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Revision of the Genus Styxosaurus and Relationships of the Late Cretaceous Elasmosaurids (Sauropterygia: Plesiosauria) of the Western Interior Seaway

Elliott Armour Smith

REVISION OF THE GENUS *STYXOSAURUS* AND RELATIONSHIPS OF THE LATE CRETACEOUS ELASMOSAURIDS (SAUROPTERYGIA: PLESIOSAURIA) OF THE WESTERN INTERIOR SEAWAY

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Approved by
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Dr. Habiba Chirchir, Committee Member
Dr. Herman Mays, Committee Member

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APPROVAL OF THESIS

We, the faculty supervising the work of Elliott Armour Smith, affirm that the thesis, *Revision of the Genus* *Styxosaurus* *and Relationships of the Late Cretaceous Elasmosaurids (Sauropterygia: Plesiosauria) of the Western Interior Seaway* meets the high academic standards for original scholarship and creative work established by the Department of Biological Sciences and the College of Science. The work also conforms to the formatting guidelines of Marshall University. With our signatures, we approve the manuscript for publication.

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5/27/2020

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5/28/2020

Dr. Habiba Chirchir, Department of Biological Sciences — Committee Member — Date

DEDICATION

Dedicated to my loving parents for supporting me on my journey as a scientist.

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ABSTRACT

Growing evidence indicates that elasmosaurid plesiosaurs from the Late Cretaceous Western Interior Seaway are members of a single clade, the Styxosaurinae. The styxosaurines are reported to be mostly Campanian in age, and taxa within the clade obtain the longest necks, by number of cervical vertebrae, of any known vertebrate. The styxosaurines are morphologically diverse and include taxa that exhibit a secondary reduction in neck length. Given the evolutionary plasticity of postcranial characters in plesiosaurs in general, and neck length in elasmosaurs, scrutiny of cranial osteology is pertinent to advancing understanding of Western Interior Seaway elasmosaurids. This study finds that an elasmosaurid specimen (UNSM 50132) from the Cenomanian of Nebraska is remarkably similar in cranial morphology to the Campanian *Styxosaurus snowii* (KUVP 1301). The phylogenetic affinity of UNSM 50132 was tested with a cladistic analysis with 94 Operational Taxonomic Units (OTU) and 270 anatomical characters, utilizing the Serratos et al. (2017) character matrix with changes and additions. The analysis supports five unambiguous synapomorphies for the genus *Styxosaurus*: (1) dorsomedian ridge of premaxilla located posteriorly (19.1); (2) dorsal portion of squamosal reflected anteriorly in lateral view (61.1); (3) posteromedian ridge on the supraoccipital (77.1); (4) a sharp ridge or keel located adjacent to the mandibular symphysis (114.1); (5) a retroarticular process that is shorter in anteroposterior length than the glenoid (116.0). Five additional ambiguous synapomorphies that support the monophyly of *Styxosaurus* include: lateral expansion of the maxilla that supports caniniform teeth, anisodont dentition, anterior embayment of the squamosal arch, an elongate posteromedian process of the premaxilla, a rugose boss on the ectopterygoid, parietals that form a sagittal crest that rises above the cranial roof, and elongate anterior to middle cervical centra. 67% of 100 bootstrap replicates support the monophyly of UNSM 50132, *Styxosaurus snowii*, *Styxosaurus browni*, and *Styxosaurus* sp. (SDSM 451). UNSM 50132 was previously referred to the genus *Thalassomedon*, a taxon considered to be outside of the Styxosaurinae. The recommended referral of UNSM 50132 to the genus *Styxosaurus* pushes back the earliest occurrence of Styxosaurinae in the Western Interior Seaway by over ten million years. Maximum parsimony analysis suggests that all Western Interior Seaway elasmosaurids belong to a single clade, including the genera *Libonectes* and *Thalassomedon*. *Libonectes* and *Thalassomedon* have been previously recovered as outgroup taxa to a clade composed of the sister relationship of Western Interior Seaway elasmosaurids and Aristonectinae. This study provides additional context for furthering understanding of the origins of Elasmosauridae in the Early Cretaceous.

CHAPTER 1

BACKGROUND

Overview

Elasmosauridae is a family of Plesiosauria (Reptilia: Sauropterygia) that evolved near the Jurassic-Cretaceous boundary and went extinct at the Cretaceous-Paleogene boundary (O'Keefe, 2001; Benson and Druckenmiller, 2014). By the Early Cretaceous, elasmosaurs had achieved a cosmopolitan distribution, found in marine sedimentary strata in Australia (Kear, 2005), Alberta (Druckenmiller and Russell, 2006), and Colombia (Carpenter, 1999). The Late Cretaceous would be marked by the evolution of two distinct, subfamily-level clades of Elasmosauridae: Styxosaurinae and Aristonectinae (Otero, 2016). Aristonectine elasmosaurs are found in Late Cretaceous strata of extreme southern latitudes of Antarctica (Cabrera, 1941) and New Zealand (Otero et al., 2016). The aristonectines are characterized by their numerous homodont teeth and secondarily short necks, and may have been benthic filter-feeders, a feeding strategy convergent with that of mysticete cetaceans (O'Keefe et al., 2017; O'Gorman, 2020). The styxosaurines are characterized by their extremely long necks with as many as 76 cervical vertebrae (Kubo et al., 2012). However, the styxosaurines are morphologically diverse, with *Nakonanectes* possessing 39-42 cervical vertebrae, suggesting a secondarily evolved reduction of neck length within the clade (Serratos et al., 2017).

Non-Pacific elasmosaurs from North America lived in the Western Interior Seaway, a shallow, epeiric sea that covered the center of the craton during much of the Cretaceous Period (Everhart, 2005). For over 150 years, fossils have been collected from sedimentary strata deposited by the Western Interior Seaway (Cope, 1869; Everhart, 2005). During the 19th and 20th centuries, elasmosaur taxonomy suffered from the proposal of dozens of *nomen dubia*, the result of poor type specimen selection (Carpenter, 1999). A much-needed revision of Elasmosauridae from the Western Interior Seaway by Carpenter (1999) validated only five genera, *Elasmosaurus*, *Hydralmosaurus*, *Libonectes*, *Styxosaurus*, and *Thalassomedon*. As cladistic analyses began to illuminate the nature of plesiosaur relationships (O'Keefe, 2001; Ketchum and Benson, 2010; Benson and Druckenmiller, 2014), a clearer understanding of elasmosaur ingroup relationships began to emerge (Otero, 2016; Serratos et al., 2017; O'Gorman, 2020). Despite several conflicting results from phylogenetic analyses due to disparate taxon sampling and utilization of different matrices (Serratos et al., 2017), the phylogenetic results of Serratos et al. (2017) and Otero (2016) were largely in congruence in supporting the subfamily-level clades Styxosaurinae and Aristonectinae as nodes. O'Gorman (2020) recovered all Pacific elasmosaurids within a single clade, Wedellonectia. Included within Wedellonectia are the aristonectine elasmosaurids (O'Gorman, 2020).

What remains to be understood is the relationship of the Aristonectinae plus Styxosaurinae clade to more basal elasmosaurids. In order to stabilize ingroup relationships of Elasmosauridae, and to constrain timing of clade origination, a more thorough dataset of comparative cranial anatomy is needed. Three elasmosaur specimens are redescribed: *Thalassomedon hanningtoni* (DMNH 1588), *Styxosaurus snowii* (KUVP 1301) and a new unassigned elasmosaurid, UNSM 50132. These specimens are scored based on the Serratos et al. (2017) character matrix, with changes and additions listed in Appendix B.

Purpose of Study

The purpose of this study is to redefine the genus *Styxosaurus* and the subfamily Styxosaurinae, and to evaluate the temporal range of both the genus and subfamily Styxosaurinae. This will illuminate the timing of elasmosaurid evolution and add greater context to the unstable relationships found at the base of Elasmosauridae. This study aims to use comparative cranial anatomy to evaluate the synapomorphies that define the genus S*tyxosaurus* and the subfamily Styxosaurinae. This study also serves to improve understanding of the cranial anatomy of Late Cretaceous elasmosaurids. Elasmosaurid cranial anatomy is known from a limited number of complete skulls, and many important taxa contain only partial or poorly preserved skulls.

Evolution of Sauropterygia

Sauropterygia is an extinct clade of aquatic diapsid reptiles that originated in the Early Triassic and went extinct at the K/Pg mass extinction (Neenan et al., 2013). Early radiations of Sauropterygia include the nothosaurs (Cheng et al., 2004), the turtle-like placodonts (Neenan et al., 2013), and the flippered Plesiosauria (O'Keefe, 2001). The origins of Plesiosauria are in the Late Triassic (Wintrich et al., 2017), and they underwent an initial radiation following the Late Triassic mass extinction (Benson et al., 2012).

A phylogenetic analysis of basal Sauropterygia with a focus on the placodonts by Neenan et al. (2013) defined Sauropterygia as containing two sister clades: Placodontiformes and Eosauropterygia (Fig. 1). Eosauropterygia includes the Pachypleurosauria, Nothosauroidea, and the group that gave rise to plesiosaurs, the Pistosauroidea (Neenan et al., 2013). Rieppel (2000) summarized a body of knowledge on basal sauropterygians in a detailed monograph that diagnosed major subclades based on important morphological traits. A few notable morphological traits in his diagnosis of Sauropterygia include large premaxillae, absence of lacrimal, and upper temporal fenestrae larger than orbits. Rieppel (2000) reported postcranial characters diagnosing Sauropterygia including: a reduction in the epicondyles of the humerus; radius and ulna of equal length; three or more sacral ribs; and pectoral fensestration. The order

Pistosauroidea (Fig. 1) includes Plesiosauria nested within, and is diagnosed by characters including the constriction of the parietals forming a sagittal crest, and the absence of a quadratojugal.

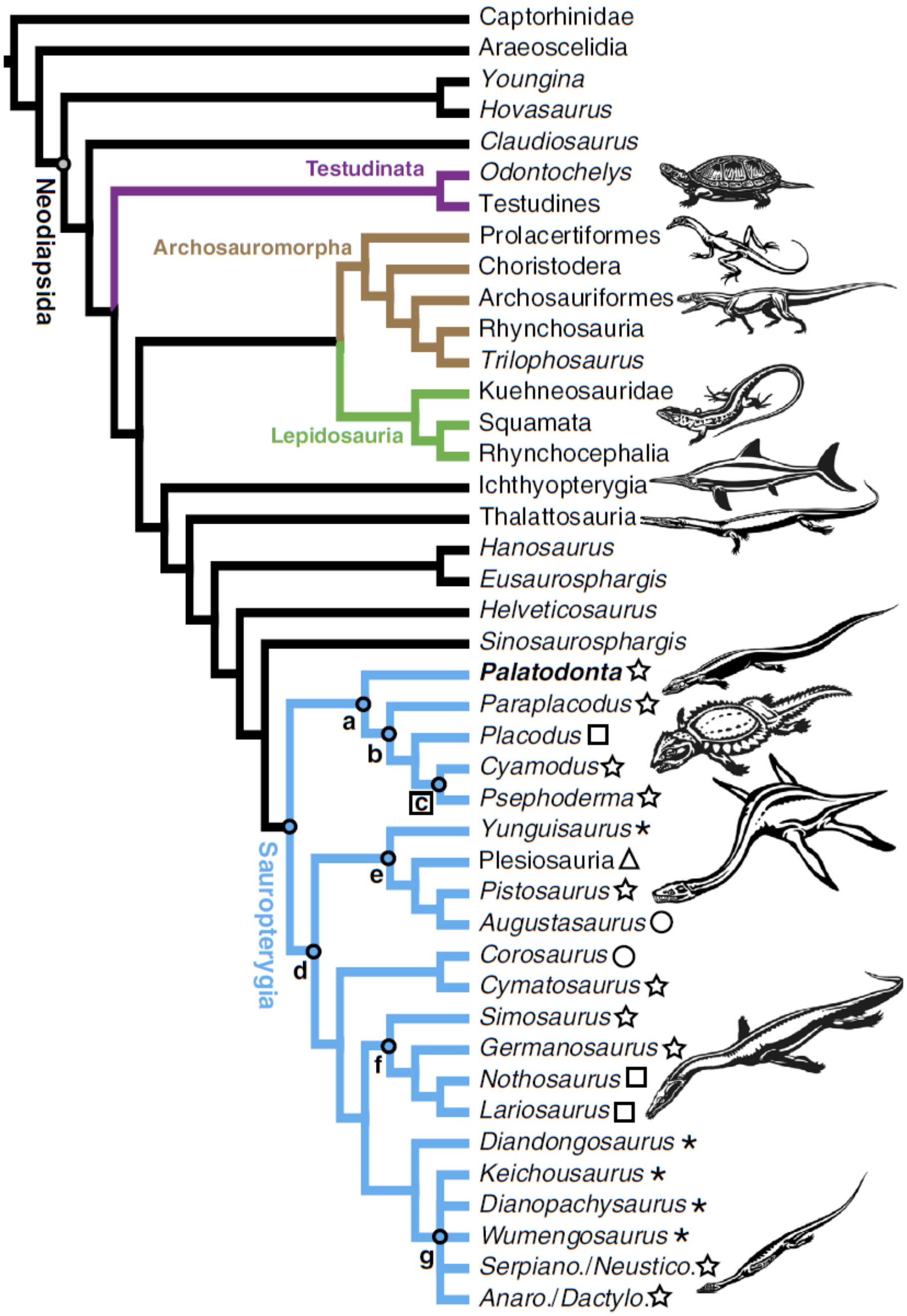

Figure 1. Relationships of Sauropterygia among major clades of Diapsida from a phylogenetic analysis by Neenan et al. (2013). A) Placodontiformes B) Placodontia C) Cyamodontoidea D) Eosauropterygia E) Pistosauroidea F) Nothosauroidea G) Pachypleurosauria. Reprinted by permission from Springer Nature (2013), see Appendix D.

Plesiosauria: Evolution, Paleobiology, and Systematics

Plesiosaur Origins

The earliest neoplesiosaurian is from the Triassic, *Rhaeticosaurus mertensi*, of the Rhaetian of Germany (Wintrich et al., 2017). This specimen documents an important transition in sauropterygian evolution, showing a series of character acquisitions that separate basal pistosaurs and true plesiosaurians. *Rhaeticosaurus mertensi* is considered to be a basal pliosaurid from the results of a phylogenetic analysis and character states including a stiff trunk and neck, reduced tail, large cervical subcentral foramina, and propodials of the same size and shape (Wintrich et al., 2017). The Jurassic was marked by the evolution of three important plesiosaurian clades: Rhomaelosauridae, Pliosauridae, and Plesiosauroidea (Benson and Druckenmiller, 2014). Rhomaelosauridae reached its peak diversity in the Early Jurassic (Benson et al., 2012). Coeval with the radiation of rhomaelosaurs, the more highly nested clades Plesiosauroidea and Pliosauridae begin to radiate in the Early Jurassic (Benson and Druckenmiller, 2014).

Changing Views On Plesiosaur Cladistics and Phylogenetics

Before more rigorous cladistic analyses began to revise much of the understanding of the relationships of fossil organisms, plesiosaurs were thought to fit into one of two morphotype-based categories: the long-necked plesiosaurs and short-necked pliosaurs. A revision of the Plesiosauria by O'Keefe (2001) demonstrated that cryptoclidids and polycotylids, short-necked plesiosaurs, were nested within Plesiosauroidea, rather than within the short-necked Pliosauridae (Fig. 2). Cladistic evidence supported the idea that plesiosaur morphospace was more fluid, and that the pliosauromoph (large head, short neck, large flippers) evolved at least three times (O'Keefe, 2002). Additional datasets with more inclusive taxon sampling have subsequently clarified our understanding of plesiosaurian relationships. A phylogenetic analysis by Benson and Druckenmiller (2014) advanced the hypothesis that Leptocleidia and Elasmosauridae are sister taxa, the clade Xenosparia. In this analysis, Xenosparia, along with the brachaucheninine pliosaurs are interpreted to be the only plesiosaurian lineages that crossed the Jurassic-Cretaceous boundary (Benson and Druckenmiller, 2014).

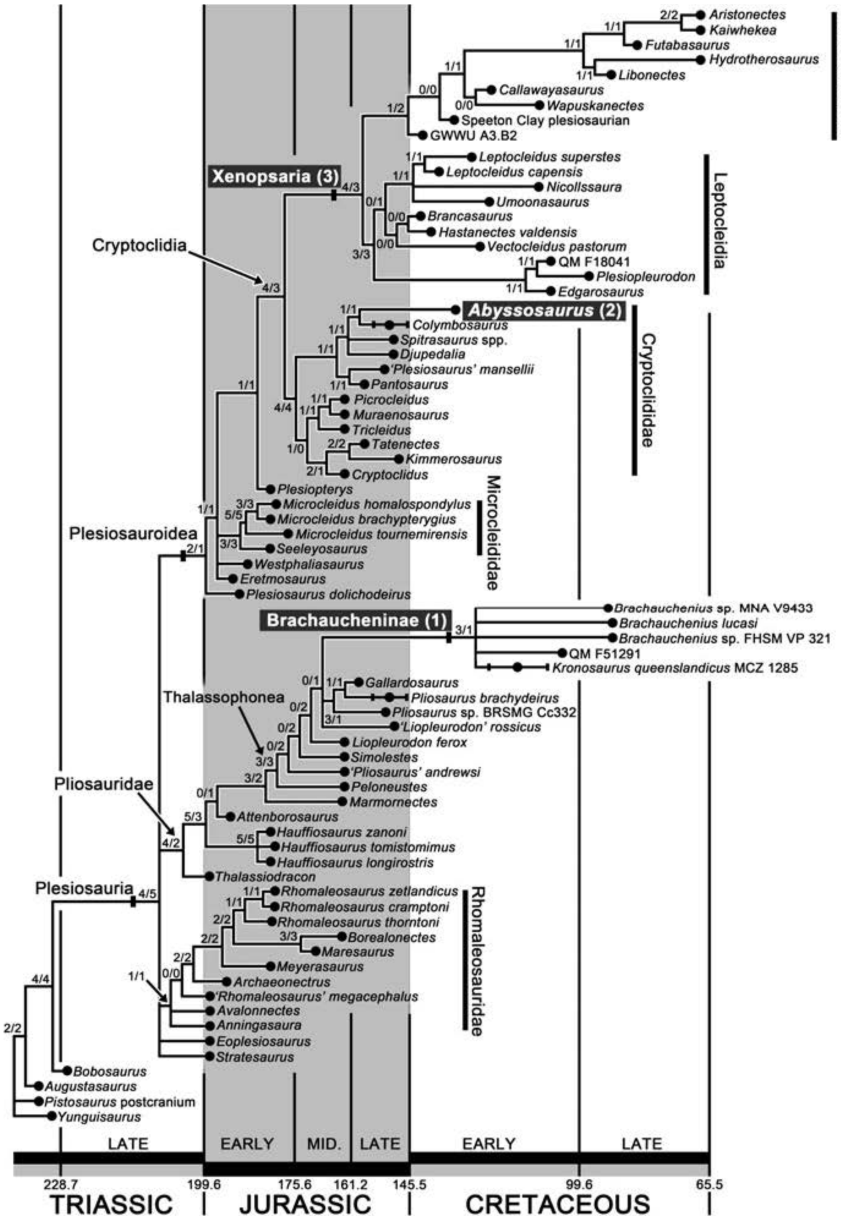

Figure 2. **Phylogenetic analysis of Plesiosauria by Benson and Druckenmiller (2014).** Only the brachaucheninaed pliosaurs and xenosparians cross the Jurassic-Cretaceous boundary. Reprinted by permission from John Wiley and Sons, 2013, see Appendix D.

