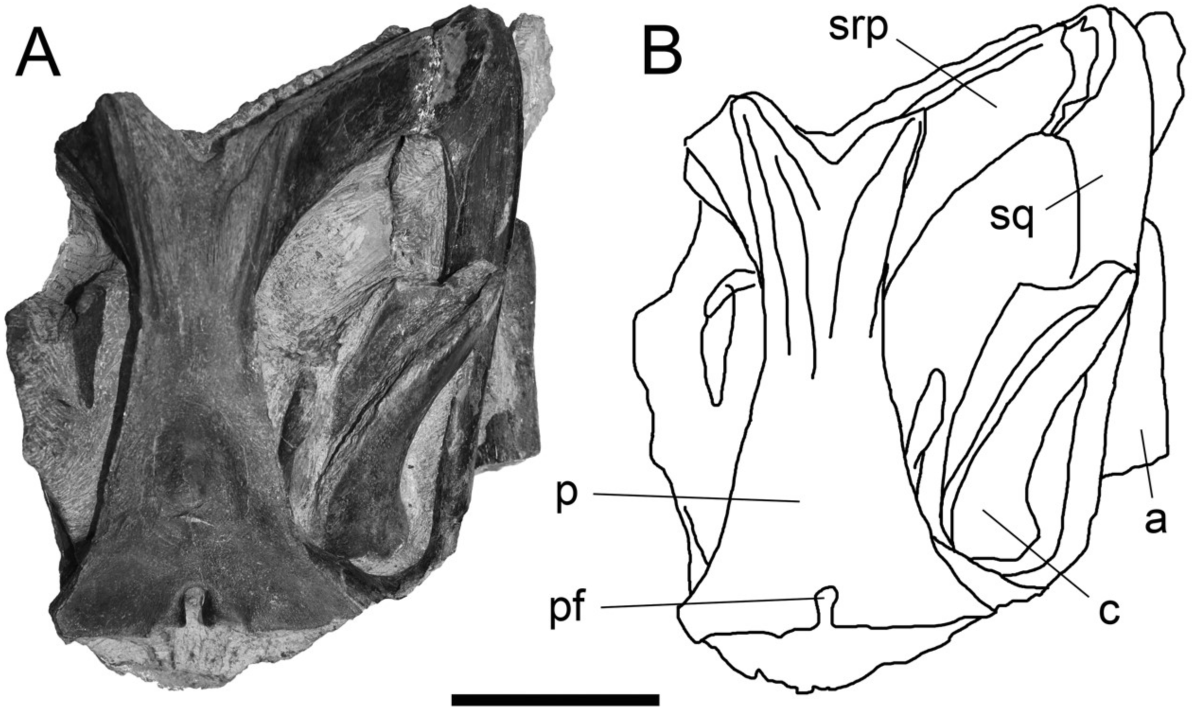

FIGURE 5.3. Block with skull elements of holotype assigned to *Tylosaurus neumilleri* SDSM 75705 (Martin, 2007). **A**, photograph of the block. **B**, schematic drawing indicating the cranial elements. Scale bar equal to 10 cm.

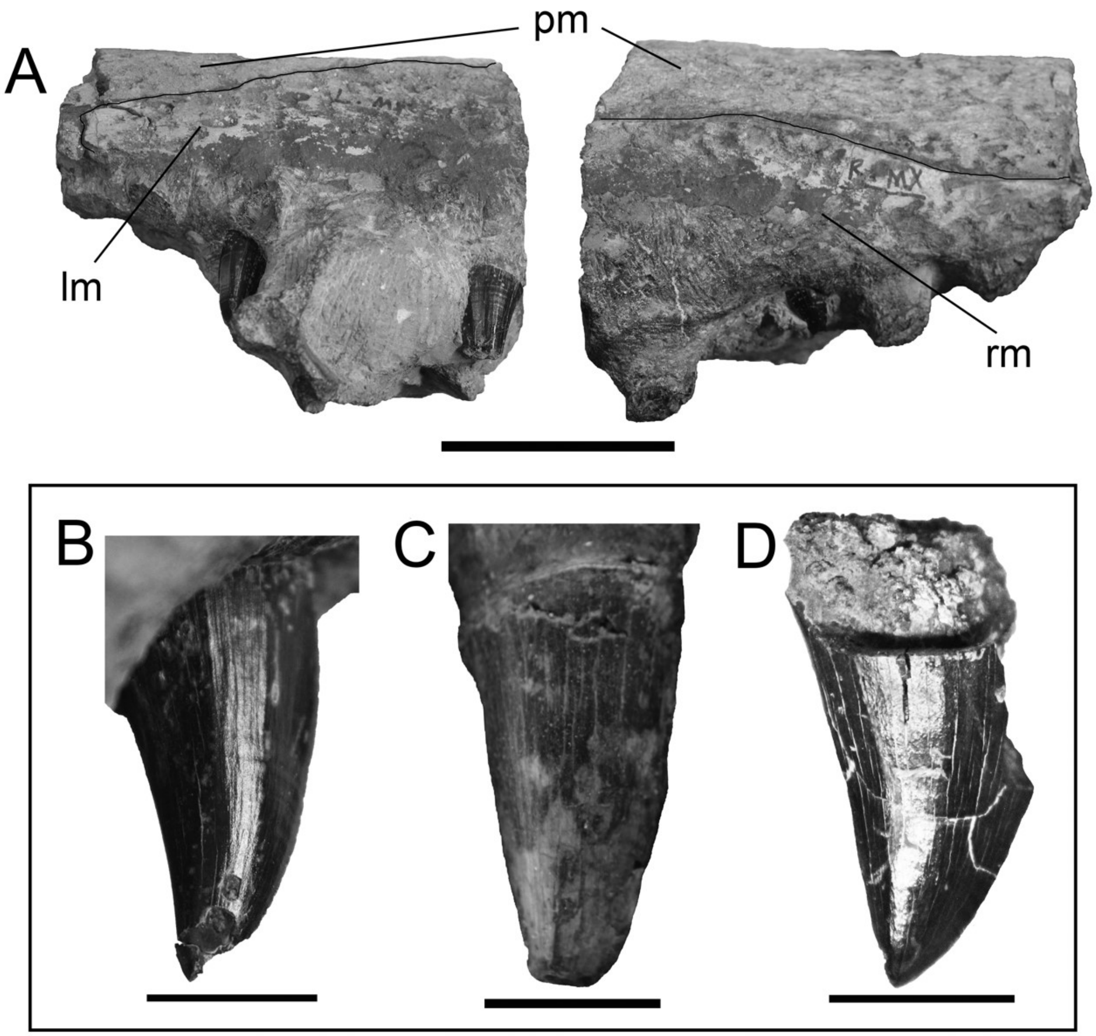

FIGURE 5.4. Fragment of a jaw of the holotype of *Tylosaurus neumilleri*, and marginal teeth of *T. neumilleri* and *T. pembinensis*. **A**, left and right sides of fragmented premaxilla and maxilla, holotype of *T. neumilleri* SDSM 75705; scale bar equal to 10 cm. **B**, tooth of the holotype of *T. neumilleri* SDSM 75705; scale bar equal to 2 cm. **C**, tooth of *T. saskatchewanensis* RSM P2588.1; scale bar equal to 2 cm. **D**, tooth of *T. pembinensis* MDM M77.05.07; scale bar equal to 2 cm.

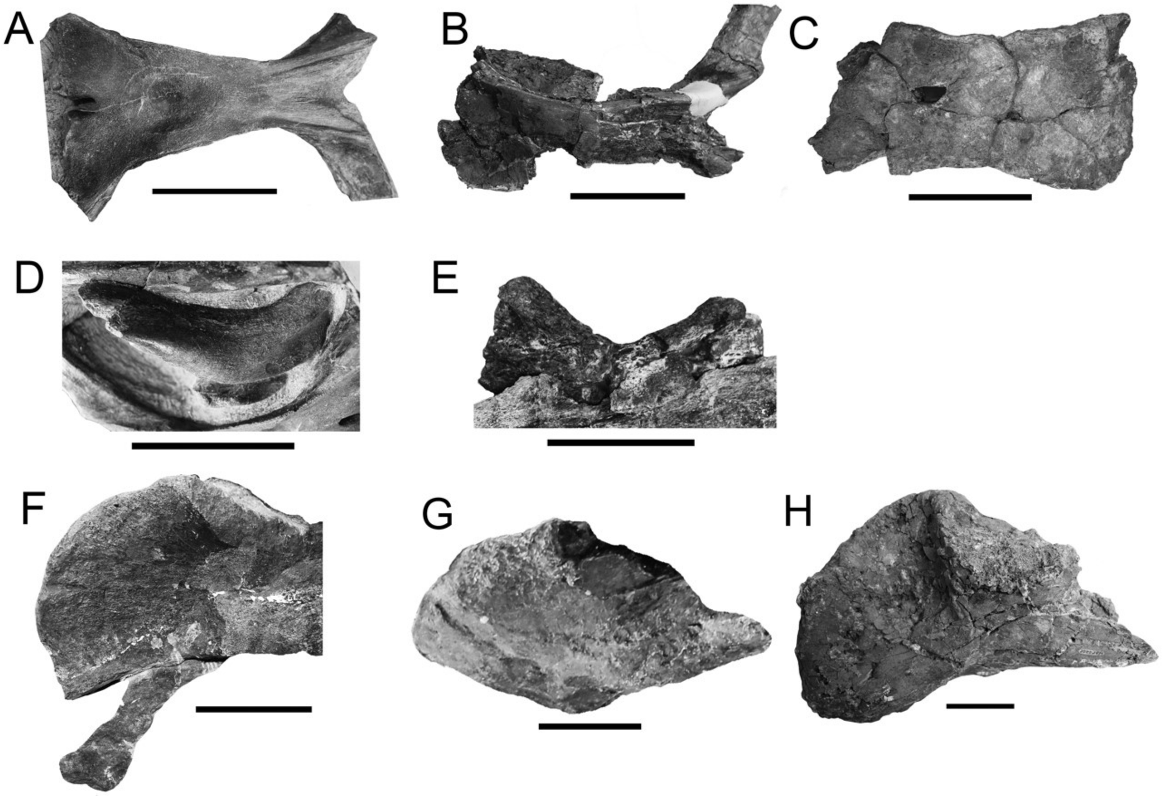

FIGURE 5.5: Comparison of cranial elements between *Tylosaurus neumilleri* and *Tylosaurus pembinensis*. **A**, parietal of *T. neumilleri* SDSM 75705; scale bar equal to 10 cm. **B**, parietal of *T. saskatchewanensis* RSM P2588.1; scale bar equal to 10 cm. **C**, partial parietal of *T. pembinensis* MDM M74.06.06; scale bar equal to 10 cm. **D**, coronoid of *T. neumilleri* SDSM 75705; scale bar equal to 10 cm. **F**, coronoid of *T. pembinensis* MDM M77.05.07; scale bar equal to 10 cm. **F**, articular of *T. neumilleri* SDSM 75705; scale bar equal to 5 cm. **G**, articular of *T. saskatchewanensis* RSM P2588.1; scale bar equal to 5 cm. **H**; articular of *T. pembinensis* MDM M74.05.06, scale bar equal to 5 cm.

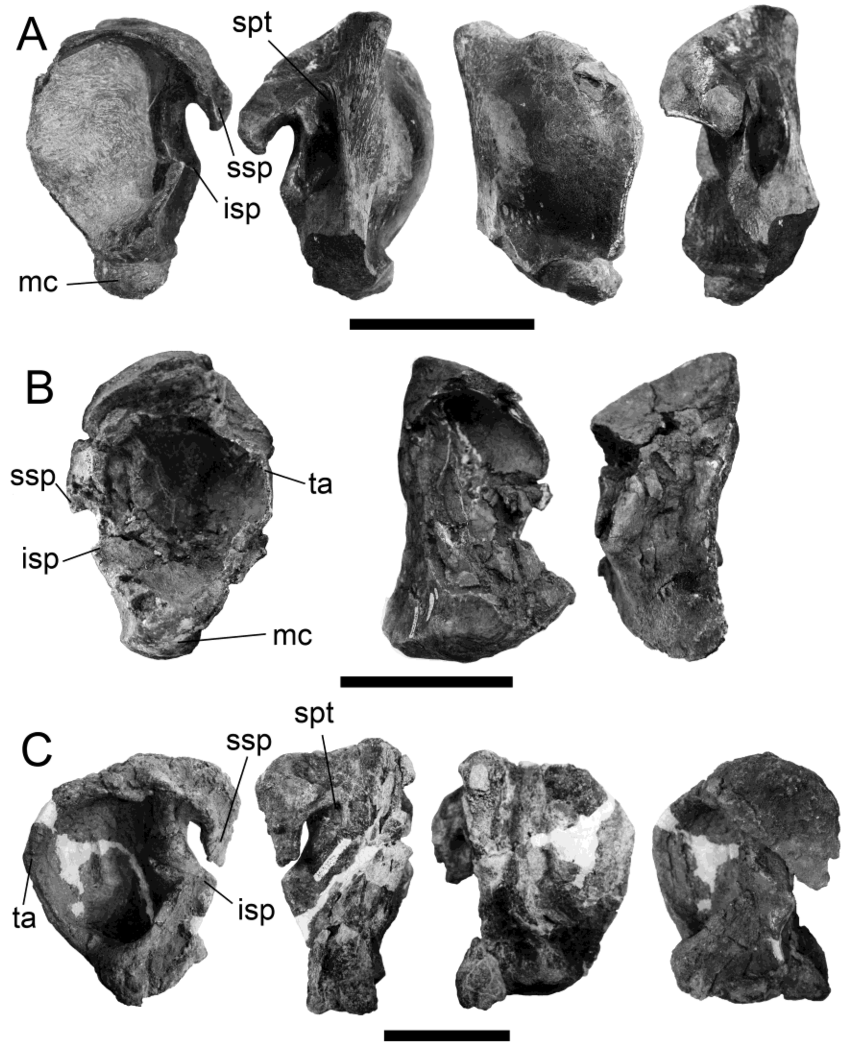

FIGURE 5.6: Comparison of quadrates of specimens assigned to *Tylosaurus neumilleri* and *Tylosaurus pembinensis*. **A**, left quadrate of the holotype of *T. neumilleri* SDSM 75705, views from left to right: lateral, medial, anterior, posteromedial. **B**, right quadrate of *T. saskatchewanensis* RSM P2588.1 in lateral view, followed by the left quadrate in lateral and posteromedial views; scale bar equal to 10 cm. **C**, left quadrate of *T. pembinensis* MDM M77.05.07, views from left to right: lateral, medial, anterior, posterolateral. Both scale bars equal to 10 cm.

