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Revision of polycotylid plesioaur systematics (sauropterygia plesiosauria) and description of the axial osteology of a juvenile polycotylid

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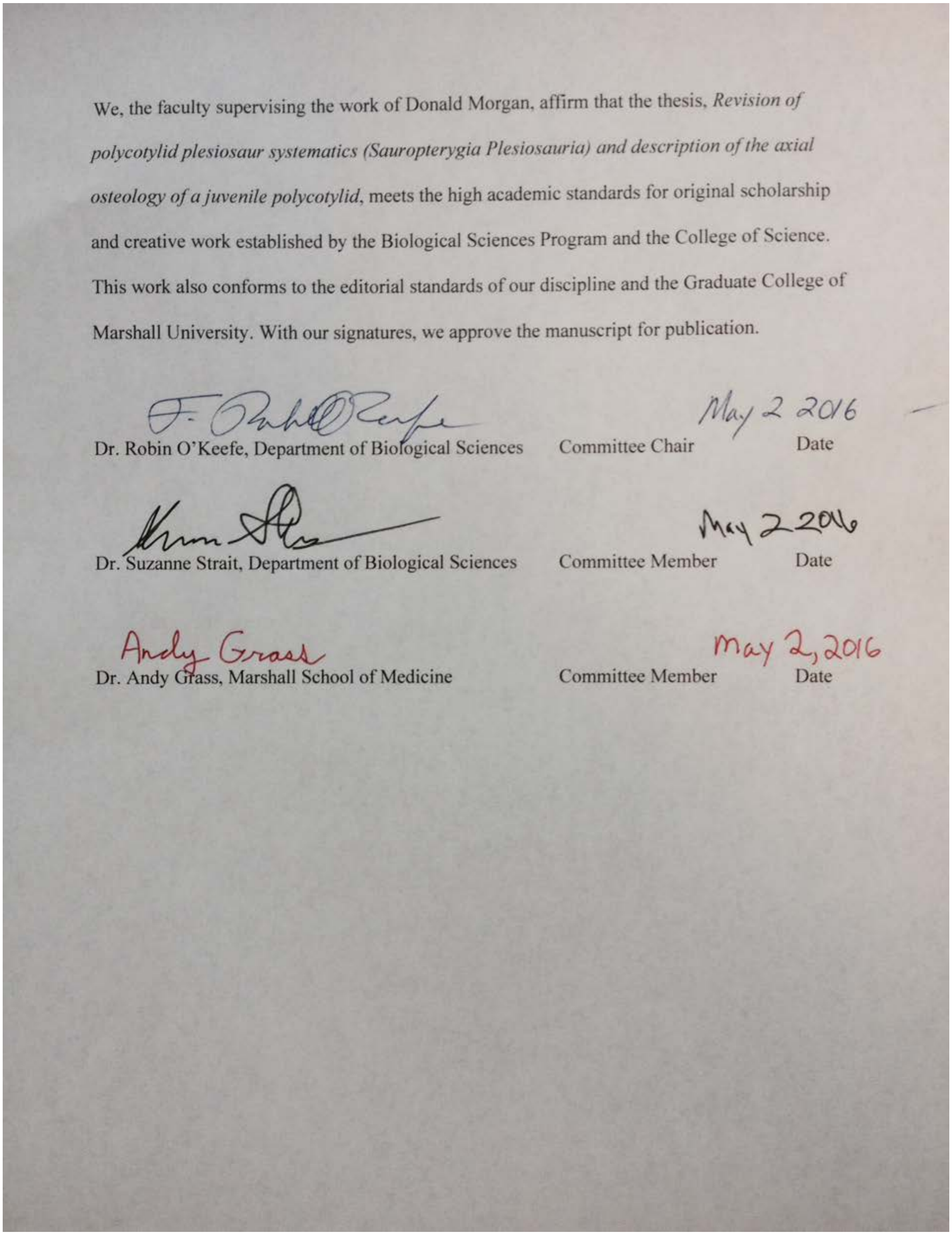
REVISION OF POLYCOTYLID PLESIOAUR SYSTEMATICS (SAUROPTERYGIA PLESIOSAURIA) AND DESCRIPTION OF THE AXIAL OSTEOLOGY OF A JUVENILE POLYCOTYLID

A thesis submitted to
the Graduate College of
Marshall University
In partial fulfillment of
the requirements for the degree of
Master of Science
in
Biological Science
by
Donald Joseph Morgan III
Dr. F. Robin O'Keefe, Committee Chairman
Dr. Suzanne Strait
Dr. Andrew Grass

Marshall University
May 2016



We, the faculty supervising the work of Donald Morgan, affirm that the thesis, *Revision of polycotylid plesiosaur systematics (Sauropterygia Plesiosauria) and description of the axial osteology of a juvenile polycotylid*, meets the high academic standards for original scholarship and creative work established by the Biological Sciences Program and the College of Science. This work also conforms to the editorial standards of our discipline and the Graduate College of Marshall University. With our signatures, we approve the manuscript for publication.

May 2 2016
Dr. Robin O'Keefe, Department of Biological Sciences Committee Chair Date

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ABSTRACT

The polycotylids were a clade of plesiosaurs that proliferated during the Cretaceous period. Despite recent research efforts, evolutionary relationships among polycotylid species remain unresolved. In this study, a phylogenetic analysis incorporating a large taxon sampling from the Polycotylidae was used to parse out the evolutionary relationships among the taxa. The main focus was to assign two polycotylid specimens from the Wallace Ranch to a formal species. A study on the axial osteology of the juvenile Wallace Ranch polycotylid was also performed, as the development of the axial column of a polycotylid plesiosaur has been poorly understood and may have phylogenetic implications. This study revealed that the two Wallace Ranch specimens form a well-supported clade, and feature a mosaic of character states found in currently described species, and may represent a new species. The monophyly of the genus *Dolichorhynchops,* was not supported in the current analysis. *D. bonneri*, *D. tropicensis,* and the Wallace Ranch specimens are more closely related to *Trinacromerum*. Therefore a formal re-description of the two genera *Dolichorhynchops* and *Trinacromerum* is required. The study also revealed that the three skeletons attributed to the species *Polycotylus latipinnis* do represent members of the same species. However, the study did not support the close relationship between *D. bonneri* and *P. latipinnis,* and that the similarity seen between the two species is attributed to a convergence in large body size. The cranial osteology of the juvenile Wallace Ranch polycotylid provides a rare insight into the development and fusion pattern of a polycotylid skull, and reveals some possible ontogenetic characters, which should be excluded from future phylogenetic analyses. After analyzing the axial osteology of the juvenile Wallace Ranch specimen, the individual was most likely a neonate at the time of death. The understanding of the morphological changes during ontogeny provides better insight into intraspecific variation in a polycotylid species. The current study revealed, Polycotylidae feature a basal clade, a polyphyletic genus *Dolichorhynchops*, with an expanded *Trinacromerum*, and supports the previous assignment of three specimens to the species *P. latipinnis*.

CHAPTER 1

INTRODUCTION

The Polycotylidae is a large clade of plesiosaurs that was first described from the Cretaceous deposits of the North American Western Interior Seaway. Cope (1869) described the first polycotylid, *Polycotylus latipinnis,* and there are currently over 18 described species of polycotylids (McKean 2012). The polycotylids were not restricted to the North American Western Interior Seaway, and reached a cosmopolitan distribution in the Late Cretaceous period (Druckenmiller and Russell 2009). The first of the polycotylids appeared in the Albain (100.5–113.0 mya), and the group proliferated into the Maastrichtian, where they, along with countless other species, perished in the Cretaceous-Tertiary extinction (Carroll 1988; O'Keefe 2001).

The classification of the polycotylids within the Plesiosauria has been contentious for over 100 years (Williston 1925; Person 1963; Brown 1981; Carpenter 1996; O'Keefe 2001; Druckenmiller and Russell 2008; Ketchum and Benson 2010). Recent phylogenetic analyses suggest that the polycotylids are a clade within the Plesiosauroidea, rather than the Pliosauroidea (O'Keefe 2001, 2008; Ketchum and Benson 2010; Benson et al. 2012a; Druckenmiller and Benson 2014; Schumacher and Martin 2015). The ontogeny of plesiosaurs is scarcely known, as articulated juvenile plesiosaur fossil are rare in the fossil record, and the assignment of isolated juvenile remains of a plesiosaur to a specific taxon can be problematic. Most of the material found for juvenile plesiosaurs include postcranial remains, and the taxonomic utility of fragmentary postcranial material makes the utility of such fossil material dubious.

Purpose of Study

The purpose of this study is to elucidate the phylogenetic relationships among polycotylids, and to describe the axial osteology of a juvenile polycotylid plesiosaur and compare it to another juvenile plesiosaurs, and the associated adult specimen UNSM 51033. A cladistics analysis will be used to differentiate the evolutionary relationships among the polycotylid taxa. This will be the first cladistic analysis to include all known species of polycotylids and will hopefully clarify the interrelationships among members of a clade that diversified over a short period of time. The description of the juvenile polycotylid (UNSM 55180) will be the first description of the axial osteology of a young juvenile polycotylid. The presence of juvenile plesiosaurs in the fossil are rare, and *Cryptoclidus eurymerus* is the only species that features a true growth series for a plesiosaur (Andrews 1910; Brown 1981; Caldwell 1997). The most complete juvenile specimens belong to *Thalassiodracon hawkinsi* (BMNH 1336), *Atychodracon megacephalus* (BMNH 2018, 2020, and 2021), and to (SMNS 51141) (Vincent 2010). Other less complete juvenile plesiosaurs include *Leptocleidus* sp. (SAM P15980), *Eurycleidus arcuatus* (OUM J.28585), and *Plesiosaurus dolichodeirus* (YPM PU3352) (Kear 2007, Storrs 1997 and Vincent 2010). However, the cranial anatomy of any juvenile Plesiosaur has not been described from North America, and the only other known fairly complete juvenile axillary material from a polycotylid is known from (LACM 129629) the embryo, which does not feature a head (O'Keefe and Chiappe 2011). Therefore, the description of the cranial anatomy of a juvenile polycotylid while elucidate the changes during ontogeny to the skull, and understand the evolutionary patterns of the polycotylid skull.