Plesiosaur Paleobiology

Plesiosaurs were likely all predators of some variety, and evidence for a range of prey items has been reported including fish, ammonites, and other invertebrates (Sato and Tanabe, 1998; Motani, 2009). Evidence from biomechanical experiments indicates that plesiosaurs likely swam with an "underwater flight" method of locomotion, utilizing all four flippers in tandem for propulsion, maximizing locomotory efficiency (Muscutt et al., 2017). Fossil evidence for sophisticated life history in plesiosaurians has been demonstrated in the subfamily level clade, Polycotylidae. A remarkable specimen of *Polycotylus latippinus* preserves a fetal skeleton within the abdominal region, direct evidence that this animal gave birth to live young (O'Keefe and Chiappe, 2011). The estimated size of the fetal specimen suggests that polycotylids likely had maternal care and lived in social groups, analogous to modern day cetaceans (O'Keefe and Chiappe, 2011). Histological evidence supports the hypothesis that polycotylids had prolonged fetal gestation, and had rapid growth rates early in ontogeny (O'Keefe et al., 2019). Evidence from other reptilian lineages, both extinct and extant, indicates that viviparity may have been ancestral to Sauropterygia (Blackburn and Sidor, 2014).

Elasmosauridae: Evolution, Paleobiology, and Systematics

Late Jurassic-Early Cretaceous: Elasmosaurid Origins

Bardet and others (1999) determined that *Occitanosaurus tournemirensis* of the Lower Jurassic of France was the earliest elasmosaurid. However, this taxon lacks diagnostic features of the Elasmosauridae. The premaxillae of *Occitanosaurus tournemirensis* do not contact the parietals posteriorly, and the frontals articulate along the midline. *Occitanosaurus tournemirensis* was recovered in a cladistic analysis as the sister taxon to *Microcleidus*, with the immediate outgroup as *Muraneosaurus*. However, this analysis lacked thorough taxon-sampling, and

Benson and Druckenmiller (2014) would recover *Muraneosaurus* as a cryptoclidid plesiosaur. There is little support for *Occitanosaurus touremirensis* as an elasmosaurid, therefore it is highly unlikely that Elasmosauridae had first evolved in the Early Jurassic; the long-neck microcleidids were therefore convergent on the body plan of Cretaceous elasmosaurids.

The Jurassic-Cretaceous transition was a key interval of faunal turnover within Plesiosauria. In a phylogenetic analysis of plesiosaurians, Benson and Druckenmiller (2014) recovered support for most Cretaceous plesiosaurians as belonging to a single clade, Xenosparia. Clade Xenosparia comprises Leptocleidia (sister relationship between Leptoclididae and Polycotylidae) and Elasmosauridae (Fig. 2). Otero (2016) determined Elasmosauridae had an Early Cretaceous origin, utilizing the Benson and Druckenmiller (2014) phylogenetic matrix. O'Keefe (2001) determined that *Brancasaurus brancai* was the most basal elasmosaurid, while Benson and Druckenmiller (2014) recovered *Brancasaurus brancai* as a leptoclidid. Despite minor differences, these authors both determined that elasmosaurids had evolved by the Early Cretaceous. Elasmosaurs from the Early Cretaceous are rare and relatively unknown. Currently, only three valid elasmosaur genera are known from the Early Cretaceous. Two are from the southern hemisphere: *Callawayasaurus colombiensis* (Carpenter, 1999) and *Eromangasaurus carinognathus* (Kear, 2005). Only one elasmosaur genus is known from the Early Cretaceous of North America, *Wapuskanectes betsynichollsae* of the lowermost Albian Clearwater Formation of Alberta (Druckenmiller and Russell, 2006).

Late Cretaceous: Elasmosaurids Diversify

The earliest appearance of an elasmosaurid in the Late Cretaceous of North America is *Thalassomedon hanningtoni*, from the Cenomanian of Colorado (Welles, 1943). Thalassomedon was 11.6 meters in length (Welles, 1952), and the appearance of this taxon demonstrates that elasmosaurids had attained large body sizes in the Western Interior Seaway by the Cenomanian. The next elasmosaur taxon to appear in sedimentary strata of the Western Interior Seaway is *Libonectes morgani*, from the lower Turonian Britton Formation of Texas (Carpenter, 1999). Both taxa are recovered as basal to Styxosaurinae in phylogenetic analyses (Otero, 2016; Serratos et al., 2017). The skull of the holotype specimen of *Libonectes* (SMUSMP 69120) has been described in detail in multiple scientific publications (Welles and Bump, 1949; Carpenter, 1997; Carpenter, 1999; Araújo and Polcyn, 2013). The skull of *Thalassomedon hanningtoni* (DMNH 1588) has received less attention, figured only in a description published by Carpenter (1999) and an unpublished dissertation by Sato (2002).

There is a notable lack of elasmosaurid material from the Coniacian through the Santonian, except for a partial skeleton, YPM 1640, from the Lower Coniacian Fort Hays Limestone (Everhart, 2006). This absence may be attributed to either preservation or paleoenvironmental biases (Everhart, 2006). The Turonian record of elasmosaurids is sparse as well, with only one known taxon, *Libonectes morgani*, from the Britton Formation of Texas (Carpenter, 1999). The record of WIS elasmosaurs continues with *Elasmosaurus platyurus* and *Styxosaurus snowii* from the earliest Campanian (Otero, 2016). *Styxosaurus snowii* is known from the Smoky Hill Chalk Member of the Niobrara Formation (Sachs et al., 2018), and *Elasmosaurus platyurus* is known from the Sharon Springs Formation of the Pierre Shale (Sachs, 2005), both of which are earliest Campanian; the Smoky Hill Chalk Member of the Niobrara Formation underlies the Sharon Springs Formation (Miall et al., 2008). The holotype specimen of *Elasmosaurus platyurus* (ANSP 18001) was originally described by Cope (1869), and is interpreted to possess 71 cervical vertebrae, one of the highest cervical vertebrae counts of any known vertebrate, living or extinct (Sachs et al., 2013). The cranium of this specimen is incomplete, with only the rostral portion preserved, paired premaxillae and anterior mandibles (Sachs, 2005). Elasmosaur remains have also been recovered from the Maastrichtian Horseshoe Canyon Formation of Alberta, and the depositional environment indicates elasmosaurs may have inhabited estuarine or fluvially-influenced settings, inland from shore (Sato and Wu, 2006). The elasmosaurid fossil record indicates this clade became speciose and morphologically disparate while adapting to different environments.

Evolution of the Aristonectinae

The aristonectine plesiosaurs of the Austral Late Cretaceous are a highly derived clade of filter-feeding elasmosaurids (O'Keefe et al., 2017). The aristonectines are characterized by their high number of maxillary and dentary teeth, and an occiput placed significantly anterior to the glenoid of the suspensorium (O'Keefe et al., 2017). The phylogenetic position of the Aristonectinae has been controversial. *Aristonectes parvidens* was originally described by Cabrera (1941), who originally suggested this taxon was an elasmosaurid. Gasparini and colleagues (2003) referred the genus *Aristonectes* to the Elasmosauridae based on several synapomorphies, including: a long, straight jugal-postorbital suture; orbit smaller than supratemporal fenestra; absence of anterior interpterygoid vacuity, platycoelous cervical vertebrae, and lateral ridges on the anterior cervical vertebrae. Brown (1993) referred *Aristonectes* to the Cryptoclididae. O'Keefe and Street (2009) erected a subfamily, Aristonectidae, that included the Cretaceous Austral aristonectines within the Cryptocleidoidea, based on a series of cranial and postcranial characters, including the presence of more than 30 maxillary teeth, and the presence of more than 32 cervical vertebrae. Subsequent phylogenetic analyses by Benson and Druckenmiller (2014), Otero et al. (2014), Otero (2016), and Serratos et al. (2017) would support the hypothesis of Gasparini et al. (2003) and Cabrera (1941), that the aristonectines are in fact a highly derived clade of elasmosaurids. Otero et al (2014) recognized that *Aristonectes quiriquinensis* has a series of features that are convergent with cryptoclidoids, including: a large skull, a relatively long neck, anteriorly directed neural spines, and a posterior symphysis of the coracoids.

While the monophyly of Aristonectinae is well-supported and replicated across phylogenetic analyses, the relationship of the Aristonectinae to the rest of the Elasmosauridae is less well-known. The phylogenetic analyses of Otero (2016) and Serratos et al. (2017) are largely in congruence; however, their topologies are slightly different, with biogeographic implications. A phylogenetic analysis by Otero (2016) recovered the taxon *Hydrotherosaurus alexandrae* from the Maastrichtian Moreno Formation of California to be outside of both Styxosaurinae and Aristonectinae. Serratos et al. (2017) found *Hydrotherosaurus* to be within Styxosaurinae. A study of elasmosaurid phylogeny by O'Gorman (2020) found the Aristonectinae to be nested within an exclusively Pacific clade named Wedellonectia. Non-aristonectine members of this group include *Vegasaurus molyi*, *Kawanectes lafquenianum*, *Aphrosaurus furlongi*, *Morenosaurus stocki*, *Futabasaurus suzkukii*, and *Tuarangisaurus keyesi*.

Elasmosaurid Paleobiology and Paleoecology

Elasmosaurids were immediately recognized by paleontologists to be macropredators. Cope (1869) in his original description of the taxon *Elasmosaurus platyurus* noted the elongate "canine-like" teeth and fish remains discovered under the dorsal vertebrae, suggesting that the animal was piscivorous. The extremely long neck of some elasmosaurid species is considered by researchers to be an evolutionary novelty (Noe et al., 2017). The long neck of elasmosaurids has been interpreted as an adaptation for acquisition of fast-moving, pelagic prey (Thulborn and

Turner, 1993); however, there is notable evidence that elasmosaurids pursued a variety of benthic marine invertebrates as well (McHenry et al., 2005).

Gastroliths are found consistently associated with articulated elasmosaur skeletons. Cicimurri and Everhart (2001) reported a skeleton of an elasmosaur from the Sharon Springs Member of the Pierre Shale (Campanian) with gastroliths, and the remains of teleost fish. The ubiquitous presence of gastroliths, and evidence from tooth crown wear, has been cited in support of the hypothesis that elasmosaurs specialized in swallowing prey whole and relying upon gastroliths for digestion (Kear et al., 2017). Collin and Janis (1997) argued that limitations on the pharyngeal apparatus prevented marine reptiles from evolving suspension-feeding analogous to that of modern baleen whales. However, the aristonectine elasmosaurid *Morturneria seymourensis* (O'Keefe et al., 2017) has dozens of homodont teeth that are interpreted to be an adaptation for benthic filter-feeding.

Relationships of Elasmosauridae: Reaching a Consensus

Prior to the widespread adoption of cladistic methods for determining evolutionary relationships, plesiosaur interrelationships were plagued by a morphotype-based taxonomy (O'Keefe, 2001). The definitions of clades within Plesiosauria have undergone a suite of changes and revisions. Brown (1993) attempted to revise the taxonomy of Plesiosauroidea by evaluating the morphology of the temporal region and anterior cervical vertebrae of Elasmosauridae and Cryptoclididae. Brown (1993) diagnosed Elasmosauridae as having five pairs of premaxillary teeth, with enlarged premaxillary and maxillary teeth punctuated by smaller teeth adjacent to the premaxilla-maxilla contact. He noted a reduction in dentary teeth, and a lack of significant emargination of the lower temporal bar. He also noted unique characters in the braincase of elasmosaurids, including an occipital condyle formed exclusively by the basioccipital, and a constricting groove occurring on the occipital condyle. The application of cladistic analyses on fossil taxa would result in a major restructuring on plesiosaur ingroup relationships, and the diagnosis of Elasmosauridae would be updated iteratively (O'Keefe, 2001; Druckenmiller and Russell, 2008; Ketchum and Benson, 2010; Benson and Druckenmiller, 2014). O'Keefe (2001) in a cladistic revision of the Plesiosauria provided a node-based definition of Elasmosauridae as "including *Brancasaurus*, *Styxosaurus*, their most recent common ancestor, and all descendants." In this analysis, Elasmosauridae was diagnosed by three cranial characters: "anterior quadrate embayment absent (reversal); premaxilla excluded from border of external naris; vomer extends posterior to internal nares." The five postcranial characters diagnose Elasmosauridae in this analysis: "number of cervical rib heads reduced to one; coracoids long with deep median embayment; ventro-medial margin of pubis concave; ulna not lunate (reversal); epipodials wider than long." A cladistic analysis of Elasmosauridae was reported in an unpublished dissertation by Sato (2002), which would include characters that would be incorporated into future plesiosaurian cladistic datasets (Benson and Druckenmiller, 2014). Sato (2002) built off the work of O'Keefe (2001) and investigated the Bearpaw Formation elasmosaurid fauna.

Otero (2016) attempted to clarify elasmosaurid relationships by focusing on the alpha-taxonomy of the genus *Styxosaurus*. A significant result of this study was the declaration of the genus *Hydralmosaurus* (Welles, 1943) a *nomen dubium*, and referring the specimen this taxon was based on, AMNH 1495, to an indeterminate species of *Styxosaurus*. The author also erected a new subfamily level clade, Styxosaurinae, with the type species as *Styxosaurus browni* (AMNH, 5835, holotype). Styxosaurinae was diagnosed as a "clade of Campanian elasmosaurds from the Western Interior Seaway" with 60 or more cervical vertebrae, elongate middle cervical centra, and a plesiomorphic number (17-19) of dorsal vertebrae. Styxosaurinae was defined phylogenetically (Fig. 3) as “the genera *Terminonatator*, *Styxosaurus* (=’*Hydralmosaurus*’), *Albertonectes*, *Elasmosaurus*, their most recent common ancestor and all descendants.”

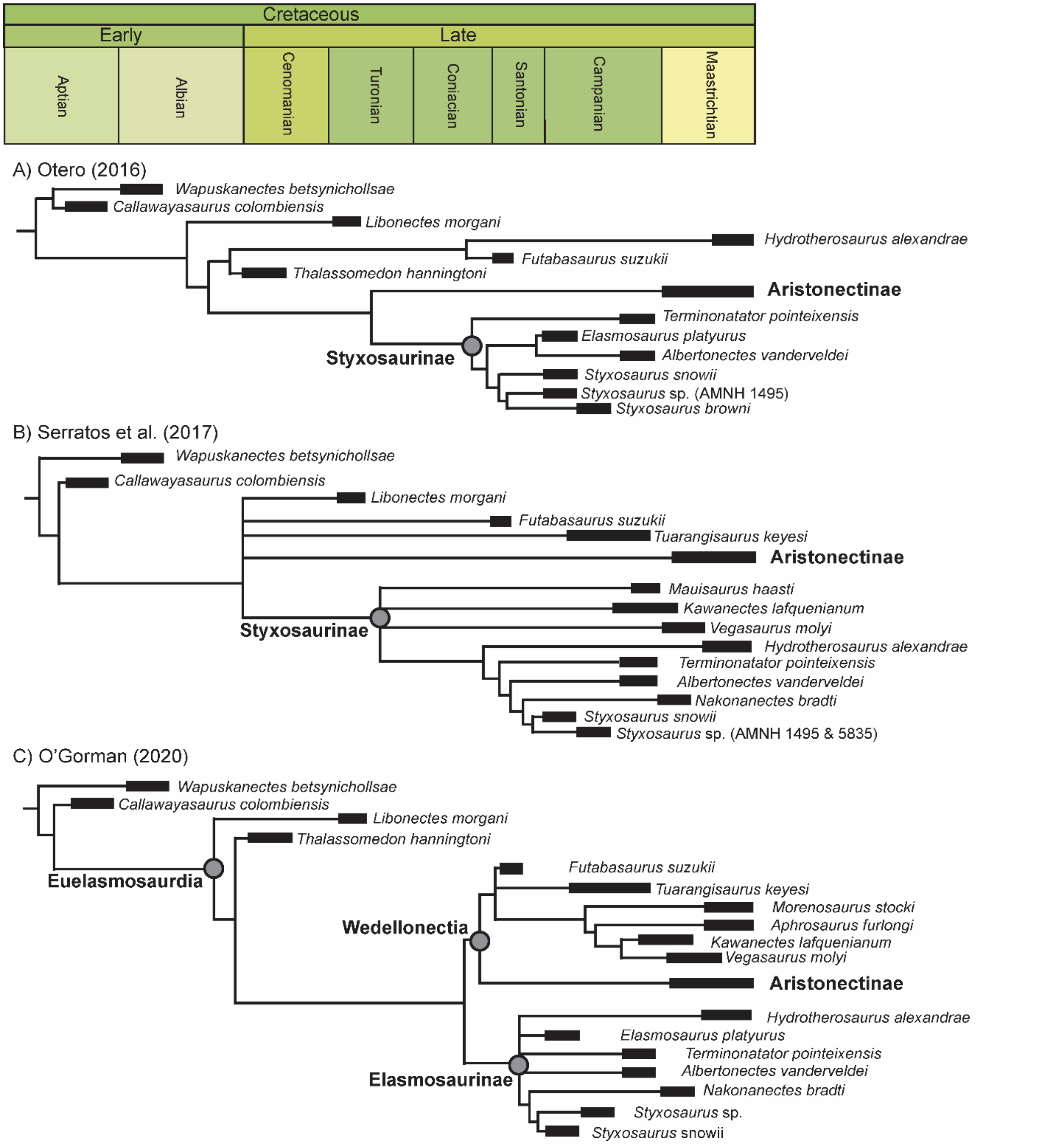

Figure 3. Phylogenetic analyses of Elasmosauridae. A) Otero (2016); Serratos et al. (2017); and C) O’Gorman (2020). Figure © 2020 Elliott Armour Smith.