CHAPTER SIX

PHYLOGENETIC RELATIONSHIPS OF THE TYLOSAURINAE (SQUAMATA: MOSASAUROIDEA)

ABSTRACT

Tylosaurinae Williston, 1897, is a monophyletic clade, reconstructed in most analyses as the sister group of the Plioplatecarpinae Dollo, 1884. The most distinctive characteristic of the group is an elongate edentulous rostrum on the premaxilla. Members of the tylosaurine subfamily are divided into two genera: *Tylosaurus* Marsh, 1872, and *Taniwhasaurus* Hector, 1874. When all arguably valid tylosaurine species are included in a single phylogenetic analysis, some clades are in well supported phylogenetic positions, such as the clade *T. proriger* (Cope, 1869) + *T. bernardi* (Dollo, 1885), and *T. pembinensis* (Nicholls, 1988) + *T. saskatchewanensis* n. sp. from Saskatchewan, while the relationships between other members appeared unresolved, such as *T. gaudryi* (Thevenin, 1896), and *T. nepaeolicus* (Cope, 1874), and the species considered within the genus *Taniwhasaurus*. When *T. gaudryi* (Thévenin, 1896), and *Ta. 'mikasaensis'* Caldwell et al., 2008, are removed from the analysis, due to their lack of diagnostic and/or informative materials, *T. nepaeolicus* appeared as the basal taxon of the clade *T. pembinensis* + *T. saskatchewanensis*, which is itself the sister group of the clade *T. proriger* + *T. bernardi*. The genus *Taniwhasaurus*, however, is resolved not as a clade, but as successive branches along the stem, with *Ta. oweni* Hector, 1874 at the base of *Tylosaurus*, and *T. antarcticus* (Novas et al., 2002), basal to the clade *Ta. oweni* + *Tylosaurus*. Based on morphological characters seen in the holotype of *'T'. capensis* Broom, 1912, I suggest a re-assignation to *Taniwhasaurus capensis*, based on the flutes and facets in the crown of the two preserved replacement teeth. Reassessment of the Japanese species *Ta. 'mikasaensis'* indicates that the various specimens do not displays sufficient diagnostic characters to differentiate a species distinct from *Taniwhasaurus*

oweni. The North Atlantic Circle Basin distribution for species of the genus *Tylosaurus* from the Coniacian to the Maatrichtian is supported, and a cosmopolitan distribution is suggested of the genus *Taniwhasaurus*, at least from the Santonian to the Maastrichtian, with species recovered along the Pacific and Indian Ocean Basins and Antarctica.

INTRODUCTION

Mosasaurs were a successful group of squamates, diverse and widespread during the Upper Cretaceous, that evolved paddle like limbs and radiated into aquatic environments (Caldwell, 2012). Tylosaurinae Williston, 1897, is a clade/subfamily of mosasaurs broadly distributed around the world, with records from North America (Cope, 1869, 1874; Russell, 1967; Nicholls, 1988), Europe (Dollo, 1885; Lingham-Soliar, 1992; Lindgren and Siverson, 2002; Bardet et al., 2006), Africa (Broom, 1912; Antunes, 1964), Antarctica (Novas et al, 2002), Japan (Caldwell et al., 2008), and New Zealand (Welles and Gregg, 1971; Caldwell et al., 2005). Among mosasauroids, tylosaurines include some of the largest bodied marine lizards ever known, such as *T. bernardi* from Belgium, which is estimated to have been 12.2 m long (Lindgren, 2005).

There have been attempts to examine the position of Mosasauroidea within Squamata (Rieppel, 1980; Carroll and deBraga, 1992; deBraga and Carroll, 1993; Caldwell et al., 1995; Caldwell, 1996; Conrad, 2009; Gauthier et al., 2012; Reeder et al., 2015), and the relationships of the lineages within Mosasauroidea (Bell 1993, 1997; Caldwell 1996, Polcyn and Bell, 2005; Caldwell and Palci, 2007, LeBlanc et al., 2012; Palci et al., 2013; Jiménez-Huidobro and Caldwell, 2016; Chapter 2). However, none of these studies have been focused on tylosaurine mosasaurs, and none included a revision of all tylosaurine species and thus all valid terminal taxa. Bullard (2006), in his analysis of tylosaurine mosasaurs, demonstrated the monophyly of the Tylosaurinae, and that *Tylosaurus bernardi* (=*H. bernardi*) and *Taniwhasaurus oweni* are basal in the Tylosaurinae, and *T. pembinensis* and *T. saskatchewanensis* are the crown of the clade.

However, Bullard (2006) was unable to resolve relationships between the different tylosaurines. By adding a revised list of terminal taxa, derived from first hand observation of all known tylosaurine mosasaur taxa, and many specimens, to a modified version of a pre-existing data matrix, the analysis presented here seeks to establish the phylogenetic relationships of Tylosaurinae on a global scale. A secondary goal is to assess the status of the two genera that form this group, *Tylosaurus* and *Taniwhasaurus*, and examine them in paleobiogeographic terms.

MATERIALS AND METHODS

Most of the specimens of tylosaurine mosasaurs were personally examined and studied by me, or both M. W. Caldwell and me. Photographs were taken using a Canon EOS 2ti and edited in Photoshop CS6 for Macintosh computer. Measurements were taken using a tape measure.

Phylogenetic analysis was completed using the data matrix from Chapter 3 (Jiménez-Huidobro et al., 2016), which was derived in sequence from Palci et al. (2013), LeBlanc et al. (2012), Caldwell and Palci (2007), and Bell (1997). The modified data matrix of 45 ingroup taxa and 128 morphological characters was analyzed using a traditional (heuristic) search in TNT 1.1 (Goloboff et al., 2008) with TBR, 1000 replicates and 10 trees saved per replication. The outgroup used in the analysis corresponds to the anguimorph lizard genus *Varanus*. The resulting trees were analyzed in Mesquite 3.03 for Mac, and edited in Adobe Illustrator CS6 for Mac. A second analysis was performed excluding *T. gaudryi*, *Ta. 'mikasaensis'*, and *'Tylosaurus'* *capensis*, because all of these terminal taxa suffer from a small number of scoreable characters thus leading to large numbers of missing data.

GEOGRAPHIC AND STRATIGRAPHIC OCURRENCES

There are two described genera of Tylosaurinae: *Tylosaurus* Marsh, 1872, and *Taniwhasaurus* Hector, 1874; a third genus, *Hainosaurus*, Dollo, 1885, has recently been formally recognized as the junior synonym of *Tylosaurus* (Lindgren, 2005; Bullard and Caldwell, 2010; Jiménez-Huidobro and Caldwell, 2016).

Turonian

The earliest record of a tylosaurine mosasauroid corresponds to a specimen from the upper Turonian of Chihuahua, northern Mexico assigned to *Tylosaurus* (Loera-Flores, 2013), although due to lack of preparation it was not diagnosed at the species level at the time of description. Another early species of tylosaurine is *T. imbeensis* Antunes, 1964, from the upper Turonian of Iembe, Angola (Fig. 6.1). Unfortunately, the holotype was lost in a fire in Lisbon (Jacobs et al., 2006), and although there is a new specimen mentioned by Jacobs et al. (2006) and Mateus et al. (2012), it has never been described or figured.

Coniacian (Fig. 6.1A)

Tylosaurus nepaeolicus was described from the upper Coniacian of the lower Smoky Hill Chalk, Kansas; the current species range is from the upper Coniacian to the lower Santonian of the Kansas Chalk (Russell, 1967), and from the Boquillas Formation of Texas (Bell et al., 2012) (Fig. 6.1). A more recently described tylosaurine species, *T. kansasensis* from the upper Coniacian of the lower Smoky Hill Chalk of Kansas, has now been synonymized with *T. nepaeolicus* (Jiménez-Huidobro et al., 2016; Chapter 3).

Santonian (Fig. 6.1B)

The type species *Tylosaurus proriger* was recovered from the lower Campanian of the Upper Smoky Hill Chalk, near Monument Rocks, Gove County, Kansas (Cope, 1869; Everhart, 2001). The current range of the species is from the upper Santonian to the middle Campanian (Fig. 6.1). Two more tylosaurine taxa from the Santonian have been found outside of North America: *T. gaudryi* from the upper Santonian to lower Campanian of Eclusier Vaux near Péronne, France (Thévenin, 1896), was described based on an incomplete skull, and the second species corresponds to a specimen assigned to *'T'. capensis* by Broom (1912) from the Santonian of Pondoland, South Africa. The latter taxon was based on an almost complete frontal with fragments of parietal and postorbitofrontal attached, as well as two jaw fragments.

Campanian (Fig. 6.1C)

The Campanian of North America was characterized by a more diverse assemblage of tylosaurines: *T. pembinensis* Nicholls, 1988, from the middle Campanian of the Pembina Member of the Pierre Shale of Manitoba, Canada, and *T. saskatchewanensis* (Chapter 4) from the upper Campanian of the Bearpaw Formation of

Saskatchewan, Canada. A former species, *Tylosaurus neumilleri* Martin, 2007, was re-assigned to *T. saskatchewanensis* (Chapter 5).

From Europe, *Tylosaurus ivoensis* Persson, 1963, was described from the lower Campanian of Sweden, based on isolated teeth and vertebrae. The Western Pacific tylosaurine, *Taniwhasaurus,* also diversified during the Campanian (Fig. 6.1C): *Ta. 'mikasaensis'* was described based on a skull block that includes an upper and lower jaws and a partial frontal, from the upper Santonian-lower Campanian boundary, near Mikasa City, central Hokkaido, Japan (Caldwell et al., 2008). A second taxon, *Ta. oweni*, was described from the lower Haumurian (lower to middle Campanian) of the Haumuri Bluff, Conway Siltstone Formation, South Island of New Zealand (Welles and Gregg, 1971; Caldwell et al., 2005). And finally, *Ta. antarcticus* was recovered from the upper Campanian to the lower Maastrichtian of the Santa Marta Formation, James Ross Island, Antarctica (Novas et al., 2002; Martin, 2006; Fernández and Martin, 2009; Fernández and Gasparini, 2012).

Maastrichtian (Fig. 6.1D)

The youngest record of tylosaurine mosasaurs is held by *Tylosaurus bernardi* (Dollo, 1885) from the lower Maastrichtian of the Ciply Phosphatic Chalk of Belgium; this species was formerly the type species of the genus *Hainosaurus*, that later was synonymized with *Tylosaurus* (Jiménez-Huidobro and Caldwell, 2016; Chapter 2). From South America, a number of isolated teeth were recovered from the upper Maastrichtian of the Quiriquina Formation in Chile; however, due to the lack of information, these could only be classified as indeterminate Tylosaurinae (Jiménez-Huidobro et al., 2015).

RESULTS

Phylogenetic Analysis

Two phylogenetic analyses were performed in order to establish relationships within Tylosaurinae. The first analysis was performed using all valid tylosaurine taxa: *T. proriger*, *T. nepaeolicus*, *T. pembinensis*, *T. saskatchewanensis*, *T. bernardi*, *Ta. oweni*, *Ta. antarcticus*, and three problematic taxa, *T. gaudryi*, *Ta. capensis* and *Ta. 'mikasaensis'*. A second analysis was performed excluding the last three species due to the number of missing characters, and the problem of diagnosing these taxa to the species level.

The traditional search in the first analysis (Fig. 6.2A) resulted in 33 most parsimonious trees of 430 steps in length (C.I. = 0.3651; R.I. = 0.7321). The Tylosaurinae is found to be monophyletic (Bremer Support = 3), and is the sister group of Plioplatecarpinae, similar to the results obtained by Palci et al. (2013), LeBlanc et al. (2012), and Bell (1997). The genus *Tylosaurus* is monophyletic as well, although weakly supported (Bremer = 1), with *T. proriger* + *T. bernardi* and *T. pembinensis* + *T. saskatchewanensis* as terminal taxa within the clade. The relationship between *T. nepaeolicus*, *T. gaudryi* and the other species of *Tylosaurus* remains unresolved at the base of the *Tylosaurus* branch. *Tylosaurus proriger* appears as the sister group of *T. bernardi*, in a well-supported clade (Bremer = 10), and this latter clade emerges as the sister group of *T. pembinensis* + *T. saskatchewanensis* clade (Bremer = 8 and Bootstrap = 59).

By comparison to *Tylosaurus*, the genus *Taniwhasaurus* is not recovered as a monophyletic group. Rather, *Taniwhasaurus capensis* and *Ta. 'mikasaensis'* appear as a clade of basal most tylosaurines, although this is a weakly supported clade (Bremer = 1). This clade of taniwhasaurs is the sister to *Taniwhasaurus antarcticus* + all other tylosaurines (*Ta. oweni* + *Tylosaurus* [Bremer = 1]).

When *Tylosaurus gaudryi*, *Taniwhasaurus capensis*, and *Ta. 'mikasaensis'* are excluded (Fig. 6.2B), the traditional search resulted in 49 most parsimonious trees, with the same number of steps as the previous analysis, 428 steps (C.I. = 0.3668; R.I. = 0.7292). The monophyletic clade Tylosaurinae is now strongly supported (Bremer = 10 and Bootstrap = 82). The genus *Tylosaurus* is monophyletic and well supported (Bremer = 4 and Bootstrap = 72). *T. proriger* and *T. bernardi* are sister taxa; the clade *T. proriger* + *T. bernardi* is strongly supported (Bremer = 10 and Bootstrap = 63). The other crown clade is composed of *T. pembinensis* and *T. saskatchewanensis* (Bremer = 6 and Bootstrap = 66). *Tylosaurus nepaeolicus* appears at the base of the clade *T. pembinensis* + *T. saskatchewanensis* (Bremer = 6). The genus *Taniwhasaurus* resolves as *Ta. oweni* as sister to all *Tylosaurus*, with *Ta. antarcticus* at the base of the clade.

DISCUSSION

Phylogenetic relationships and Systematic Palaeontology of Tylosaurinae

Russell (1967) recognized only three tylosaurine species: the North American *T. proriger* and *T. nepaeolicus*, and the Belgian *T. bernardi* (formerly *Hainosaurus bernardi*). Bullard (2006), in his phylogenetic analysis included *T. proriger*, *T.*

nepaeolicus, *T. 'kansasensis'*, *T. pembinensis*, *T. bernardi* (= *H. pembinensis*), *T. saskatchewanensis,* and *Ta. oweni*. After that thesis project, this is the first attempt to study the phylogenetic relationships of tylosaurine mosasaurs.

The phylogenetic results show the monophyly of the subfamily Tylosaurinae, and when synapomorphies were mapped, the characters that define the subfamily are the frontal olfactory canal not ventrally embraced by descending process (12[0]); frontoparietal suture with oblique median frontal and parietal ridges almost horizontal (15[1]); teeth surface not coarsely textured (72[0]); and zygosphene and zygantra absent (81[0]), in addition to the edentulous rostrum, twelve to thirteen maxillary teeth, thirteen to fourteen dentary teeth, prefrontal overlaps with postorbitofrontal above the orbit, and coracoid bigger than scapula (Russell, 1967; PJH pers. obs.). When *T. gaudryi*, *Ta. 'mikasaensis'* and *Ta. capensis* are removed from the analysis, the autapomorphies that define the subfamily are characters 2[2], 6[1], 12[0], and 15[1], in addition to the prefrontal contacting the postorbitofrontal above the orbits (27[1]), and both bones laterally overlapping (28[1]), quadrate suprastapedial process moderately long, ending near the midheight (40[1]), anterior projection of the dentary anterior to first dentary tooth (57[0]), and long anterior projection of the dentary (58[1]). The diagnosis of the subfamily seems to be better supported in the last analysis, when missing data is excluded.

The genus *Tylosaurus* appears as a monophyletic group. When all taxa are included, *T gaudryi* appears in a polytomy with *T. nepaeolicus* and the other *Tylosaurus* (Fig. 2A). In the second analysis (Fig. 2B), the autapomorphies that characterize the genus are tooth fluting absent (74[0]), if carina is present, it has serrations (77[1]), and cervical vertebrae length proportions equal or longer than other vertebrae (91[1]). In the first analysis (Fig. 2A), *T. gaudryi* and *T. nepaeolicus* appear in an unresolved polytomy between them and the clade containing the other tylosaurs. When *Ta. gaudryi*, *Ta 'mikasaensis'* and *Ta. capensis* are removed from the analysis, *T. nepaeolicus* was revealed as basal to *T. pembinensis* and *T. saskatchewanensis* (Fig. 2B), based on, the high and triangular posteroventral ascending tympanic rim of the quadrate (45[1]), the thick tympanic ala of the quadrate (46[1]) in addition to the presence of hypapophyses on eight (or posterior) vertebra (83[1]). The two younger North American tylosaurines, *T. pembinensis* and *T. saskatchewanensis*, are characterized by the following autapomorphies: lateral sutural flange and median sutural flange of the frontal posteriorly extended to invade the parietal (16[2]); the maxillopremaxillary suture ends between the fourth and ninth maxillary teeth (32[1]); and the articular retroarticular process presents an extreme inflection of almost 90º, appearing nearly horizontal (69[1]). In the second analysis the group is defined only by the articular retroarticular process that presents an extreme inflection of almost 90º (69[1]). In both analyses, *T. proriger* and *T. bernardi* appear as sister group, characterized by the single autapomorphy quadrate conch with shallow alar concavity (47[1]).