Sauropterygian Taxonomic Relationships

The plesiosaurs are an extinct clade of sauropterygian reptiles that proliferated throughout the Mesozoic era. The term Sauropterygia was first defined by Richard Owen in 1860 to include plesiosaurs and nothosaurs (Storrs 1993 and Rieppel et al. 2000). The sauropterygians were a monophyletic clade of derived aquatic diapsids, with a contentious position within the Sauria (Joyce 2015; Schoch and Sues 2015). Within the Permian, there was a major radiation of diapsid clades. The rapid divergence of the Permian Diapsida generated confusion within the taxonomic relationships of stem-diapsid clades (Joyce 2015; Schoch and Sues 2015). The Sauropterygia most likely diverged from other primitive saurian clades during the Late Permian or Early Triassic period (Rieppel et al. 2000). The crown group Sauropterygia features major clades such as the Placondontia, Nothosauroidea, and Pistosauriodea, which includes Plesiosauria (Figure 1.1) (Rieppel 1999; Rieppel et al. 2000; Sato et al. 2006; Le-Tian Ma et al. 2015). The following synapomorphies unite the sauropterygian clade: a single upper temporal fenestra in the roof of the skull; a closed palate, in which the pterygoids cover the braincase ventrally; absence of the supratemporal, postpareital, and tabular bones; restracted nares, with the nostrils closer to the orbit margin rather than the tip of the snout; large retroarticular process on the mandible; three to six cervical vertebrae; absence of an ossified sternum; separate scapula and coracoid bones; pectoral fenestra in the pectoral girdle and a thyroid fenestra in the pelvic girdle; scapula lies superficial to the clavicle (posterior portion of the clavicle overlies the anterior portion of the scapula); a small ilium; and the absence of humeral ectepicondylar foramen (Ketchum and Benson 2010). The group Eosauropterygia includes all of the clades of Sauropterygia except for the placodonts, which is the sister group to the clade (Figure 1) (Rieppel et al. 2000; Sato 2006; Le-Tian Ma et al. 2015). Within the Eosauropterygia, the Plesiosauria is a derived clade, most closely related to the Pistosauridae (Rieppel et al. 2002; Sato et al. 2006; and Le-Tian Ma et al. 2015). The pistosaurians resembled early plesiosaurs in superficial appearance, but featured a palate more akin to a nothosaur, rather than a plesiosaur (Rieppel et al. 2002). The sister clade relationship of the Pistosauridae and the Plesiosauroidae are bolstered by eight unique synapomorphies shared between both clades. The uniting synapomorphies are: retraction of the external naris to the posterior half of the preorbital portion of the skull, a parietal crest, contact of the squamosals along the midline of the posterior apex of the skull, a “box-like” suspensorium, presence of the posterior interpterygoid vacuities, dorsal vertebrae featuring evenly rounded facets on the transverse process, and the absence of a deltopectoral crest on the humerus (Ketchum and Benson 2010).

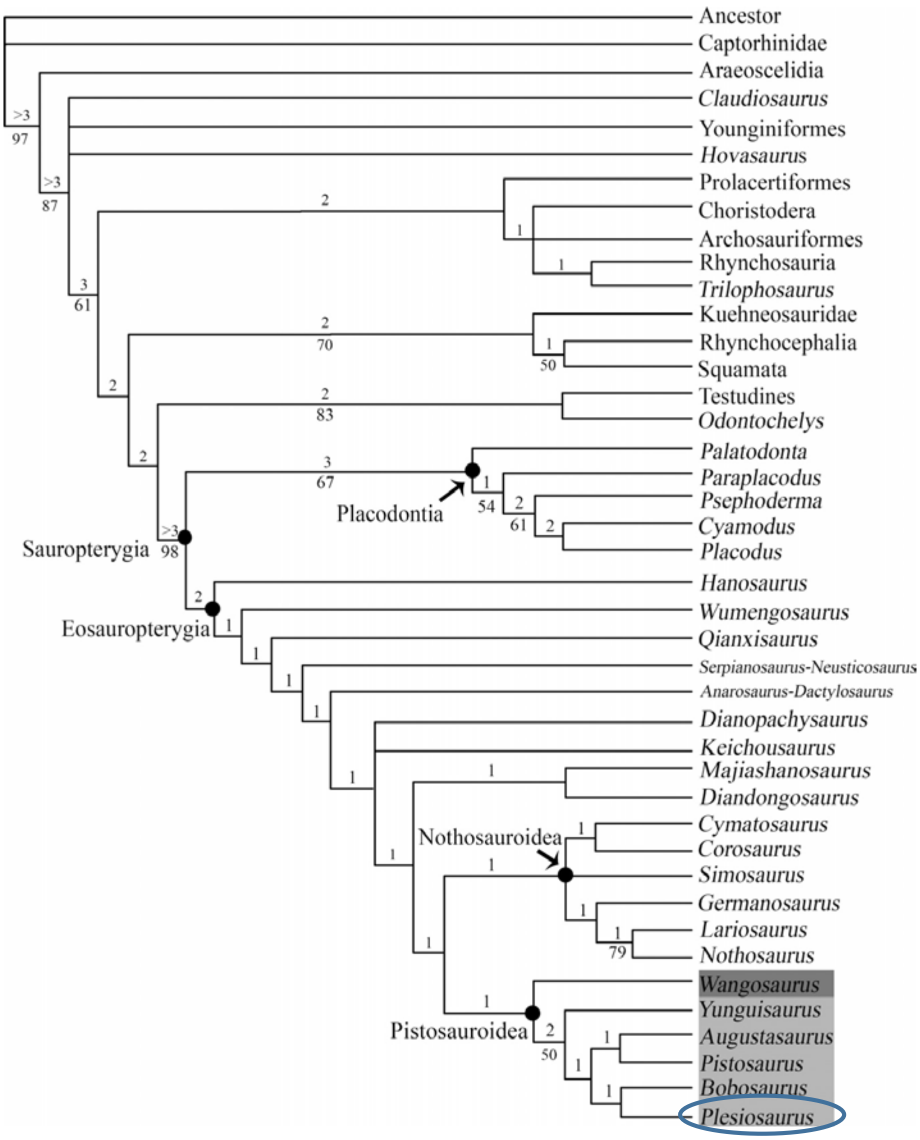

Figure 1 Overview of Sauropterygian Systematics. Overview of Sauropterygian systematics, and relationships to other diapsids (Le-Tian Ma et al. 2015). The sister taxon to the plesioaurs are the pistosaurids, and all are members of the Pistosauroidea are highlighted. This figure illustrates the split between the Eosauropterygia from the Placodontia. Among the Sauropterygia, the Plesiosauria were the only clade to flourish until the end of the Mesozoic era. Figure is from Le-Tain Ma et al. (2015).

Plesiosauria Systematics

At the base of the Plesiosauria, there is a polytomy comprising of the three main lineages, the Rhomaleosauridae, Pliosauridae, and Plesiosauroidea (Figure 1.2) (Benson and Druckenmiller 2014). These lineages most likely diverged from one another in the Late Triassic, and the fossil record for Plesiosauria from this time period is scarce, thus making resolution of this polytomy problematic until more fossils from the Late Triassic are found (Benson and Druckenmiller 2014). Until recently, the rhomaleosaurs and the pliosaurs were put into their own clade, the Pliosauroidea, and all the other Plesiosauria that were more closely related to *Plesiosaurus dolichodeirus*, are placed into the Plesiosauroidea (O'Keefe 2001; Ketchum and Benson 2010; 2011). However, modern phylogenetic analysis on the more basal plesiosaurian taxa has revealed that the Pliosauroidea was a paraphyletic grouping (Benson and Druckenmiller 2014). The clade known as the rhomaleosaurs were large bodied plesiosaurs which featured broad and elongated heads and moderated long necks, and they were prevalent throughout the early and mid-Jurassic. The Rhomaleosauridae is defined as all taxa more closely related to *Rhomaleosaurus victor* than to *Leptocleidus superstes*, *Pliosaurus brachydeirus*, or *Polycotylus latipinnis* (Khun 1961). The rhomaleosaurs are united by the following synapomorphies: the premaxilla having a dorsomedian foramen present, a significantly inclined suspensorium, and a bowed mandible (Ketchum and Benson 2010). The pliosaurs proper, were collectively termed as plesiosaurs with large heads and short necks; however, this broad categorical classification by body shape arose multiple times within the Plesiosauria, and the true Plisoauridae is a monophyletic grouping of all taxa more closely related to *P. brachydeirus,* than to *L. superstes*, *P. victor*, or *P. latipinnis* (Carpenter 1996; 1997; O'Keefe 2001; Ketchum and Benson 2010).

The Pliosauridae are united by the following unambiguous synapomorphies: the coronoid of the mandible is present with a long lingual process, the ventral surface of cervical centra are flat or only slightly convex, the dorsal tip of the ilium flares dorsally with an asymmetrical flare that is wider posteriorly, and a convex tibia (Ketchum and Benson 2010).

The final stem group of the Plesiosauria is known as the Plesiosauroidea, and this group includes a diverse assemblage of plesiosaurs, including the Elasmosauridae, Plesiosauridae, Polycotylidae, Leptocleididae, Cryptoclididae, and the Microcleididae (Ketchum and Benson 2010; Benson et al. 2012b; Benson and Druckenmiller 2013). The Plesiosauroidea is defined as all taxa more closely related to *P. dolichodeirus* than to *P. brachyderius* and *R. victor* (Ketchum and Benson 2010; Benson and Druckenmiller 2014). The family known as the Microcleididae, was a primitive group of Plesiosauroideia, which flourished from the early to mid-Jurassic period (Benson and Druckenmiller 2014). The Microcleididae include taxa that are more closely related to *Microcleidus homalospondylus* than to *P. dolichodeirus*. The uniting synapomorphies of the clade are: widely separated posterior cervical rib facets, posteriormost dorsal rib facets split between the centrum and neural arch, the medial surface of the iliac blade anteroposteriorly concave, and a prominent flange extends anteriorly from the proximal half of the radius (Benson and Druckenmiller 2014). The Cryptocleididae were present from the Jurassic to the early Cretaceous. The Cryptoclididae are defined as all taxa more closely related to *Cryptoclidus eurymerus* than to *P. latipinnis*, *E. platyurus*, *L. superstes*, and *P. dolichodeirus* (Ketchum and Benson 2010). The Cryptoclididae monophyly is supported by numerus cranial and postcranial synapomorphies, such as: the anterior extent of the jugal ventral to the orbit lies ventral to the posterior third of the orbit, the jugal is narrow and vertically oriented, the temporal emargination was moderately embayed, the presence of ornamentation of the surface around the orbit, the pineal foramen contacts the frontals anteriorly, the absence of an elongated medial process of the ventral ramus of the squamosal contacting the quadrate, the paraoccipital process contacts the posterior ramus of the pterygoid, the presence of atlas ribs and rib facets, the axis rib articulates partially with the atlas centrum, and the ventral plates of the scapula contact one another at the ventral midline (Ketchum and Benson 2010). The next major grouping of plesiosaurs includes the derived Plesiosauroidea taxa from the Cretaceous called the Xenopsaria, and includes the families Elasmosauridae, Polycotylidae, and Leptocleididae (Figure 2) (Benson and Druckenmiller 2014). However, previous analysis from Benson et al. (2013b), Ketchum and Benson (2010), and O'Keefe (2001), did not recover this clade, and the validity of this gouping of elsamosaurs, leptocleidids, and polycotylids remains tentative. The Elasmosauridae were an enigmatic group of Cretaceous plesiosaurs with extremely long necks and small heads (O'Keefe 2001; Ketchum and Benson 2010). The Elasmosauridae is defined as all taxa more closely related to *Elasmosaurus platyurus* than to *Cryptoclidus eurymerus*, *L. superstes*, *P. dolichodeirus*, or *P. latipinnis*. The monophyly of the clade is supported by the following synapomorphies: closing of the pineal foramen, a massive quadrate, the cross-sectional shape of the teeth in the anterior half of the tooth row was oval, the lateral surface of anterior cervical centra is present, the articular face of the cervical centra are nearly flat, and the presence of a posterior intercocracoid vacuity/embayment (Ketchum and Benson 2010). The sister clade to the Elasmosauridae is the Leptocleidia, which includes the families Leptocleididae and Polycotylidae (Ketchum and Benson 2010). The Leptocleidia is defined as including all taxa more closely related to *L. superstes* and *P. latipinnis* and all of their descendants (Ketchum and Benson 2010; Benson et al. 2012b). The position of the leptocleidid's been uncertain until recent phylogenetic analyses. Their position has jumped from a sister taxon to the rhomaleosaurs to a derived clade of pliosaurs, and is now nested as a derived member of the Plesiosauroidea, most closely related to the polycotylids and the elasmosaurs (O'Keefe 2001; Druckenmiller and Russell 2008; and Ketchum and Benson 2010). The Leptocleididae, is a monophyltic clade which features all taxa more closely related to the *L. superstes* than to *C. eurymerus, E. platyurus, P. dolichodeirus, P. latipinnis, R. victor,* or *P. brachydeirus* (Ketchum and Benson 2010). The unambiguous synapomorphy that unites the Leptocleididae clade is that the frontals participate in the margin of the temporal fenestration (Ketchum and Benson 2010). The synapomorphies shared within the Leptocleidia will be discussed in the next section, which is primarily focused on polycotylid systematics.