An important contribution to understanding Western Interior Seaway elasmosaurids was made by the discovery of *Nakonanectes bradti* (Serratos et al., 2017). *Nakonanectes* is unusual in having a relatively low number of cervical vertebrae (39-42), a reversal also found in the Aristonectinae (Otero, 2016). However, *Nakonanectes* was found to be nested within the long-necked Styxosaurinae, indicating that this taxon had experienced a reduction in neck elongation independent from the reduction in neck vertebrae in Aristonectinae (Fig. 3). Serratos et al. (2017) reported character support for the monophyly of this group that included the presence of a squamosal bulb, anteroposteriorly oriented dorsal spines, and a reduced number of dorsal vertebrae (17-19).

The most recent contribution to elasmosaurid phylogeny was published by O'Gorman (2020), in a paper revising the holotype of *Aphrosaurus furlongi*, of the Maastrichtian aged Moreno Formation of California. The topology he recovered indicated that Pacific elasmosaurid taxa including *Morenosaurus stocki*, *Aphrosaurus furlongi*, *Kawanectes lafquenianum*, and *Vegasaurus molyi* form a monophyletic sister group to the Aristonectinae (Fig. 3).

Geological Setting

Overview of the Western Interior Basin

In the Early Cretaceous, beginning about 120 Ma, crustal thickening related to the thrust-folding of the Sevier Orogeny caused the development of a foreland basin in what are now the Rocky Mountain and Colorado Plateau regions of the North American Cordillera (Blakey and Ranney, 2018). This axis of this foreland basin would stretch from southern Alaska and northwestern Canada to the Gulf of Mexico, and would become inundated with a shallow, saline body of water known as the Western Interior Seaway. During the latter part of the Early Cretaceous and nearly the entirety of the Late Cretaceous, the Western Interior Seaway separated the landmass of eastern North America from western North America (Blakey and Ranney, 2018). Sandstones such as the Mesa Verde Group track cycles of transgression and regression during the Cretaceous, and grade eastward into dark-colored marine shales such as the Mowry Formation and Pierre Shale Group (Blakey and Ranney, 2018). The Western Interior Basin experienced a series cycles of marine transgression and regression during the Cretaceous Period, which are elucidated based on the stratigraphic distribution of major facies (Kauffman and Caldwell, 1993). Tectonic and eustatic mechanisms determined the distribution of facies at the basin center (Miall et al., 2008). An extensive fossil record of marine invertebrates adds an immense level of detail to the stratigraphy of marine deposits. The Upper Cretaceous fossil record of ammonites and inoceramid clams has been used to define distinct biozones that are correlative throughout the Western Interior Basin, and some taxa are globally correlative (Cobban et al., 2006). During the Late Cretaceous, North America occupied middle to high paleolatitudes (from 30 degrees to 85 degrees north) and ranged from tropical climate in what is now the southwestern United States and Mexico to a temperate climate in what is now Alaska and Canada (Robinson and Kirschbaum, 1995).

Major Transgressive-Regressive Cycles of the Cretaceous

Sedimentary strata are divided into stratigraphic stages with discrete ages that are globally standardized by the International Commission on Stratigraphy (ICS, 2020). The actual intervals of geologic time that are represented by these stages are called ages and are calibrated by radiometric dating. The Western Interior Basin of North America records many of the ages of the Cretaceous period, shown on the geologic timescale in Figure 4.

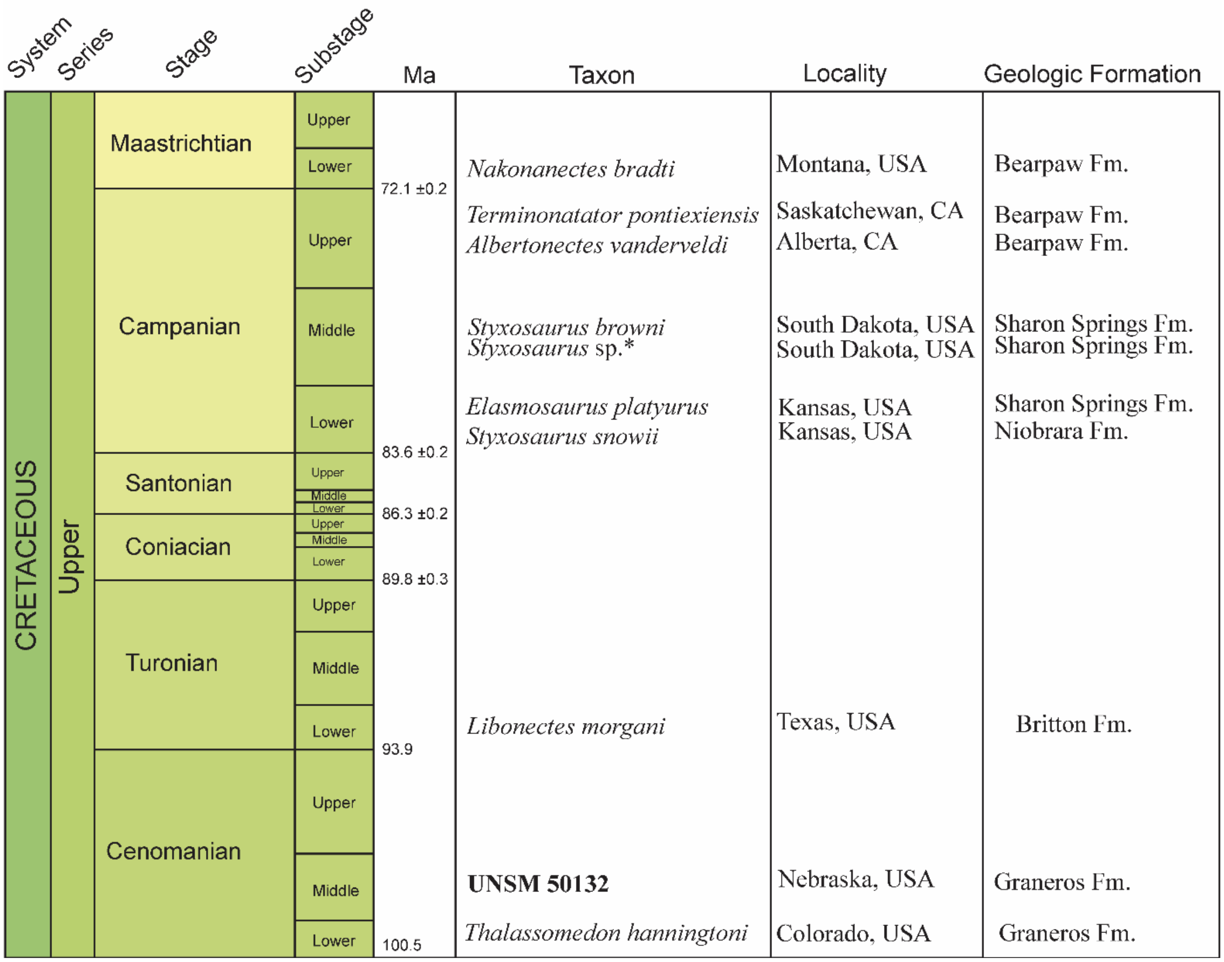

Figure 4. Chronostratigraphic occurrences of Late Cretaceous elasmosaurids from the Western Interior Seaway. Stage boundaries from the International Commission on Stratigraphy (ICS, 2020). *Two referred specimens of *Styxosaurus* sp. include AMNH 1495 from Iowa and SDSM 451 from South Dakota. Figure © 2020 Elliott Armour Smith.

The beginning of the Early Cretaceous (Berriasian to the Barremian) of the Western Interior basin is marked by a regional unconformity attributed to a lack of sedimentation, the result of an interval of quiet tectonism (Miall et al., 2008). This period of quiet tectonism in the Early Cretaceous is represented by conglomerates that were deposited over much of the Western Interior, the result of an eastward tectonic uplift with eastward trending paleo-flow, similar to modern day Alberta (Miall et al., 2008). Above the regional Barriasian-Barremian unconformity and overlying gravels, a series of marine transgressions are recorded throughout the Western

Interior Basin (Miall et al., 2008). The Skull Creek-Kiowa transgression records the first time the waters of the northern Western Interior Basin would become connected with the neo-Tethyan waters of the south (Kauffman and Caldwell, 1993).

The beginning stage of the Late Cretaceous, the Cenomanian, would be characterized by a marine transgression cycle known as the Greenhorn cyclothem, which resulted in the deposition of the Mowry Shale, the Greenhorn Formation, and the Carlile Shale (Robinson and Kirschbaum, 1995). Due to high rates of seafloor spreading, global sea levels would rise to their highest in Earth's history during the Turonian, nearly 300 meters higher than today (Miall et al., 2008). During the Conacian-Santonian, a relative lack of sedimentation in the interior basin resulted in the deposition of the chalky Niobrara Formation, which grades westerly into the silt-shale dominated Mancos Formation (Miall et al., 2008).

The Campanian was an interval of increased fold-thrust tectonism of the Sevier Orogeny, which created a sediment source for progradational clastic wedges represented by the Judith River Formation of Montana, and south to the upper facies of the Mesaverde Group in Utah (Miall et al., 2008). Near the Campanian-Maastrichtian boundary, the Western Interior Seaway would become closed off from the Gulf of Mexico due to Laramide orogenesis, although the WIS would remain open to the north (Blakey and Ranney, 2018). The last great marine deposition of the Western Interior Basin occurred during the Campanian and Maastrichtian and resulted in the deposition of the Bearpaw Formation, which is primarily confined to Montana and southern Canada (Miall et al., 2008).

Vertebrate Faunas of the Western Interior Seaway

Upper Cretaceous marine sedimentary strata of the Western Interior Basin contain an extremely well-sampled vertebrate fauna, with a high level of taxonomic diversity. Cenomanian faunas of the Graneros Shale of Nebraska contained a diversity of chondrichthyans (Meglei et al., 2013) and osteichthyans (Jansen et al., 2012). Turonian vertebrate faunas of the Carlile Shale of Kansas were dominated by a comparable diversity of chondrichthyans and osteichthyans (McIntosh et al., 2016). The Late Cretaceous Western Interior Seaway also hosted a diversity of hesperornithoform diving seabirds, which thrived on the warm and productive waters of the basin (Wilson, 2019). Other marine reptiles included the mosasaurs, which evolved from a relatively small-bodied squamate ancestor in the early part of the Late Cretaceous, and by their demise at the Maastrichtian-Danian boundary, they had achieved a cosmopolitan distribution, were taxonomically diverse, and had a wide range of ecologies, including pursuit predation and durophagy (Ross, 2009). The rich Late Cretaceous plesiosaur faunas of the Western Interior Seaway included brachaucheniid pliosaurs, polycotylids, and elasmosaurs (Schumacher and Everhart, 2005).

Fossil Specimens

Institutional Abbreviations

ANSP, Academy of Natural Sciences, Philadelphia, PA; **AMNH**, American Museum of Natural History, New York, NY; **DMNH**: Denver Museum of Nature and Science, Denver, CO; **KUVP**, University of Kansas Museum Natural History Museum, Lawrence, KS; **SDSM**, South Dakota School of Mines and Technology, Rapid City, SD; **UNSM**: University of Nebraska State Museum, Linclon, NE; **YPM**, Yale Peabody Museum, New Haven, CT

Specimen Selection

In this study, four elasmosaur specimens were selected for their relevance to resolving ingroup relations within North American Elasmosauridae. The following is a taxonomic summary of all the species involved in this study. These specimens were chosen to assess the alpha taxonomy of two Western Interior Seaway elasmosaurid genera: *Thalassomedon* and *Styxosaurus*.

KUVP 1301 – *Styxosaurus snowii* (Holotype)

KUVP 1301 is the holotype specimen of *Styxosaurus snowii*, a large-bodied elasmosaur known from a cranium, 28 of the anterior-most cervical vertebrae, and a possible ilium (Carpenter, 1999; Everhart, 2006). The specimen was collected in 1890 by E.P. West in Logan County, Kansas on Hell Creek (Everhart, 2006). It is from the Upper Smoky Hill Chalk Member of the Niobrara Formation (Fig. 4), which is likely lowermost Campanian. First described as '*Cimoliosaurus' snowii* by Williston (1890), he reported a complete skull of the animal and the first 28 cervical vertebrae. The skull of KUVP 1301 received additional description by Cope (1894) and Williston (1903). In 1906, Williston referred KUVP 1301 to *'Elasmosaurus' snowii*, along with a juvenile elasmosaur specimen, YPM 1644, which consists of cervical vertebrae, dorsal vertebrae, a partial pectoral girdle, a partial pelvic girdle, and a humerus (Carpenter, 1999). Welles (1943) erected a new genus, *Styxosaurus*, and referred KUVP 1301 to this new genus. Carpenter (1999) validated the designation of KUVP 1301 as a holotype specimen for the genus *Styxosaurus* (Welles, 1943). The skull of KUVP 1301 would receive additional description by Welles (1952). Carpenter (1999), in his revision of Elasmosauridae from the Western Interior Seaway, referred a series of specimens with *nomen dubia* to the genus *Styxosaurus*. Sachs and colleagues (2018) re-described KUVP 1301 and re-diagnosed the taxon based on what the authors argued is a unique combination of synapomorphies.

UNSM 50132 – Unassigned Styxosaurine

UNSM 50132 comprises a complete skull with brittle deformation, a complete cervical series of 63 cervical vertebrae, three dorsal vertebrae, and a fore-paddle (pers. observ.). The specimen is from the Graneros Formation (Fig. 4), which is known to be Cenomanian in age (Carpenter, 1999). This specimen was first discovered in 1964 on the farm of Adolph Rezac by Hal DeGraw of the Nebraska Geological Survey and University of Nebraska, Charles Osborn of the Bureau of Reclamation, and Phil Emory of the United States Geological Survey (Schultz, 1965). These geologists were studying exposures of Cretaceous shales and limestones along the North Oak Creek valley (Schultz, 1965). UNSM 50132 was studied by Samuel P. Welles, and he informally referred the specimen to the taxon *Thalassomedon hanningtoni* in a University of Nebraska news bulletin (Welles, 1970). Carpenter (1999) validated this unofficial referral, and listed UNSM 50132 as a referred specimen of *Thalassomedon hanningtoni*.

DMNH 1588 – *Thalassomedon hanningtoni* (Holotype)

DMNH 1588 is the holotype specimen of *Thalassomedon hanningtoni*, first described by Welles (1943), and consists of a nearly complete skeleton, including a skull with brittle deformation. DMNH 1588 was discovered in Baca County, Colorado, 13 miles north of the town of Pritchett (Carpenter, 1999). The specimen comes from the uppermost facies of the Graneros Formation (Welles, 1943), which is known to be Cenomanian in age (Carpenter, 1999). A chronostratigraphic study of the Western Interior Basin by Shang and colleagues (2018) placed the age of the Graneros Formation near Pueblo, Colorado, to be between 94.2 Ma and 96.4 Ma. Welles (1952) recognized *Thalassomedon hanningtoni* to be one of the largest known plesiosaurs in existence. Carpenter (1999) revised the diagnosis of *Thalassomedon hanningtoni* and referred two additional specimens to the taxon. One of these specimens is FMNH 12009, a partial skeleton with over 60 vertebrae, a pectoral girdle, and a fore-paddle (Carpenter, 1999). FMNH 12009 was previously named '*Elasmosaurus serpentinus'* (Riggs, 1939) and '*Alzadasaurus serpentinus*' (Welles, 1943). This specimen was not evaluated and is not considered further here.

The other specimen Carpenter (1999) referred to *Thalassomedon hanningtoni* was UNSM 50132, described above.

CHAPTER 2

CRANIAL OSTEOLGY OF THE LATE CRETACEOUS ELASMOSAURIDS OF THE WESTERN INTERIOR SEAWAY

KUVP 1301 – *Styxosaurus snowii* (Holotype)

General Description of the Skull

In overall shape, *Styxosaurus snowii* has an elongate rostrum, with a prominent hump between the anterior edges of the orbits (Fig 5). The beak index (the percentage of preorbital length to total skull length), is 42. The external nares are posteriorly placed near the anterior edge of the orbit. The orbits face antero-laterally and are ventrally expanded while constricted dorsally (Fig. 5). The temporal bar is constricted in its middle portion, while the ventral edge of the temporal bar deflects ventrally near the mandibular articulation (Fig. 5, 6). The parietals are laterally concave, with a prominent sagittal crest (Fig. 5). The squamosal arch meets the cranial roof near the parietals in a slightly expanded fashion, with notable rugosity (Fig. 5). The cranium of *Styxosaurus snowii* (Fig. 5, 6) is well-preserved, with intact bone surface on much of the cranial surface, except for some cracks and perforations. These cracks and perforations are related to the mediolateral crushing of the skull. The upper and lower jaws are completely occluded. The area around the right external naris is crushed in a medially concave direction. The right orbit has experienced little deformation and is mostly intact. The right jugal is thin and has been crushed onto the right lateral side of the braincase. On the right side of the skull there is a crack between the massive anterior process of the squamosal, and the dorso-medial oriented process of the squamosal arch. From right lateral view, the braincase appears relatively intact, with a prominent crack occurring near the parietal-braincase suture (Fig. 5).

In left lateral view (Fig. 6), the cranium has occluded jaws with the teeth in an extremely good state of preservation. The left orbit is badly cracked and deformed, with the postorbital bar broken in at least three places. There is a prominent crack running from the massive anterior process of the left squamosal that travels down through the posterior left mandible. Like the right squamosal, there is a prominent crack between the massive anterior process of the left mandible and the dorsally oriented process of the squamosal. The mandibles appear to be nearly contacting one another medially due to crushing.