The genus *Taniwhasaurus* does not appear as a monophyletic group. In the first analysis, *Ta. capensis* and *Ta. 'mikasaensis'* appear as sister groups, sharing the presence of facets in the teeth surface (73[0]), a character that is also seen in *Ta. oweni*. The latter appears at the base of the clade *Tylosaurus*, sharing with them the quadrate suprastapedial ridge wide, broadly rounded and curving downwards, especially above the stapedial pit (42[1]). *Taniwhasaurus antarcticus* appeared at the base of *Ta. oweni* + *Tylosaurus*, sharing an anterior ventral condyle of the quadrate with distinct deflection (51[1]). When *Ta. capensis, Ta. 'mikasaensis'* and *T. gaudryi* are removed, the relationship between *Ta. oweni* and *Ta. antarcticus* are unsolved. When the diagnostic characters suggested for *Ta. oweni* (Caldwell et al., 2005) and *Ta. antarcticus* (Novas et al., 2002; Martin and Fernández, 2007; Fernández and Martin, 2009) are compared, the only different characters are the shape of the frontoparietal suture, which is almost straight in *Ta. antarcticus*, and not in *Ta. oweni*, and the absence of facets in *Ta. antarcticus* teeth, while the teeth in *Ta. oweni* are faceted. Only a few specimens have been assigned to *Ta. antarcticus* (Fernández and Gasparini, 2012), where the holotype is the most complete and best preserved, followed by a partial skull of a juvenile specimen from Vega Island (Martin et al., 2007); more material from Vega and Seymour Islands referred to the species correspond to isolated vertebrae and teeth, none of them well preserved. The species from New Zealand, *Ta. oweni*, was poorly described until a new specimen was found in the Haumuri Bluff (Caldwell et al., 2005). New specimens from Antarctica will enable us to hypothesize its relationship with *Ta. oweni*.

The only specimen available of *Ta. capensis* shows more affinities with *Taniwhasaurus* species, than *Tylosaurus*. The flutes visible on the teeth crowns have not been seen in any species of *Tylosaurus*, and it is considered here diagnostic for the genus *Taniwhasaurus* (Martin and Fernández, 2007; Caldwell et al., 2008). Therefore, it is here removed from *Tylosaurus* and placed in *Taniwhasaurus*. This re-assignment expands the geographic range of the genus *Taniwhasaurus* to the Indian Ocean. The taniwhasaur *Ta. 'mikasaensis'* does not have enough diagnostic characters to be considered a different species, since the characters exhibited by the holotype and referred specimens are shared with other species of *Taniwhasaurus*. Therefore, it is considered appropriate to assign the Japanese specimens to a generic level, as indeterminate *Taniwhasaurus*.

Order SQUAMATA Oppel, 1811

Family MOSASAURIDAE Gervais, 1852

Subfamily TYLOSAURINAE Williston, 1897

Genus *TYLOSAURUS* Marsh, 1872

Type Species—*Tylosaurus proriger* (Cope, 1869) from Niobrara Formation, western Kansas, USA.

Generic Diagnosis—(1) twelve to thirteen maxillary teeth; (2) prefrontal does not contribute to external nares; (3) frontal overlaps supraorbital portion of prefrontal; (4) frontal does not contribute to the orbit; (5) ventroposterior process on jugal present; (6) ten to eleven pterygoid teeth; (7) broad projection of dentary anterior to first dentary tooth; (8) thirteen teeth on dentary; (9) if teeth present carina, it have serrations; (10) unfluted marginal teeth; (11) six to seven pygals, 33 to 34 caudal chevron-bearing and 56 to 58 terminal caudals; (12) scapula smaller than coracoid, convex superior border of scapula; (13) radial process absent in the humerus; (14) elongated radius, same length of metacarpal one and two; (15) ischium well expanded medially at symphysis; (16) distal end of femur more expanded than proximal; (17) phalangeal formula of pes 5-8-8-8- (modified from Russell, 1967).

Locality/Age—Turonian to lower Maastrichtian (Dollo, 1885; Loera-Flores 2013; Jiménez-Huidobro and Caldwell, 2016).

Discussion—The current knowledge of the genus *Tylosaurus* involves a North Atlantic Circle Basin (Jiménez-Huidobro and Caldwell, 2016) distribution, with the following species: The type species, *T. proriger*, was described from a partial snout and thirteen associated vertebrae (Cope, 1869). *Tylosaurus imbeensis* from Angola is the oldest tylosaurine species ever mentioned, however, it will be not considered in this analysis, due to the lack of available specimens. *Tylosaurus nepaeolicus* is the next oldest known tylosaurine taxon, from the upper Coniacian-lower Santonian of the Kansas Chalk. Another species with the same geographic and stratigraphic distribution, *T. kansasensis*, named by Everhart (2005) was later recognized as representing subadult specimens of *T. nepaeolicus* (Jiménez-Huidobro et al., 2016; Chapter 3). From northern North America, *T. pembinensis*, formerly *Hainosaurus pembinensis*, was later synonymized by Bullard and Caldwell (2010). A second species, the younger North American tylosaurine *T. saskatchewanensis*, was described from the upper Campanian of Saskatchewan (Bullard 2006; this thesis, chapter 4). Some representatives of *Tylosaurus* have been found in Europe: *T. gaudryi* from France was firstly assigned to *Mosasaurus gaudryi* (Thevenin, 1896); later, due to the edentulous rostrum, and some similarities with a Belgian specimen, it was re-assigned to *Hainosaurus gaudryi* (Bardet, 1990), and finally to *Tylosaurus gaudryi* (Lindgren, 2005).

The Belgian species *Hainosaurus bernardi* was re-assigned to *Tylosaurus bernardi*, due to the lack of diagnosis of the former genus *Hainosaurus* (Jiménez-Huidobro and Caldwell, 2016; Chapter 2). And finally, the Swedish *Tylosaurus ivoensis* (Persson, 1963), previously *Mosasaurus ivoensis* and synonymized to *Tylosaurus* by Lindren and Siverson (2002), which consists only of isolated teeth and vertebrae; the teeth in this species show ornamentation based on facets and flutes, more typical of *Taniwhasaurus*; however, *T. ivoensis* still needs further analysis, and it will not be considered here.

TYLOSAURUS PRORIGER (COPE, 1869)

Synonymy—*Macrosaurus proriger* Cope, 1869

Leiodon proriger (Cope, 1870)
Liodon proriger (Cope, 1870)
Rhinosaurus proriger (Marsh, 1871)
Rhamphosaurus proriger (Cope, 1872)

Emended diagnosis—(1) maxillopremaxillary suture terminates posteriorly the fourth maxillary tooth; (2) frontal with well developed medial crest; (3) prefrontal overlaps with postorbitofrontal; (4) frontal invades posteriorly the parietal through dorsal medial and lateral alae; (5) suprastapedial process of the quadrate long, reaches about midheight of the shaft; (6) infrastapedial process of the quadrate moderately developed; (7) tympanic ala thin; (8) teeth without flutes; (9) humerus and femur equal in length.

Locality/Age—upper Santonian to lower Campanian of the Kansas Chalk, Niobrara Formation (Cope, 1869; Russell, 1967), Mooreville Chalk of Alabama (Russell and Applegate, 1970; Kiernan, 2002), Taylor Group of Texas, and the Pierre Shale of Kansas and South Dakota (Russell, 1967).

Referred Material—AMNH 221; 1493; 1529; 1535; 1555; 1560; 1585; 1592; YPM 1268; 1288; 1302; 3873; 3977; 3978; 3981; 3984; 3987; 3990; 3993; 3999; KU 1020; 1023; 1032; 1033; 1084; 1115; 1135; 1194; 5033; FHSM VP 3; 393; SDSM 10439; NHMUK R3628. Not all referred specimens are listed here.

TYLOSAURUS NEPAEOLICUS COPE, 1874

Synonymy—*Tylosaurus kansasensis* Everhart, 2005.

Revised diagnosis—*T. nepaeolicus* differs from other species of *Tylosaurus* by the following combination of character-states: (1) premaxillo-maxillary suture terminates posteriorly above midpoint between third and fourth maxillary tooth; (2) prefrontal overlaps with postorbitofrontal; (3) frontal with dorsal medial midline in juveniles, but poorly developed or absent in adult; (4) lateral borders of parietal table slightly convex; (5) infrastapedial process of quadrate poorly developed or absent; (6) suprastapedial process of quadrate long, reaching about half length of complete bone; (7) tympanic ala thick; (8) mandibular condyle of the quadrate lateromedially broad; (9) lateral crest of tympanic ala ends posteriorly near mandibular condyle.

Locality/Age—Lower Smoky Hill Chalk, Niobrara Formation, Kansas, from the upper Coniacian to lower Santonian.

Referred Material—FHSM VP 7262, 2209, 13742; NHMUK R3624; AMNH 124, 134, 1524, 15,61, 1565, 2167, 2319; MCZ 1592, 1604, 1626; YPM 3969, 3970, 3974, 3979, 3980, 3992. Not all referred specimens are listed here.

TYLOSAURUS BERNARDI DOLLO, 1885.

Synonymy—*Hainosaurus bernardi*.

Holotype—IRScNB R23 (ex IRScNB 1564?) Skull moderately complete; pectoral girdle fairly complete; dissociated limb bones and incomplete vertebral series, not well preserved.

Emended Diagnosis—(9) vertical ramus of the jugal thick; (2) vertical ramus of the jugal presents a visible suture to articulate with the postorbitofrontal, instead of a deep excavation; (3) tympanic ala of the quadrate thin; (4) frontal midline dorsal eminence moderately developed; (5) parietal table rectangular in shape, wider in the anterior than posterior end; (6) ventromedial process of postorbitofrontal projects laterally.

Locality/Age—upper Lower Maastrichtian Ciply Phosphatic Chalk, in La Malogne, near the town of Mesvin, Mons Basin, southwestern Belgium (Robaszynski, 1989; Robaszynski and Christensen, 1989; Robaszynski and Martin, 1988).

Referred Material—IRScNB 3672, consisting of a partial skull (upper and lower jaw, left postorbitofrontal, left quadrate), 17 vertebrae and few podial elements.

TYLOSAURUS SASKATCHEWANENSIS n.sp.

Holotype—RSM P2588.1. Moderately complete and articulated skull, associated with a quite complete and disarticulated postcranium. The vertebral column is almost complete, except for a few vertebrae in the caudal series; among the appendicular elements only the phalanges are missing.

Diagnosis—(1) extensive overlap of premaxilla onto the frontal; (2) anterior process of the frontal extending anteriorly up to half of the length of the external naris; (3) frontal with a well-developed dorsal midline crest; (4) exclusion of the prefrontal from the dorsal rim of the orbit, by a long anterior process of the postorbitofrontal; (5) suprastapedial process of the quadrate moderate in size; (6) infrastapedial process of the quadrate rounded, and located high on the quadrate shaft, almost touching the suprastapedial process; (7) tympanic ala of the quadrate thick; (8) femur longer than the humerus; (9) 55

(+8) vertebrae anterior to chevron bearing caudals; (10) rounded astragalus with big semicircular crural foramen.

Locality/Age—near Herbert Ferry on the shore of lake Diefenbaker, Snakebite Member, Bearpaw Fm., Saskatchewan, Canada, upper Campanian (Kauffman and Caldwell, 1993).

Genus *TANIWHASAURUS* Hector, 1874

Type Species—*Taniwhasaurus oweni* (Hector, 1874) from Campanian of Haumuri Bluff, Conway Siltstone Formation, South Island, New Zealand.

Generic Diagnosis—(1) prefrontal excluding maxilla from contact with frontal; (2) frontal shield-shaped rather than triangular; (3) narial opening beginning between third and fourth maxillary tooth; (4) thirteen to fourteen teeth in maxilla; (5) thirteen to fourteen dentary teeth; (6) marginal dentition distally slender, posteromedially recurved with narrow and distinct lateral fluting and medial striation; (7) if teeth are carinated, they have no serrations; (8) predental rostrum of premaxilla with dorsal sagittal crest; (9) base of ectopterygoid process broad anteroposteriorly; (10) distal end of ectopterygoid process forming thick, rounded tubercle facing ventrolaterally and slightly posteriorly; posteroventral process of jugal present; (11) quadrate shaft distinctly deflected laterally around midheight; (12) suprastapedial process roughly 50% or more of quadrate height; (13) suprastapedial process not constricted in dorsal view; (14) infrastapedial process small (modified from Caldwell et al., 2008).

Locality/Age—upper Santonian to lower Maastrichtian (Novas et al., 2002; Caldwell et al., 2008).

Discussion—Hector (1874) described two species from the lower Haumurian of the Haumuri Bluff (=lower/middle Campanian, Upper Cretaceous) of New Zealand: *Taniwhasaurus oweni and Tylosaurus haumuriensis*. Caldwell et al. (2005) synonymized *T. haumuriensis* with *Ta. oweni*. The type species *Ta. oweni* was described based on the lectotype (NMNZ R1536, Welles and Gregg, 1971:51), two paralectotypes and six referred specimens. *Ta. oweni* remained poorly known until Caldwell et al. (2005) re-described it based on a newly collected skull from the same locality. A second species, *Ta. antarcticus*, was described based on an almost complete skull and associated postcranial material from the upper Campanian of the Northwestern James Ross Island, Antarctica. The specimen was first described by Novas et al. (2002) as *Lakumasaurus antarcticus*. However, Martin and Fernández (2007) noted similarities of the species from Antarctica with *Ta. oweni*, synonymizing the genus with *Taniwhasaurus*.

TANIWHASAURUS OWENI HECTOR, 1874

Synonymy—*Leiodon haumuriensis* Hector, 1874
Leiodon amuriensis Hector, 1880
Tylosaurus haumuriensis (Hector) Williston, 1898

Revised diagnosis—(1) prefrontal excluding maxilla from contact with frontal; (2) broad overlap of prefrontal and postorbitofrontal above orbit, excluding frontal from orbital margin; (3) frontal shield-shaped rather than triangular; (4) narial opening beginning above third to fourth maxillary tooth position; (5) 13 to14 teeth in maxilla; (6) predental rostrum of premaxilla with dorsal sagittal crest; (7) small predental process on anterior tip of dentary; (8) infrastapedial process small (modified from Caldwell et al., 2005).

Locality/Age—Haumuri Bluff, in the Conway Siltstone Formation, south of Kaikoura, South Island, New Zealand. The horizon is lower Haumurian (lower-middle Campanian).

Referred Material—NMNZ R1532 snout composed of right dentary, maxilla, premaxilla, prefrontal, and partial right jugal; KHM N99-1014/1-5 skull block in five parts (including upper jaw, pterygoid, snout, lower jaw, three caudal vertebrae, and a small block with skull bones); NMNZ 1541 teeth and three vertebrae; NMNZ 1537 fragment of jaw; CM Zfr 143 jaw, pterygoid, and teeth; NHMUK R840 block with cranial elements.

TANIWHASAURUS ANTARCTICUS (NOVAS ET AL. 2002)

Synonymy—*Lakumasaurus antarcticus* Novas et al., 2002.