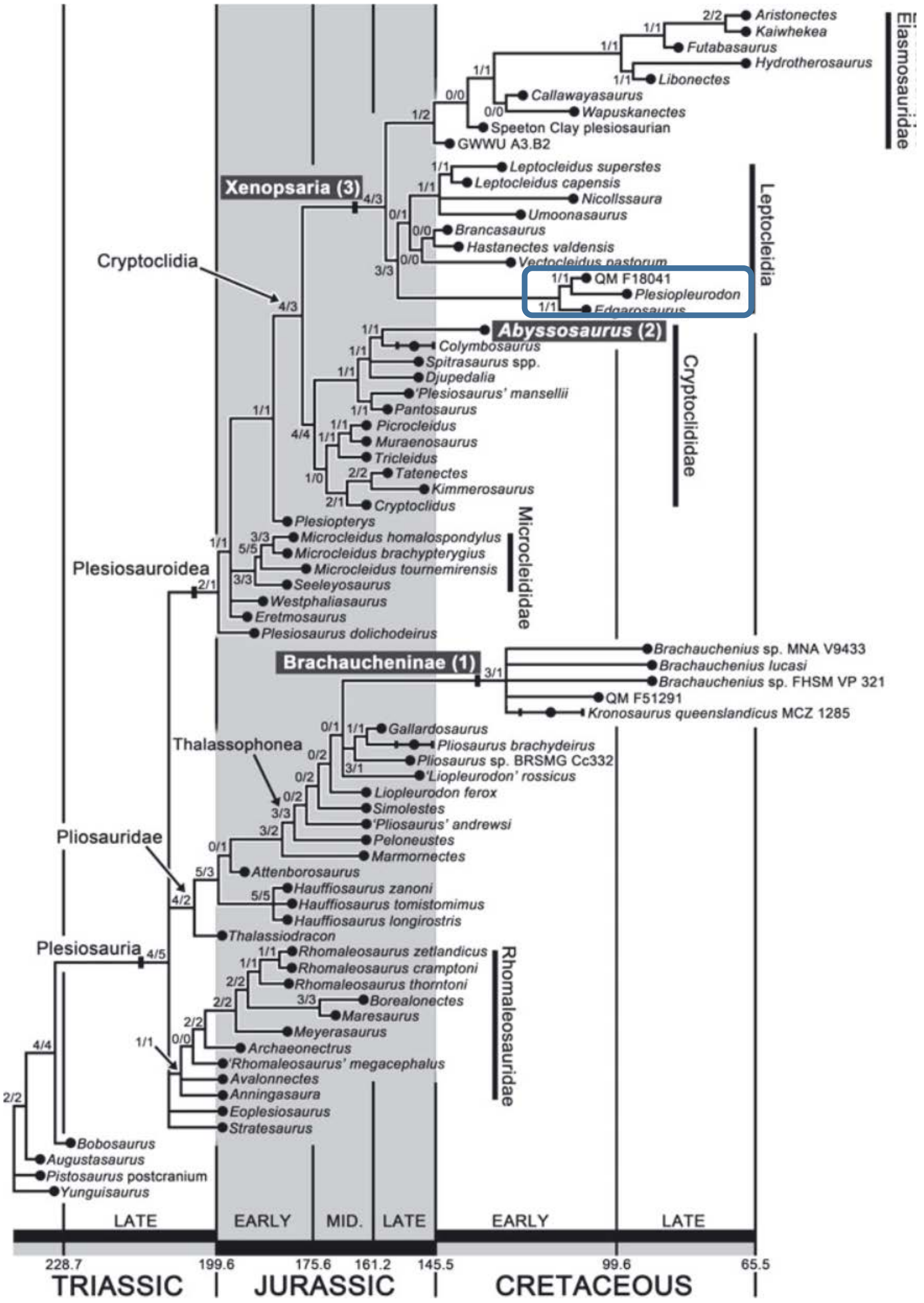

Figure 2 Plesiosauria Phylogeny. The most recent phylogeny of Plesiosauria including taxa from all major clades. There is a polytomy at the base of Plesiosauria. The polycotylids are nested as one of the most derived members of the Plesiosauroidea. The polycotylids were also one of three clades to survive into the Late Cretaceous. Figure is from Druckenmiller and Benson (2014).

Leptoclidida and Polycotylidae Systematics.

The sister taxon to the Polycotylidae is the Leptocleididae, a clade once considered to be more closely related to rhomaleosaurs, rather than a derived Plesiosauroidea clade (Figure 2 and 3) (Ketchum and Benson 2010; Benson et al. 2012; Shumacher and Martin 2015). However, recent phylogenetic evidence suggests that the Leptocleididae are a monophyletic group, and are firmly nested within Plesiosauridea, closely related to both the polycotylids and the elasomosaurids. The leptocleidids and the polycotylids are united via the following characteristics of their cranial and postcranial anatomy: the parietal is transverly flared posteriorly so that its contact with the squamosal is more than half the width of the posterior cranium, the dorso-ventral trough occupies the lateral surface of the mandible and is bound dorsally and ventrally by robust lateral ridges, possession of an S-curved humerus, and the posterior portion of the skull table is abruptly raised (Benson et al. 2012b). Most of the leptocleidids are known from the Early Cretaceous, while the polycotylids were predominately a Late Cretaceous clade of plesiosaurs. *Niccolssaura borealis*, one of the latest surviving leptocleidids, is Albian in age, and coexisted with the basal polycotylid, *Edgarosaurs muddi*, and the two species were similar in structuring of the palate and rostrum. The leptocleidids and polycotylids most likely diverged from one another in the Early Cretaceous, during the Aptian age (113-125 mya), which featured a diversity of leptocleidid species (Benson et al. 2012b). However, a true transitionary form between a leptocleidid and polycotylid plesiosaur still remains to be found.

Polycotylidae is supported by the following unambiguous synapomorphies: the premaxilla does not participate in the margin of the external naris, and premaxilla dorsomedian ridge is broad (Ketchum and Benson 2010). Other previous studies have noted that the

Polycotylidae can be described as having an ischium longer than the pubis; maxillary/squamosal suture present, which is formed by the posterior expansion of the maxilla; pterygoids with distinct medial processes that meet behind the posterior interpterygoid vacuity; pterygoid plates that are dished; a scoop-like or long mandibular symphysis; splenial included in the mandibular symphysis; longitudinal pectoral bar present and formed by both the clavicle and coraoid; supernumerary ossifications in both the propodeal and epipodial rows (Carpenter 1996; O'Keefe 2004; 2008; Albright et al. 2007).

The North American Polycotylid plesiosaurs are morphologically similar, and differentiation among species has been debated since there first discovery. The synonymy of the genera *Polycotylus*, *Dolichorhynchops*, and *Trinacromerum* was explored by Williston (1908; 1925), however he did believe that the three taxon were most likely different species. Welles (1962) also questioned the distinction between *Polycotylus*, *Dolichorhynchops,* and *Trinacromerum*, and suggested that with the fragmentary remains of both *P. latipinnis* and *T. bentonianum*, were not diagnostically different from *Dolichorhynchops osborni* and should be synonymized with *D. osborni*. Carpenter (1996), in his redescription of the North American polycotylids, maintained that there were 4 valid species of polycotylids, *D. osborni*, *P. latipinnis,* *T. bentonianum,* and *T. kirki*. However, two specimens that were assigned as the adult growth stage of *D. osborni* by Carpenter (1996), were later identified by Adams (1997) to belong to *T. bonneri,* and O'Keefe (2008) found this material to actually be part of the genus *Dolichorhynchops,* and the species was named *D. bonneri*. However, O'Keefe (2008) stated that the species D. *bonneri* possessed a mosaic of characters of *T. bentonianum*, *D. osborni*, and *P. latipinnis*.

Other polycotylids have been found from all over the world; as well as, new polycotylid discoveries in North America. There are currently 4 members of the genus *Dolichorhynchops*, but the most recent phylogenetic analyses do not support the monophyly of this genus (Ketchum and Benson 2010; Benson et al. 2012b; Schumacher and Martin 2015). All recognized species of the family Polycotylidae are being analyzed in this study, along with two additional specimens originally attributed to species *D. osborni*, UNSM 55810 and UNSM 50133. The validity of the material assigned to the species *P. latipinnis* is also being evelauted in this study. Currently, there are 3 additional specimens other than the holotype assigned to the species, and only one specimen contains significant cranial material (O'Keefe 2004; O'Keefe and Chiappe 2011; Schumacher and Martin 2015).

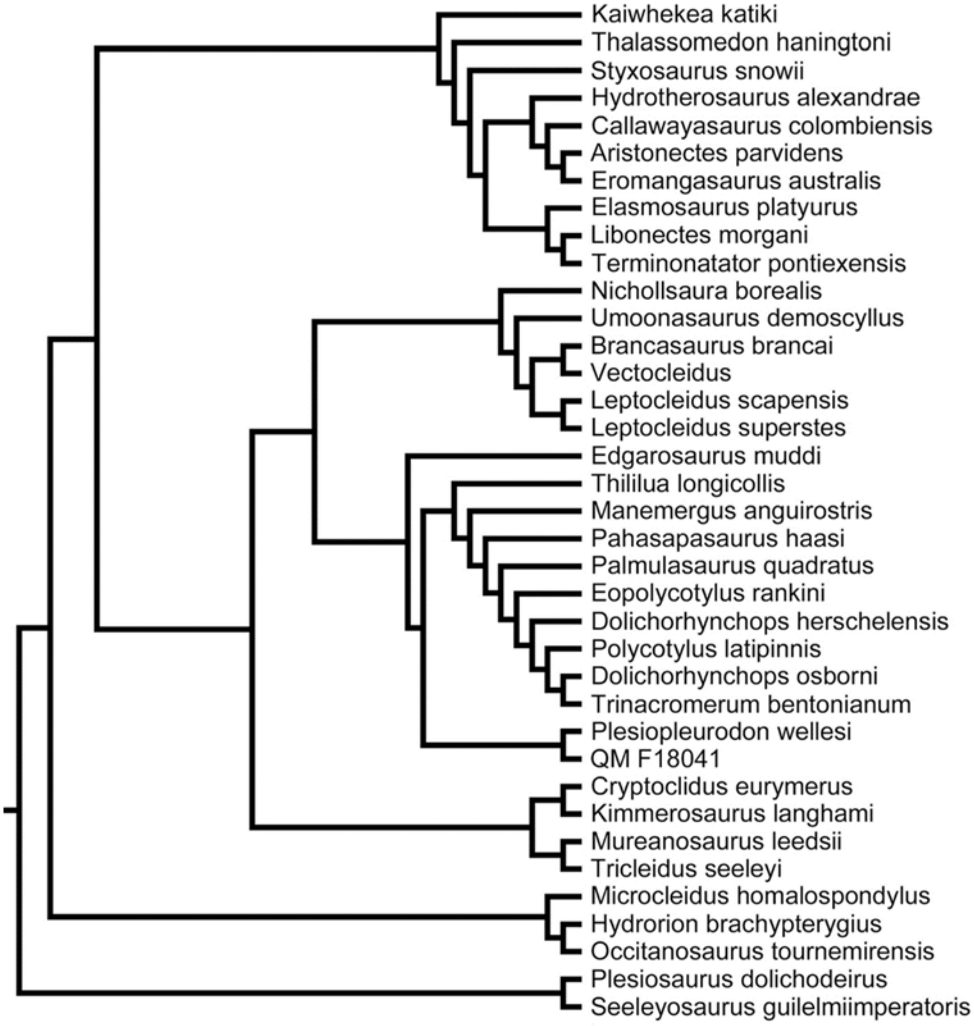

Figure 3 Polycotylid Phylogeny. Current phylogenetic relationships of the polycotylid plesiosaurs. This analysis illustrates that the genus *Dolichorhynchops* is paraphyletic. Represents the most extensive analysis of Polycotlyid systematics until the current study. However, this study by Schumacher and Martin (2015), did not report any support statistics with their phylogeny. The cladogram is from Schumacher and Martin (2015).