Dorsal Elements of the Skull

Premaxilla. The premaxillae are expanded and robust anteriorly (Fig. 5, 6), and relatively gracile and constricted posteriorly. Each premaxilla forms the anterior margin of the external naris and contacts the maxilla posteriorly. The premaxilla-maxilla suture travels antero-ventrally from the inferior edge of the external naris to the alveolar tooth row (Fig. 5). The premaxillae have a thin, posterior process that contacts the frontal immediately dorsal to the external naris (Fig. 5). The contact between the frontal and the posterior process of the premaxilla is highly interdigitated. The posterior tip of this process contacts the postfrontal laterally. The posterior processes of the premaxillae meet the parietals posteriorly, and the pineal foramen appears to be closed. The premaxillae contact one another medially along the sagittal midline, and the posterior processes of the premaxillae form a prominent hump between the anterior edges of the orbits. In right lateral view (Fig. 5), three antero-posteriorly oriented grooves occur on the anterior tip of the right premaxilla. A scattering of small pits occurs on the alveolar margins, which are relatively expanded on the lateral edge of the tooth crowns. There are five alveoli in each premaxilla. Several larger pits occur near the medial margin with the premaxilla.

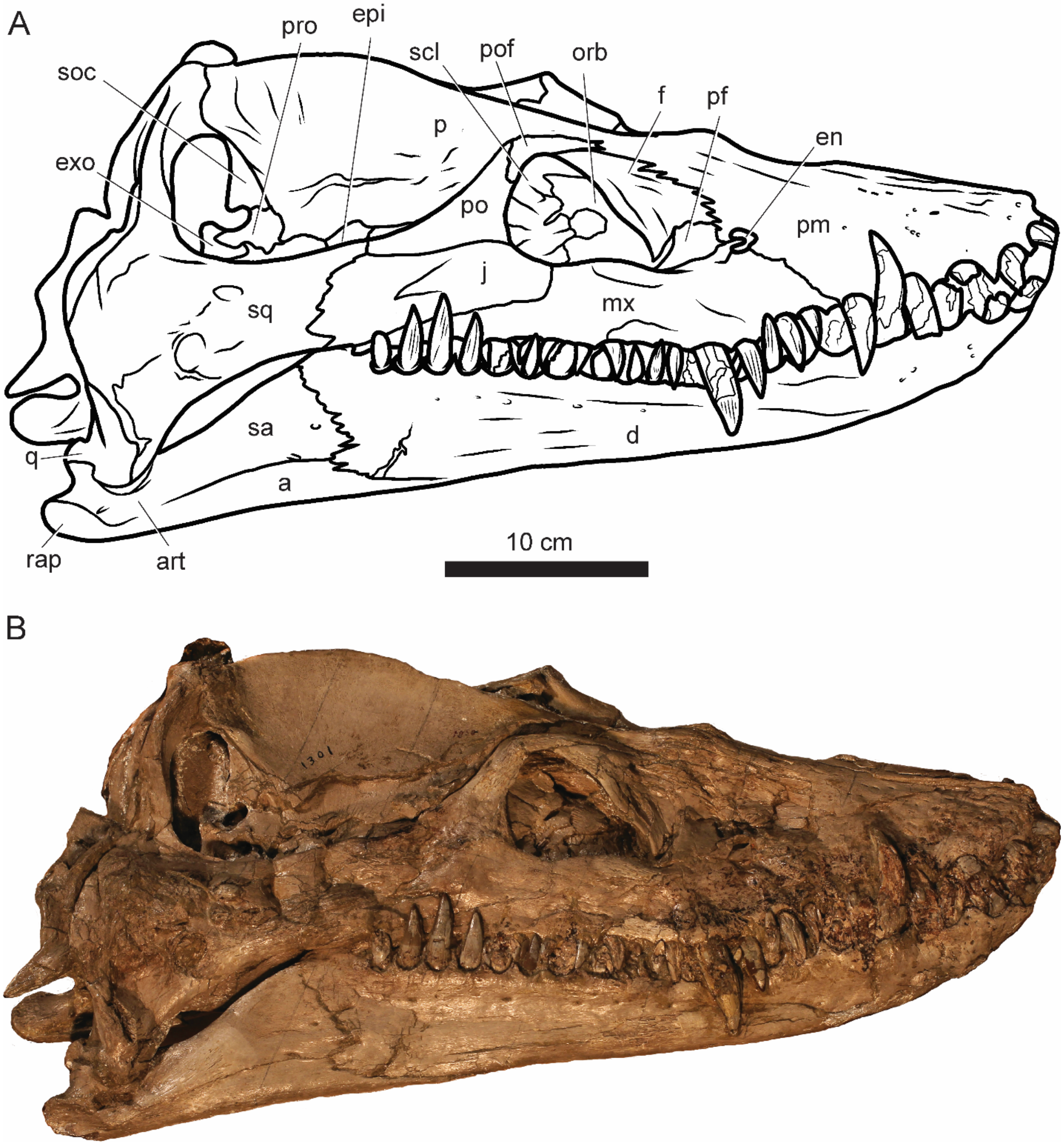

Figure 5. Cranium of KUVP 1301, holotype specimen of *Styxosaurus snowii,* in right lateral view. Interpretation (A) and photo (B). Abbreviations: **a**, angular; **art**, articular; **d**, dentary; **en**, external naris; **exo**, exoccipital; **epi**, epipterygoid; **f**, frontal; **j**, jugal; **mx**, maxilla; **orb**, orbit; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **scl**, sclerotic ring; **soc**, supraoccipital; **sq**, squamosal. Illustration and photograph © 2020 Elliott Armour Smith.

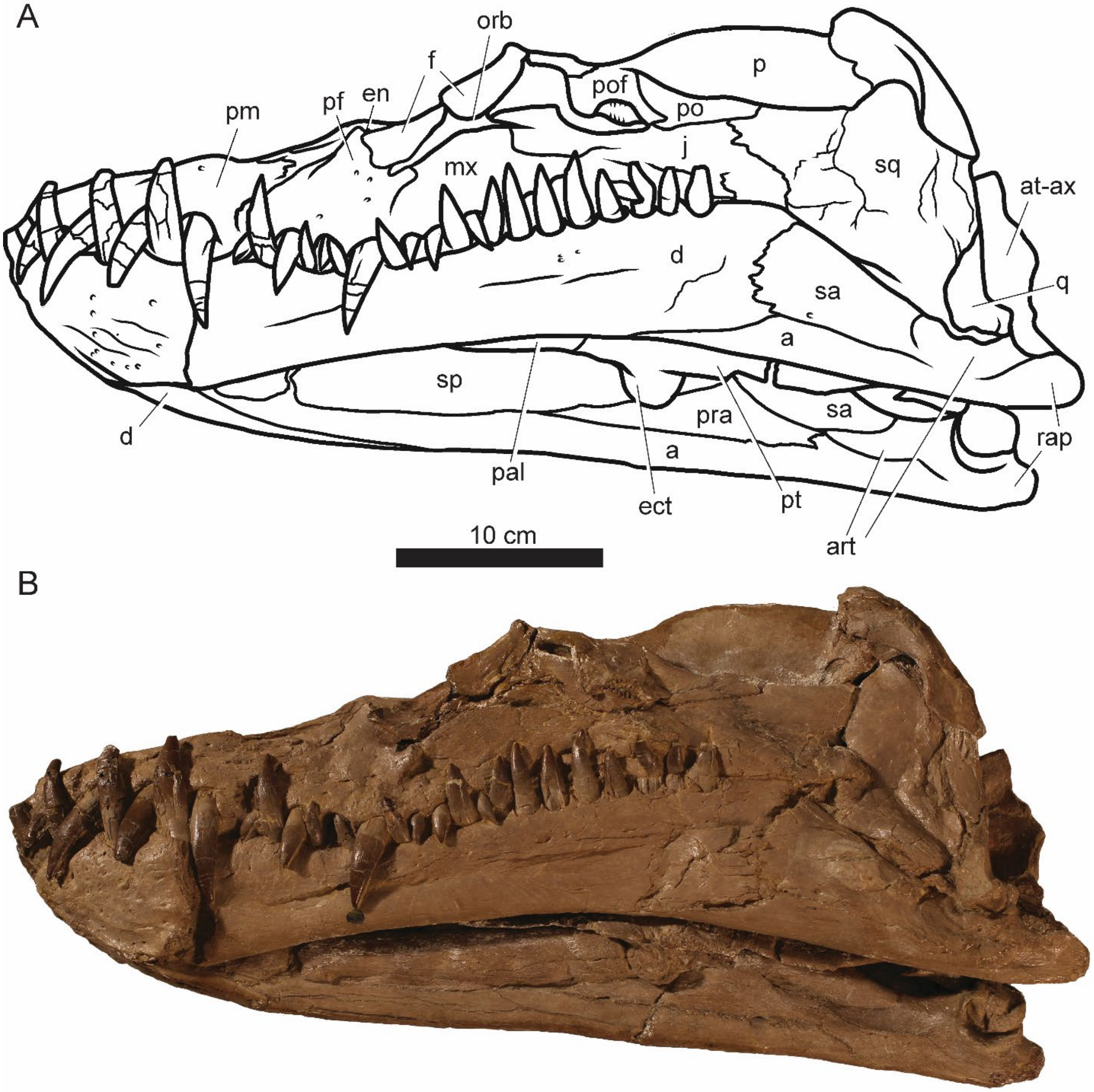

Figure 6. Cranium of KUVP 1301, holotype specimen of *Styxosaurus snowii*, in left lateral view. Interpretation (A) and photo (B). Abbreviations: **a**, angular; **at-ax**, atlas-axis; **art**, articular; **d**, dentary; **en**, external naris; **exo**, exoccipital; **epi**, epipterygoid; **f**, frontal; **j**, jugal; **mx**, maxilla; **orb**, orbit; **p**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **scl**, sclerotic ring; **soc**, supraoccipital; **sp**, splenial; **sq**, squamosal. Illustration and photograph © 2020 Elliott Armour Smith.

Maxilla. The maxilla forms the ventral margin of the external naris and contacts the premaxilla anteriorly. The premaxilla-maxilla suture travels anteriorly from the ventral margin of the external naris towards the alveolar tooth row, and extends between the fifth and sixth alveoli of the upper jaw. There are eleven alveoli in the maxilla. The fourth alveolus (ninth overall) bears a large caniform tooth, and the alveolar margin is bulbous and expanded here. The maxilla generally lacks the pits found on the anterior and medial margin of the premaxilla. The maxilla contacts the prefrontal dorsally along a sinuous suture. The maxilla forms the ventral margin of the orbit. The anterior and ventral margin of the orbit on the maxilla contains a raised area that is spatulate in shape, and points posteriorly along the ventral margin of the orbit. This condition is seen in *Thalassomedon hanningtoni* (Carpenter, 1999), unassigned styxosaurine UNSM 50132, *Terminonatator pointexiensis*, and a referred specimen of *Styxosaurus* sp., SDSM 451 (pers. observ.). The dorsal margin of the maxilla (Fig. 5) forms the inferior edge of the external naris and contacts the ventral margin of the prefrontal in a sinuous fashion from the naris towards the anterior orbit margin. The anterior edge of the ventral orbit margin is dorsally bowed, a condition observed in *Nakonanectes bradti* (Serratos et al., 2017), unassigned styxosaurine UNSM 50132, *Styxosaurus browni* (Otero, 2016), and *Kaiwhekea katiki* (Cruickshank and Fordyce, 2002). This condition is referred to as a "reniform orbital outline" (Benson and Druckenmiller, 2014). The maxilla contacts the jugal posteriorly, with this suture beginning at the posterior edge of the ventral orbit margin. The maxilla-jugal suture is dorso-ventrally oriented, for a length of 1.6 cm, before changing direction abruptly, to a posterior direction. The angle of the jugal-maxilla suture is deflected approximately 10 degrees ventrally from horizontal. The maxilla-jugal suture ends on the ventral margin of the temporal bar, just posterior to the termination of the maxillary alveoli. The length of this portion of the jugal-maxilla suture is 10 cm. Thirteen alveloli are visible in both the left and right maxillae.

Jugal. The jugal is thin and flat in the mediolateral direction, forming the anterior temporal bar, and the postero-ventral orbit margin. The jugal contacts the postorbital dorsally, beginning at the posterior margin of the orbit. The jugal-postorbital suture travels posteriorly and intersects the temporal bar. The tripartite contact between the postorbital, jugal, and squamosal occurs near the dorsal margin of the temporal bar. The squamosal-jugal suture is relatively obscured from cracking and deformation, but where visible, it appears to be interdigate.

Prefrontal. The prefrontal is a triangular shaped bone that contacts the maxilla ventrally, the premaxilla anteriorly, and the frontal superiorly and posteriorly. In right lateral view, the frontal-prefrontal suture appears to be displaced out of articulation. The frontal-prefrontal suture is straight with an anterior interdigitation halfway along its margin. The ventral margin of the prefrontal is sinuous in appearance as it trends from the anterior orbit margin to the external naris. The anterior margin of the prefrontal has a constricted, pointed process that forms the ventral margin of the external naris. There is some dissociation of the cranial elements around the margin of the external naris, so this process is out of articulation. The frontal and maxilla nearly meet along the anterior margin of the orbit, almost blocking the prefrontal entirely from the anterior margin of the orbit. This is like the condition observed in *Nakonanectes*, and unassigned styxosaurine UNSM 50132.

Frontal. The frontal is a thin, fan-shaped element that forms the anterior margin of the orbit. It contacts the prefrontal posteriorly, and the premaxilla medially. The frontal contacts the premaxilla medially along a highly interdigate suture. The anterior margin of the frontal contacts the prefrontal beginning at the anterior-inferior margin of the orbit, and begins trending dorsally, with shift in angle to horizontal as the suture travels anteriorly towards the orbit. The frontal-prefrontal contact gives the anterior frontal margin a right-angle appearance. This condition of the frontal-prefrontal contact is shared by other styxosaurines*:* *Styxosaurus* sp. SDSM 451 (personal obs.); unassigned styxosaurine UNSM 50132 (pers. observ.); *Nakonanectes bradti* (Serratos et al., 2017).

Postfrontal. The postfrontal contributes to the superior margin of the orbit, and articulates with frontal anteriorly, along an anteromedially-trending suture that points in the direction of the premaxillary boss. The posterior suture of the postfrontal articulates in a moderately interdigitate fashion and travels medially from the orbit margin towards the sagittal crest, along the axis of the postorbital bar. In right lateral view, the orbit is crushed against the midsagittal plane, and the medial margin of the postfrontal is visible within a wide, anteroposterior running crack adjacent to the sagittal crest (Fig. 5). In left lateral view, the left orbit is completely crushed with the postorbital bar and the anterior orbit margin broken into three distinct pieces. The ventral margin of the left prefrontal can be seen in this view. In right lateral view, the posterior margin of the postfrontal appears to contact the anterior margin of the temporal fenestra, similar to the condition seen in UNSM 50132 (personal obs.), and *Nakonancetes bradti* (Serratos et al., 2017). This is similar to the basal condition of non-plesiosaurian sauropterygians including *Augustasaurus hagdorni* (Rieppel et al., 2002) and *Cymatosaurus* (Rieppel, 1994); and also similar to basal plesiosaurians including *Macroplata tuniceps* (Ketchum and Smith, 2010).

Postorbital. The postorbital is an elongate element that forms the posterior margin of the orbit and the anterolateral margin of the temporal fenestrae. The anterior margin of the postorbital forms the dorsoventrally oriented, posterior margin of the orbit. The posterodorsal process of the postorbital contacts the posterior margin of the postfrontal.

Parietal. The parietal is a broad, deep, and plate-like element that articulates anteriorly with the premaxillae along the midline, and posteriorly with the suspensorium at the intersquamosal suture. Posteroventrally, the parietal contacts the posterodorsal process of the suproccipital. The parietal contacts the braincase ventrally with horizontal sutures to the prootic and epipterygoid (Fig. 5). In right lateral view, the temporal bar obstructs the view of the contact of the parietal with some of the braincase elements, and the basal articulation with the braincase is obstructed. In left lateral view, the lateral surface of the parietal is strongly convex, forming a prominent sagittal crest. A prominent sagittal crest is a feature of many other elasmosaurs including UNSM 50132 (personal obs.), *Nakonanectes bradti* (Serratos et al., 2017), *Libonectes morgani* (Carpenter, 1999), SDSM 451 (personal obs.) and *Thalassomedon hanningtoni* (personal obs.). The anterior process formed by the interparietal suture contacts the premaxillae between the orbits.

Squamosal. The squamosal is a broad and deep element that forms the lateral margin of the temporal region and attaches the suspensorium to the basicranium at the squamosal-parietal contact. The anterior margin of the squamosal contacts the other elements of the temporal bar, the postorbital and the jugal. The squamosal contacts the postorbital along the dorsal margin of the temporal bar and the lateral margin of the temporal fenestra. This condition prevents the jugal from contacting the margin of the temporal fenestra. The squamosal-postorbital contact is short, travelling from the temporal fenestra a short distance ventrally to the contact with the jugal, which is highly interdigitate as it travels posteroventrally to the inferior margin of the temporal bar. The posterior portion of the squamosal is the deepest, with the posteroventral margin of the squamosal lapping onto the lateral surface of the quadrate. The squamosal-quadrate suture follows the posterior margin of the quadrate ramus. The posterodorsal margin of the squamosal leads to a prominent posterodorsal process, which travels dorsomedially, and slightly anteriorly, towards the parietals, and the other squamosal. The inter-squamosal contact forms a prominent bulb-like extension, as seen in other styxosaurine elasmosaurids (Serratos et al., 2017). The anterior margin of the posterodorsal process of the squamosal is concave, and forms a rounded lip on the dorsal margin, a condition seen in other styxosaurine elasmosaurs including UNSM 50132 (personal obs.), and SDSM 451 (personal obs.).

Quadrate – The quadrate is only partially visible in right lateral (Fig. 5) and left lateral (Fig. 6) view. In both left and right lateral views, the bilobate articular process of the quadrate is visible.