Revised diagnosis— prefrontal forming part of the narial opening; broad overlap of prefrontal and postorbitofrontal above orbit, excluding frontal from orbital margin; frontal with relatively straight lateral sides; narial opening beginning between third and fourth maxillary tooth position; striated dentition; premaxilla with orsal ridge; relatively short predental rostrum; dorsal quadrate deflected laterally; long, narrow dorsal margin of quadrate; suprastapedial with a large medial projection distinctly offset from the line of the suprastapedial process; suprastapedial process of quadrate long, deeply grooved, and directed ventromedially; infrastapedial process small; ventromedial suture of prefrontal sigmoidal rather than broadly convex; posterior extension of postorbitofrontal extends beyond the supratemporal fenestra.

Locality/Age— Dinosaurio River, Santa Marta Formation, James Ross Island, Antarctica, uppermost Campanian (Crame et al., 2004).

TANIWHASAURUS INDET 1. – “*Taniwhasaurus mikasaensis*” (Fig. 3)

Specimens— MCM.M0009 fragment of a skull; MCM.A600 skull elements: quadrate, jugal, postorbitofrontal, parietal and coronoid; MCM.M10 two dorsal vertebrae; MCM.A1008 two intermedial, one terminal, and one dorsal vertebrae.

Locality/Age—East bank of Kikumen Creek, near to Mikasa city, Hokkaido, Northern Japan. The horizon is upper Santonian – lower Campanian.

Discussion–The holotype assigned to *Ta. ‘mikasaensis’* MCM.M0009 is a fragment of skull, and it is the only specimen with teeth preserved (Fig. 6.3A). The dental characters present in this specimen are attributable to the genus *Taniwhasaurus*, such as the presence of flutes in the crown, character seen in *Ta. oweni* (Caldwell et al., 2005) and *Ta. antarcticus* (Martin and Fernández, 2007) (Fig. 6.4). The lack of serrations in the carinae is also a character seen in *Taniwhasaurus* species. Some referred specimens include skull elements (Fig. 6.3B) and isolated vertebral elements (Fig. 6.3C). The squamosal process of the postorbitofrontal is also long in *Ta. antarcticus*, almost until the posterior end of the supratemporal fenestra; the posterior process of the postorbitofrontal it is not known in *Ta. oweni*. The internarial bar of the premaxilla overlaps with the anterior portion of the frontal, as in all tylosaurine mosasaurs; the overlapping almost at the level of the anterior border of the orbit also happens in *T. saskatchewanensis* (this thesis, Chapter 4). The jugal does not show any unique character, being similar to that of *Ta. oweni* (Caldwell et al., 2005), where the vertical ramus is slightly posteriorly recurved as well.

TANIWHASAURUS INDET. 2 ("Tylosaurus capensis")

Specimens—SAM-PK-5265, nearly complete frontal with fragments of parietal and postorbitofrontals, a fragment of jaw, and a cervical vertebra (Fig. 6.5).

Locality/Age—Chalk of the Transkei (= Pondoland), South West of Umzamba, South Africa. The horizon is Santonian.

Remarks—The original diagnosis by Lingham-Soliar (1992) included the size of the parietal foramen and the distance of it from the frontoparietal suture. They are not included here because both characters seem to be variable along the genus *Tylosaurus* (Jiménez-Huidobro and Caldwell, 2016).

Discussion–The holotype corresponds to a large tylosaurine specimen, consisting of a smooth frontal, with the frontal midline crest absent, thus differing from that of *Ta. antarcticus* and *Ta. oweni* (Novas et al, 2002; Caldwell et al, 2005). Both median sutural flanges (cf. Bell, 1997) are visibly rounded, not sharp or pointed, and softly invade the parietal; lateral sutural flanges are not developed. The result is a frontoparietal suture that is slightly sinusoidal. The anterior portion of the parietal is attached to the frontal, with the parietal opening visible, located only in the parietal, far from the suture (Fig. 6.5A). Fragments of both the left and right postorbitofrontals are attached to each side of the frontal. Jaw fragments exist, but there is little data preserved meriting description (Fig. 6.5B). There is a complete replacement tooth appearing in the jawbone, along with a fragmented replacement tooth, which has a broken apex of the crown. The teeth are cylindrical in shape, sharp, and slightly labiolingually compressed. Both teeth are fluted and faceted (Fig. 6.5C), differing from those in the various *Tylosaurus* species which have no facets, but similar to the enamel ornamentation seen in teeth of *Ta. oweni* and *Ta.*

antarcticus; in addition, it has been established that the fluting condition of the crown is a character seen only in the genus *Taniwhasaurus* amongst tylosaurines (Martin and Fernández, 2007; Caldwell et al., 2008). However, due to preservation, it is not possible to establish the presence of carinae.

CONCLUSIONS

The results of the phylogenetic analysis presented here support the monophyly of the clade Tylosaurinae, as suggested by Bullard (2006), and contrary to Bell (1997) who suggested that the inclusion of *T. bernardi (=H. bernardi)* into the analysis would render the group paraphyletic. Four valid taxa of *Tylosaurus* were recovered: *T. proriger* from the upper Santonian-lower Campanian of the Western Interior Seaway, and *T. bernardi* from the lower Maastrichtian of Belgium, both forming a well-supported clade; and *T. pembinensis* from the middle Campanian, and *T. saskatchewanensis* from the upper Campanian, both from northern North America, forming another clade. The earliest recognized species, *T. nepaeolicus* from the upper Coniacian-lower Santonian of the Western Interior Seaway, was recovered as basal to the clade of all other species of *Tylosaurus*.

The genus *Taniwhasaurus* is a paraphyletic assemblage, even when the poorly known species of taniwhasaurs and tylosaurs were removed from the analysis. *Taniwhasaurus oweni* from the lower-middle Campanian of New Zealand, and *Ta. antarcticus* from the upper Campanian-lower Maastrichtian of Antarctic Peninsula are distinguished by only a few characters, such as the unfaceted teeth in *Ta. antarcticus*, and its almost straight frontoparietal suture. Unfortunately, none of the species is known from a complete specimen, making it difficult to differentiate them, and so the conservative approach is taken here of retaining these taxa until new data supports them more robustly, or suggests synonymization.

My results support a North Atlantic Circle Basin distribution for the genus *Tylosaurus*, suggested by Jiménez-Huidobro and Caldwell (2016). However, I suggest that species from the genus *Taniwhasaurus* were not endemic as previously suggested (Martin and Fernández, 2007), but rather enjoyed a cosmopolitan distribution, with records from the North and South Pacific, Indian Ocean, and Antarctica. These patterns are crucial to understanding the evolution of tylosaurine mosasaurs, and the evolution of mosasauroids on a global scale.

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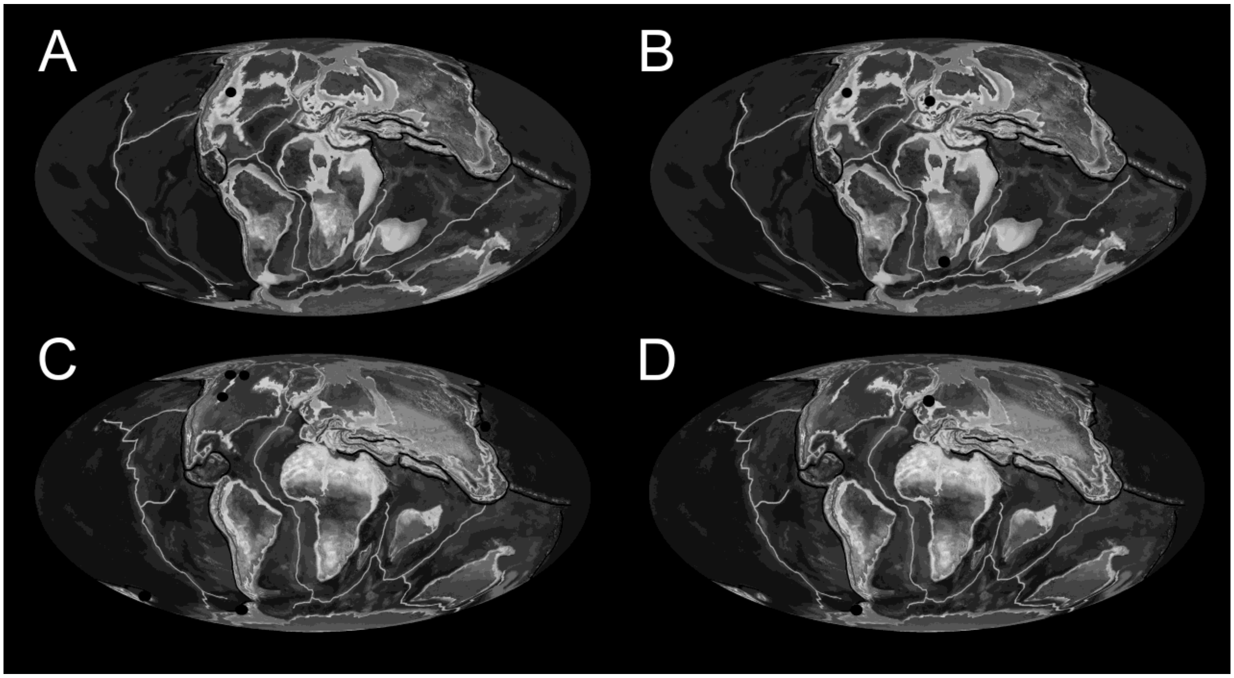

FIGURE 6.1. Geographical distribution of tylosaurine species, according to geochronological stages in the Late Cretaceous: **A**, Coniacian. **B**, Santonian. **C**, Campanian. **D**, Maastrichtian. © Ron Blakey, Colorado Plateau Geosystems.

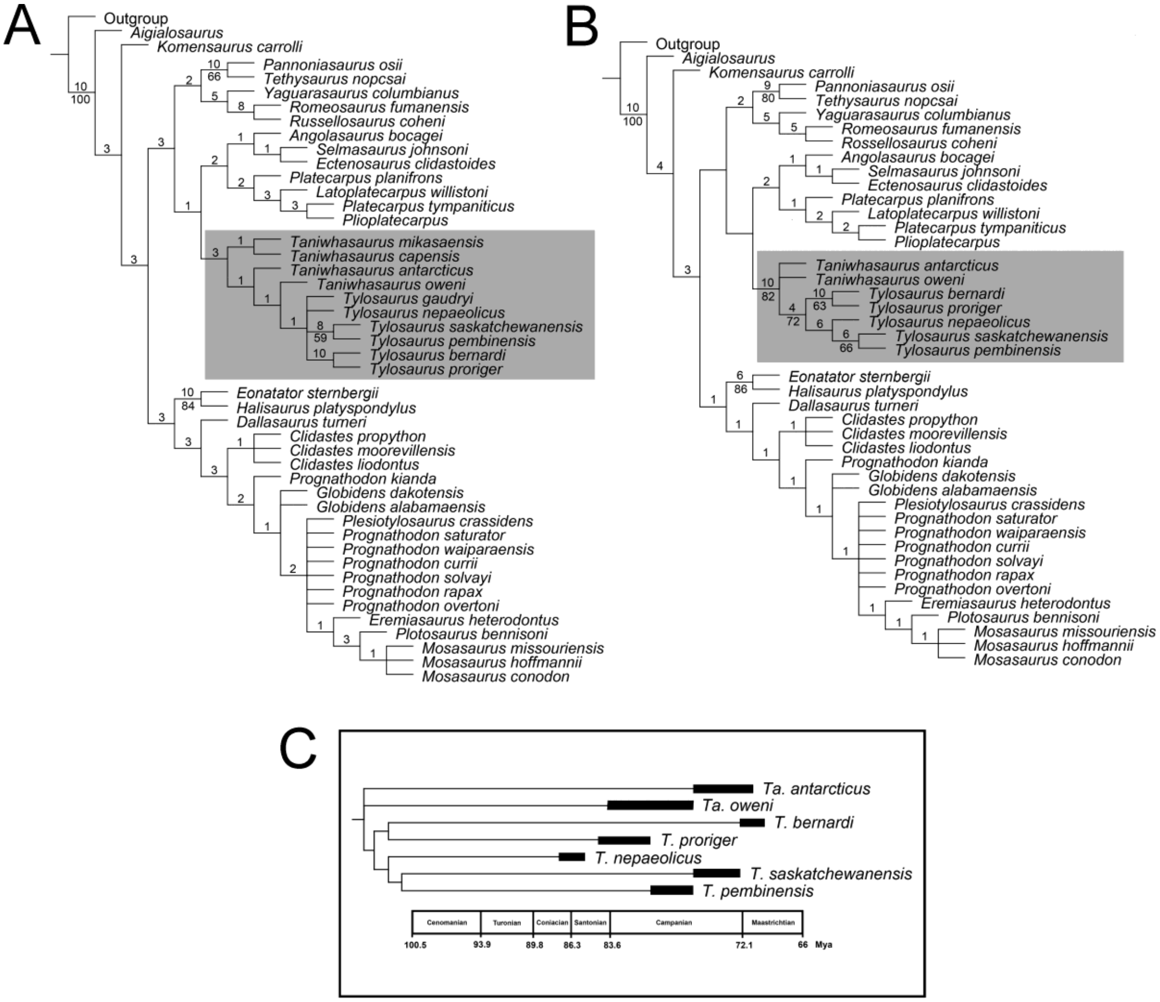

FIGURE 6.2. Strict consensus trees. **A**, strict consensus tree obtained from 33 most parsimonious trees (MPTs) of 430 steps (C.I. = 0.3651; R.I. = 0.7321) of all tylosaurine species. **B**, strict consensus tree obtained from 49 MPTs of 428 steps (C.I. = 0.3668; R.I. = 0.7292), exluding *T. capensis, T. gaudryi* and *Ta. 'mikasaensis'*. Values above nodes indicate Bremer (decay) indices, and below nodes indicate Bootstrap indices (only values over 50% are shown). **C**, ingroup relationships depicted in **B,** with paleobiostratigraphic distribution.