Polycotylid Origins and Trends.

The origin of the polycotylids remains unclear, as the earliest members of the family do not appear until the Albian stage of the Cretaceous in two geographically distant locations, North America and Australia (Druckenmiller 2009). However, the position of the Australian specimen, QM F18041, remains uncertain. The material was not observed by the author and the specimen still lacks a formal description. Therefore, the biogeographic origin of the Polycotylidae cannot be addressed presently. The diversity of the polycotylids throughout the Cretaceous suggests two peaks in diversity, the first in the Turonian and the second in the Campanian respectively. However, the peaks in fossil and species abundance might also reflect the access of better marine fossil deposits, than an actual peak in diversity (see Figures 4 and 5). The polycotylids do not seem to exhibit any correlation with body size throughout time, as there are both large and small polycotylids in the Albian/Cenomanian and Campanian (Figure 4). The diversity in body sizes throughout the Late Cretaceous most likely indicates that the polycotylids were taking advantage of different niches. However, some of the morphological disparity among erected polycotylid species could be due to sexual dimorphism rather than speciation. Schumacher (2007) and Schumacher and Martin (2015) have previously speculated this for the numerous polycotylid species during the Cretaceous, and the variability of the morphology in ilium for polycotylids might be attributed to sexual dimorphism. This assertion of sexual dimorphism in the ilium has not been quantitatively analyzed, and the results of this analysis are present in the appendix.

Sexual dimorphism usually comes in two major forms, the first being size dimorphism and the second being the presence of secondary sexual characteristics (Shine 1989; Watkins 1998; Hone et al. 2012). Size dimorphism is prevalent throughout Animalia, and is when one sex is larger in overall body size than the other (Hone et al. 2012). Most commonly the females are the larger sex in reptiles and amphibians, and this is reversed in mammals and some birds, where the males are larger to fight over mating access to harems (Hone et al. 2012). The acquisition of secondary sexual characteristics are either in the form of displays to attract mates or intimidate rivals, or features to fight off rivals for access to potential mates (Shine 1989; Hone et al. 2012). The thin sagittal crests in the polycotylids could be secondary sexual characters used to attract mates, as is seen in the nuchal crests of marine iguanas (Watkins 1998). It is also possible for multiple factors, such as, ontogeny and sexual selection to influence intraspecific variation within a species (Hone et al. 2012). Another marine species, the common bottlenose dolphin (*Tursiops truncates*), features high levels of intraspecific variation in skeletal characters and the species also exhibits sexual dimorphism (Nummela et al. 2004). The morphology of the premaxilla, the number of teeth in the mandible, and the nasal bone morphology vary among individuals within the species (Nummela et al. 2004). The formation of the melon during ontogeny influences the formation and morphology of the apex of the skull, while sexual selection drives overall body size and the number of teeth found in an individual (Nummela et al. 2004). It is possible that the variation observed in the morphology of skulls attributed to different species of polycotylids could be a product of intraspecific variation within a species. Therefore, the species of Polycotylids should be reevaluated to ensure the validity of each taxon.

Another hallmark characteristic of polycotylids is a lengthened rostrum, which caused the traditional misplacement of the polycotylids into the Pliosauroidea clade (White 1940; Persson 1963; Brown 1981). It has been asserted that as the polycotylids became more derived, rostrum length in comparison to overall skull size increased (Gasparini et al. 2001). The functional purpose for the slender and elongate rostrum in the polycotylids has yet to be explored. I hypothesize, that as the polycotylids became more derived, they developed into more specialized feeders, convergent to the crocodilian fish specialists *Gavialis gangeticus* and *Tomistoma schlegelii* of southern Asia (Piras et al. 2010). The slender snouted *G. gangeticus* and *T. schlegelii* use a slashing motion with their jaws to both stun in capture fish. The slender snouted morphology enables greater angular acceleration than broad snouted animals, thus the end of the rostrum in elongated/slender taxa moves at a greater velocity (Cuff and Rayfield 2013). The tubular morphology of the rostrum of derived polycotylids is also similar to *G. gangeticus* and *T. schlegelii,* which has been shown as an adaption for the reduction drag when thrusting the head underwater (Cuff and Rayfield 2013). However, until a comprehensive biomechanical analysis of the polycotylid skull is performed, these ideas on convergence in feeding strategy remain speculative.

	Geologic Stage	**MYA**	**North American Polycotylids**	**African Polycotylids**	**Asian and Australian Polycotylids**	**South American and Antarctic Polycotylids**
Cretaceous Period	Maastrichitian	70.6-65.5	*D. herschelensis*			*Sulchusuchus erraini*
	Campanian	83.5-70.6	*D. herschelensis, D. osborni, D. bonneri,* and *P. latipinnis,* UNSM 50133, UNSM 55810, ROM 29010		SGU 104a/37	*Sulchusuchus erraini*
	Santonian	85.8-83.5			*Georgiasaurus penzensis*	
	Coniacian	89.3-85.8				MACN Pv 19.781
	Turonian	93.5-89.3	*T. bentonianum, P. quadratus, E. rankini,* and *D. tropicensis*	*T. longicollis* and *M. anguirostris*		
	Cenomanian	99.6-93.5	*P. wellesi, P. haasi*		UMUT MV 19965	
	Albian	112.0-99.6	*E. muddi*		QM F18041	
	Aptian	125.0-112.0				
	Barremian	129.4-125.0				
	Hauterivian	132.9-129.4				
	Valanginian	139.8-132.9				
	Berriasian	145.0-139.8				

Figure 4 Polycotylid Diversity Throughout Time. Compilation of all the polyotylid species occurrence in throughout the Cretaceous period. Cosmopolitan diversity of Polycotylidae occurred early in their evolution or their appearance in the fossil record. Based on Druckenmiller and Russell (2009), but also includes all other known polycotylid species (and potential species) and removal of all leptocleidid taxa.

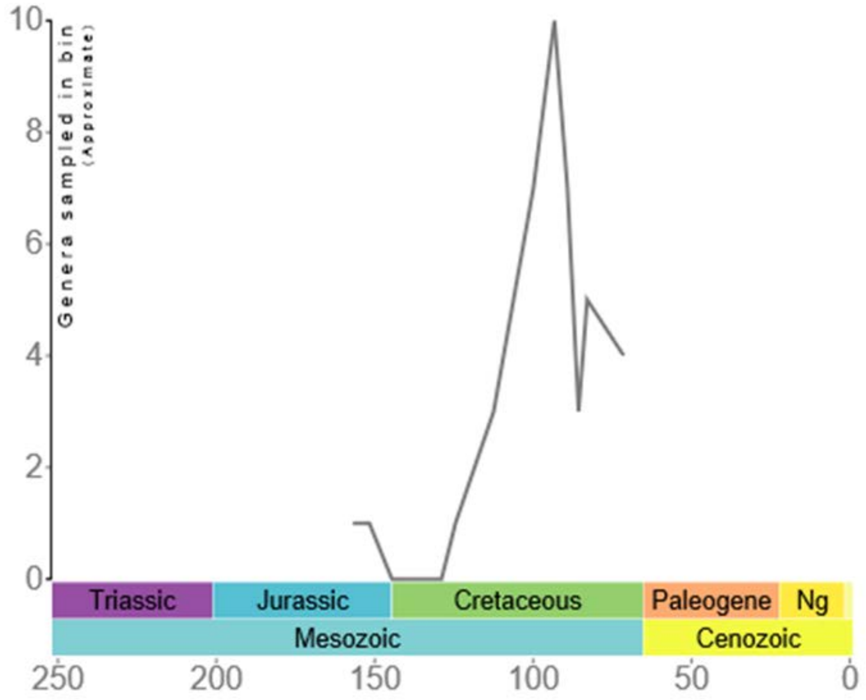

Figure 5 Diversity of polycotylid fossil incidences throughout time. A sharp peak in global fossil abundance for polycotylids is seen during the being of the Late Cretaceous and another smaller peak right before the end of the Cretaceous. These peaks correlate with the Turonian and Campanian peaks in species diversity seen in the Western Interior Seaway. Figure was created by the author in the Paleobiology Database (PaleoBioDB).

Wallace Ranch Specimens

The two fossil skeletons discussed in this thesis both come from the Wallace Ranch of South Dakota. The deposits are from the Sharon Springs member of the Pierre Shale, which is Campanian in age. The two specimens of interest are UNSM 50133 (adult) and UNSM 58810 (juvenile). The two polycotylids may represent the presence of parental care, as the two specimens were found nearby one another, and the total body size and state of ossification of UNSM 58810 seems to indicate that the individual died and a young ontogenetic stage. However, to verify this claim, a detailed quarry map of the two specimens would be essential, but a quarry map only exists for UNSM 58810, and since the two specimens were collected at different times the claim remains speculative. Both specimens were assigned to the species *D. osborni* by Carpenter (1996) and were both treated as juveniles, with the adult stage being KUVP 4001 and 4002. However, both KUVP 4001 and 4002 were determined to be from a different taxon by Adams (1997) as *Trinacromerum bonneri*, and by O'Keefe (2008) as *Dolichorhynchops bonneri*. However, the material from the Wallace Ranch was not thoroughly studied along with the KUVP specimens to determine if the two Wallace Ranch skulls actually belonged *to D. osborni*. In O'Keefe (2008) both the Wallace Ranch skulls were assigned to the family Polycotylidae, but both of the skulls featured characteristics of both *D. bonneri* and *D. osborni*, and the lack of restoration to either of the skulls made the placement of them to a given species tentative.

Based on O'Keefe and Byrd (2012), where the appendicular osteology of UNSM 58810 was examined, the study concluded that the individual was a polycotylid, and most likely belonged to the Family Polycotylidae, due to the morphology of the clavicle being triradiate. In Christina Byrd's unpublished Master's thesis (2012), she further used the morphology of the ilium to place UNSM 58810 into the genus *Dolichorhynchops*. However, the placement of a polycotylid into a specific genus based upon ilial morphology should be done cautiously, as ilium shape and curvature are highly variable throughout Polycotylidae. Examination of the adult skull from the Wallace Ranch UNSM 50133 and the juvenile UNSM 58810 have enabled a more detailed description and cladistic analysis of the material. The skulls of UNSM 55810 and 50133 will be discussed in greater detail in the following chapters.

Geological Background of the Wallace Ranch.