Braincase

Much of the braincase is intact and visible in left lateral view (Fig. 5). The supraoccipital contacts the parietal anterodorsally, forming a tall and thin dorsal process. Along the posterior end of the supraoccipital, a small, ventrally oriented protrusion of bone is identified as the posteromedian process of the supraoccipital, a feature identified in other plesiosaurian braincases (O'Keefe, 2006; Sato et al., 2011). The left exoccipital-opisthotic is partially visible, as it is hidden by the right prootic and the right temporal bar (Fig. 6).

Palate

The cranium of KUVP 1301 is preserved with extensive mediolateral deformation, causing the mandibles to nearly contact one another at the midline. This state of preservation prevents direct observation of most of the palate surface. In left lateral view, however, the right lateral margin of the palate can be seen between the mandibles. Posteriorly, the right pterygoid can be seen, as it travels anteriorly to the pterygoid flange. The pterygoid flange terminates in a rugose boss that is primarily formed by the ectopterygoid. This condition is also seen in

Nakonanctes bradti (Serratos et al., 2017). Anterior to the ectopterygoid boss, the palatine bone is visible (Fig. 6).

Mandible

The mandibles are in excellent condition and visible in both right lateral (Fig. 5) and left lateral (Fig. 6) views. There are 17 alveoli in each dentary. The lateral views of the left and right anterior dentaries display numerous neurovascular foramina, as is seen in other elasmosaurids including *Nakonanectes bradti* (Serratos et al., 2017) and UNSM 50132 (pers. observ.). The surfaces of the anterior dentary are rugose (Fig. 5) and have shallow, anteroposteriorly oriented grooves (Fig. 6). The dentary is 73% of the length of the mandibular ramus. The coronoid process is dorsal to the alveoli of the posterior dentary, is visible near the ventral to the temporal bar (Fig. 5). The coronoid process is comprised mainly of the dentary (Fig. 5). The angular and surangular compose the posterior portion of the mandible between the coronoid and the glenoid (Fig. 5). The surangular is deep anteriorly, and constricted posteriorly, and fused to the articular along a suture that is not visible (Fig. 6). In lateral view, the angular is a thin, splint-like element that contacts the surangular ventrally along a suture and extends ventrally below the dentary (Fig. 5; Fig. 6). In medial view, the angular is long and thin, contacting the prearticular and splenial dorsally (Fig. 6). The splenial and prearticular are heavily sutured to the articular, and the Meckelian canal appears to be closed (Fig. 6). Due to mediolateral crushing, the mandibular symphysis is partially obscured, but the anterior margin of the right angular appears to contribute to the mandibular symphysis (Fig. 6). The articular is a well-ossified element that composes the glenoid of the mandible. In lateral view, the articular has a small indentation below the glenoid (Fig. 5; Fig. 6). Posterior to the glenoid, the articular forms the dorsal margin of the retroarticular process, which is dorsally concave (Fig. 5). In medial view, the articular forms the semicircular glenoid, and the dorsal margin of the retroarticular process. The left retroarticular process appears to be complete (Fig. 6), but the right retroarticular process appears to be partially broken (Fig. 5).

Dentition

The teeth of *Styxosaurus snowii* are strongly anisodont (Fig. 6), as is the condition among other Western Interior Seaway elasmosaurids including: UNSM 50132 (pers. observ.), *Thalassomedon* (pers. observ.), and *Nakonanectes* (Serratos et al., 2017). The anterior dentary teeth and anterior premaxillary teeth are posteriorly recurved (Fig. 6). The most pronounced caniniform teeth are the fifth premaxillary tooth on the left side (Fig. 6) and the fourth maxillary tooth on the right side (Fig. 5). The most pronounced maxillary tooth occurs in the area that is laterally expanded to form the caniniform bases or roots (*sensu* Benson and Druckenmiller, 2014; character state 2.1). The posterior maxillary teeth are small, with little pronouncement of the crown beyond the alveolar row. The posterior dentary teeth are medially recurved and cover most of the maxillary alveolar row of the posterior maxilla (Fig. 6), the condition observed in both *Styxosaurus* and *Thalassomedon*.

UNSM 50132 – Unassigned Styxosaurine

General Description of the Skull

UNSM 50132 is installed in an active exhibit at the University of Nebraska State Museum, which prevents the right lateral view of the skull and the palate from being visible. The cranium is visible in left lateral view (Fig. 7) with some brittle distortion, but sutural contacts are largely intact. It is large (56.4 cm in length), with an elongate rostrum, has a beak index of 39, which is typical for elasmosaurs (Sato, 2003). The pineal foramen is apparently closed, and the dentition is strongly anisodont, with an expanded maxillary margin housing a large caniniform tooth with posterior recurvature. The posterior dentary teeth are laterally procumbent and cover the alveoli of the posterior maxillary teeth. The orbit margin possesses a reniform orbit margin, a diagnostic character of derived elasmosaurids (O’Gorman, 2020). The supratemporal fenestrae are large, with a pronounced sagittal crest. The suspensorium is curved and posteriorly inclined. The ventral margin of the temporal bar curves along the posterior edge. The retroarticular process is relatively short (5 cm).

The postfrontal is a relatively small (Fig. 7), triangular element that occurs in a tripartite area posterior to the frontal, medial to the postorbital, and anterior to the parietal. The postorbital bar is broken through its midsection, which obscures the lateral contact of the postorbital. It is not clear if the postfrontal reaches the orbit margin (Fig. 7). The posterior edge of the postfrontal bears a strut-like ossification that clearly contacts the anterior edge of the supratemporal fenestra. On both left and right prefrontals there is a small foramen that perforates the dorsal surface. The contact between the parietals and the posteromedian processes of the premaxillae separate the contact between the postfrontals along the dorsal midline. The parietals have a pronounced sagittal crest, a condition considered to be a synapomorphy of Sauropterygia (Rieppel, 2000). The anterior margin of the parietals forms a point that comes into a feathered contact with the posteromedian process of the premaxillae, which lap onto the dorsal surfaces of the frontals, postfrontals, and posterolateral edge of the anterior parietals (Fig. 7). This arrangement of the dorsal skull elements obscures the pineal foramen from view. The articulation with the braincase and epipterygoid can be seen through the left supratemporal fenestra (Fig. 7). The parietals constrict posterodorsally as they meet the squamosal arch (Fig. 7).

The postorbital forms the anterolateral edge of the supratemporal fenestra, and the posterior orbit margin. The jugal laps onto the inferior margin of the postorbital laterally, and there are several neurovascular foramina that occur along this contact (Fig. 7). The postorbital bar is cracked, collapsing the orbit. Anteriorly, an isolated piece of the postorbital contacts the frontal and postfrontal anteriorly (Fig. 7). The anterior contact of the postorbital with the frontal excludes the postfrontal from the orbital margin (Fig. 7). The squamosal contacts the jugal and postorbital anteriorly along a highly interdigitate suture (Fig. 7). The body of the squamosal is dorsoventrally deep, thin, and perforated with numerous cracks. The posterior edge of the squamosal is inflected strongly anterodorsally. This appearance corresponds with the inclination of the suspensorium anteriorly. The quadrate articulates with the squamosal medially, and the bilobate articular condyle is visible in lateral view.

Braincase

The braincase of UNSM 50132 is relatively intact despite some crushing. In lateral view, the left side of the articulated braincase displays the supraoccipital, prootic, and exoccipital-opisthotic. The suproccipital bears a tall dorsal process with a posteromedian ridge. The exoccipital-opisthotic is visible just above the temporal bar, and the posteroventrally oriented paraoccipital process can be seen impressed against the cracked temporal bar (Fig. 7). The prootic appears to be in its original position, with the fenestra ovalis positioned at its posterior margin. (O'Keefe, 2006; Sato et al., 2011; Rieppel, 1994). On the anterior border of the prootic the opening for the trigeminal nerve (V) is visible, and is the facet for the epipterygoid. Ventrally, the transversely oriented basal articulation of the braincase is visible along the margin of the prootic (Fig. 7). When a loose piece of the left suspensorium is removed exposing the braincase, the basioccipital is revealed. The basioccipital lacks a notochordal pit and possesses a distinct groove on the ventral margin of the occipital condyle, a feature noted to be plesiomorphic amongst elasmosaurs (Brown, 1993).

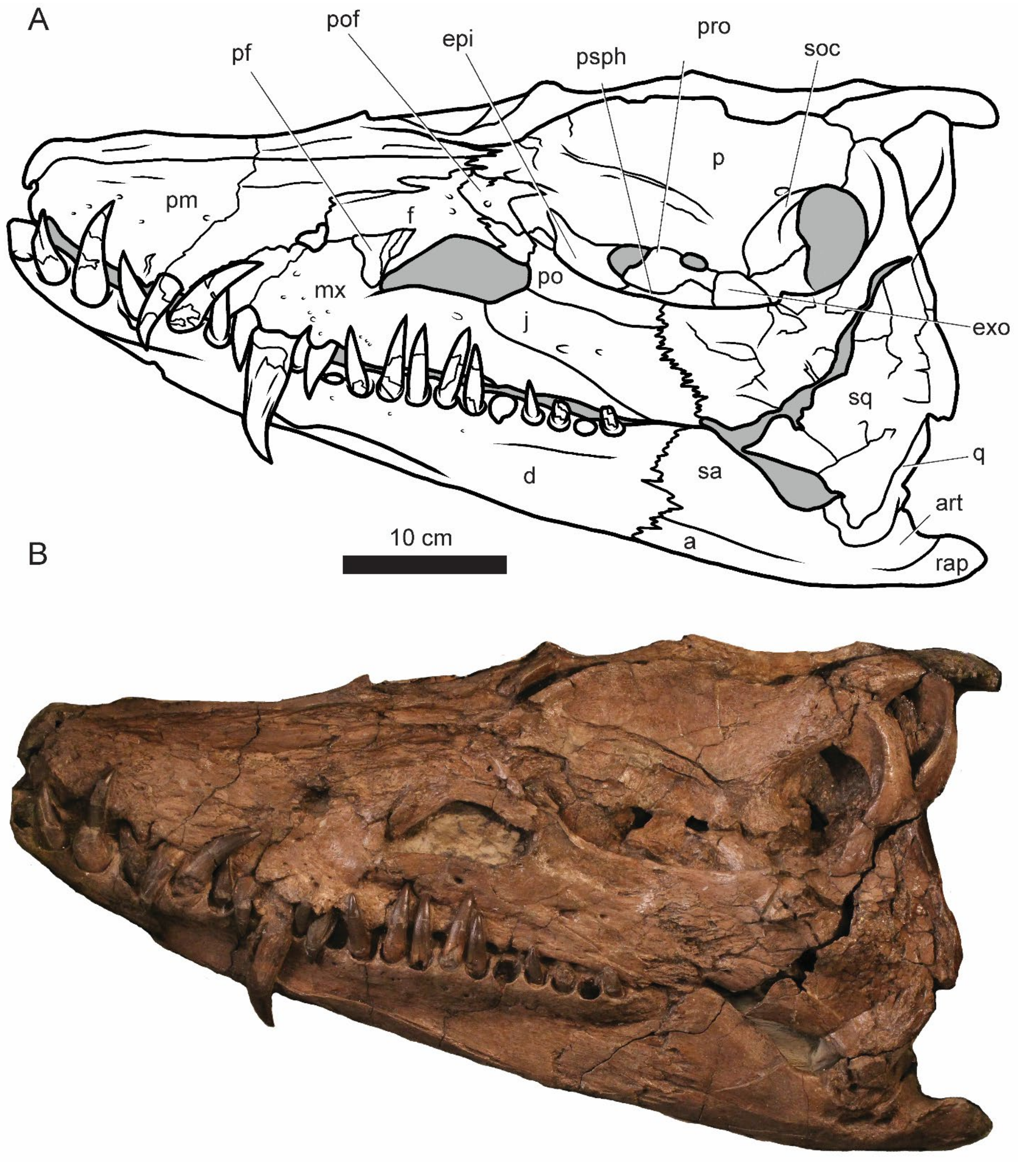

Figure 7. Cranium of UNSM 50132, unassigned styxosaurine, in left lateral view. Interpretation (A) and photo (B). Abbreviations: **a**, angular; **art**, articular; **d**, dentary; **en**, external naris; **exo**, exoccipital; **epi**, epipterygoid; **f**, frontal; **j**, jugal; **mx**, maxilla; **orb**, orbit; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pro**, prootic; **psph**, parasphenoid **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **soc**, supraoccipital; **sq**, squamosal. Illustration and photograph © 2020 Elliott Armour Smith.

Mandible

The dentary is 68% of the total length of the mandibular ramus. The alveolar tooth row is sinuous and has dramatically enlarged alveolus in the anterior dentary. The posterior dentary alveoli are oriented slightly laterally. A series of small neurovascular foramina occur just below the posterior alveolar tooth row. The dentary has a strong anteroposteriorly oriented groove below the alveolar tooth row. The coronoid eminence receives an equal contribution from the surangular and the dentary. The retroarticular process is shorter anteroposteriorly than the glenoid, and possesses a dorsally depressed surface. A sharp ridge on the lateral surface of the retroarticular process (Fig. 7) is likely the well-ossified sutural contact between the angular inferiorly and the articular superiorly.

Dentition

The skull of UNSM 50132 possesses large anterior teeth that are posteriorly recurved (Fig. 7). The teeth of UNSM 50132 bear apicobasally oriented enamel ridges as seen in *Styxosaurus snowii* (Sachs et al., 2018). The maxilla bears an extremely long caniniform tooth (83 mm from alveolus to tip) that is posteriorly recurved. The posterior dentary teeth are laterally procumbent and cover the posterior maxillary toothrow laterally (Fig. 7).

DMNH 1588 – *Thalassomedon hanningtoni* (Holotype)

General Description of the Skull

The skull is large, 46.5 cm in total length, and 27.4 cm in total height. The preorbital length of the premaxillae is relatively short, with a beak index of 33, which is shorter than is typical for elasmosaurs, about 35 (Sato, 2003). The midline of the premaxillae forms a thin dorsomedian crest on the rostrum but becomes a pronounced dorsomedian hump between the external nares (Fig. 8). The sagittal crest is pronounced and forms a prominent midline keel that rises above the skull roof (Fig. 8). The temporal bar in right lateral view is largely crushed, and there is a large crack running between the temporal region of the squamosal and the posterior edge of the suspensorium. The braincase is partially exposed in right lateral view with the supraoccipital rotated anteriorly forward, exposing the foramen magnum dorsally (Fig. 8). The mandible is only slightly mediolaterally bowed, but expresses laterally procumbent dentary teeth.

Dorsal Elements of the Skull

The premaxillae have a rugose texture with regular pitting (Fig. 8). It is not clear if any neurovascular foramina are present on the surface due to poor preservation. There is a slightly pronounced dorsomedian ridge that occurs on the contact between the premaxillae on the rostrum. The dorsomedian process of the premaxillae travels posteriorly to contact the parietals, closing the pineal foramen. It is not clear how many total premaxillary alveoli there are, but four total teeth are visible in left lateral view (Fig. 8). The maxilla is badly damaged in left lateral view, but its margins are largely intact, except for the orbit margin (Fig. 8). A mediolaterally oriented rugosity occurs on the ventral orbit margin, which is also seen in *Styxosaurus* and UNSM 50132. The prefrontal is a small, rectangular shaped element that forms the posterior edge of the external naris, like the shape of *Styxosaurus snowii* (Fig. 8). The prefrontal does not have a dorsally oriented process that laps onto the lateral edge of the anterior orbit edge as seen in UNSM 50132. The frontal-premaxilla suture is largely obscured by cracking, but frontal does not appear to fan out anteriorly as it does in *Styxosaurus snowii* (Fig. 8). The postfrontal is largely obliterated in right lateral view, and crushed in by the temporal bar in left lateral view (Fig. 9). The temporal bar is largely crushed but the relative positions of the jugal, postorbital, and squamosal can be discerned (Fig. 9). The squamosal and jugal have a highly interdigitate contact that is shared amongst Western Interior Seaway elasmosaurids including *Styxosaurus* *snowii*, *Nakonanectes bradti*, and UNSM 50132. The postorbital bar is entirely crushed, and exists as only a few unidentifiable fragments disassociated on the superior margin of the orbit. The suspensorium is inclined anteriorly, as seen in other elasmosaurids including *Nakonanects bradti* (Serratos et al., 2017), *Styxosaurus snowii*, *Libonectes, morgani* (Carpenter, 1997), and UNSM 50132. The bilobate articular surfaces of the quadrates are visible in both left lateral and right lateral views (Fig. 8, Fig. 9).

Braincase

The braincase is mostly visible in right lateral view, and largely in articulation (Fig. 8). The posterolaterally trending paraoccipital process is visible and is rather columnar and appears to have no constriction in width. The supraoccipital is small, rounded, and lacks the thin dorsal process visible in UNSM 50132 and *Styxosaurus snowii*. The right exoccipital and right supraoccipital are displaced anteriorly, exposing the foramen magnum in dorsal view (Fig. 8). Anteriorly, the prootic is hardly discernable among an extensively cracked articulation with the palate and parietals.

Palate

In left lateral or ventral view, the anatomically right-hand portion of the palate is exposed. The ventral surface of the pterygoid is dished, a condition reported by Sato (2002) (Fig. 9). The ectopterygoid tapers to a point laterally but does not possess the rugose boss seen in *Styxosaurus snowii* or *Nakonanectes bradti* (Serratos et al., 2017). Anterior to the ectopterygoid, the right palatine is visible before it disappears under the left mandibular ramus anteriorly (Fig. 8). A groove occurs on the lateral edge of the mandible along the surangular-angular suture (Fig. 8).

Figure 8. Cranium of DMNH 1588, holotype specimen of *Thalassomedon hanningtoni*, in right lateral view. Interpretation (A) and photo (B). Abbreviations: **a**, angular; **art**, articular; **d**, dentary; **en**, external naris; **exo**, exoccipital; **eppt**, epipterygoid; **f**, frontal; **fm**, foramen magum; **j**, jugal; **mx**, maxilla; **orb**, orbit; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pop**, paraoccipital process; **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **soc**, supraoccipital; **sq**, squamosal. Illustration and photograph © 2020 Elliott Armour Smith.