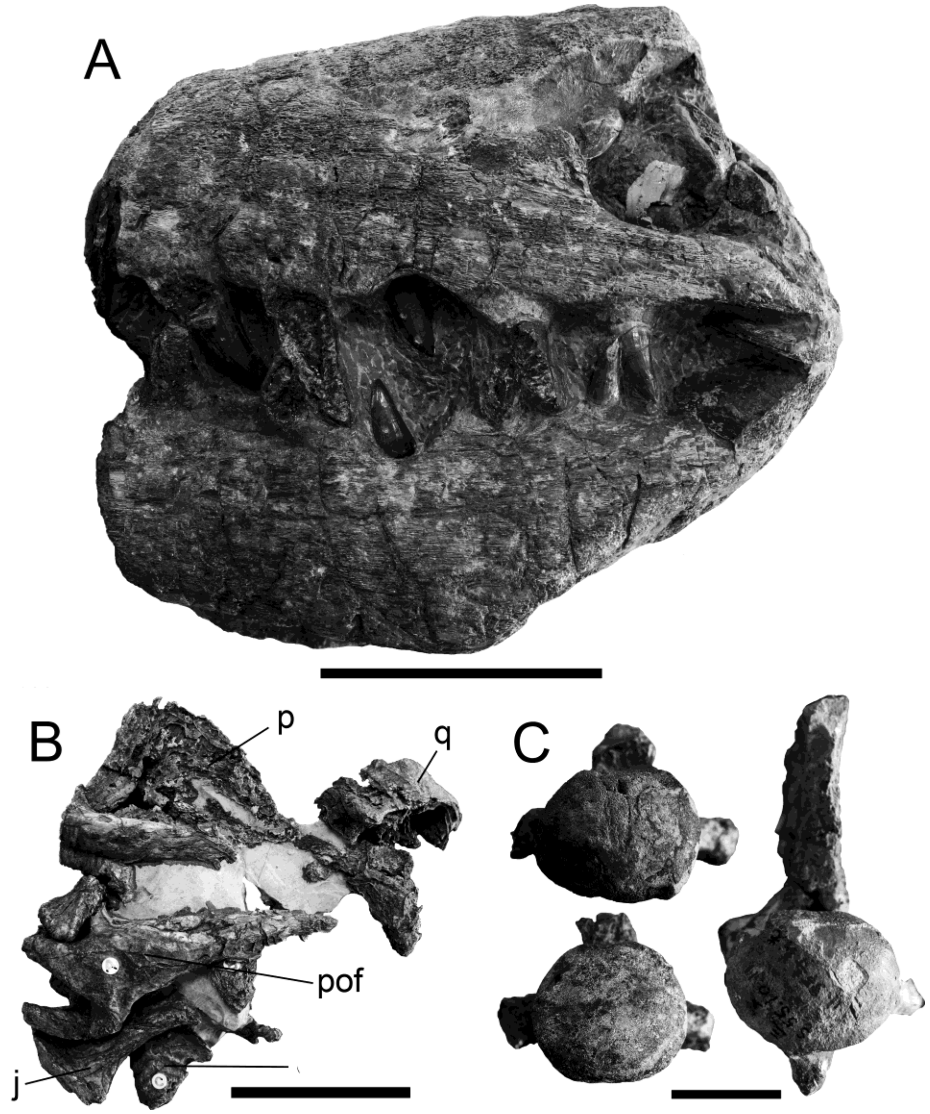

FIGURE 6.3. Japanese specimens assigned to *Taniwhasaurus 'mikasaensis'*, by Caldwell et al., 2008, here re-assigned to *Taniwhasaurus* indet. **A**, left lateral view of the holotype MCM.M0009, corresponding to a fragment of a skull. Scale bar equal to 10 cm. **B**, referred specimen MCM.A600, skull elements: quadrate, jugal, postorbitofrontal, parietal and coronoid. Scale bar equal to 10 cm. **C**, vertebral elements: left top and bottom show dorsal vertebrae, in condyle view; right shows an intermedial caudal vertebra, in condyle view. Scale bar equal to 5 cm.

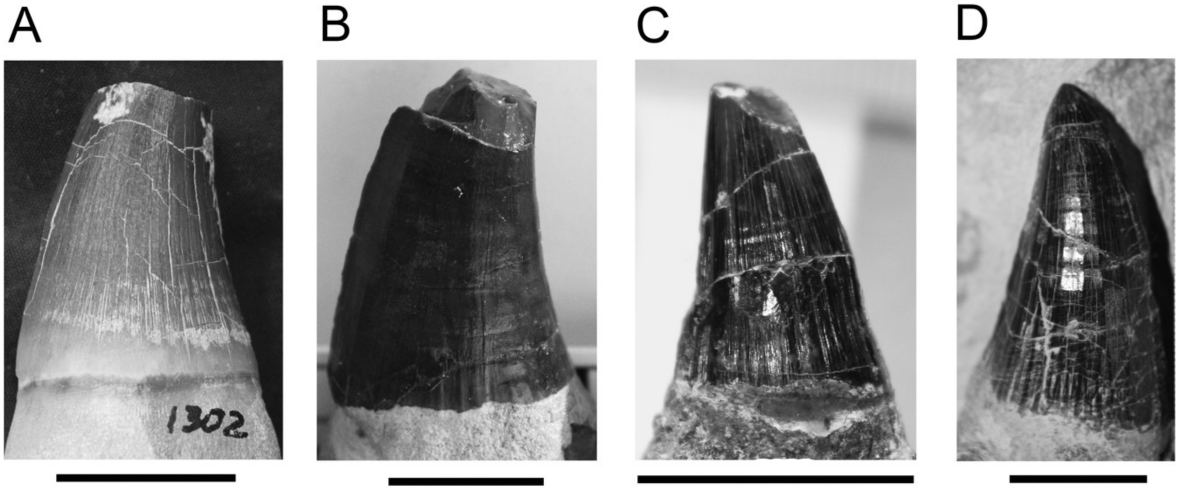

FIGURE 6.4. Comparison of marginal teeth of different species of Tylosaurinae. **A**, *T. proriger* YPM 1302. **B**, *T. bernardi* IRScNB 3672. **C**, *Ta. antarcticus* IAA 2000-JR-FSM-1. **D**, *Ta. oweni* CMNZ Zfr 143. All scale bars equal to 2 cm.

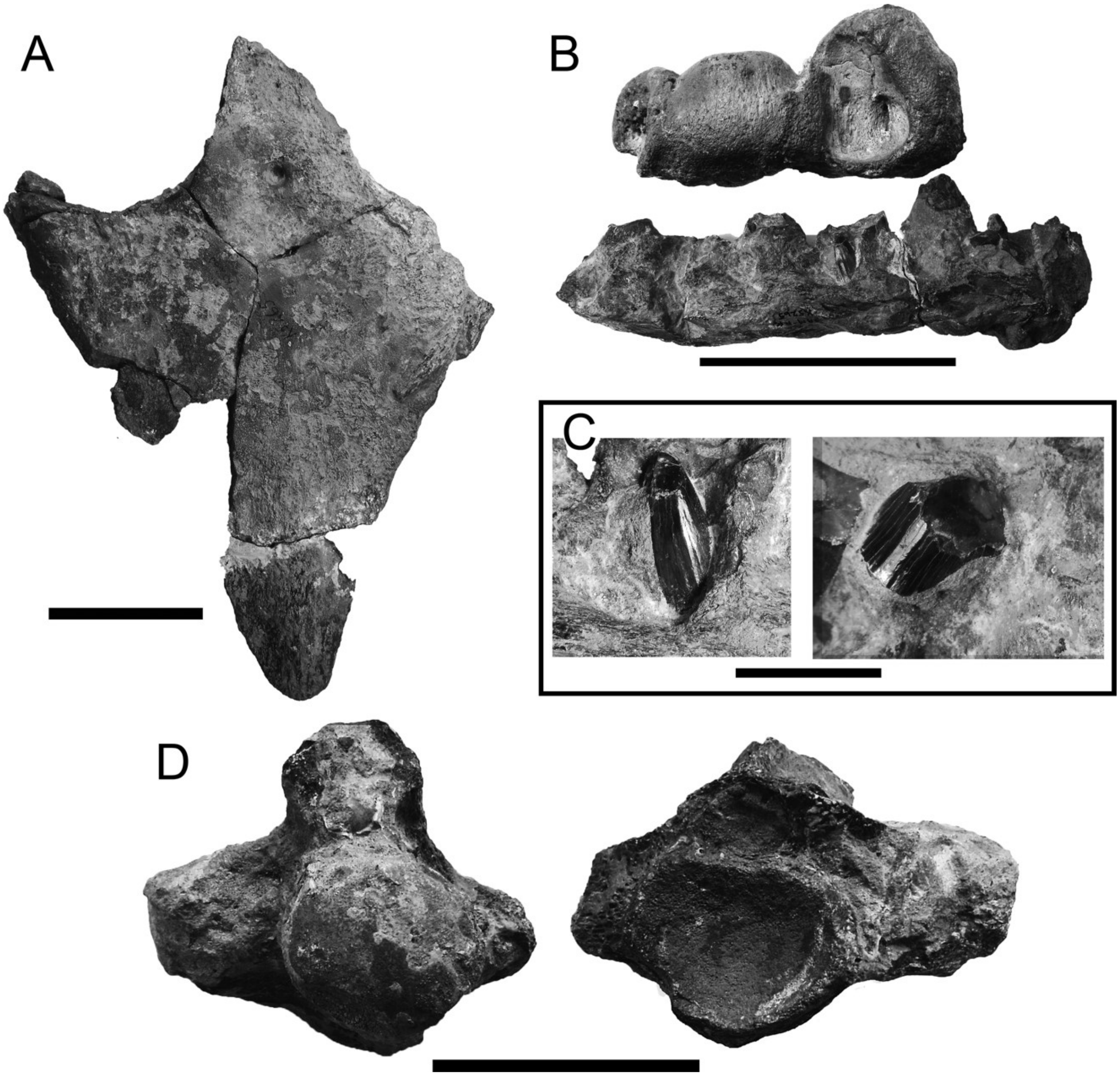

FIGURE 6.5. SAM-PK-5265, holotype of former *'Tylosaurus' capensis*, here re-assigned to *Taniwhasaurus capensis*, from Pondoland, South Africa. **A**, frontal with fragments of parietal and both postorbitofrontals. Scale bar equal to 10 cm. **B**, jaw fragments. Scale bar equal to 10 cm. **C**, close up of replacement teeth. Scale bar equal to 2 cm. **D**, cervical vertebra, left shows in condyle view, right shows in cotyle view. Scale bar equal to 5 cm.

CHAPTER SEVEN

GENERAL DISCUSSION AND CONCLUSIONS

At the beginning of this thesis project, it was commonly accepted that there were three well defined, diagnosed, and described tylosaurine genera: *Tylosaurus* Marsh, 1872, *Hainosaurus* Dollo, 1885, and *Taniwhasaurus* Hector, 1874. These three genera included the species *Tylosaurus proriger* Cope, 1869, *Tylosaurus nepaeolicus* Cope, 1874, *Tylosaurus kansasensis* Everhart, 2005, *Tylosaurus pembinensis* Nicholls, 1988, *Tylosaurus gaudryi* Thèvenin, 1896, *Tylosaurus ivoensis*, Persson 1963, *Tylosaurus capensis* Broom, 1912, *Tylosaurus imbeensis* Antunes, 1964, *Hainosaurus bernardi* Dollo, 1885, *Hainosaurus neumilleri* Martin, 2007, *Taniwhasaurus oweni* Hector, 1874, *Taniwhasaurus antarcticus* Novas et al., 2002, and *Taniwhasaurus mikasaensis* Caldwell et al., 2008. At the conclusion of this project, the number of genera has been reduced to two, and the number of valid species, to six.

Chapter Two of this thesis was intended to consider in detail the type species of the genus *Hainosaurus* and to re-diagnose that species of lower Maastrichtian mosasaur from the Ciply Phosphatic Chalk, Mons Basin, Belgium. When *H. bernardi* was reassessed, the absence of diagnostic characters supporting a generic distinction of *Hainosaurus* from *Tylosaurus* was evident. The purportedly diagnostic characters for *Hainosaurus* proposed by Lingham-Soliar (1992) were found either to be shared with other species of *Tylosaurus*, or to not be preserved in the specimens assigned to *H. bernardi* (Jiménez-Huidobro and Caldwell, 2016). Russell (1967) considered the high vertebral count to be a good diagnostic character (*H. bernardi* was diagnosed with 40 presacral vertebrae, while *Tylosaurus* possesses only about 30 presacrals). However, none of the specimens of *H. bernardi* have either a complete or articulated vertebral series. Therefore, it is not possible to use the vertebral count to diagnose the genus as the actual number of dorsals and caudals is unknown (Jiménez-Huidobro and Caldwell, 2016). Lindgren and Siverson (2002) concluded that some of the characters suggested by Lingham-Soliar (1992) were not diagnostic, and proposed a new diagnosis for *Hainosaurus* (i.e., *H. bernardi*), based mainly on tooth morphology (Lindgren and Siverson, 2002; Lindgren, 2005). Jiménez-Huidobro and Caldwell (2016) noted that *Tylosaurus* also displayed a marginal dentition with the same characteristics possessed by *Hainosaurus*. The original diagnoses by Dollo (1885) and the emended diagnoses by Lingham-Soliar (1992), Lindgren and Siverson (2002), and Lindgren (2005), of *H. bernardi*, do not differentially diagnose this taxon as generically distinct from *Tylosaurus*. The results of Chapter 2 suggested that *Hainosaurus* is a junior synonym of *Tylosaurus*, a conclusion supported by phylogenetic analysis where *T. bernardi* appears nested within the genus *Tylosaurus*, as sister taxon of the type species *T. proriger*. However, some characters still are found to diagnose the species *Tylosaurus bernardi*. The synonymy shown here suggests a broader temporal and spatial distribution of *Tylosaurus* than was previously thought (Bardet, 1990), ranging from the late Turonian (Loera-Flores, 2013) to the early Maastrichtian instead of just being restricted to the Campanian, contra Russell (1967). This re-assignment indicates a distribution of the genus *Tylosaurus* in the North Atlantic Circle Basin, rather than a restriction to only the North American epicontinental seas.

In Chapter Three, the North American species *Tylosaurus nepaeolicus* Cope, 1874, and *Tylosaurus kansasensis* Everhart, 2005, were re-described, compared and contrasted. The former species is recognized from the upper Coniacian to the lower

Santonian of the lower Smoky Hill Chalk, Niobrara Group, while the latter has only been found in the upper Coniacian of the lower Smoky Hill Chalk of Kansas. The data obtained from the two sympatric species, that also share an overlapping temporal range, showed no differences between them, indicating that *T. kansasensis* and *T. nepaeolicus* correspond to the same taxon. The diagnostic characters argued to distinguish *T. kansasensis* by Everhart (2005) are shared with *T. nepaeolicus*, and in some cases even with *T. proriger*. Furthermore, that there are no juvenile specimens reported for *T. nepaeolicus*, while all the specimens assigned to *T. kansasensis* present juvenile characters that are observed in juveniles of *T. proriger*, suggesting that the differences between *T. nepaeolicus* and *T. kansasensis* are the product of ontogenetic variation, instead of sympatric speciation. Such modification of character states between juveniles and adults are also present in specimens of *Clidastes propython*, suggesting that they can be considered as ontogenetic markers of mosasaurid lizards. The morphological similarity between subadult specimens of *T. nepaeolicus* (formerly *T. kansasensis*) and *T. proriger*, suggests that the latter is a possible paedomorph of *T. nepaeolicus*, although a gigantic one.

In Chapter Four a new species of *Tylosaurus* was described based on previous unpublished work by Bullard (2006). The specimen is characterized by a unique set of characters that distinguish it from all the other species of the genus. *Tylosaurus saskatchewanensis* n. sp. from the upper Campanian of the Bearpaw Formation, southern Saskatchewan, represents a large tylosaurine diagnosed by characters of the prefrontal and postorbitofrontal, quadrate, premaxilla and frontal, humerus and femur, astragalus, and a high vertebral count anterior to the chevron bearing caudals. In terms of phylogenetic relationships, *T. saskatchewanensis* is nested within the genus *Tylosaurus*, as the sister taxon of *T. nepaeolicus*. This new species represents the youngest known North American species of *Tylosaurus*.

In Chapter Five, a tylosaurine mosasaur from the upper Campanian of the lower Pierre Shale of South Dakota, U.S.A. was re-assessed. The species was described by Martin (2007), based on a single, very incomplete specimen. Morphological characters to diagnose the material as *Tylosaurus* are present in the single quadrate, a parietal and two teeth. However, the material does not show characters to diagnose a new species and so *T. neumilleri* is considered nomen dubium. The few characters visible on the specimen show strong similarities to both *T. pembinensis* (Bullard, 2006; Bullard and Caldwell, 2010) and *T. saskatchewanensis* (Bullard, 2006; Chapter 4). Therefore the specimen is considered as *Tylosaurus* sp.