The Wallace Ranch sediments are from the Sharon Springs Formation of the Pierre Shale Group. The Pierre Shale Group is broken into 8 formations, with the Sharon Springs Formation being the oldest. The Sharon Springs Formation is characterized by its dark black, highly organic, fissile shale with abundant bentonites (Gries and Martin 1985). The formation was first described in Kansas, but was later found to extend north into South Dakota (Martin et al. 2007). The Sharon Springs Formation differs from the other parts of the Pierre Shale with its high radioactivity, erosion resistance, and its darker color via organic content clay stones (Martin et al. 2007). The age of the Sharon Springs Formation dates the Mid-Campanian (80.54 ± 0.55 Ma), and the Formation is broken down into three members the Nicholas Creek Member, Boyer Bay Member, and the Burning Brule Member (Figure 6). The Wallace Ranch locality is part of the Burning Brule Member of the Sharon Springs Formation, and is one of the most organic rich shales in the lower Pierre Shale group (Bertog 2011). The skeletons of both UNSM 58810 and UNSM 50133 both contain a high amount of gypsum. The formation of gypsum forms as a precipitate from saline water in sedimentary rocks (Burchett 1970), thus indicating that the two polycotylids were living in a marine environment, rather than a fresh water system.

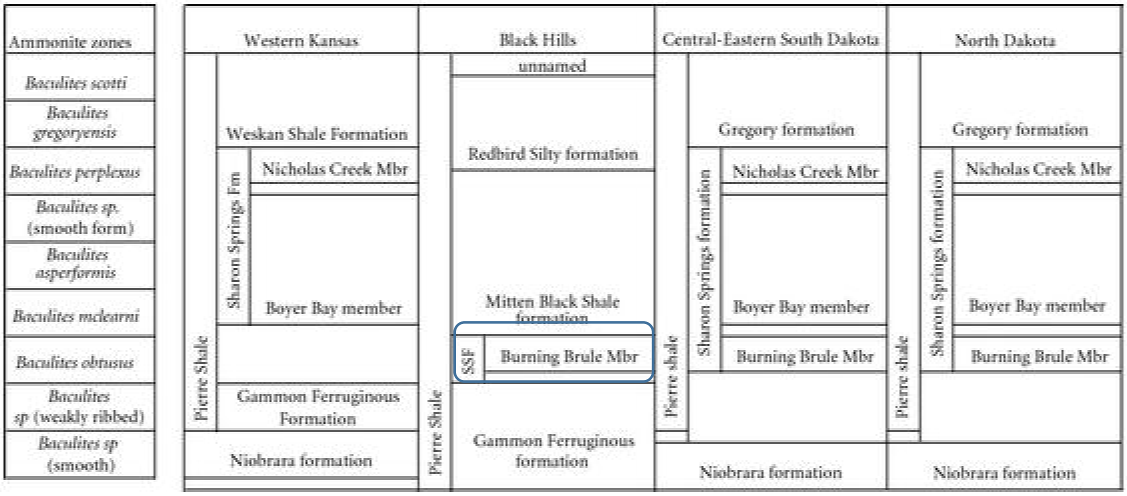

Figure 6 Overview of the Stratigraphy of the Lower Pierre Shale. The Burning Brule Member of the Pierre Shale, which contains the Wallace Ranch, is circled. This figure was taken from Martin et al. (2007).

Dermal and endochondral ossification

The axial skeleton consists of the skull, vertebrae and ribs, while the girdle elements and limbs are considered the appendicular skeleton. The bones of the axial skeleton are formed by either endochondral or dermal ossifications. The endochondral ossifications are first present as cartilage during early development and gradually ossify from their cartilaginous precursors. Cartilage is defined as a type of connective tissue with a rubbery matrix, consisting of chondrocytes contained in lacunae (Romer 1956; Hall 2005). The dermal ossifications are formed from intramembranous ossifications, in which there is no cartilaginous precursor for the bone, and the bone develops directly from condensed mesenchyme (Romer 1956; Hall 2005).

Ossification of the skull.

The skull consists of three regions based upon their developmental origins: the chondrocranium, splanchnocranium, and the dermatocranium. The chondrocanium develops from endochondral ossification and consists of the bones of the brain case, nasal capsule, ethmoid plate, otic capsule, and orbital cartilage (Romer 1956 and Jollie 1962). Most of the chondrocranium arises from the migration of neural crest cells during early development (Romer 1956; Liem et al. 2001; Rieppel 1992; Werneberg et al. 2015). The occipital complex, which consists of the exoccipital, basiocciptal, and supraoccipital arise from mesodermal sclerotome rather than from neural crest cells, and form the posterior margin of the braincase (Liem et al. 2001; Werneberg et al. 2015).

The splanchnocranium arises from the first pharyngeal arch and forms the palatoquadrate cartilage and Meckelian cartilage (Liem et al. 2001; Rieppel 1992; 1993a; Werneberg et al. 2015). From the palatoqudrate cartilage, the epipterygoid bone is formed, while the ossifications of Meckel's cartilage form the quadrate and the articular bones (Liem et al. 2001). Most of the skull bones are dermal in origin, which is unlike a majority of the rest of the postcranial skeleton in tetrapods (Rieppel 1992; 1993a; Liem et al. 2001). The dermatocranium arises from ectomesenchyme cells and the mesodermal dermatome (Werneberg et al. 2015). The ossifications included in the dermatocranium include: the premaxilla, maxilla, nasals, lacrimal, prefrontal, frontal, postfrontal, postorbital, jugal, squamosal, parietal, vomer, palatine, ectopterygoid, pterygoid, parasphenoid, dentary, splenial, angular, surangular, prearticular, and coronoid (Liem et al. 2001).

The sequence of ossification in modern reptilian skulls starts with the dermatocranuim (Rieppel 1992; 1993a; 1993b). The first structures to ossify are the dermal bones of the palate and the rostral area. However, in Testudines, the postorbital ossifications are the first to appear, not the pterygoids as in other diapsids (Rieppel 1993b). The first of the endochondral ossifications to appear in extant diapsids is the ossification of the basioccipital and exoccipitals (Rieppel 1992, 1993a, 1993b). The ossification of the rest of the chondrocranium and splanchnocranium occur after the beginning of the ossification of the postcranial axial skeleton. In *Alligator mississippiensis*, the splanchnocranium ossifies before any of the chodrocranial elements (Rieppel 1992, 1993a, 1993b). *A. mississippiensis*, when born, features the more ossified and sutured cranium than in Lepidosaurs (Rieppel 1993a). The ossification of the cranium throughout ontogeny is speculative in Plesiosauria, the only described material is from R.2417 of *Cryptoclidus eurymerus* and (SMNS 51141) (Brown 1981; Vincent 2010). Interestingly, the juvenile *Cryptoclidus* (SMNS 51141), featured a retroarticular process of the articular bone which was mostly cartilaginous in R.2417 (Brown 1981).

Ossification of the Postcranial Axial Skeleton.

The postcranial axial skeleton includes the vertebral column and ribs. All of the postrcranial axial skeleton is endochodrally derived, except for the gastralia (Liem et al. 2001; Christ et al. 2007). The individual ossified vertebrae possess two main features: the centrum, which replaces the notochord and adds mechanical strength to the vertebral column, and the neural arches. The formation of the neural arches protect the spinal cord and associated vasculature (Fleming et al. 2015). The vertebral column forms embryonically from mesenchyme cells that migrate from the sclerotome portion of the somites and gather around the developing spinal cord and notochord (Liem et al. 2001; Christ et al. 2007; Fleming et al. 2015). The sclerotome then divides further into scleromites (Liem et al. 2001; Christ et al. 2007). The posterior sclerotomite unites with the anterior sclerotomite from the next posterior segment to form a vertebral segment. Ossification begins in the neural arches from a pair of neural plates, then in the centrum, and finally the proximal ends of the ribs (Liem et al. 2001). Growth of the centrum typically starts with a single ossification center derived from the condensed mesenchyme cells of the caudal portion of the scleretomes, which in turn condense and concentrate around the notochord in an intersegmental position (Liem et al. 2001; Christ et al. 2007; Fleming 2015). Bone growth then radiates from the intersegmental concentration of mesenchyme and radiates outward (Fleming et al. 2015). The ribs, like the vertebrae, are also formed from somatic scelertome (Aoyama et al. 2005). The rib developmentally is broken down into proximal and distal ends. The development of proximal end is dependent on the notochord and neural tube, and the distal ends development is dependent on surface ectoderm (Aoyama et al. 2005). The ossification of the ribs occurs after the ossification of the vertebrae are in progress (Aoyama et al. 2005). The fusion pattern of the vertebrae and ribs within Lepidosauria is variable (Maisano 2001). Some Sauria feature an anterior to posterior gradient, like *Lacerta vivipara*, *Lacerta agilis exigua*, and *Cyrtodactylus pubisulcus*. However, this gradient is not seen in most other saurian taxa, which feature a posterior to anterior gradient in the ossification of the postcranial axial column (Rieppel 1992, 1993a, 1993b; Maisano 2001, 2002). Therefore assuming that Plesiosauria followed the viviparous lepidosaurian posterior to anterior ossification gradient, for the postcranial axial column should be cautioned.

CHAPTER 2

NEW PHYLOGENETIC ANALYSIS

The phylogeny of Polycotylidae has been highly contentious over the last twenty years. The Polycotylidae have been placed from nested deeply within the Pliosauroidea, to derived members of the Plesiosauroidea (O'Keefe 2001; Druckenmiller and Russell 2008; Smith and Dyke 2008; Ketchum and Benson 2010). Multiple recent studies have affirmed the placement of the polycotylids within the Plesiosauroidea clade (O'Keefe 2001; Ketchum and Benson 2010; Benson and Druckenmiller 2014). Now that the placement of the clade of Polycotylidae within the Plesiosauroidea has been supported through numerous recent phylogenetic analyses, more focus on the evolutionary relationships within the family is needed (O'Keefe 2001; Ketchum and Benson 2010; Benson et al. 2012a; 2012b; Schumacher and Martin 2015). The purpose of this study is to elucidate the phylogenetic relationships of the taxa within the Polycotylidae, and in so doing, place the UNSM polycotylid specimens into a phylogenetic context.

For this study, all of the North American species, and most of all other polycotylids, were coded from the primary literature and personal observation, using the matrix from Ketchum and Benson (2012b), with the addition of 22 new characters. PAUP 4.0a 147 was used to analyze the matrix, via parsimony. Parsimony was the preferred method of analysis, since the evolution of morphological characters cannot be accurately modeled, and the increased resolving power of using a modeling method might be meaningless (Spencer and Wilberg 2013). In the analysis there was a total of 238 characters analyzed for the 25 taxa. The addition of the 22 new characters were to parse out the morphological differences among the polycotlyid taxa. In contrast to previous studies by Schumacher and Martin (2015), Ketchum and Benson (2010; 2011; Benson et al. 2012b) which utilized PAUP Ratchet to find trees, this analysis used a

Heuristic search method with a TBR branch swapping searching algorithm to search for the most parsimonious trees. Ketchum and Benson 2010 utilized PAUP Ratchet for speed in finding parsimonious trees, since the authors were dealing with 66 taxa, and the use of heuristic or exhaustive search methods would have been too time consuming. However, since this study was only concerned with 25 taxa rather than 66, a more reliable heuristic search was used. The heuristic search criterion was used implementing the TBR (tree bisection and reconnection) branch swapping algorithm to find the most parsimonious trees, with 10,000 replicates. The outgroup taxa were manually constrained, so that the topology found in Schumacher and Martin (2015), and Benson et al. (2012b) was recovered (Figure 7, 8, and 9). The most basal taxon of the outgroup is *Thalassicodracon hawkinsi*, which is a basal pliosaurid and is very distantly related to any of the polycotylids. This further supports that the polycotylids are derived members of the Plesiosauroidea, rather than of the Plisauroidea as previously suggested by other authors (Carpenter 1996; O'Keefe 2001; Ketchum and Benson 2010). The rest of the outgroups follow the same phylogentic pattern found in Benson et al (2012b), with *Plesiosaurus dolichodeirus* being the next taxon to branch off, followed by *Libonectes morgani*, then *Cryptoclidus eurymerus*, and finally *Nichollasaura borealis* branching as the sister taxon to the Polycotylidae. This study did not find the support of the clade Xenopsaria, which consists of the Leptocleidia and the Elasmosauridae which was recovered by Benson and Druckenmiller (2014). However, the focus of this study is concerned with the primary relationships between the polycotylids, not the basal relationships of the Plesiosauroidea clade.