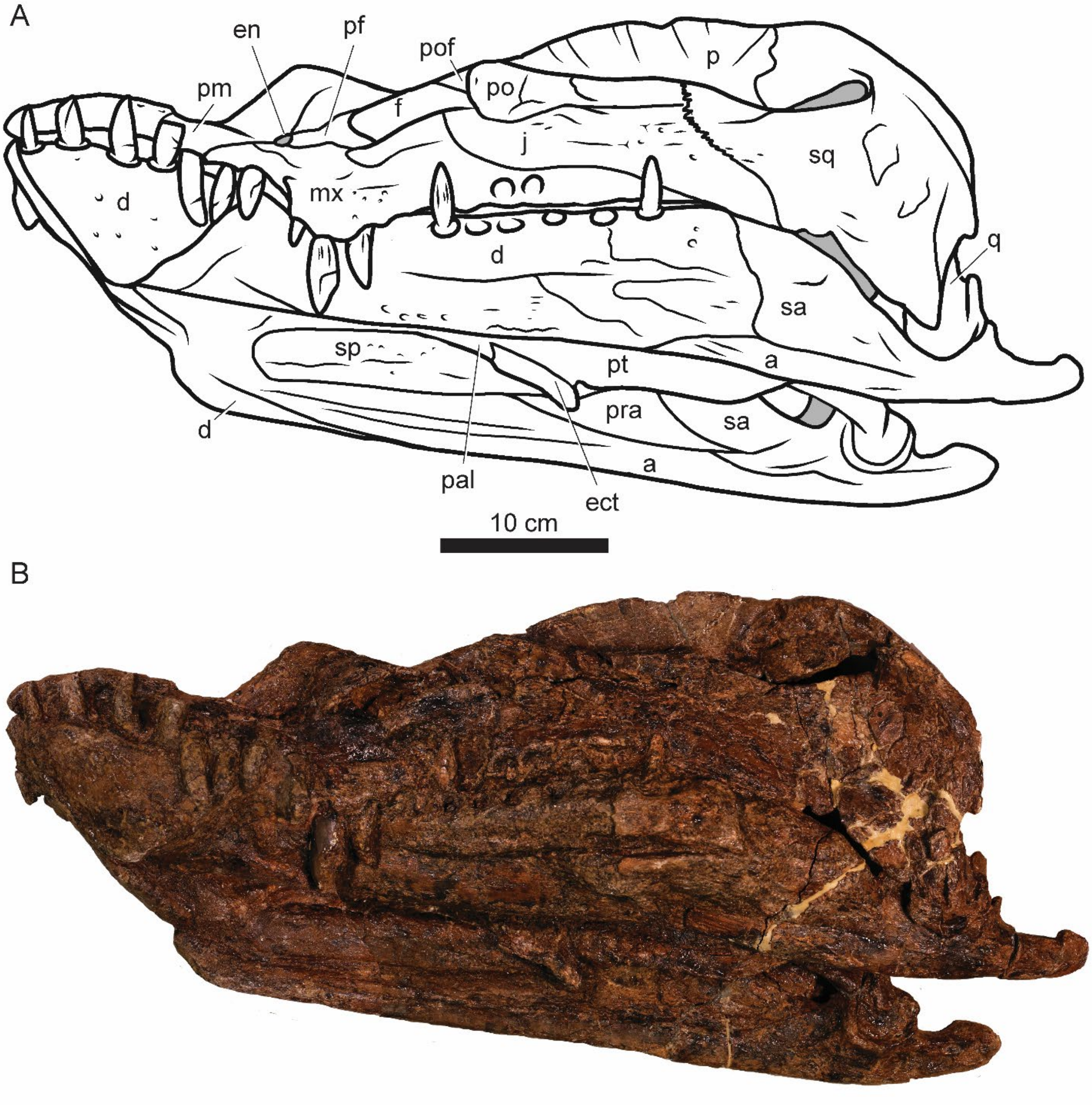

Figure 9. Cranium of DMNH 1588, holotype specimen of *Thalassomedon hanningtoni*, in left lateral view. Interpretation (A) and photo (B). Abbreviations: **a**, angular; **art**, articular; **d**, dentary; **ect**. ectopterygoid, **en**, external naris; **f**, frontal; **j**, jugal; **mx**, maxilla; **orb**, orbit; **p**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **sq**, squamosal. Illustration and photograph © 2020 Elliott Armour Smith.

Mandible

The mandibular rami are long and straight with little sinuosity or mediolateral bowing (Fig. 9). The mandible articulates anteromedially at the mandibular symphysis, which bears a modest midline keel, a feature identified in *Styxosaurus snowii* (Sachs et al., 2018), but absent in *Nakonanectes bradti*. Only the dentaries and articulars appear to converge along the mandibular symphysis; the right splenial does not appear to extend far enough anteriorly (Fig. 9). In left lateral view, the inferior margin of the splenial demarcates the Meckelian groove, a feature visible among many reptilian groups (Romer, 1956). In lateral view, the alveoli of the dentary appear to be oriented laterally (Fig. 8). The coronoid eminence is mainly composed of the surangular, however, the dentary makes a minor contribution (Fig. 8, Fig. 9). The posterior end of the mandible is well-ossified, and the surangular-angular suture is difficult to discern posteriorly. The articular is well fused to the surangular anteriorly, and to the angular inferiorly (Fig. 9). T medial view of the mandiblular ramus reveals a well-ossified prearticular, forming a relatively shallow Meckelian fossa (Fig. 9).

Dentition

On the left lateral side of the skull, four premaxillary tooth crowns are preserved, and on the left lateral side, the premaxillary tooth crowns are not visible (Fig. 9). These crowns are not elongate, and tooth crowns are relatively blunt. Anterior dentary teeth are broken, but they do not appear to have posterior recurvature indicated by the bases of the tooth crowns, unlike in UNSM 50132 (Fig. 7). The teeth are only slightly anisodont, unlike the anisodont dentition seen in *Styxosaurus snowii*, UNSM 50132, and *Nakonancetes*. In right lateral view, posterior dentary teeth are laterally procumbent, but are only slightly medially recurved, not to the degree seen in

Styxosaurus snowii or UNSM 50132. The third tooth in the maxilla appears to be elongate, or caniniform (Fig. 8, Fig. 9).

Comparative Osteology

Autapomorphic Features of UNSM 50132

UNSM 50132 exhibits a suite of unique osteological features, summarized in Table 1. A small infraorbital foramen (Fig. 9) is not visible in *Styxosaurus snowii* or *Nakonanectes bradti*. A v-shaped, anteroposteriorly oriented groove is visible on the jugal (Fig. 7). The postfrontal has a well ossified posterolateral process that forms the anterior edge of the supratemporal fenestra, and a small foramen pierces its dorsal surface (Fig. 7). The second or third maxillary tooth (7th or 8th overall) is extremely long from alveolus to tip (83 mm) and is posteriorly recurved. Also, the premaxillary dentition is posteriorly recurved.

Affinities of UNSM 50132 to *Styxosaurus snowii* (KUVP 1301)

Both *Styxosaurus snowii* and UNSM 50132 are longirostrine, with beak indexes of 42 and 39, respectively (Fig. 5, Fig. 7). Both specimens have a long posteromedian process of the premaxilla (Fig. 5, Fig. 7). These specimens also share the deep embayment on the dorsal process of the squamosal as it contributes to the squamosal arch. These specimens share a supraoccipital with a thin dorsal process and posteromedian ridge. Both skulls possess a pronounced fossa on the lateral surface of the articular (Fig. 5, Fig. 7), and a short retroarticular process. Both taxa have extremely anisodont dentition, with anterior teeth posteriorly recurved (Fig. 5, Fig. 7).

Affinities of UNSM 50132 to *Thalassomedon hanningtoni* (DMNH 1588)

UNSM 50132 shares a few traits with *Thalassomedon*; both specimens lack a squamosal “bulb,” and both lack an extensive ossification of the midline contact between the dorsal processes of the squamosals. This character is reported to be a synapomorphy of Styxosaurinae by Serratos et al. (2017). Both specimens have a circular naris, and the retroarticular process of UNSM 50132 is longer than *Styxosaurus snowii*, although not as long as *Thalassomedon hanningtoni*.

Table 1. Osteological features of Western Interior Seaway elasmosaur skulls

Osteological Feature	**Taxon**		
	UNSM 50132	***Styxosaurus snowii***	***Thalassomedon hanningtoni***
Beak index	39	42	33
External naris	Circular	Heart-shaped	Circular
Postfrontal ossification	Present	Absent	?
V-shaped groove on jugal	Present	Present	Absent
Embayment on squamosal arch	Present	Present	Absent
Squamosal bulb	Absent	Present	Present
Fossa of lateral articular	Present	Present	Absent
Retroarticular process	Shorter anteroposteriorly than glenoid	Shorter anteroposteriorly than glenoid	Longer anteroposteriorly than glenoid
Caniniform tooth crown height	83 mm	53 mm	48 mm

CHAPTER 3

PHYLOGENETIC ANALYSIS OF THE LATE CRETACEOUS ELASMOSAURIDS OF THE WESTERN INTERIOR SEAWAY

Introduction

As discussed in Chapter 1, the understanding of plesiosaur ingroup relationships has improved significantly with the proliferation of cladistic analyses (O'Keefe, 2001; Sato, 2002; Benson and Druckenmiller, 2014). However, taxon selection and discrepancies in character scoring have led to variability in the topology for Elasmosauridae (O'Gorman et al., 2015; Otero et al., 2016; Otero et al., 2014; O'Gorman et al., 2017; Sachs et al., 2018). Statistical and character support for the subfamily rank clades Aristonectinae and Styxosaurinae has been reported by Otero (2016) and Serratos et al. (2017). The phylogenetic analysis by O'Gorman (2020) proposed a new taxonomy for Elasmosauridae, which will be addressed in this chapter in the course of our consideration of a new phylogenetic analysis of Elasmosauridae. In light of the increased understanding of cranial anatomy of elasmosaurids from the Western Interior Seaway in presented in Chapter 2, a phylogenetic analysis of Elasmosauridae is necessary to interpret this morphological data.

The Benson and Druckenmiller (2014) character matrix has been utilized by several groups of authors for investigating elasmosaurid ingroup relationships (Otero, 2016; Serratos et al., 2017; O'Gorman, 2020). The Benson and Druckenmiller (2014) matrix includes 80 operational taxonomic units (OTUs), scored for on 270 morphological characters. Otero (2016) added 13 additional elasmosaurid OTUs to the Benson and Druckenmiller matrix for a total of 93 taxa. Serratos et al. (2017) added 12 additional OTUs for a total of 92 taxa.

Methods

In this cladistic analysis, the maximum parsimony method of Hennig (1966) is utilized. Three specimens described for their cranial anatomy in Chapter 2, and an additional specimen of *Styxosaurus* sp., SDSM 451 (Carpenter, 1999; Welles and Bump, 1949), were added as four additional OTUs to the Serratos et al. (2017) character matrix. These specimens were scored independently for the 270 characters: *Styxosaurus snowii* (KUVP 1301), *Styxosaurus* sp. (SDSM 451), the Nebraska elasmosaur (UNSM 50132), and *Thalassomedon hanningtoni* (DMNH 1588). A group of character state scorings were changed from the Serratos et al. (2017) matrix where there was appropriate justification. Character scoring changes to the Serratos et al (2017) matrix are summarized in Appendix B. The original character matrix was retrieved from the supplemental information of Serratos et al. (2017). Overall, there were 94 taxa scored as operational taxonomic units (OTUs) for 270 morphological characters. Modification of the character matrix and addition of OTUs was performed in Mesquite, and the updated matrix was saved as a NEXUS file. Initial tree searches were performed in PAUP*4.0a167 (Swofford, 2002), by a heuristic search, set to retrieve a population of 2000 most parsimonious trees (MPTs). Strict consensus and 50 percent majority-rule consensus trees were compared to look for unresolved branches and wildcard taxa. The initial search justified the pruning of three OTUs reported as wildcard taxa by Serratos et al. (2017): *Futabasaurus suzukii*, *Eromangasaurus australis*, and *Elasmosaurus platyurus*.

One OTU, *Mauisaurus haasti*, was deliberately removed from the analysis. A review of the original lectotype by Hector (1874) revealed that *Mauisaurus* is a hypodigm and is composed of more than one taxon (Hiller et al., 2017). Some of the referred material was determined to be an indeterminate aristonectine (Hiller et al., 2017). The authors of this review determined

Mauisaurus a *nomen dubium*. This evidence justifies the exclusion of this OTU from the analysis.

In PAUP, a heuristic search of 100 bootstrap replicates was performed by stepwise addition utilizing a tree-bisection-reconnection (TBR) algorithm. Tree was built by random addition sequences, with ten replicates per addition sequence. This analysis resulted in an unresolved Plesiosauria and Elasmosauridae. Percentage of bootstrap replicates that support a given node are reported in a 50 percent majority rule consensus tree.

Results

Initial Heuristic Search

An initial heuristic search of a population of 2000 most parsimonious trees (MPTs) generated a 50 percent majority-rule consensus tree that supported Western Interior Seaway (WIS) elasmosaurids as a monophyly (Fig. 10). The outgroup taxon to this WIS clade in this tree was *Hydrotherosaurus alexandrae*. This tree also recovered a monophyletic Aristonectinae, with a polyphyletic Wedellonectia, sensu O'Gorman (2020). Interestingly, two cryptoclidid taxa, *Abyssosaurus* and *'Plesiosaurus' mansellii* were recovered in proximity to Elasmosauridae. Abyssosaurus was recovered as the outgroup taxon to Elasmosauridae, and *'Plesiosaurus' manselli* was recovered within a clade containing the Aristonectinae (Fig. 10).

The analysis pruned of three wildcard taxa (*Eromangasaurus australis*, *Futabasaurus suzukii*, *Elasmosaurus platyurus*) recovered a more robust topology that lacked the cryptocleidid taxa (Fig. 11). In this analysis, Tuarangisaurus keyesi was recovered as the outgroup taxon to a clade composed of the sister relationship between a clade containing the Aristonectinae, and a clade containing the WIS elasmosaurids (Fig. 11).

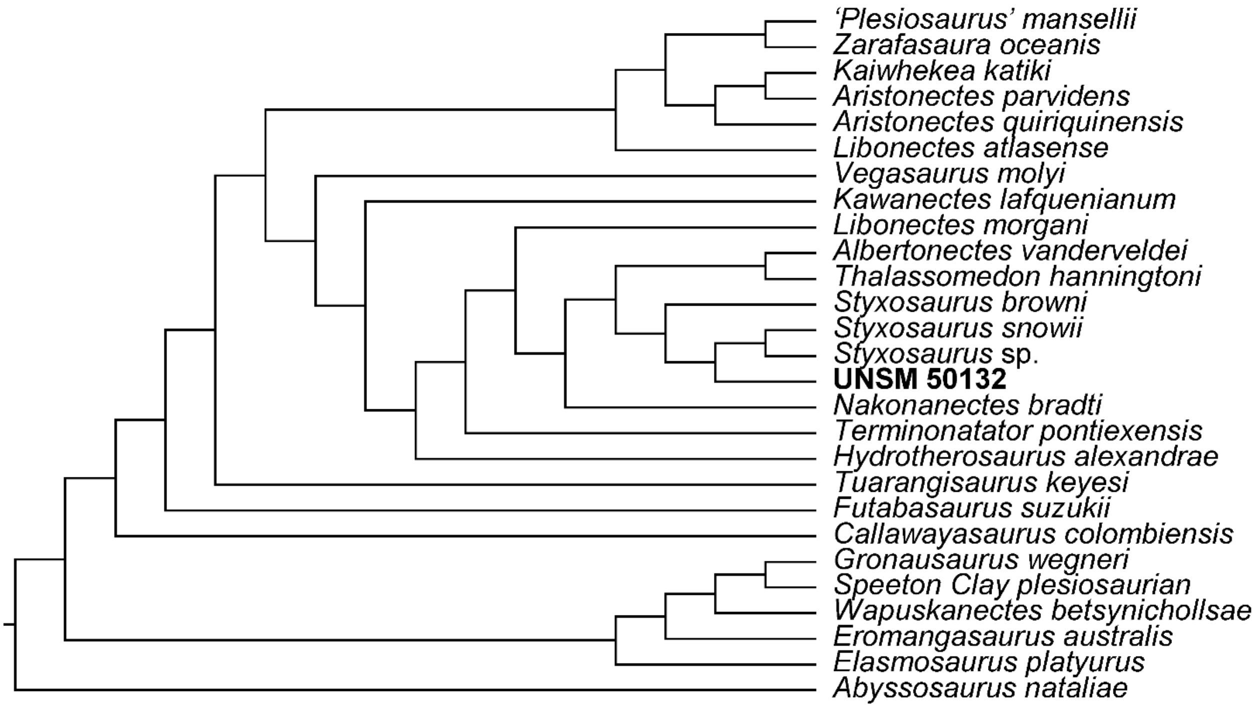

Figure 10. 50% majority rule consensus tree. Computed from a population of 20000 most parsimonious trees (MPTs), based on 94 operational taxonomic units OTUs scored for 270 morphological characters.

Bootstrap analysis

The bootstrap analysis recovered an unresolved Plesiosauria, and consequently, a partially unresolved Elasmosauridae. However, within the unresolved Elasmosauridae, four OTUs formed a monophyletic grouping: the Nebraska elasmosaur (UNSM 50132), *Styxosaurus snowii* (KUVP 1301), *Styxosaurus* sp. (SDSM 451), and *Styxosaurus browni*/*Styxosaurus* sp. (AMNH 5835 & 1495). This group was supported by 67 percent of 1000 bootstrap replicates (Fig. 12). The second node had a bootstrap percentage of 63 and supported the monophyly of three Aristonectine OTUs: *Kaiwhekea katiki*, *Aristonectes quiriquinensis*, and *Aristonectes parvidens* (Fig. 13). This clade was supported by 65 percent of bootstrap replicates.