In Chapter Six, a phylogenetic analysis included all known, and valid, tylosaurine taxa was performed. The results of the phylogenetic analysis supported the monophyly of the clade Tylosaurinae, as suggested by Bullard (2006), and contrary to Bell (1997), who suggested that the inclusion of *T. bernardi* (=*H. bernardi*) into the analysis would demonstrate the paraphyletic nature of the group. Based on morphological characters seen in the holotype of *Tylosaurus capensis* Broom, 1912, from the Santonian of South Africa, it was reassigned to *Taniwhasaurus* indet. The generic reassignment was based on the morphology of the two preserved replacement teeth; however, the poorly preserved specimen does not present enough characters to be diagnosed at the specific level. The genus *Taniwhasaurus* is not resolved as a clade, even when the poorly known species of *Tylosaurus* and *Taniwhasaurus* were removed from the analysis. *Taniwhasaurus oweni* from the lower-middle Campanian of New Zealand, and *Ta. antarcticus* from the upper Campanian to the lower Maastrichtian of Antarctic Peninsula, are the only two recognized species of the genus, distinguished by only a few characters, and are recovered at the base of the clade Tylosaurinae. The Japanese species *Taniwhasaurus mikasaensis* from the late Santonian to early Campanian of Hokkaido (Caldwell et al., 2008) is not considered here to display sufficient diagnostic characters to differentiate a species distinct from *Ta. oweni;* therefore, it is recognized as *Taniwhasaurus* indet. (Jiménez-Huidobro and Caldwell, in prep.).

Previous research suggested that the genus *Tylosaurus* was endemic to North America, known from the Turonian to the Campanian (Russell, 1967; Loera-Flores, 2013). However, the reassignment of *Tylosaurus bernardi,* and the previous reassignment of *T. gaudryi* (Lindgren, 2005), recognizes a broader temporal and spatial distribution of the genus than was previously thought (Bardet, 1990), extending to the early Maastrichtian. The new species, *Tylosaurus saskatchewanensis,* represents the youngest tylosaurine that occupied the North American epicontinental sea during the late Campanian, extending the stratigraphic range of the genus in the Western Interior Seaway. The invalidation of the species *Hainosaurus/Tylosaurus neumilleri* (Martin, 2007), and the a posteriori re-assignment to *Tylosaurus saskatchewanensis*, extends the geographic range of the species during the late Campanian, from the Bearpaw Formation of Saskatchewan to the lower Pierre Shale of Southern South Dakota.

The results of this thesis support a North Atlantic Circle Basin distribution for the genus *Tylosaurus*. On the other hand, due to the addition of records from South Africa and Japan, species from the genus *Taniwhasaurus* are not described as endemic to any geographic region (as suggested by Martin and Fernández, 2007), but rather had a cosmopolitan distribution from the Santonian (Broom, 1912; Caldwell et al, 2008) to the early Maastrichtian (Novas et al., 2002), with records from the North and South Pacific (Hector, 1874; Welles and Gregg, 1971; Caldwell et al., 2005; Caldwell et al., 2008) to South Africa (Broom, 1912) and Antarctica (Novas et al., 2002; Fernández and Gasparini, 2012).

The alpha taxonomy of the Tylosaurinae Williston, 1897, is now rather significantly modified, resulting in a much more restricted concept of "tylosaurine mosasaur". Two genera are recognized, *Tylosaurus* Marsh, 1872, and *Taniwhasaurus* Hector, 1874. Valid species of *Tylosaurus* include the North American *T. nepaeolicus* Cope, 1874, from the upper Coniacian to lower Santonian of the Niobrara and Boquillas Formation (Russell, 1967; Bell et al., 2012), *T. proriger* from the upper Santonian to lower Campanian of Niobrara, Mooreville Chalk and Taylor Group (Russell, 1967), *T. pembinensis* from the lower-middle Campanian of the Pembina Formation of the lower Pierre Shale (Nicholls, 1988; Bullard and Caldwell, 2010), and *T. saskatchewanensis* from the upper Campanian of the Bearpaw Formation and the lower Pierre Shale (Bullard, 2006; Chapter 4). Valid species of European tylosaurines include *T. bernardi* from the lower Maastrichtian of the Ciply Phosphatic Chalk of Belgium (Hector, 1874; Jiménez-Huidobro and Caldwell 2014), and *T. gaudryi* from the Santonian of France (Thèvenin, 1896; Lindgren, 2005). The distribution of the genus in North America is recognized from the late Turonian of Chihuahua, Mexico, to the late Campanian of Saskatchewan and South Dakota, while the global distribution is extended to the early Maastrichtian of Belgium, reaching the North Atlantic Circle Basin of North America and Europe. The species recognized from the genus *Taniwhasaurus* include *Ta. oweni* Hector, 1874, from the lower-middle Campanian of the Haumuri Bluff of New Zealand (Welles and Gregg, 1971; Caldwell et al., 2005), and *Ta. antarcticus* Novas et al., 2002, from the late Campanian to the early Maastrichtian of Antarctica (Martin and Fernández, 2007; Fernández and Gasparini, 2012). However, the genus was present from the Santonian to the early Maastrichtian, achieving a cosmopolitan distribution prior to its extinction. Future research using new data from the poorly known Southern Hemisphere tylosaurine mosasaurs would potentially help determine the relationships of the genus *Taniwhasaurus* within Tylosaurinae.

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Appendix 1: Data matrix used in Chapter Two and Chapter Three.

MATRIX

Outgroup 0-0000002000100-3-0000000000-0030011000000-0-0010000000051-01-0010001001000020-100-1000001010000000010-0100000000000000000001-0000

Aigialosaurus 0-00?0?02100??0?3?1010?10?00?00???10?1?1??0?011?0???00??????00??0??001000020??010?0000???00000000010-0-00000?00000000000001??0000

Komensaurus_carrolli ??20?0?000?0????????????????0000???????????1???0?01??00?0?00???????????????0000?000?0011?000?

Halisaurus_platyspondylus 10100000211000003?10101?0?00???11????1?20010000?0001??????101?000100010000101??0?????00????????1?????????????????????????1?????00

Halisaurus_sternbergi 0-100?00210000003?0010100000???0210???0020?1?000?0?01??0?1?1101?0?0100010?00100?10??00100??0011101011111001001000010111001111?010?

Dallasaurus_turneri ???????0??0???1??0????????????????????0??????????????????00010??0?1????100002?0?11??00111110?????1???0-0???01000000????????0???0?1?

Clidastes_liodontus 111000?020010?10101001111?10?1021002??1010?0000000010100{1

2}0021?10001000?10100201011000001101 01?1111010110000210101112100 01010001

211?

Clidastes_moorevillensis

1110000020010010101001111?10?1021?020?1010?000100001010020021010001 00001

010020101100000 11?101?1111??0110000210101112100010100 01211?

Clidastes_propython

111000?12001001010100111??10?1021?0???1010?0001000010100100 2101?101000010

1002010110000011?10???1?1??????000210101112 10?0???????2?10

Prognathodon_overtoni

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1001211????0?0?110?11-?1111101110012121011 1??0???010000211?

Prognathodon_rapax

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21010???00001100121101 10?00011110?????1??01?001121210111210 0010?????2?1?

Prognathodon_solvayi 0-

0000010001001010101111 1110?0030?110?1110010100?00111?141-

2?010101?00000?012110?10001011?10????????01?01???????????????????????????

Prognathodon_currii

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Prognathodon_waiparaensis

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11???0

Prognathodon_saturator

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012110?10?01011110????01??0??????????????2??????????????

Globidens_alabamaensis

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101011??0?011??0?????????????0??21010111?????????????2?1?

Globidens_dakotensis

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1}10100???????????????11001101011?00?011?10?????????????????????????????????

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Mosasaurus_conodon

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Mosasaurus_maximus

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1002110111011011O?1??11111?021001131110111210001110001211O

Mosasaurus_missouriensis

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1}0110?3002?01011101101010O2?1011?0000110111?1??11?01??00?????????2100?11?

????2?1?

Plesiotylosaurus_crassidens

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100211?????00011?10????????01100113121011121000l0?????2???

Plotosaurus_bennisoni

101001?10101??10111011?11111?0011002001000?001000110110?101?1?1???1011000 0012??010?10?011??11???1?1?02100113111011121000011??1??211?

Tylosaurus_nepaeolicus

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Tylosaurus_bernardi

121111?001110?11??1001?11001100310?21??0????2?001001001?401?1000000000000 000211100?00001010101100010110110120001000?011100????0?100

Taniwhasaurus_oweni

121111?00?21??11????01????011003?0?21??011?02000?0010???301???00?0?????0111 ?2??100????01010?????00??1????????????????????????????0?

Taniwhasaurus_antarctius

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Tylosaurus_proriger

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Yaguarasaurus_columbianus 0-

10?0?02000???0201200?11000?0?3001111??21002001100000013001???????????00?00 100??1??0?

Eremiasaurus_heterodontus

101001?10111??101?10?1?11?11?01300020?111??1??0??1?111??20021010??1011?100 0121?01??0100110?0??11111001?01???10???????????01??01??1?

Prognathodon_kianda

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Russellosaurus_coheni

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Romeosaurus_fumanensis

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Ectenosaurus_clidastoides

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Plioplatecarpus ???????0011100100-1113011?01000?0??110002110020 0?0{0 1}1100251-21101000000100000201??0??000110000????0??010110020?110012011100?????1?00

Platecarpus_planifrons 1010000001011?100-1110?11?00??13000?100021001000?0{0 1}11001500210010000001000102011010000011??0????????010110020?1100?2011100 ?????1?00

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        Platecarpus_tympaniticus     0-100000011111100-
1111011?01001300011?002110110010{0 1}1100251-
211010000001000002011001000011000001000100101100 20??1?012011100101101100
        Latoplatecarpus_willistoni   0-1000?00120111?0-111{1
2}0?1?01001300021?0021001200101110 0251-
211010000001000102011110001011??0?????0???2111?????????????????????????0
        Selmasaurus_johnsoni         101000?100011110201200011?01-
01?0??21?0011011100?000101151-
211110000001000102011010000011000???????????????????????????????????????
        Angolasaurus_bocagei
101??0?01?11???0??1100?1??00?0?30????1??2100010010001 00151-
21?010001001?00102?1??1???????????????????????????????????????????????0?
        Tethysaurus_nopcsai          0-00?0?02110??10201200?11000-
0?00??21??0010020001?20000111-?10010001000000{0 1}00-
0??10?111000???????0??1110?00?????000???????000?????0
        Pannoniasaurus_osii          0-
00?0???????????????????????0??????????01002000??200???01-
20010?00??000001020???10?1110000???0??0?????01???0???000???????00???????
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Appendix 2: Characters and character states for Appendix 1.

(1) Premaxilla predental rostrum I: total lack of a bony rostrum (0); or presence of any predental rostrum (1). In lateral profile, the anterior end of the premaxilla either exhibits some bony anterior projection above the dental margin, or the bone recedes posterodorsally from the dental margin. State 1 produces a relatively taller lateral profile with an obvious 'bow' or 'prow.'

(2) Premaxilla predental rostrum II: rostrum very short and obtuse (0); or distinctly protruding (1); or very large and inflated (2). In *Clidastes* a short, acute, protruding rostrum (state 1) produces a 'V'-shaped dorsal profile and, as far as is known, is peculiar to that genus. An alternative condition, described as 'U'- shaped, includes those taxa whose rostral conditions span the whole range of states of characters 1 and 2. Hence, the descriptive character is abandoned in favor of a more informative structure-based series.

(3) Premaxilla shape: bone broadly arcuate anteriorly (0); or relatively narrowly arcuate or acute anteriorly (1). In virtually all lizards the premaxilla is a very widely arcuate and lightly constructed element, and the base of the internarial process is quite narrow as in Aigialosaurus bucchichi. All other mosasaurids have a very narrowed premaxilla with the teeth forming a tight curve and the internarial process being proportionally wider (state 1). *Tethysaurus* was recoded as having state 0.

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

(5) Premaxilla internarial bar base shape: triangular (0); or rectangular (1). A vertical

cross-section through the junction of the internarial bar and the dentigerous rostrum produces an inverted triangle in most taxa. But in state 1, this cross-section is transversely rectangular because the broad ventral surface of the bar is planar.

(6) Premaxilla internarial bar dorsal keel: absent (0); or present (1). In state 1 a ridge rises above the level of a normally smoothly continuous transverse arch formed by the bones of the anterior muzzle.

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

(8) Frontal shape in front of the orbits: sides sinusoidal (0); or bone nearly triangular and sides relatively straight (1). In state 1, the area above the orbits is expanded and an isosceles triangle is formed by the rectilinear sides. In certain taxa, a slight concavity is seen above the orbits, but anterior and posterior to this, there is no indication of a sinusoidal or recurved edge.

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

(10) Frontal narial emargination: frontal not invaded by posterior end of nares (0); or

distinct embayment present (1). In some mosasauroids, the posterior ends of the nares are concomitant with the anterior terminus of the frontal-prefrontal suture and, therefore, there is no marginal invasion of the frontal by the opening. However, in other mosasauroids this suture begins anterior and lateral to the posterior ends of the nares, causing a short emargination into the frontal.

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

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

(13) Frontal olfactory canal embrasure: canal not embraced ventrally by descending processes (0); or canal almost or completely enclosed below (1). In state 1, very short descending processes from the sides of the olfactory canal surround and almost, or totally, enclose the olfactory nerve.

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

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

The dorsal trace of the suture can be quite complex with a portion of the parietal embraced by the posterior extension of these frontal flanges.

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

(17) Frontal invasion of parietal I: lateral sutural flange of frontal posteriorly extended (0); or median frontal sutural flange posteriorly extended (1); or both extended (2); or suture straight (3). In all mosasaurines the oblique median frontal sutural ridge extends onto the dorsal surface of the parietal table and embraces a portion of the anterior table within a tightly crescentic midline embayment. In *Plioplatecarpus* and *Platecarpus*, the lateral oblique sutural ridge from the frontal is greatly protracted posteriorly to cause a large, anteriorly convex embayment in the dorsal frontal-parietal suture. In this case the entire posterolateral corner of the frontal is extended backwards to embrace the anterolateral portion of the parietal table on both sides. Consequently, the parietal foramen is very widely embraced laterally and the oblique anterior sutural ridge of the parietal occupies a position inside the embayment within the frontal. *Dallasaurus* was recoded as ?.

(18) Frontal medial invasion of parietal II: if present, posteriorly extended median sutural flange short (0); or long (1). The median oblique sutural flange is either short, not

reaching back to the parietal foramen (state 0), or tightly embraces the foramen while extending backwards to a position even with or beyond its posterior edge (state 1).

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

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

(21) Parietal foramen size: relatively small (0); or large (1). If the foramen is smaller than or equal to the area of the stapedial pit, it is considered small. If the foramen is significantly larger or if the distance across the foramen is more than half the distance between it and the nearest edge of the parietal table, the derived state is achieved.

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

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

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

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

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

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

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

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

(30) Postorbitofrontal shape: narrow (0); or wide (1). In *Clidastes* and the *Globidensini*,

the lateral extent of the element is almost equal to half of the width of the frontal and the outline of the bone is basically squared.

(31) Postorbitofrontal transverse dorsal ridge: absent (0); or present (1). In state 1, an inconspicuous, low, and narrowly rounded ridge traces from the anterolateral corner of the parietal suture across the top of the element to disappear behind the origin of the jugal process.

(32) (modified) Maxilla tooth number: 20–24 (0); or 17–19 (1); or 15–16 (2); 12–14 (3).

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

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

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

(36) Jugal posteroventral angle: angle very obtuse or curvilinear (0); or slightly obtuse, near 120^{o} (1); or 90^{o} (2). *Aigialosaurus* was recoded as having state 1, *Russellosaurus* and *Tethysaurus* were recoded as having state 2.

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

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

(39) Pterygoid tooth row elevation: teeth arise from robust, transversely flattened, main shaft of pterygoid (0); or teeth arise from thin pronounced vertical ridge (1). In state 0, the teeth emanate from the relatively planar surface of the thick, slightly dorsoventrally compressed main shaft of the pterygoid. In state 1, a tall, thin dentigerous ridge emanates ventrally from a horizontal flange that forms the base of the quadratic ramus and the ectopterygoid process, thus causing the main shaft to be trough-shaped. Although the outgroup we selected (*Varanus*) does not possess pterygoid teeth we decided to code the primitive condition as state 0 because that is the condition observed in fossil varanoids like *Ovoo gurval* and basal anguimorphs like *Ophisaurus apodus*.