For this analysis, 19 of the total 238 characters were ordered. The character weighting scheme used in the analysis followed the same procedure as Ketchum and Benson (2010; 2011; Benson et al. 2012b). All quantitative characters were treated as ordered for this analysis, and therefore, large changes in character states in quantitative characters would add more steps onto the cladogram. All quantitative characters had up to 26 possible different character states, which is the maximum number of character states possible for MacClade to process. The actual assignment of character states was ascertained via gap coding, which is based on the distribution of mean values for a given character (Schols et al. 2004; Ketchum and Benson 2010, 2011; Benson et al. 2012b). All quantitative characters were given the weight of 1, and all other characters were given a weight of 26 to avoid overweighting quantitative characters which potentially have a large number of steps. The reasoning for treating all quantitative characters as ordered, is that most morphological characters, whether coded quantitatively or qualitatively, are fundamentally quantitative. Therefore, when coding quantitative characters, they should be analyzed as continuous traits (Weins 2001).

Taxonomic units and descriptions

Out-Group

Genus: *Thalassiodracon* Storrs and Taylor (1996)
Species: *Thalassiodracon hawkinsi*

Type Material: BMNH 2018 (lectotype), CAMSM J.46986

Type Locality: Blue Lias Formation, Pre-planorbis Beds, Rhaetian/Hettangian boundary, of Street, Somerset, UK

Age: Rhaetian-Hettangian boundary (Triassic-Jurassic)

Referred Material: CAMSM J.46986

Remarks: Basal plesiosaur, recent phylogenetic analyses place *T. hawkinsi* at the base of the Pliosauroidea clade.

Genus: *Libonectes* Carpenter (1996)

Species: *Libonectes morgani* (Welles, 1949).

Type Material: SMUSMP 69120 (Holotype)

Type Locality: Britton Formation, near Cedar Hill, Texas, USA.

Age: Coniacian

Referred Material: SNUSMP 69120

Remarks**:** Basal elasmosaurian plesiosaur, skull refigured by Carpenter (1996), features a well preserved palate and braincase.

Genus: *Nichollssaura*

Species: *Nichollssaura borealis*

Type Material: TMP 94.122.01

Type Locality: Wabiskaw Member, Clearwater Formation, from near Fort McMurray, Alberta, Canada

Age: Early Albian, Lower Cretaceous

Referred Material: TMP 94.122.01 Druckenmiller & Russell (2008b; 2009)

Remarks: Leptocleidid plesiosaur, recent phylogenies place this taxon as a sister group to the Polycotylids. Material includes a well preserved skull and a nearly complete postcranial skeleton.

Genus: *Plesiosaurus*

Species: *Plesiosaurus dolichodeirus*

Type Material: BMNH 39490, BMNH 41101, OUMNH J.13809

Type Locality: Black Ven Marl Formation, Lower Lias Group, of Charmouth, Dorset, UK

Age: Late Sinemurian, Lower Jurassic

Referred Material: BMNH 39490, BMNH 41101, OUMNH J.13809 Storrs (1997)

Remarks: Early basal plesiosaur, placed as a basal member of the Plesiosauroidea. The palate of *P. dolichodeirus* exhibits the primitive condition for the Plesiosauroidea.

In-Group Taxa

Genus*:* *Polycotylus* Cope (1869)

Species: *Polycotylus latipinnis* Cope (1869)

Type Material: USNM 27678 and AMNH 1735 (holotype), YPM 1125 (paratype)

Type Locality: Smoky Hill Chalk Member, Niobrara Formation, Hesperornis zone, Smoky Hill River, 22.5 km east of Fort Wallace in Logan County, Kansas, USA

Age: Santonian-Campanian, Late Cretaceous

Referred Material: USNM 27678 and AMNH 1735 (holotype), YPM 1125 (paratype)

Remarks: The holotype is split between the USNM and AMNH which consists of a partial ilium, metapodial, vertebrae, and phalanges and propodeal. Paratype, assigned by O'Keefe (2004), which was comprised of a most complete postcranial skeleton and parts of the braincase. Overall large body sized Polycotylid from North America.

Genus: *Dolichorhynchops* Williston (1902)

Species: *Dolichorhynchops osborni* Williston (1902)

Type Material: KUVP 1300 (holotype), FHSM VP404, MCZ 1064

Type Locality: Smoky Hill Chalk Member, Niobrara Formation, Hesperornis Zone of Wallace, Logan County, Kansas, USA

Age: Santonian-Campanian, Late Cretaceous

Referred Material: KUVP 1300 (holotype), FHSM VP404, MCZ 1064

Remarks: Known from multiple specimens, including multiple skulls. The skull has been described by multiple authors, and features a well preserved palate. It was a small body sized Polycotlyid from North America.

Genus: *Dolichorhynchops* Williston (1902)

Species: *Dolichorhynchops bonneri* O'Keefe (2008)

Type Material: KUVP 40002 (Holotype) KUVP 40001 (Paratype)

Type Locality: Wyoming, northern Niobrara County, Johnson Ranch and South Dakota, southern Fall River County, Wallace Ranch

Age: Lower Campanian

Referred Material: KUVP 40002 (Holotype) KUVP 40001 (Paratype)

Remarks: Features a mostly complete skull and a mostly complete postcranium. The individual was first attributed to be an adult *D. osborni* (Carpenter 1996), and was later assigned to the genus Trinacromerum (1997). The skull was re-described by O'Keefe (2008), and was reassigned to the genus Dolichorhynchops.

Genus: *Dolichorhynchops* Williston (1902)

Species: *Dolichorhynchops herschelensis* Sato (2005)

Type Material: RSM P2310.1 Sato (2005)

Type Locality: Southwest of Herschel, Saskatchewan, Canada

Age: Bearpaw Formation (late Campanian to early Maastrichtian, Late Cretaceous)

Referred Material: RSM P2310.1

Remarks: features a mostly complete skull, with a well preserved palate, some vertebrae, paddles, and pectoral and pelvic girdle elements. A small Polycotylid, and one of the last known members of the family.

Genus: *Dolichorhynchops* Williston (1902)

Species: *Dolichorhynchops tropicensis* McKean (2012)

Type Material: MNA V10046

Type Locality: Tropic Shale, Kane County, Utah

Age: Turonian

Referred Material: MNA V10046 MNA V9431

Remarks: Partial skeleton, with fragmentary skull, most of the postcranial material is also present. Small polycotylid plesiosaur, and the earliest occurring member of its genus.

Genus*:* *Trinacromerum* Cragin (1891)

Species: *Trinacromerum bentonianum* Cragin (1888)

Type Material: USNM 10945 (holotype), USNM 10946 (paratype)

Type Locality: Fairport Chalk Member of the Carlile Shale Formation, near the fork of Solomon River, near Downs, Osborne County, Kansas, USA

Age: Turonian

Referred Material: USNM 10945 (holotype), USNM 10946 (paratype) and KUVP 5070

Remarks: Well-known Polycotylid plesiosaur with multiple skeletons and skulls. However, a detailed view of the palate of this taxon is not well known. Overall a moderate sized Polycotylid, larger than *Dolichorhynchops* but smaller than *Polycotylus*.

Genus: *Pahasapasaurus* Schumacher (2007)

Species: *Pahasapasaurus haasi* Schumacher (2007)

Type Material: AMM 98.1.1 (holotype)

Type Locality: Maloney Creek, just south of the Belle Fourche River, Butte County, South Dakota

Age: Cenomanian

Referred Material: AMM 98.1.1 (holotype)

Remarks: partial skull, portions of left front and rear paddles, poorly preserved vertebral column and rib portions

Genus: *Palmula* Albright et al. (2007)

Species: *Palmula quadtraus* Albright et al. (2007)

Type Material: MNA V9442 (holotype)

Type Locality: Tropic Shale Formation, middle–upper Pseudoaspidoceras flexuosum Zone, Grand Staircase-Escalante National Monument, Kane County, Utah, USA

Age: Turonian

Referred Material: MNA V9442 (holotype)

Remarks: Only fragments of the mandible and rostrum, parts of propodials, vertebrae and girdle elements.

Genus: *Eopolycotylus* Albright et al. (2007)

Species: *Eopolycotylus rankini* Albright et al. (2007)

Type Material: MNA V9445 (holotype)

Type Locality: Tropic Shale Formation, middle to upper Pseudoaspidoceras flexuosum Zone, of Glen Canyon National Recreation, Kane County, Utah, USA

Age: Turonian, Late Cretaceous

Referred Material: MNA V9445

Remarks: Only fragmentary remains of the mandible, parts of the propodials, vertebrae and girdle elements.

Genus: *Edgarosaurus* Druckenmiller (2002)

Species: *Edgarosaurus muddi* Druckenmiller (2002)

Type Material: MOR 751 (holotype)

Type Locality: Shell Creek Member, 'Thermopolis Shale' within or just below the *Neogastroplites haasi* zone, of Edgar, Montana, USA

Age: Upper Albian, Early Cretaceous

Referred Material: MOR 751 (holotype)

Remarks: Primitive Polycotylid, with a well preserved skull a few vertebrae with partial front paddle.

Genus: *Thililua* Bardet et al. (2003)

Species: *Thililua longicollis* Bardet et al. (2003)

Type Material: MHNGr.PA.11710

Type Locality: Unit 4 of the Cenomanian–Turonian limestone bar, near Goulmima, Er-Rachidia, Morocco

Age: Early Turonian, Late Cretaceous

Referred Material: MHNGr.PA.11710

Remarks: Well preserved skull and vertebral column. The palate is not prepared, thus inhibiting vital analysis of the skull.

Genus: *Manemergus* Buchy et al. (2005)

Species: *Manemergus anguirostris* Buchy et al. (2005)

Type Material: SMNK-PAL 3861

Type Locality: Goulmima, Morocco

Age: Early Turonian (Late Cretaceous)

Referred Material: SMNK-PAL 3861

Remarks: Features a complete skull, vertebrae, pectoral and pelvic girdles, and propodials.

Genus: *Plesiopleurodon* Carpenter (1996)

Species: *Plesiopleurodon wellesi* Carpenter (1996)

Type Material: CM 2815 (holotype)

Type Locality: Belle Fourche Shale, near Connamp Creek, Rattlesnake Hills, Natrona County, Wyoming, USA

Age: earliest Cenomanian, Upper Cretaceous

Referred Material: CM 2815 (holotype)

Remarks: Initially described as a Pliosaur, but recent analysis has placed the taxon firmly within the base of the Polycotylid family. Only the skull and pectoral girdle has been described for this taxon is known, and the palate has not been prepared.

Genus: QM F18041

Species: QM F18041

Type Material: QM F18041

Type Locality: Lower part of the Allaru Formation, of Richmond, Queensland, Australia

Age: Late Albian

Referred Material:

Remarks: This specimen is not formally described or accessible.