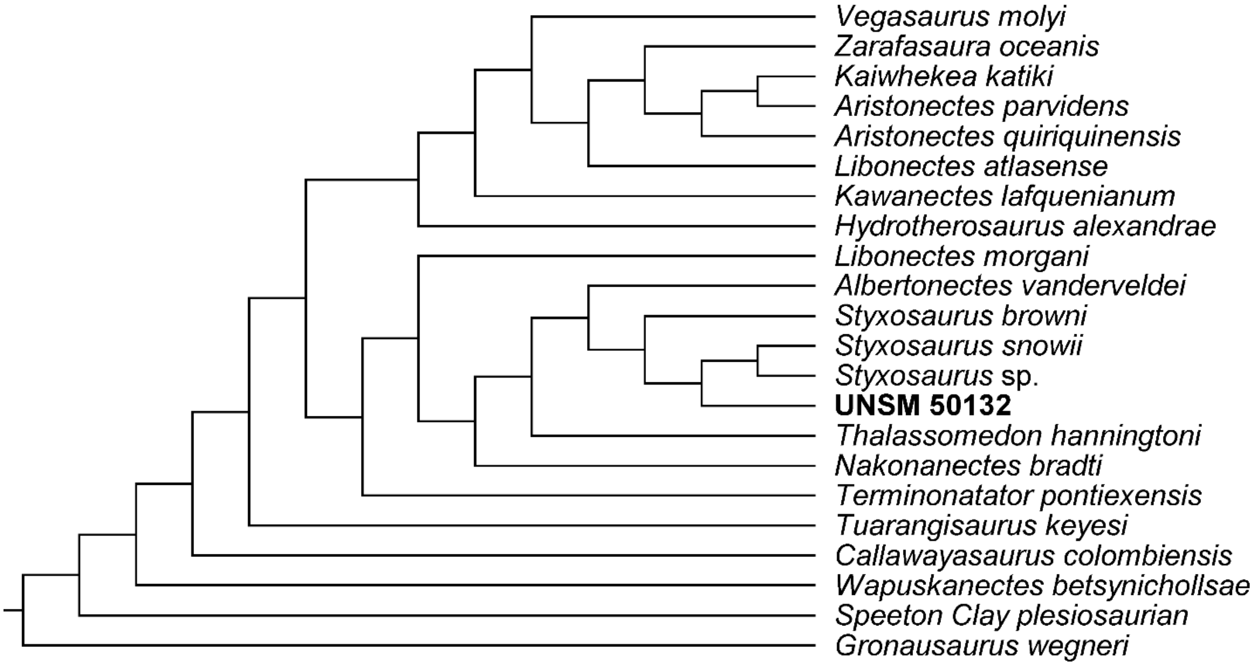

Figure 11. 50% majority rule consensus tree with 'wildcard' taxa pruned. Computed from a population of 20000 MPTs (91 OTUs; 270 characters). Three OTUs were omitted: *Elasmosaurus platyurus*, *Futabasaurus suzukii*, and *Eromangasaurus australis.*

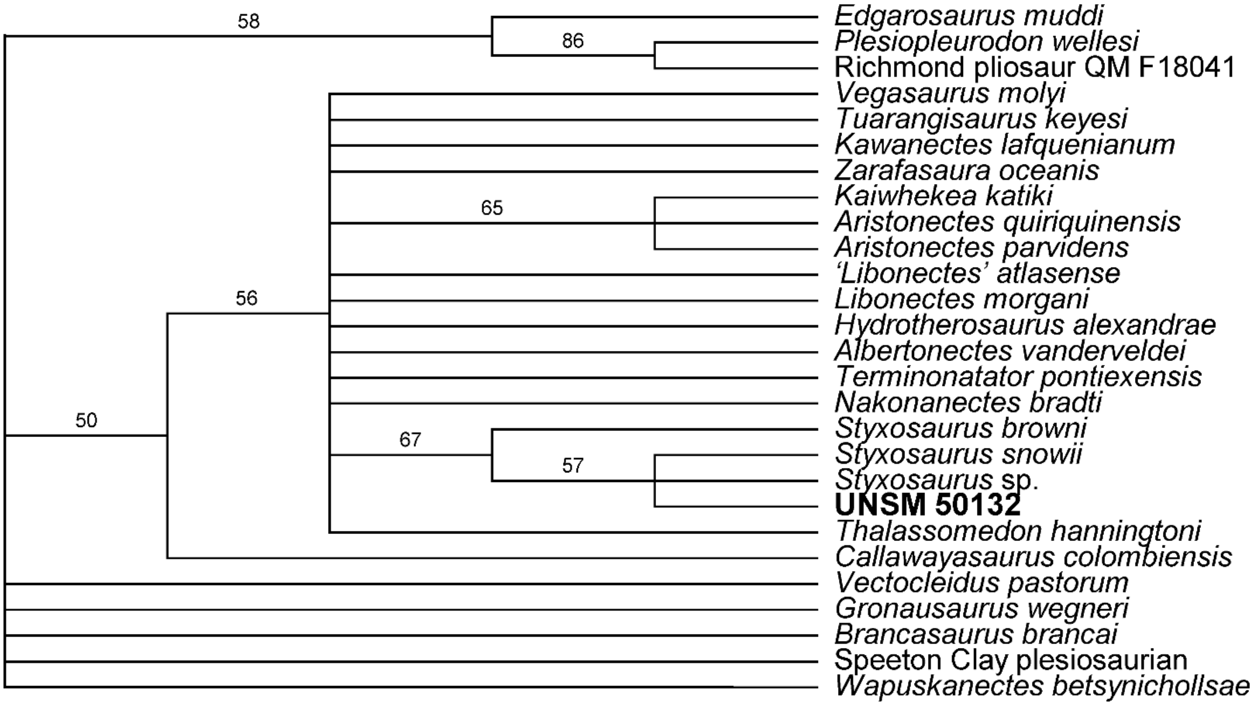

Figure 12. Bootstrap analysis of 100 replicates for Elasmosauridae. Values indicate percentage of bootstrap replicates that support node. Note that elasmosaurids such as *Callawayasaurus* occur in a polytomy with an unresolved Plesiosauria.

Revised Diagnosis of *Styxosaurus*

The bootstrapped phylogenetic analysis 91 taxa (Fig. 12) supported five unambiguous synapomorphies for the genus *Styxosaurus*: (1) dorsomedian ridge of premaxilla located posteriorly (19.1); (2) dorsal portion of squamosal reflected anteriorly in lateral view (61.1); (3) posteromedian ridge on the supraoccipital (77.1); (4) a sharp ridge or keel located adjacent to the mandibular symphysis (114.1); (5) a retroarticular process that is shorter in anteroposterior length than the glenoid (116.0).

Additional ambiguous synapomorphies that support the monophyly of *Styxosaurus* include: lateral expansion of the maxilla that supports caniniform teeth (Benson and Druckenmiller, 2014; character 2), reniform orbit margin (Benson and Druckenmiller; character 5), anterior embayment of the squamosal arch, an elongate posteromedian process of the premaxilla, a rugose boss on the ectopterygoid (Benson and Druckenmiller; character 109, state 2), parietals that form a sagittal crest that rises above the cranial roof (Benson and Druckenmiller, 2014; character 50, state 3), and elongate anterior to middle cervical centra (Benson and Druckenmiller, 2014; character 153, state 2).

Discussion

Taxonomic Status of UNSM 50132 and the Monophyly of *Styxosaurus*

The initial heuristic search utilizing the Serratos et al. (2017) character matrix for a sample of 1000 topologies displayed at 50% majority rule consensus supported the monophyly of Western Interior Seaway elasmosaurids (Fig. 12). However, this initial search lacked statistical robusticity, and bootstrap analyses utilizing the heuristic search recovered a topology that was more robust, despite its lack of resolution. Despite the ambiguity of relationships in Elasmosauridae, most trees (67%) supported the monophyly of *Styxosaurus* (Fig. 12). The monophyly of UNSM 50132 and three *Styxosaurus* OTUs across a range of dataset sizes (number of OTUs) suggest that this is a single taxonomic entity.

Styxosaurine Relationships

By comparing the large and small datasets with a bootstrap analysis, we can make inferences about the robustness of styxosaurine relationships. It is evident that among the large dataset, *Styxosaurus* is supported in monophyly amongst an unresolved Elasmosauridae. In the pruned set of unstable Pacific taxa, *Styxosaurus* is still recovered as monophyletic, with weaker support for all Western Interior Seaway elasmosaurids as monophyletic.

Effectively, this analysis supports the hypothesis that the most recent common ancestor of Styxosaurinae likely evolved in the later part of the Early Cretaceous (Fig. 13). The recovery of Pacific elasmosaurid taxa and Aristonectinae as paraphyletic with respect to Styxosaurinae is an interesting result but is likely an artifact of a lack of Pacific elasmosaurid taxa in the early part of the Late Cretaceous. These lineages appear to have a long duration from diversification to appearance in the fossil record under this topology (Fig. 13).

Response to O'Gorman (2020) on the Establishment of Elasmosaurinae

In a paper revising the Pacific taxon *Aphrosaurus furlongi*, O'Gorman (2020) reported a phylogenetic analysis that created a single clade of southern hemisphere elasmosaurids. This clade contained the Aristonectinae, and was termed Weddellonectia. O'Gorman (2020) revised the Western Interior Seaway elasmosaurids to a single subfamily level clade, which he named Elasmosaurinae.

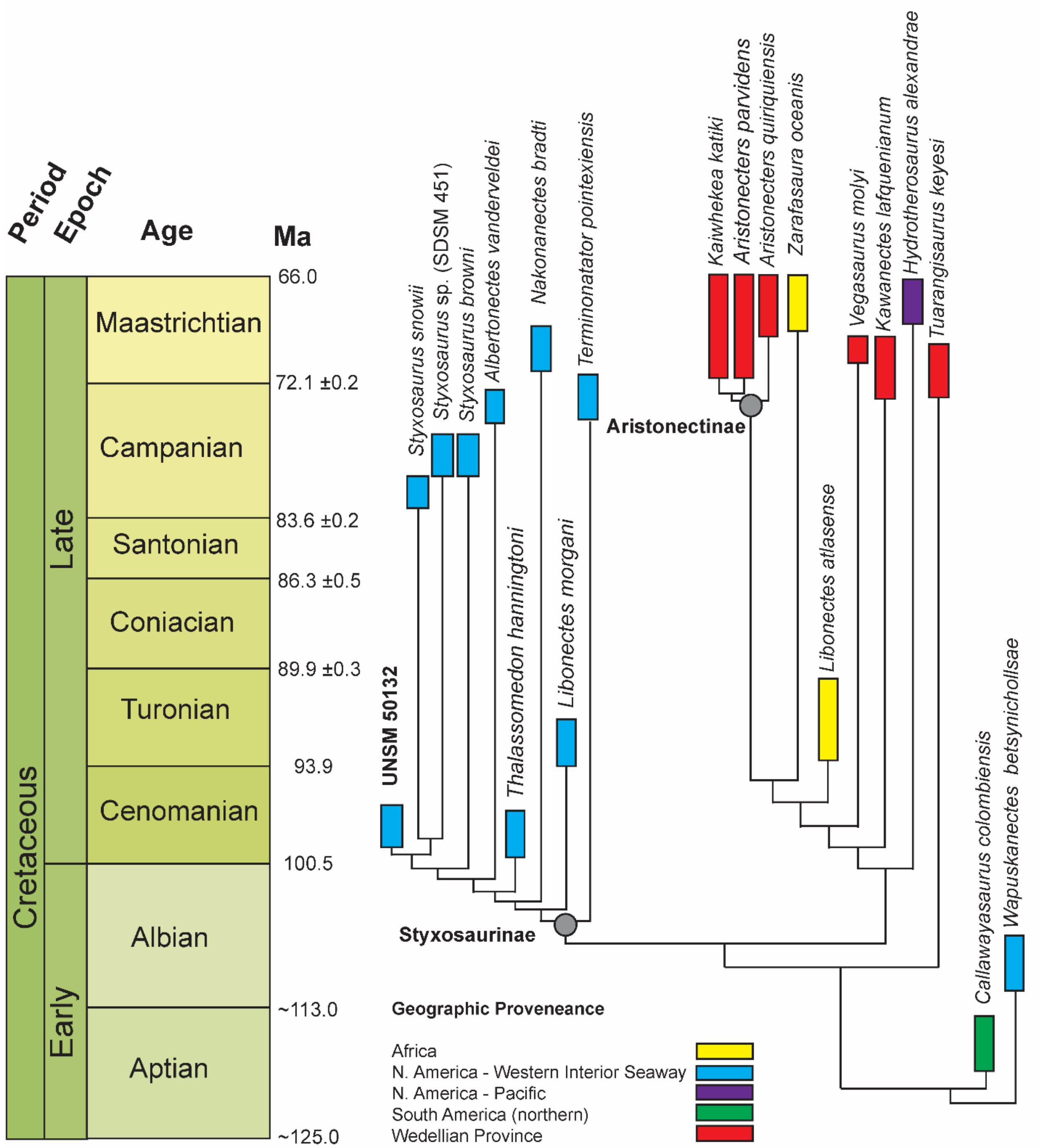

Figure 15. Time-calibrated phylogeny of Elasmosauridae. Based on maximum parsimony analysis of 92 OTUs scored for 270 morphological characters based on the Serratos et al. (2017) matrix. Changes to character scoring summarized in Appendix B. Figure © 2020 Elliott Armour Smith.

Serratos et al. (2017) posited that if future studies were to recover *Elasmosaurus platyurus* within the subfamily Styxosaurinae, then Styxosaurinae should be abandoned in favor of the subfamily Elasmosaurinae. These authors cite taxonomic rules that the subfamily name Elasmosaurinae has the same authority and date as the family name Elasmosauridae (Cope, 1869) under Article 36.1 of the ICZN (1999). O'Gorman (2020) defined Elasmosaurinae phylogenetically as "the most inclusive clade that contains *Elasmosaurus platyurus* but not *Aristonectes quiriquinensis*." The author did not designate a type species of Elasmosaurinae. Although not explicitly mentioned, it is likely the consequence of this designation is that *Elasmosaurus platyurus* (Cope 1869) would become the type species for this subfamily.

This is taxonomically problematic because the holotype specimen (ANSP 10081) comprises a largely incomplete skull, and a vertebral series with many damaged or missing neural spines, neural arches, and zygapophyses. The pectoral and pelvic girdles were originally preserved, but have since been lost (Sachs, 2005). The incompleteness of ANSP 10081 is the result of the colorful history of the specimen, first published by Edward Drinker Cope (1869). Best practices in paleontological field techniques were in their infancy, and the specimen was not collected with plaster jacketing (Davidson and Everhart, 2017). This resulted in much of the skeleton becoming badly damaged.

Even though names within a family level taxon have the same authorship and date at every rank (Article 36.1; ICZN, 1999), it is important that a clade defined on morphology alone has a type specimen that is relatively complete and phylogenetically informative. Serratos et al. (2017) justifiably excluded *Elasmosaurus platyurus* from the definition of Styxosaurinae to resolve this issue. Otero (2016) designates *Styxosaurus browni* (AMNH 5835) as the type species of Styxosaurinae, which is justifiable given the presence of a complete skull, mostly complete cervical series, and appendicular material. The cladistic analysis presented in this chapter adds further support to the genus *Styxosaurus* as a phylogenetically informative reference taxon, and to the lack of diagnostic-ness of elasmosaurs.

Reconstructing Elasmosaurid Phylogeny: Temporal and Geographic Biases

The Benson and Druckenmiller (2014) matrix has been foundational in resolving plesiosaur relationships, and has yielded replicated support for Styxosaurinae (Otero, 2016; Serratos et al., 2017) and Aristonectinae (O'Gorman, 2020) as distinct, subfamily level clades. The monophyly of these two clades is supported by cladistic, morphological, and paleogeographic evidence (Otero, 2016; Serratos et al., 2017; O'Gorman, 2020). While our implementation of the matrix itself is extremely detailed and well-constructed, the results obtained from maximum parsimony (Swofford, 2002) do not display a high-level of resolution across Plesiosauria, or more specifically, Elasmosauridae in general (Fig. 12). These results support the notion that homoplasy is a prevalent factor in the evolution of Elasmosauridae, and that Bayesian methods may be more appropriate in evaluating elasmosaurid relationships, and plesiosaur relationships in general.

Many elasmosaurid (*Zarafasaurus oceanus* (Vincent et al., 2011), '*Libonectes' atlasense* (Buchy, 2005), *Vegasaurus molyi* (O'Gorman et al., 2015), and *Hydrotherosaurus alexandrae* (Welles, 1943) taxa have relatively weak affinity to Styxosaurinae or Aristonectinae as clades in the initial tree searches, and within the bootstrap analysis. A plausible explanation for the weakness in affinity of these taxa to either clade is that the taxon sampling is too poor in the temporal interval in which both clades evolved in order to assess ancestral character states. Many of the most important elasmosaurid fossils outside of the Western Interior Seaway have been found in the Weddellean Province of Antarctica (O'Keefe et al., 2017), South America (Otero et al., 2014), and New Zealand (Otero, 2016). However, there have been relatively few reported occurrences elsewhere. Africa has only two reported elasmosaurs, '*Libonectes*' *atlasense* (Buchy, 2005), and *Cardiocorax mukulu* (Araujo et al., 2015). In Eurasia, the record of Elasmosauridae is extremely sparse, with some published material form the Maastricht type area in southern Belgium (Mulder et al., 2000), and some from Late Cretaceous strata of the former USSR (Storrs et al., 2000), but no named taxa. It is plausible that additional type specimens in the Early Cretaceous would add additional character resolution to elasmosaurid phylogeny.

These results indicate that ancestral relationships of Cretaceous clades of Plesiosauroidea need further evaluation. Benson and Druckenmiller (2014) report that three clades of plesiosaurians cross the Jurassic-Cretaceous boundary: Xenosparia, Cryptoclididae, and Brachaucheninae. Benson and Druckenmiller (2014) indicate that cryptocidids are represented in the Cretaceous fossil record by a single taxon, *Abyssosaurus nataliae* (Berezin, 2011). An alternative hypothesis to the Xenosparian hypothesis is one put forth by O'Keefe and Street (2009), that aristonectines are derived Cretaceous cryptoclidids. The recognition of 'Cimoliosauridae'-grade cervical vertebrae from Early Cretaceous deposits in Russia (Storrs et al., 2000; Berezin, 2011) call for further investigation.