(40) Pterygoid tooth size: anterior teeth significantly smaller than marginal teeth (0); or anterior teeth large, approaching size of marginal teeth (1). As per the argument discussed for character 40 we coded the outgroup as having state 0.

(41) Quadrate suprastapedial process length: process short, ends at a level well above midheight (0); or of moderate length, ending very near midheight (1); or long, distinctly below midheight (2). *Russellosaurus* was recoded as having state 2.

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

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

(44) Quadrate suprastapedial process fusion: no fusion present (0); or process fused to, or

in extensive contact with, elaborated process from below (1). A posterior rugose area may be inflated and broadened mediolaterally to partially enclose the ventral end of a broad and elongate suprastapedial process as in *Halisaurus*. In *Globidens*, *Prognathodon*, and *Plesiotylosaurus*, the process is fused ventrally to a narrow pedunculate medial extension of the tympanic rim. A similar condition is present in *Ectenosaurus*, except that the tympanic rim is not medially extended and has a short projection that overlaps a portion of the suprastapedial process posteriorly.

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

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

(47) Quadrate ala thickness: ala thin (0); or thick (1). In state 0, the bone in the central area of the ala is only about 1 mm thick in medium-sized specimens and that area is usually badly crushed or completely destroyed. Alternatively, the ala extends from the main shaft with only minor thinning, providing a great deal of strength to the entire bone. *Tethysaurus* was recoded as having state 0.

(48) Quadrate conch: ala and main shaft encompassing a deeply bowled area (0); or alar

concavity shallow (1). A relatively deeper sulcus in the anterior part of the intratympanic cavity and more definition to the ala and the main shaft are features of state 0. *Tethysaurus* was recoded as having state 0.

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

(50) Quadrate ala groove: absent (0); or long, distinct, and deep groove present in anterolateral edge of ala (1); or groove along dorsal margin of quadrate ala (2).

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

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

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

(54) Basioccipital tubera size: short (0); or long (1). Long tubera are typically parallel-sided in posterior profile and protrude ventrolaterally at exactly 45° from horizontal. Short tubera have relatively large bases that taper distally, and emanate more horizontally.

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

(56) Basioccipital canal: absent (0); or present as a pair separated by a median septum

(1); or present as a single bilobate canal (2).

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

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

(59) Dentary anterior projection length: short (0); or long (1). In state 1, the projection of bone anterior to the first tooth is at least the length of a complete tooth space. *Russellosaurus* was recoded as not applicable.

(60) Dentary medial parapet: parapet positioned at base of tooth roots (0); or elevated and strap-like, enclosing about half of height of tooth attachment in shallow channel (1), or strap equal in height to lateral wall of bone (2). States 1 and 2 are possible sequential stages of modification from a classically pleurodont dentition to the typical mosasaur 'sub-thecodont' dentition. *Tethysaurus* was recoded as ?.

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

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

(63) Coronoid shape: coronoid with slight dorsal curvature, posterior wing not widely fan-shaped (0); or very concave above, posterior wing greatly expanded (1). *Ectenosaurus* was recoded as having state 0.

(64) Coronoid posteromedial process: small but present (0); or absent (1). *Russellosaurus*

was recoded as having state 0, *Ectenosaurus* was recoded as having state 1.

(65) Coronoid medial wing: does not reach angular (0); or contacts angular (1). *Aigialosaurus* was recoded as ?.

(66) Coronoid posterior wing: without medial crescentic pit (0); or with distinct excavation (1). In state 1, there is a posteriorly open, 'C'-shaped excavation in the medial side of the posterior wing of this element. *Dallasaurus* was recoded as ?.

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

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

(69) Surangular-articular lateral suture trace: suture descends and angles or curves anteriorly (0); or is virtually straight throughout its length (1). In state 1, the suture trails from the glenoid posteriorly about halfway along the dorsolateral margin of the retroarticular process, then abruptly turns anteriorly off the edge and strikes in a straight line for the posterior end of the angular. *Aigialosaurus* was recoded as ?.

(70) Articular retroarticular process inflection: moderate inflection, less than 60^{o} (0); or extreme inflection, almost 90^{o} (1).

(71) Articular retroarticular process innervation foramina: no large foramina on lateral

face of retroarticular process (0); or one to three large foramina present (1).

(72) Tooth surface I: teeth finely striate medially (0); or not medially striate (1). In "Russellosaurinae," medial tooth striations are very fine and groups of tightly spaced striae are usually set apart by facets, leading to a fasciculate appearance. *Angolasaurus* was recoded as ?, *Aigialosaurus* was recoded as having state 1.

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

(74) Tooth facets: absent (0); or present (1). *Halisaurus* teeth are smoothly rounded except for the inconspicuous carinae. *Clidastes* is described in numerous places as having smooth unfaceted teeth, but many immature individuals and some larger specimens have teeth with three distinct facets on the medial faces. Adult *Tylosaurus* proriger has indistinct facets. *Mosasaurus* has taken this characteristic to the extreme. *Russellosaurus*, *Tethysaurus*, *Angolasaurus*, *Ectenosaurus*, *Platecarpus* (*P. planifrons* and *P. tympaniticus*), and *Plioplatecarpus* have been recoded as having state 0.

(75) Tooth fluting: absent (0); or present (1). In *Ectenosaurus*, and some *Platecarpus planifrons*, several broadly rounded vertical ridges alternate with shallow, round-bottomed grooves completely around the teeth. *Tethysaurus* was recoded as having both states 0 and 1, because grooves can be observed in larger specimens. *Angolasaurus* was recoded as having state 1.

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

(77) Tooth carinae I: absent (0); or present but extremely weak (1); or strong and elevated (2). *Halisaurus* exhibits the minimal expression of this character (state 1) in that its marginal teeth are almost perfectly round in cross-section; the carinae are extremely thin and barely stand above the surface of the teeth.

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

(79) Tooth replacement mode: replacement teeth form in shallow excavations (0); or in subdental crypts (1). All mosasauroids that can be evaluated have an 'anguimorph' type of tooth replacement, which is to have interdental positioning of replacement teeth and resorption pits associated with each. *Angolasaurus* was recoded as ?.

(80) Atlas neural arch: notch in anterior border (0); or no notch in anterior border (1). *Dallasaurus* was recoded as ?.

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

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

outgroup we selected (*Varanus*) does not possess zygosphene and zygantra we decided to code the primitive condition as present because these structures can be observed in primitive varanoids like *Saniwa*.

(83) Zygosphene and zygantra number: present on many vertebrae (0); or present on only a few (1). As per the argument discussed for character 84 we coded the outgroup as having state 0.

(84) Hypapophyses: last hypapophysis occurs on or anterior to seventh vertebra (0); or on eight or posteriorly (1).

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

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

(87) Synapophysis ventral extension: synapophyses extend barely or not at all below ventral margin of cervical centra (0); or some extend far below ventral margin of centrum (1). In state 1, two or more anterior cervical vertebrae have rib articulations that dip well below the centrum, causing a very deeply concave ventral margin in anterior profile.

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

(89) Vertebral condyle shape I: condyles of anterior-most trunk vertebrae extremely dorsoventrally depressed (0); or essentially equidimensional (1). In state 0, posterior

height: width ratios of anterior trunk vertebrae are close to 2:1. In state 1, they are between to 4:3 and 1:1.

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

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

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

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

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

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

(96) Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0); or several spines dorsally elongated behind middle of tail (1). *Dallasaurus* was recoded as ?.

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

(98) Haemal arch articulation: arches articulating (0); or arches fused to centra (1).

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

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

(101) Scapula/coracoid size: both bones about equal (0); or scapula about half the size of coracoid (1). *Dallasaurus* was recoded as ?.

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

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

(104) Scapula posterior emargination: posterior border of bone gently concave (0); or

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

(105) Scapula-coracoid suture: unfused scapula-coracoid contact has interdigitate suture anteriorly (0); or apposing surfaces without interdigitation (1). *Dallasaurus* was recoded as ?.

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

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

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

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

(110) Humerus glenoid condyle: if present, condyle gently domed and elongate, ovoid in proximal view (0); or condyle saddle-shaped, subtriangular in proximal view and depressed (1); or condyle highly domed or protuberant and short ovoid to almost round in proximal view (2). In some taxa, the condylar surfaces of the limbs were finished in thick cartilage and there was no bony surface of the condyle to be preserved. This condition is scored as not represented. In some taxa, the glenoid condyle extends more proximally than does the postglenoid process (state 2), and it is not ovoid as state 0. *Dallasaurus* was

recoded as having state 0.

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

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

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

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

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

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

(117) Ulna contact with centrale: broad ulnare prevents contact (0); or ulna contacts centrale (1). In state 1, the ulnare is omitted from the border of the antebrachial foramen.

There is usually a well-developed faceted articulation between the ulna and the centrale (or intermedium, as used by Russell, 1967).

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

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

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

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

(122) Phalanx shape: phalanges elongate, spindle-shaped (0); or blocky, hourglass-shaped (1). *Mosasaurus* and *Plotosaurus* have phalanges that are slightly compressed and anteroposteriorly expanded on both ends. *Dallasaurus* was recoded as ?.

(123) Ilium crest: crest blade-like, articulates with sacral ribs (0); or elongate, cylindrical, does not articulate with sacral ribs (1).

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

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

(126) Ischiadic tubercle size: elongate (0); or short (1). In state 0, the tubercle is as long

as the shaft of the ischium is wide, but it is only a short narrow spur in state 1.

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

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

(129) Hyperphalangy: absent (0); or present (1). Hyperphalangy is defined as presence of one or more extra phalanges as compared to the primitive amniote formula of 2-3-4-5-3.

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

(131) Ectopterygoid process of pterygoid: distal portion of process not offset anterolaterally and/or lacking longitudinal grooves and ridges (0); distal portion of process is offset anterolaterally and bears longitudinal grooves and ridges (1).

Appendix 3: Data matrix used in Chapter Four and Chapter Six.

MATRIX

Outgroup 0-000002000100-3-0000000000-0030011000000-0-0010000000051-01-0010001001000020-100-10000010100000010-0100000000000000000000001-0000

Aigialosaurus 0-00?0?2100??0?3?1010?10?00?00????10?1?1??0?011?0???00???????00?????001000020??010?0000???000000010-0-00000?00000000000001??0000

Komensaurus_carrolli

???????????????????????????????????????20?0?000?0????????????????0000???????????1???0?01??00?00???????????????0000?000?0011?000?

Halisaurus_platyspondylus

1010000211000003?10101?0?00???11????1?20010000?0001???????101?000100010000101??0-????00??????1?????????????????????????1?????00

Halisaurus_sternbergi 0-100?0210000003?0010100000???0210???0020?1?000?0?01??0?1?1101?0?0100010?00100?10-?00100??0010101111110010010000101110011111?010?

Dallasaurus_turneri

??????0??0???1??0????????????????????0??????????????????00010??0?1????100002?0?11??00111110???1???0-0???01000000????????0???0?1?

Clidastes_liodontus

111000020010?10101001111?10?1021002??1010?0000000010100{1 2}0021?10001000?10100201011000001101011110101100002101011121000101000121 1?

Clidastes_moorevillensis

1110000200100101010011111?10?1021?020?1010?000100001010020021010001000010100201011000001 1?101111??0110000210101112100010100012 11?

Clidastes_propython

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Prognathodon_overtoni

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Prognathodon_rapax

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Prognathodon_solvayi 0-0000100010010101011111110?0030?110?1110010100?00111?141-2?010101?00000?012110?10001011?10??????01?01?????????????????????????

Prognathodon_currii

1000???0111??????10???11?11?0030?120??1???????0????1???51-

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Prognathodon_waiparaensis

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1???0

Prognathodon_saturator

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12110?10?01011110??01??0??????????????2???????????????

Globidens_alabamaensis

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101011??0?011??0??????????0??21010111????????????2?1?

Globidens_dakotensis

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?10

Mosasaurus_conodon

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Mosasaurus_hoffmanni

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0021101110110110?1?1111?0210011311101112100011100012110

Mosasaurus_missouriensis 11100110011??10111001?11?11?002001???1000?00100?1{0 1}0110?3002?0101110110101002?1011?0000110111??11?01??00?????????2100?11??????2?1?

Plesiotylosaurus_crassidens 11101?10?11??10111001111?1110031?1??01100?10110?0?1011?2002111011100??10100211?????00011?10??????011001131210111210001 0?????2???

Plotosaurus_bennisoni 10100110101??10111011?11111?0011002001000?001000110110?101?1?1???10110000012??010-10?011??11?1?1?02100113111011121000 11??1??211?

Tylosaurus_proriger 121001001110?11101001?1100110031002100011102001100100104012100000000000000211100-0000101010010101101100100010001011100101001100

Tylosaurus_nepaeolicus 121001001{0 1}10?11101001?1100110030002110011102110100100 1?40121000000000000000211100-100010101???0?????????100010001?1?100?????1?00

Tylosaurus_bernardi 121001001110?11101001?11001100310?21?00????20011001001?4012100000000000000211100-0000101010010101101100100010 00?011100???01100

Tylosaurus_pembinensis 121???001?10?11201001?11001100310 02??0011102110?001001?4012100000001100000211100-?0001010110?0101101100100010001??????1010?1100

Tylosaurus_saskatchewanensis

121001001?10?11201001?11?01100310021???1??02110?0000???40121?0??000010000

00211100-10001010120?0?01101100100010001????0010100110?

Tylosaurus_gaudryi

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Taniwhasaurus_oweni

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020?100-???01010???00??1????????????????????????????0?

Taniwhasaurus_antarcticus

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Taniwhasaurus_capensis

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Taniwhasaurus_mikasaensis

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Yaguarasaurus_columbianus 0-

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Eremiasaurus_heterodontus

10100110111??101?10?1?11?11?01300020?111??1??0??1?111??20021010??1011?1000
121?01??0100110?0?1111001?01???10???????????01??01??1?

Prognathodon_kianda

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Russellosaurus_coheni

101??0020001110201200011000?0120?121100210020011200000121-
11000000100100000100???1

Romeosaurus_fumanensis

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00?????01101??0???????0-11??00?00?00???????????????1

Ectenosaurus_clidastoides

1110000200111102011100 01?00?011101110001001210111 0??00230020001000000100
010201001001001???0??????010110021???0012010100?????1110

Plioplatecarpus ??????0011100100-
1113011?01000?0??1100021100200?0{0 1}1100251-21101000000100000201??0-
?000110000??0??010110020?110012011100?????1?00

Platecarpus_planifrons 101000001011?100-
1110?11?00??13000?100021001000?0{0
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Platecarpus_tympaniticus 0-10000011111100-
1111011?01001300011?002110110010{0 1}1100251-21101000000100000201100-
00001100000001001011002 0??1?01201110010110110 0

Latoplatecarpus_willistoni 0-10000120111?0-111{1
2}0?1?01001300021?00210012001011100251-
21101000000100010201111000101 1??0???0???2111??????????????????????????0

Selmasaurus_johnsoni 1010001000111102012000 11?01-
01?0??21?0011011100?000101151-
21111000000100010201101000001 1000????????????????????????????????????

Angolasaurus_bocagei
101??001?11???0??1100?1??00?0?30????1??210001001000100151-
21?010001001?00102?1??1??0?

Tethysaurus_nopcsai 0-00?002110??10201200?11000-
0?00??21??0010020001?20000111-?10010001000000{0 1}00-
0??10?111000?????0??1110?00?????000???????000?????0

Pannoniasaurus_osii 0-
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20010?00??000001020???10?1110000????0?????01???0???000???????00???????

Appendix 4: Characters and character states for Appendix 3.