Genus: SDSM 23020

Species: SDSM 23020

Type Material: SDSM 23020

Type Locality: Niobrara Formation, of southwestern South Dakota, Conger Ranch Locality

Age: Lower Campanian

Referred Material: SDSM 23020

Remarks: Nearly complete skull and a mostly complete postcranial skeleton, attributed to the species *P. lattipinnis*.

Genus: unassigned

Species: unassigned

Type Material: UNSM 50133

Type Locality: Sharon Springs Member, of the Pierre Shale of South Dakota

Age: Campanian

Referred Material: UNSM 50133

Remarks: Juvenile Polycotlyid, with a partial skull, most of the vertebral column, paddles and limb girdles.

Genus: unassigned

Species: unassigned

Type Material: UNSM 55180

Type Locality: Sharon Springs Member, of the Pierre Shale in South Dakota

Age: Campanian

Referred Material: UNSM 55180

Remarks: Remains include a complete skull, a few vertebrae, some of the girdle elements and the paddles are present.

Genus: *Sulcusuchus* (O'Gorman and Gasparini 2013)

Species: *Sulcusuchus erraini* (O'Gorman and Gasparini 2013)

Type Material: MPEF 650

Type Locality: La Colonia Formation, Argentina

Age: Campanian/Maastrichtian

Referred Material: MPEF 650

Remarks: Partial skull with fragments of the premaxilla and maxilla, along with well-preserved pterygoid plates.

New Character List

217. Parsphenoid anterior interpterygoid participation

    0= none 1= rounded 2=triangular

218. Squamosal shape in temporal fenestration

    0= broad and curved 1= slender and S-curved

219. Swollen premaxillary process

    0= absent 1= present

220. Pterygoid plate posterior termination

    0= terminate close to the posterior interpterygoid vacuity 1= extends far beyond posterior interpterygoid vacuity

221. Frontal foramen

    0= present 1= absent

222. Pterygoid plate lateral morphology

    0=straight 1= rounded

223. Squamosal orientation

    0= vertical and flush with the back of the skull 1= trending posterior to the occipital condyle

224. Parasphenoid striated

    0= no 1= yes

225. Sagittal crest morphology

    0= none 1= low 2= high 3= sharp peak

226. Position of external nares

    0= anterior to orbit 1= parallel to orbit

227. Frontal presence on rostrum

    0= not on rostrum 1= short extension 2= long process on the rostrum

228. Quadrate ventral morphology

    0= broad and irregular 1= slender projection 2= spherical

229. Parasphenoid morphology

    0= slender 1= robust

230. Anterior interpterygoid vacuity (O’Keefe 2008)

0= absent 1= slit-like 2= broad with round ends

231. Interlocking distal phalanges anterior to fifth phalangeal row (O'Keefe 2008)

0= absent 1= present

232. Coaracoid posterior morphology

0= flat 1= rounded process 2= long pointed process

233. Cadual chevron articulation

0= shared articulation between most caudal vertebrae 1= single articulation with one vertebrae in most of caudal series

234. Number of facets at distal end of humerus

0= 2 1= 3 2= 4 3= 5

235. Number of facets at the distal end of the femur

0= 2 1= 3 2= 4 3= 5

236. Amphocelous vertebrae

0= no/not strongly 1= yes

237. Direction of the ectopterygoid branching off the pterygoid plates

0= horizontal 1= anterior 2=posterior

238. Size of the retroarticular process

0= small 1= enlarged

Results of the Phylogenetic Analysis

The phylogenetic analysis yielded 10 most parsimonious trees. A strict consensus tree (Figure 7), a 50% majority rules consensus tree, and a bootstrap consensus tree (Figure 8) were generated from the ten most parsimonious trees found from the heuristic search. The strict consensus tree and the 50% majority rules consensus trees had the same tree topology and the interrelationships among the taxa were same. The bootstrap consensus tree, constructed via the fast step-wise addition algorithm in PAUP, yielded a polytomy for all of the polycotylid taxa. The bootstrap tree did provide support for the clade of QMF 18041 and Plesiopleurodon wellesi, and the clade formed by the Wallace Ranch polycotylids (Figure 8). The tree length was 10,174, with a consistency index of 0.5251, retention index of 0.5148, homoplasy index of 0.4749, and a rescaled consistency index of 0.2703. The tree length refers to the number of steps, or character state changes that are required to account for the variation in character states seen in all of the analyzed taxa (Baum and Smith 2013). The consistency index measures how the characters fit onto a tree. Trees with a higher consistency index have lower levels of homoplasy than trees with a low consistency index. The homoplasy index indicates the lack of consistency between the tree topology and the distribution of characters states among the taxa (Baum and Smith 2013). The retention index measures the amount of homoplasy, but also measures how well synapomorphies fit on the tree. The retention index is calculated by taking the maximum number of character state changes and subtracting them from the actual number of character changes seen on the tree, and dividing that number by the maximum number of changes on the tree minus the minimum number of character changes in the data matrix. The ranges for the retention index scale are from 0-1, with 0 equaling the maximum homoplasy possible for the set of characters and 1 meaning that there is no homoplasy in any of the characters (Farris 1989). The final analyzed metric is the Rescaled consistency index, which is equal to the consistency index multiplied by the retention index and that number subtracted by 1 (Farris 1989; Baum and Smith 2013).

Next, wildcard taxa were excluded from the analysis. For taxa in which most of the characters for that taxon are unknown, the taxa can destabilize the topology of the trees recovered from a parsimony analysis (Wilkinson 2003; Ketchum and Benson 2010). Pruning of wildcard taxa *a posteriori* does not alter the relationships amongst the remaining taxa in the cladogram. Wildcard taxa are defined as taxa that occupy a range of phylogenetic positions among the most parsimonious trees, and cause the formation of polytomies at the least conclusive clade that the taxon falls within, and thus destabilize the tree (Wilkinson 2003; Ketchum and Benson 2010). To identify wildcard taxa, an Adams consensus tree was generated, and the taxa that formed polytomies in the Adams consensus tree which featured the most missing character information were removed. The taxa that were excluded are *Sulcusuchus eraini*, *Eopolycotylus rankini*, *Pamulasaurus quadratus*, and the holotype material for *Polycotylus latipinnis*. After the exclusion of these OTUs, 2 most parsimonious trees were recovered. The new tree length was 10,076, with a consistency index of 0.5301, a homoplasy index of 0.4699, a retention index of 0.5133, and a rescaled consistency index of 0.2721. The deletion of the wildcard taxa decreased the number of character changes in the most parsimonious trees require by 98 steps and the consistency index increased by 0.005 (Baum and Smith 2013).

Bremer support values were then calculated for each of the nodes of the consensus tree. Bremer support, also known as the decay index, is a measure of support for a clade based on the difference in tree length between the shortest tree that features that clade and the shortest tree that lacks a clade (Baum and Smith 2013). Therefore, the Bremer support value measures how much longer the cladogram could be before the collapse of the clade. Clades that feature low Bremer support are not well supported by the parsimony analysis, and vice versa. Most of the clades for the polycotylid taxa, as seen in Figure 2.3, do not feature high Bremer support values, which are regarded as being 3 or higher (Baum and Smith 2013). Most of the polycotylid clades do not feature high Bremer support values (Figure 9), with only the UNSM specimens having a decay index of 3.

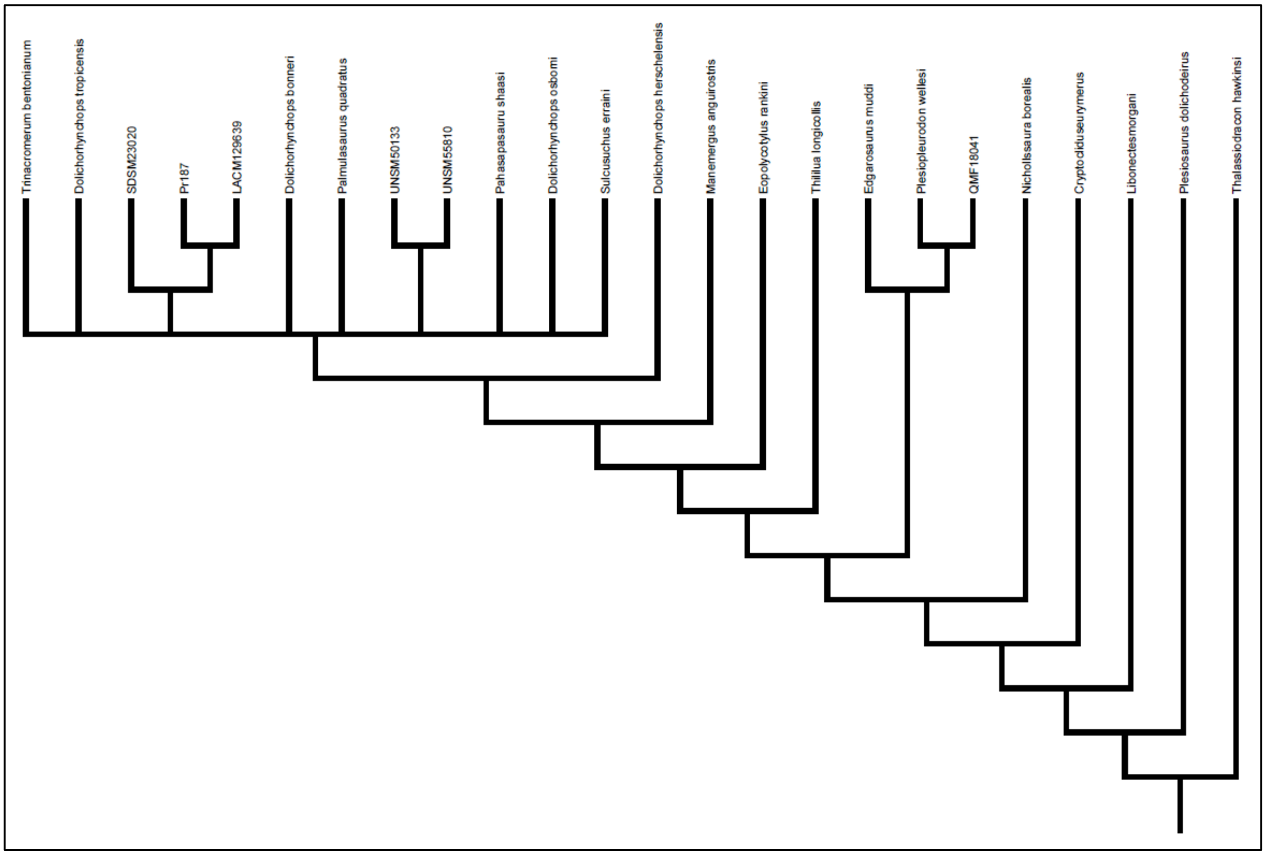

Figure 7 Strict Consensus Tree of the 10 MPTs. The trees were found via a heuristic search criterion. All taxa are present in this analysis.