The results of this phylogenetic analysis support a hypothesis that Western Interior Seaway elasmosaurids are a monophyletic group (Fig. 13) and may be much more temporally and geographically extensive than previously reported (O'Gorman, 2020; Otero, 2016; Serratos et al., 2017). Our paraphyletic recovery of the southern hemisphere taxa (Wedellonectia *sensu* O'Gorman, 2020) may be an artifact of poor taxon sampling in Cenomanian through Santonian strata worldwide rather than a lack of support for a monophyletic southern hemisphere clade. Perhaps the most parsimonious explanation is a southern hemisphere clade and a northern hemisphere clade, but there is no *a priori* reason to believe that geographic occurrence should reflect evolutionary relatedness. Major clades of marine amniotes are known to have large geographic ranges and a high degree of homoplasy, and limited barriers to dispersal (Kelley and Pyenson, 2015). Therefore, multiple lines of evidence, not just cladistics, should be implemented to thoroughly assess evolutionary history of clades.

Conclusions

The osteological data presented in Chapter 2 and the phylogenetic analysis in this chapter provide evidence that the Styxosaurinae are an older, more inclusive, and more well-established clade in the Western Interior Seaway than previously reported by Otero (2016) and Serratos et al. (2017). The monophyly of UNSM 50132 with *Styxosaurus* supports Cenomanian as the latest appearance of the Styxosaurinae in the Western Interior Seaway. The monophyly of all Western Interior Seaway elasmosaurids is less well supported than the monophyly of *Styxosaurus*, but is still a plausible hypothesis in the overall evolutionary history of Elasmosauridae. Additional elasmosaurid taxa in Cenomanian-Santonian aged strata worldwide will support one of two hypotheses. The first is the O’Gorman hypothesis, that Pacific elasmosaurid taxa including Aristonectinae (Wedellonectia) form a monophyletic group with an evolutionary history lasting most of the Late Cretaceous. The second is that the Wedellonectia are a paraphyletic or polyphyletic group that reflect multiple lineages at the base of the elasmosaurid tree. The origin of Styxosaurinae as a clade being pushed back in time does not refute the potential monophyly of Wedellonectia, but it does suggest strongly that a deeper look back in time is needed to resolve elasmosaurid phylogeny.

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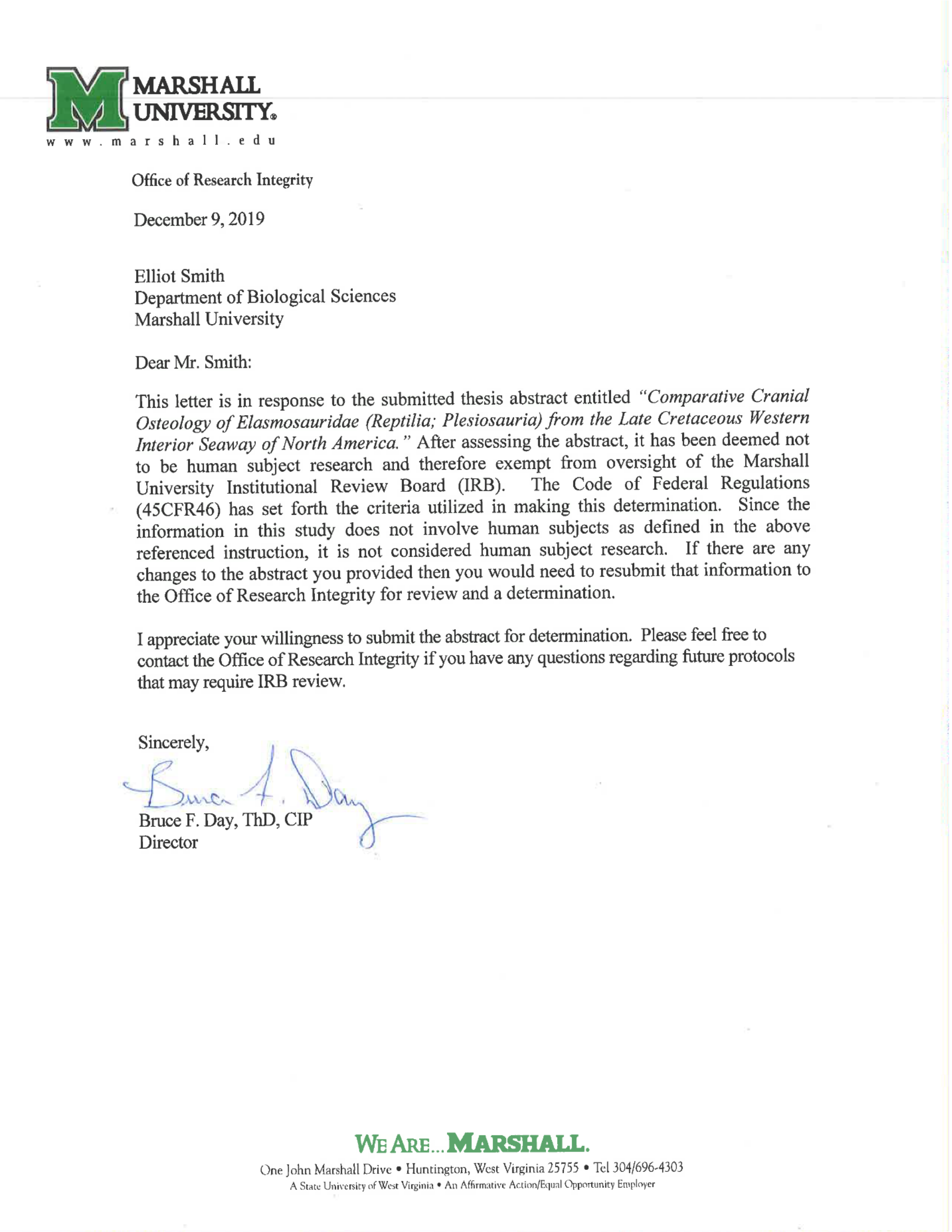
APPENDIX A

MARSHALL UNIVERSITY INSTITUTIONAL REVIEW BOARD LETTER



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Office of Research Integrity

December 9, 2019

Elliot Smith
Department of Biological Sciences
Marshall University

Dear Mr. Smith:

This letter is in response to the submitted thesis abstract entitled *"Comparative Cranial Osteology of Elasmosauridae (Reptilia; Plesiosauria) from the Late Cretaceous Western Interior Seaway of North America."* After assessing the abstract, it has been deemed not to be human subject research and therefore exempt from oversight of the Marshall University Institutional Review Board (IRB). The Code of Federal Regulations (45CFR46) has set forth the criteria utilized in making this determination. Since the information in this study does not involve human subjects as defined in the above referenced instruction, it is not considered human subject research. If there are any changes to the abstract you provided then you would need to resubmit that information to the Office of Research Integrity for review and a determination.

I appreciate your willingness to submit the abstract for determination. Please feel free to contact the Office of Research Integrity if you have any questions regarding future protocols that may require IRB review.

Sincerely,

Bruce F. Day
Bruce F. Day, ThD, CIP
Director

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APPENDIX B

CHANGES TO SERRATOS ET AL. (2017) CHARACTER MATRIX

2. Maxilla, lateral expansion of maxilla posterior to maxilla-premaxilla suture accommodates expanded caniniform bases [‘roots’]: absent (0); present (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of “?” changed to 2.1. Lateral expansion of maxilla is present in Otero (2016) and photos provided by DJ Morgan.

Styxosaurus snowii: Score of 2.0 changed to 2.1. It is clear that KUVP 1301 has a lateral expansion of the maxilla to accommodate a large caniniform tooth.

7. Relative skull length compared to length of dorsal series: 0.20–0.30 (0); 0.31–0.39 (1); >0.40 (2).
Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of “?” was changed to 7.0, the ratio of skull length to dorsal series can be extrapolated from AMNH 1495 (Otero, 2016).

15. Premaxilla contact along the dorsal midline: contacts anterior extension of frontals only (0); partially overlaps the frontal along the midline (1); overlaps the entire length of the frontal along the dorsal midline and contacts the parietal (2).

Styxosaurus snowii: Score of “?” changed to 15.2. KUVP 1301 has a posteromedian process that entirely overlaps the frontals and contacts the parietals.

16. Premaxilla, posterior termination: tapering and non-interdigitating or weakly interdigitating (0); broad, deeply interdigitating suture with the frontal or parietal (1).

Styxosaurus snowii: Score of “?” changed to 16.0. KUVP 1301 has a tapering contact of the posterior premaxilla, as the posteromedian process thins posteriorly to contact the parietals.

18. Premaxilla, morphology of dorsomedian ridge: narrow and crest-like (taller than wide) (0); broad, occupying most of the internarial width of the rostrum (1); posterior mound (2).

Hydrotherosaurus alexandrae: Score of “0/2” was changed to “?”. This skull is badly deformed and the original morphology is difficult to discern (Welles, 1943).

Styxosaurus snowii: Score of 18.2 changed to 18.0/2. KUVP 1301 has a narrow and crest like dorsomedian ridge, but also has a posteriorly oriented hump, justifying the mutli-state designation of this character.

20. Premaxilla dorsomedian foramen: absent (0); present (1).

Styxosaurus snowii: Score of “?” changed to 20.0. There is no premaxilla dorsomedian foramen present. Premaxilla is entirely intact so this state can be evaluated.

22. Premaxilla, constriction of posteromedian process at level of external naris: absent (0); present, and does not expand to original width posterior to naris (1); present, but premaxilla expands to original width posterior to naris (2).

Styxosaurus snowii: Score of "?" changed to 22.1. It is clear that the premaxillae constrict at the level of the external naris.

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" was changed to 22.1. It is clear in S. *browni* that the posteromedian process tapers to a point posterior to the nares.

23. Premaxilla-maxilla sutures: converging posteromedially gradually, for entire length (0); anterior portion extends dorsomedially then abruptly curves posteriorly, resulting in a parallel-sided appearance of the posterior process of the premaxilla (1).

Styxosaurus snowii: Score of "?" changed to 23.0. It is clear that the premaxilla-maxilla suture converges gradually posteromedially for their entire length; these sutures do not run parallel to one another at any point.

29. Posteromedial extension of the maxilla: extends to anteromedial margin of the external naris (0); extends to midpoint of the medial margin of the external naris (1); extends posteromedial to the external naris (2).

Styxosaurus snowii: Score of ?" changed to 29.0. It is clear that the maxilla extend to the anteromedial margin of the external naris.

34. Lacrimal: absent, maxilla participates in orbit margin (0); present, maxilla excluded from orbit margin (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" changed to 34.0. It is clear that the maxilla makes an edge of the orbit, and the lacrimal is absent (Otero, 2016).

36. Postfrontal participation in orbital margin: participates (0); does not participate, excluded by postorbital-frontal contact (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of 36.0 changed to 36.1. Contrary to Serratos et al. (2017) I interpret that the postfrontal contributes to the rim of the orbit.

Styxosaurus snowii: Score of 36.1 changed to 36.0. From my examination of this skull, I interpret that the postfrontal does contribute to the orbit margin.

44. Pineal foramen: present (0); absent (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" changed to 44.1. It is clear from Otero (2016) and DJ Morgan photos that pineal foramen is absent.

52. Parietal, anterior extension: short or absent, parietal extends to the level of the temporal bar (0); long, parietal extends to orbital midlength or more anteriorly (1); very long, parietal extends to anterior orbit margin or more anteriorly (2).

Styxosaurus snowii: Score of "?" changed to 52.1. The anterior margin of the parietal is clearly visible.

54. Squamosal arch, cross section of dorsal process of squamosal: dorsoventral/mediolateral width subequal to or less than anteroposterior width (0); anteroposteriorly compressed (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" changed to 54.1. It is clear from Otero (2016) and DJ Morgan photos that dorsal process of squamosal is inflected anterodorsally.

61. Squamosal, outline of posterior margin in lateral view: approximately straight (0); dorsal portion inflected abruptly anterodorsally (1).

Styxosaurus snowii: Score changed from "?" to 66.1. It is clear that the anterodorsal portion of the squamosal is inflected anteriorly in lateral view.

63. Notochordal pit on occipital condyle: absent (0); present (1).

Nakonanectes bradti: Score of 63.1 changed to 63.0. Serratos et al. (2017) reports that the occipital condyle lacks a notochordal pit in the specimen description.

66. Ventral process of the basioccipital: absent, weakly developed or wide, flat, relatively smooth, with a thin plate present [small 'step' between condyle and ventral surface of basioccipital] (0); very prominent, ventrally projecting plate present (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of 66.0 changed to "?". It is not visible.

67. Foramen magnum, proportion of foramen enclosed by supraoccipital: less than one-third (0); approximately half (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of 67.0 changed to "?". Foramen magnum is not visible (Otero, 2016).

76. Supraoccipital morphology in lateral view: wider than tall (0); or taller than wide (1).

Styxosaurus snowii: Score changed from "?" to 76.1. It is clear that the supraoccipital is taller than wide in lateral view; it has a prominent dorsal process.

77. Posteromedian ridge of supraoccipital: present (0); absent (1).

Styxosaurus snowii: Score of "?" changed to 77.1. It is clear in lateral view that this ridge is present.

99. Pterygoids, midline contact posterior to posterior interpterygoid vacuity: absent (0); present posteriorly, but very small (1); present, pterygoid contact for more than two-thirds of their anteroposterior length posterior to posterior interpterygoid vacuity (2).

Libonectes morgani: Score of 99.2 changed to 99.1. It is clear from photos in Serratos et al. (2017) supplemental information that the pterygoids do have a midline contact posterior to the posterior interpterygoid vacuity. The contact is small, and not more than two thirds length of the contact between the pterygoids anterior to the posterior interpterygoid vacuity.

110. Ectopterygoid/pterygoid boss, transverse width: approximately as wide mediolaterally as long anteroposteriorly (0); >1.5 times as wide mediolaterally as long anteroposteriorly (1).

Styxosaurus snowii: Changed from 110.1 to 110.0. This character scoring was justified by the left lateral view of the skull, exposing the anatomical-right side of the palate.

114. Structure of the dentary along the ventral surface of the mandibular symphysis: no ventral elaboration (0); forms raised ventral platform or sharp keel/ridge adjacent to symphysis (1).

Styxosaurus snowii: Changed from 114.0 to 114.1. There is clearly a keel on the mandibular symphysis.

116. Length of retroarticular process: shorter than or subequal to glenoid anteroposterior length (0); longer than glenoid (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" changed to 116.0. It is clear from Otero (2016) that the retroarticular process is short like *Styxosaurus snowii*.

Styxosaurus snowii: Score changed from 116.1 to 116.0. The retroarticular process is shorter anteroposteriorly than the glenoid, on both medial and lateral sides.

127. Surangular, fossa and longitudinal crest on medial surface anterior to glenoid: prominent longitudinal crest forms ventral margin of deep, dorsomedially facing surangular fossa (0); prominent longitudinal crest forms medial margin of mediolaterally expanded dorsal surface of surangular bearing shallow, dorsally facing fossa (1); crest and surangular fossa weak or absent, dorsal portion of surangular 'blade-like' (2); dorsolaterally facing fossa bounded laterally by a sharp crest (3).

Styxosaurus snowii: Score changed from "?" to 127.2. The surangular lacks a fossa and a crest, is thin and blade-like in appearance.

130. Articular, deep anteroposteriorly oriented cleft [notch] posterior to glenoid: absent (0); present (1); cleft absent, but dorsal surface is strongly concave mediolaterally (2).

Styxosaurus snowii: Score of 130.0 changed to 131.1. In lateral view this cleft is seen on the dorsal margin of the retroarticular process.

133. Regularity of maxillary dentition: homodont (0); heterodont (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" changed to 133.1. It is clear from Otero (2016) and DJ Morgan photos that the 4th maxillary tooth is large and caniniform.

131. Number of premaxillary teeth: four (0); five (1); six (2); seven or more (3).

Styxosaurus snowii: Score changed from 131.1 to 131.0. There are four premaxillary teeth.

134. Diastema at premaxillary-maxillary suture: absent (0); present (1).

Styxosaurus browni/*Styxosaurus* sp. (AMNH 5835 & 1495): Score of "?" changed to 134.0. It is clear from Otero (2016) and DJ Morgan photos that there is no diastema at the maxilla-premaxilla contact.

150. Axial neural spine: transversely narrow (0); transversely broad (1).

Styxosaurus snowii: Score of 150.0 changed to "?". Neural spines are not well preserved enough to evaluate this character.

152. Number of cervical vertebrae: <15 (0); 18–23 (1); 24–29 (2); 30–36 (3); 37–49 (4); 50–59 (5); >60 (6).

Styxosaurus snowii: Score changed from "?" to 152.6. Although this specimen does not contain a complete vertebral series, other referred specimens of Styxosaurus have more than 60 cervical vertebrae; it can be inferred that KUVP 1301 had more than 60 cervical vertebrae.

157. Anterior cervical neural spines, morphology: curve posterodorsally (0); inclined straight posterodorsally (1); inflected anterodorsally (2); inapplicable in some pistosaurians that have extremely low neural spines (?).

Styxosaurus snowii: Score changed from 157.0 to "?". The neural spines are not complete enough to evaluate this condition.

164. Cervical zygapophyses, combined width: broader than the centrum (0); subequal to the centrum (1); or distinctly narrower than the centrum (2).

Styxosaurus snowii: Score changed from "?" to 164.2. It is clear that the zygapophyses are much narrower than the centrum in lateral view.

168. Cervical zygapophyses, median contact between left and right zygapophyseal facets: absent for most/all of length (0); present for most of anteroposterior length (1).

Styxosaurus snowii: Score changed from “?” to 168.1. The zygapophyses are visible in lateral view and appear to have a median contact for most of their length.

171. Cervical vertebrae, proportions of anterior cervical neural spines: taller than their anteroposterior length (0); longer than tall (1); anteroposteriorly short and ‘rod-like’, approximately as long anteroposteriorly as the transverse width (2); as long as tall (3).

Styxosaurus snowii: Score changed from “?” to 171.1. It is clear that the cervical vertebrae neural spines are longer than tall, because the first four vertebrae appear to have neural spines intact.

173. Cervical centrum, proportional width: mediolateral width subequal to height or less (0); at least 1.2 times as wide mediolaterally as high dorsoventrally (1).

Styxosaurus snowii: Score changed from “?” to 173.1. Although this specimen is mounted into the wall, the right lateral half of the vertebrae are visible and double that width is approximately greater than the dorsoventral height.

APPENDIX C

CHARACTER MATRIX

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Rhomaleosaurus_cramptoni

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