(1) Premaxilla predental rostrum I: total lack of a bony rostrum (0); or presence of any predental rostrum (1). In lateral profile, the anterior end of the premaxilla either exhibits some bony anterior projection above the dental margin, or the bone recedes posterodorsally from the dental margin. State 1 produces a relatively taller lateral profile with an obvious 'bow' or 'prow.'

(2) Premaxilla predental rostrum II: rostrum very short and obtuse (0); or distinctly protruding (1); or very large and inflated (2). In *Clidastes* a short, acute, protruding rostrum (state 1) produces a 'V'-shaped dorsal profile and, as far as is known, is peculiar to that genus. An alternative condition, described as 'U'- shaped, includes those taxa whose rostral conditions span the whole range of states of characters 1 and 2. Hence, the descriptive character is abandoned in favor of a more informative structure-based series.

(3) Premaxilla shape: bone broadly arcuate anteriorly (0); or relatively narrowly arcuate or acute anteriorly (1). In virtually all lizards the premaxilla is a very widely arcuate and lightly constructed element, and the base of the internarial process is quite narrow as in Aigialosaurus bucchichi. All other mosasaurids have a very narrowed premaxilla with the

teeth forming a tight curve and the internarial process being proportionally wider (state 1). *Tethysaurus* was recoded as having state 0.

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

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

(6) Premaxilla internarial bar dorsal keel: absent (0); or present (1). In state 1 a ridge rises above the level of a normally smoothly continuous transverse arch formed by the bones of the anterior muzzle.

(7) Frontal shape in front of the orbits: sides sinusoidal (0); or bone nearly triangular and sides relatively straight (1). In state 1, the area above the orbits is expanded and an isosceles triangle is formed by the rectilinear sides. In certain taxa, a slight concavity is seen above the orbits, but anterior and posterior to this, there is no indication of a sinusoidal or recurved edge.

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

(9) Frontal narial emargination: frontal not invaded by posterior end of nares (0); or distinct embayment present (1). In some mosasauroids, the posterior ends of the nares are

concomitant with the anterior terminus of the frontal-prefrontal suture and, therefore, there is no marginal invasion of the frontal by the opening. However, in other mosasauroids this suture begins anterior and lateral to the posterior ends of the nares, causing a short emargination into the frontal.

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

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

(12) Frontal olfactory canal embrasure: canal not embraced ventrally by descending processes (0); or canal almost or completely enclosed below (1). In state 1, very short descending processes from the sides of the olfactory canal surround and almost, or totally, enclose the olfactory nerve.

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

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

embraced by the posterior extension of these frontal flanges.

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

(16) Frontal invasion of parietal I: lateral sutural flange of frontal posteriorly extended (0); or median frontal sutural flange posteriorly extended (1); or both extended (2); or suture straight (3). In all mosasaurines the oblique median frontal sutural ridge extends onto the dorsal surface of the parietal table and embraces a portion of the anterior table within a tightly crescentic midline embayment. In *Plioplatecarpus* and *Platecarpus*, the lateral oblique sutural ridge from the frontal is greatly protracted posteriorly to cause a large, anteriorly convex embayment in the dorsal frontal-parietal suture. In this case the entire posterolateral corner of the frontal is extended backwards to embrace the anterolateral portion of the parietal table on both sides. Consequently, the parietal foramen is very widely embraced laterally and the oblique anterior sutural ridge of the parietal occupies a position inside the embayment within the frontal. *Dallasaurus* was recoded as ?.

(17) Frontal medial invasion of parietal II: if present, posteriorly extended median sutural flange short (0); or long (1). The median oblique sutural flange is either short, not reaching back to the parietal foramen (state 0), or tightly embraces the foramen while

extending backwards to a position even with or beyond its posterior edge (state 1).

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

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

(20) Parietal foramen size: relatively small (0); or large (1). If the foramen is smaller than or equal to the area of the stapedial pit, it is considered small. If the foramen is significantly larger or if the distance across the foramen is more than half the distance between it and the nearest edge of the parietal table, the derived state is achieved.

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

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

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

(24) Parietal suspensorial ramus compression: greatest width vertical or oblique (0); or

greatest width horizontal (1). In *Tylosaurus*, the anterior edge of the ramus begins very low on the lateral wall of the descending process, leading to formation of a proximoventral sulcus, but the straps are horizontal distally.

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

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

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

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

(29) Postorbitofrontal shape: narrow (0); or wide (1). In *Clidastes* and the *Globidensini*, the lateral extent of the element is almost equal to half of the width of the frontal and the

outline of the bone is basically squared.

(30) Postorbitofrontal transverse dorsal ridge: absent (0); or present (1). In state 1, an inconspicuous, low, and narrowly rounded ridge traces from the anterolateral corner of the parietal suture across the top of the element to disappear behind the origin of the jugal process.

(31) Maxilla tooth number: 20–24 (0); or 17–19 (1); or 15–16 (2); 12–14 (3).

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

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

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

(35) Jugal posteroventral angle: angle very obtuse or curvilinear (0); or slightly obtuse, near 120° (1); or 90° (2). *Aigialosaurus* was recoded as having state 1, *Russellosaurus* and *Tethysaurus* were recoded as having state 2.

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

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

(38) Pterygoid tooth row elevation: teeth arise from robust, transversely flattened, main shaft of pterygoid (0); or teeth arise from thin pronounced vertical ridge (1). In state 0,

the teeth emanate from the relatively planar surface of the thick, slightly dorsoventrally compressed main shaft of the pterygoid. In state 1, a tall, thin dentigerous ridge emanates ventrally from a horizontal flange that forms the base of the quadratic ramus and the ectopterygoid process, thus causing the main shaft to be trough-shaped. Although the outgroup we selected (*Varanus*) does not possess pterygoid teeth we decided to code the primitive condition as state 0 because that is the condition observed in fossil varanoids like *Ovoo gurval* and basal anguimorphs like *Ophisaurus apodus*.

(39) Pterygoid tooth size: anterior teeth significantly smaller than marginal teeth (0); or anterior teeth large, approaching size of marginal teeth (1). As per the argument discussed for character 40 we coded the outgroup as having state 0.

(40) Quadrate suprastapedial process length: process short, ends at a level well above midheight (0); or of moderate length, ending very near midheight (1); or long, distinctly below midheight (2). *Russellosaurus* was recoded as having state 2.

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

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

(43) Quadrate suprastapedial process fusion: no fusion present (0); or process fused to, or in extensive contact with, elaborated process from below (1). A posterior rugose area may be inflated and broadened mediolaterally to partially enclose the ventral end of a

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

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

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

(46) Quadrate ala thickness: ala thin (0); or thick (1). In state 0, the bone in the central area of the ala is only about 1 mm thick in medium-sized specimens and that area is usually badly crushed or completely destroyed. Alternatively, the ala extends from the main shaft with only minor thinning, providing a great deal of strength to the entire bone. *Tethysaurus* was recoded as having state 0.

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

Tethysaurus was recoded as having state 0.

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

(49) Quadrate ala groove: absent (0); or long, distinct, and deep groove present in anterolateral edge of ala (1); or groove along dorsal margin of quadrate ala (2).

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

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

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

(53) Basioccipital tubera size: short (0); or long (1). Long tubera are typically parallel-sided in posterior profile and protrude ventrolaterally at exactly 45° from horizontal. Short tubera have relatively large bases that taper distally, and emanate more horizontally.

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

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

(56) Dentary tooth number: 20–24 (0); 17–19 (1); 15–16 (2); 14 (3); 13 (4); 12 (5). It is

easy to assume this character is correlated with the number of maxillary teeth, except that is not the case in *Ectenosaurus clidastoides*, which has 16 or 17 maxillary teeth and only 13 dentary teeth.

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

(58) Dentary anterior projection length: short (0); or long (1). In state 1, the projection of bone anterior to the first tooth is at least the length of a complete tooth space. *Russellosaurus* was recoded as not applicable.

(59) Dentary medial parapet: parapet positioned at base of tooth roots (0); or elevated and strap-like, enclosing about half of height of tooth attachment in shallow channel (1), or strap equal in height to lateral wall of bone (2). States 1 and 2 are possible sequential stages of modification from a classically pleurodont dentition to the typical mosasaur 'sub-thecodont' dentition. *Tethysaurus* was recoded as ?.

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

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

(62) Coronoid shape: coronoid with slight dorsal curvature, posterior wing not widely fan-shaped (0); or very concave above, posterior wing greatly expanded (1). *Ectenosaurus* was recoded as having state 0.

(63) Coronoid posteromedial process: small but present (0); or absent (1). *Russellosaurus* was recoded as having state 0, *Ectenosaurus* was recoded as having state 1.

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

Aigialosaurus was recoded as ?.

(65) Coronoid posterior wing: without medial crescentic pit (0); or with distinct excavation (1). In state 1, there is a posteriorly open, 'C'-shaped excavation in the medial side of the posterior wing of this element. *Dallasaurus* was recoded as ?.

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

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

(68) Surangular-articular lateral suture trace: suture descends and angles or curves anteriorly (0); or is virtually straight throughout its length (1). In state 1, the suture trails from the glenoid posteriorly about halfway along the dorsolateral margin of the retroarticular process, then abruptly turns anteriorly off the edge and strikes in a straight line for the posterior end of the angular. *Aigialosaurus* was recoded as ?.

(69) Articular retroarticular process inflection: moderate inflection, less than 60^{o} (0); or extreme inflection, almost 90^{o} (1).

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

(71) Tooth surface I: teeth finely striate medially (0); or not medially striate (1). In

"Russellosaurinae," medial tooth striations are very fine and groups of tightly spaced striae are usually set apart by facets, leading to a fasciculate appearance. *Angolasaurus* was recoded as ?, *Aigialosaurus* was recoded as having state 1.

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

(73) Tooth facets: absent (0); or present (1). *Halisaurus* teeth are smoothly rounded except for the inconspicuous carinae. *Clidastes* is described in numerous places as having smooth unfaceted teeth, but many immature individuals and some larger specimens have teeth with three distinct facets on the medial faces. Adult *Tylosaurus* proriger has indistinct facets. *Mosasaurus* has taken this characteristic to the extreme. *Russellosaurus*, *Tethysaurus*, *Angolasaurus*, *Ectenosaurus*, *Platecarpus* (*P. planifrons* and *P. tympaniticus*), and *Plioplatecarpus* have been recoded as having state 0.

(74) Tooth fluting: absent (0); or present (1). In *Ectenosaurus*, and some *Platecarpus planifrons*, several broadly rounded vertical ridges alternate with shallow, round-bottomed grooves completely around the teeth. *Tethysaurus* was recoded as having both states 0 and 1, because grooves can be observed in larger specimens. *Angolasaurus* was recoded as having state 1.

(75) Tooth inflation: crowns of posterior marginal teeth conical, tapering throughout (0); or crowns of posterior marginal teeth swollen near the tip or above the base (1).The rear

teeth of *Globidens* and *Prognathodon overtoni* are distinctly fatter than other mosasauroid teeth, but those of *P. rapax* are also swollen immediately distal to the base.

(76) Tooth carinae I: absent (0); or present but extremely weak (1); or strong and elevated (2). *Halisaurus* exhibits the minimal expression of this character (state 1) in that its marginal teeth are almost perfectly round in cross-section; the carinae are extremely thin and barely stand above the surface of the teeth.

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

(78) Tooth replacement mode: replacement teeth form in shallow excavations (0); or in subdental crypts (1). All mosasauroids that can be evaluated have an 'anguimorph' type of tooth replacement, which is to have interdental positioning of replacement teeth and resorption pits associated with each. *Angolasaurus* was recoded as ?.

(79) Atlas neural arch: notch in anterior border (0); or no notch in anterior border (1). *Dallasaurus* was recoded as ?.

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

(81) Zygosphenes and zygantra: absent (0); or present (1). This character assesses only the presence of zygosphenes and zygantra, not their relative development. Nonfunctional and functional are considered as present. Although the outgroup we selected (*Varanus*) does not possess zygosphene and zygantra we decided to code the primitive condition as present because these structures can be observed in

primitive varanoids like *Saniwa*.

(82) Zygosphene and zygantra number: present on many vertebrae (0); or present on only a few (1). As per the argument discussed for character 84 we coded the outgroup as having state 0.

(83) Hypapophyses: last hypapophysis occurs on or anterior to seventh vertebra (0); or on eight or posteriorly (1).

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

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

(86) Synapophysis ventral extension: synapophyses extend barely or not at all below ventral margin of cervical centra (0); or some extend far below ventral margin of centrum (1). In state 1, two or more anterior cervical vertebrae have rib articulations that dip well below the centrum, causing a very deeply concave ventral margin in anterior profile.

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

(88) Vertebral condyle shape I: condyles of anterior-most trunk vertebrae extremely dorsoventrally depressed (0); or essentially equidimensional (1). In state 0, posterior height: width ratios of anterior trunk vertebrae are close to 2:1. In state 1, they are between to 4:3 and 1:1.

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

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

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

(92) Presacral vertebrae number I: relatively few, 32 or less (0); 33 to 38 (1); or numerous, 39 or more (2). Here, presacral vertebrae are considered to be all those anterior to the first bearing an elongate transverse process.

(93) Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0); or several spines dorsally elongated behind middle of tail (1). *Dallasaurus* was recoded as ?.

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

(95) Haemal arch articulation: arches articulating (0); or arches fused to centra (1).

(96) Tail curvature: no structural downturn of tail (0); or tail with curved posterior

portion (1).

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

(98) Scapula/coracoid size: both bones about equal (0); or scapula about half the size of coracoid (1). *Dallasaurus* was recoded as ?.

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

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

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

(102) Scapula-coracoid suture: unfused scapula-coracoid contact has interdigitate suture anteriorly (0); or apposing surfaces without interdigitation (1). *Dallasaurus* was recoded as ?.

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

fan-shaped, with gently concave, nearly equidistant sides.

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

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

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

(107) Humerus glenoid condyle: if present, condyle gently domed and elongate, ovoid in proximal view (0); or condyle saddle-shaped, subtriangular in proximal view and depressed (1); or condyle highly domed or protuberant and short ovoid to almost round in proximal view (2). In some taxa, the condylar surfaces of the limbs were finished in thick cartilage and there was no bony surface of the condyle to be preserved. This condition is scored as not represented. In some taxa, the glenoid condyle extends more proximally than does the postglenoid process (state 2), and it is not ovoid as state 0. *Dallasaurus* was recoded as having state 0.

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

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

of the bone.

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

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

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

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

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

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

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

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

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

(119) Phalanx shape: phalanges elongate, spindle-shaped (0); or blocky, hourglass-

shaped (1). *Mosasaurus* and *Plotosaurus* have phalanges that are slightly compressed and anteroposteriorly expanded on both ends. *Dallasaurus* was recoded as ?.

(120) Ilium crest: crest blade-like, articulates with sacral ribs (0); or elongate, cylindrical, does not articulate with sacral ribs (1).

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

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

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

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

(125) Appendicular epiphyses: formed from ossified cartilage (0); or from thick

unossified cartilage (1); or epiphyses missing or extremely thin (2). Ends of the limb bones show distinct vascularization and rugose surfaces indicating an apparently thick non-vascularized, unossified cartilage cap. Extremely smooth articular surfaces suggest the epiphyses were excessively thin or perhaps even lost.

(126) Hyperphalangy: absent (0); or present (1). Hyperphalangy is defined as presence of one or more extra phalanges as compared to the primitive amniote formula of 2-3-4-5-3.

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

(128) Ectopterygoid process of pterygoid: distal portion of process not offset anterolaterally and/or lacking longitudinal grooves and ridges (0); distal portion of process is offset anterolaterally and bears longitudinal grooves and ridges (1).

(129) sacrum: present (0); absent (1).