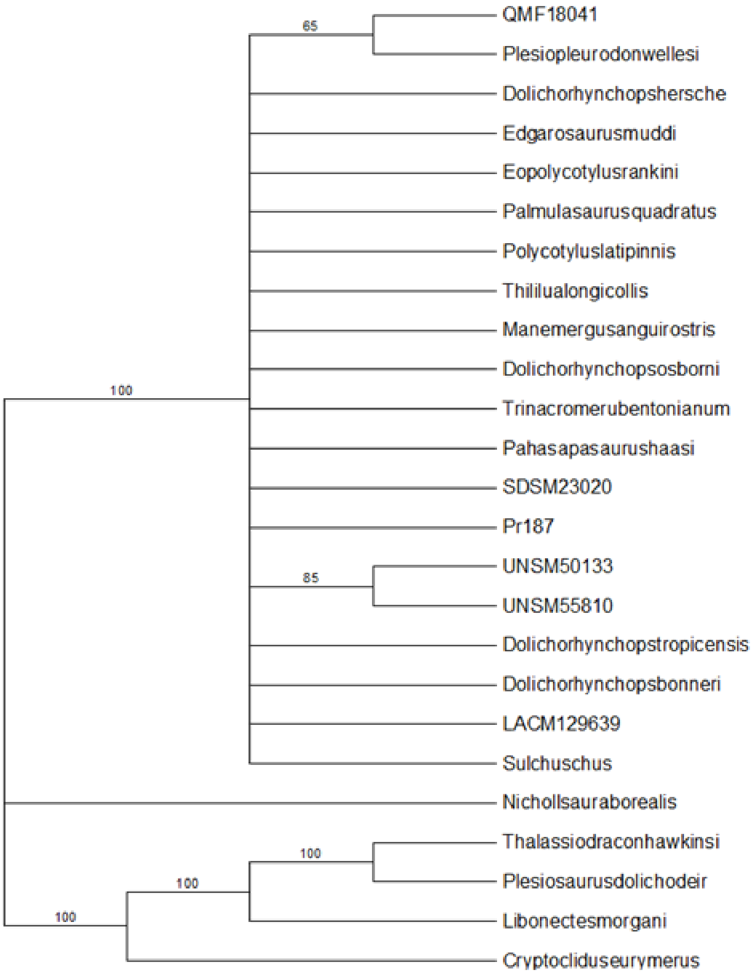

Figure 8. Bootstrap Consensus Tree. The tree was calculated in PAUP 4.0a 147. The numbers on the branches are the bootstrap values. The Polycotylidae was recovered as a monophyletic clade, but the differentiation among the in-group taxa cannot be resolved. The bootstrap consensus tree does provide support for the UNSM clade and the clade of *P. wellesi* and QMF 18041

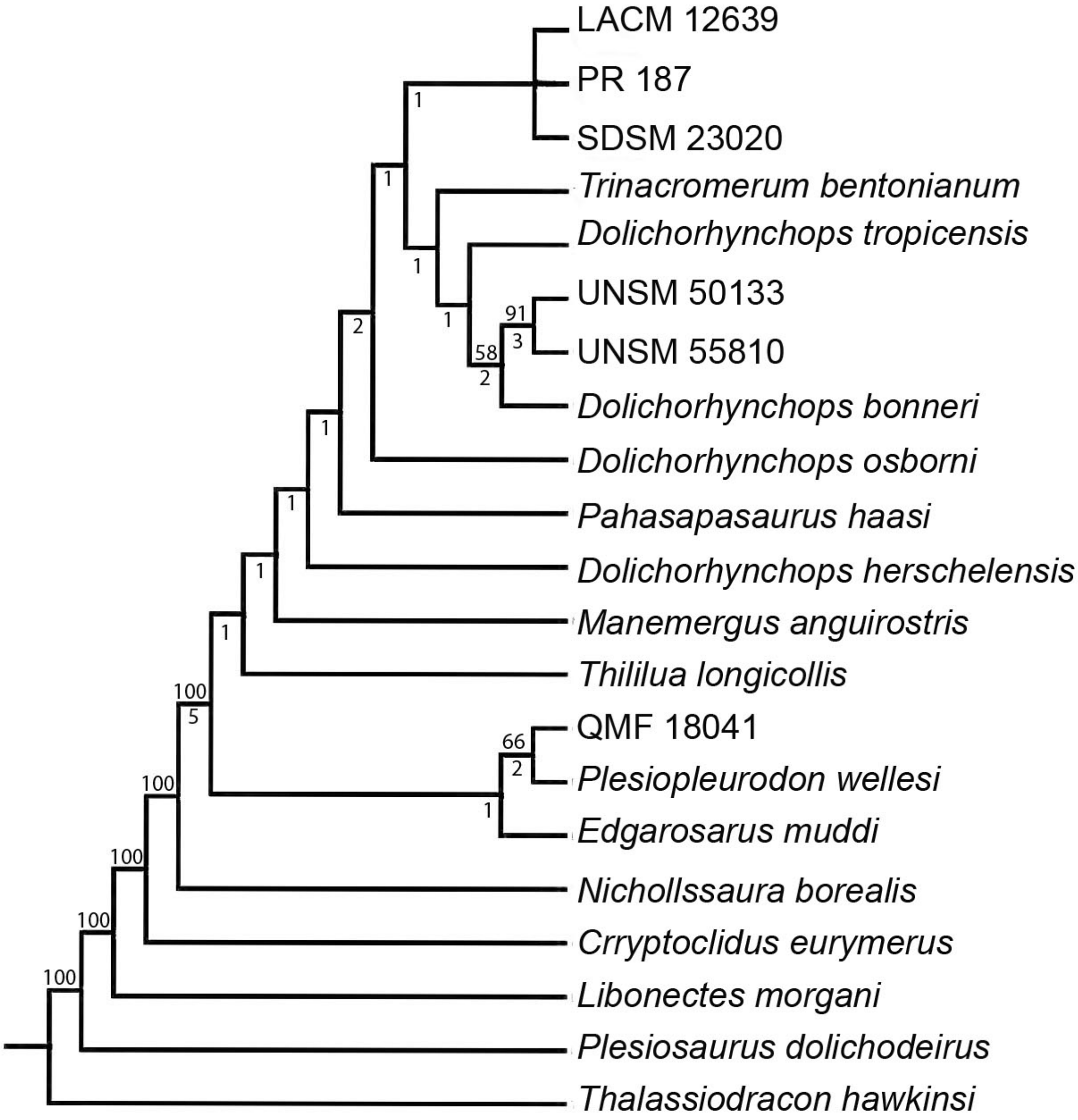

Figure 9 Consensus tree of the 2 MPTs. The tree was found after the exclusion of wildcard taxa. The clade featuring LACM 12639, PR 187, and SDSM 23020 represent the species *Polycotylus latipinnis*. The numerical values on the top of the nodes represent the bootstrap support for each clade (only bootstrap values greater than 50% were reported), and the Bremer support values for each of the clades are reported underneath each of the nodes. All Bremer support values were calculated manually in PAUP 4.0a 147. The taxa excluded from this consensus tree include *Eopolycotylus rankini*, P*almula quadtraus*, *Polycotylus latipinnis* (holotype), and *Sulcusuchus erraini*.

UNSM Specimens.

The Pierre Shale polycotylids UNSM 50133 and UNSM 55810 came out as sister taxa, with a high Bremer support value. Finding that the two UNSM specimens are closely related supports the assignment of the taxa to the same species. Both the adult and the juvenile specimens possess broad parasphenoids with triangular cultiform processes that project far into the anterior interpterygoid vacuity. The two UNSM specimens appear to be closely related to *D. bonneri*, and might represent members of the same species. However, the overall body size of *D. bonneri* is larger than that of the adult Wallace Ranch specimen UNSM 50133. Also, *D. bonneri* differs from the two Wallace ranch specimens by featuring pterygoid plates that do not extend far beyond the posterior interpterygoid vacuity, more anteriorly positioned external nares, and the lack of a large triangular cultiform process of the parashenoid. The characters supporting the monophyly of the Wallace Ranch clade include: the presence of the parasphenoid in the anterior interpterygoid vacuity, the triangular cultiform process, the long extension of the frontal on the rostrum, a robust parasphenoid, and the posterior morphology of the coracoid being flat. Two other polycotylid specimens also seem appear similar to the Wallace ranch polycotylids, ROM 29010 and AMNH 5834. Future analysis of polycotylid systematics should also include ROM 29010 and AMNH 5834 as taxonomic units to see if they are indeed members of the same species as UNSM 50133 and UNSM 55810.

Wildcard Taxa.

The first of the taxa to branch off within the Polycotylidae is *Pamulasaurus quadratus*. First described by Albright et al. (2007) *P. quadratus* consists of fragmentary girdle elements and a portion of the rostrum. This taxon is from the Cenomanian and is not expected to be placed as a basal taxon to all other polycotylids. However due to *P. quadratus'* fragmentary remains, and the fact that its position varies within the ten most parsimonious trees, indicates that P. quadratus is a wildcard taxon. This is also the case for *Eopolycotylus rankini, Polycotylus latipinnis* (holotype material) and *Sulcusuchus erraini.* Until more fossil complete fossil remains of *P. quadratus*, *E. rankini*, and *S. erraini* are obtained, the phylogenetic placement of these taxa within Polycotylidae will remain speculative.

Basal Polycotylids.

The geologically oldest members of the polycotylid family include QMF18041, *P. wellesi*, *E. muddi*, and *Pahasapasaurus haasi*. These four taxon do not form a monophyletic clade, however there is evidence of a basal clade contains *E. muddi*, *P. wellesi*, and QMF18041. QMF1804 is an undescribed polycotylid from Australia, and the nature of the specimen is speculative, since there are no publications formally describing the osteology of the specimen. However, *P. wellesi* was initially described by Carpenter (1996) and partially redescribed by Benson and Druckenmiller (2014). The entire skeleton needs to be redescribed as no palatal view is known from the specimen, and a detailed description of the cranial and postcranial elements is still lacking. When examining the skull of *P. wellsi*, it is clear that the skull resembles that of the leptocliedid, *N. borealis* (Figure 10). Both taxa do not possess the elongated rostrum seen in more derived polycotylids such as *D. osborni* and *P. latipinnis*. The morphology of the surangular, squamosal, and quadrate are very similar between the two species. The posterior extension of the squamosal is oriented so that it points posteriorly rather than vertically. The squamosal is also more gracile in its ventral half in *P. wellesi* and *N. borealis* than in other polycotylids, and the ventral extension of the quadrate is small and spherical. This condition is also seen in *T. bentonianum* and UNSM 50133, but not in other polycotylid species. The surangular in *P. wellesi* and *N. borealis* features a massive dorsal expansion, unlike the more slender jaw of derived polycotylids. Description of the palate of *P. wellesi* is needed to see if it resembled the polycotylid condition of high fenestration and enlongated pterygoids, or an intermediate condition more similar to the leptocleidid condition seen in *N. borealis,* with the large palatines and a mostly closed palate.

Edgarosaurs muddi formed a clade with QMF1804 and *P. wellesi*, when all the taxa were included, and with the exclusion of the wildcard taxa, the basal polycotylid clade of QMF1804 and *P. wellesi* retained a Bremer support value of 2, which was higher than most clades. However, the larger basal polycotylid clade, which also included *P. wellesi,* did not have high Bremer support (Figure 9). Unlike *P. wellesi* and QMF1804, the palate of *E. muddi* is well preserved. The palatal view of *E. muddi* is not as fenestrated as *D. osborni* or *T. bentonianum*, but does feature long and slender anterior projections of the pterygoids, and a well formed anterior interpterygoid vacuity (Figure 11). However, like in the leptocleidids, *E. muddi* has broad and wide palatines which constitute most of the lateral sides of the ventral surface of the skull (Figure 11). This condition is not seen in more derived polycotylids, as the palatines become more slender and reduced. *E. muddi* also features a primitive leptocleidid condition in the number of cervical vertebrae it possesses (26), which is more than any other polycotylid expect for *Polycotylus latipinnis* which also has 26 cervical vertebrae.

Interestingly, *Pahasapasaurus haasi* did not fall out with the rest of the early polycotylids in the basal clade. Rather *P. haasi*, fell out as a derived member of the Polycotylids, more closely related to the later polycotylids such as *Dolichorhynchops osborni* than to *E. muddi* or *P. wellesi*. Unlike the more derived polycotylids, *P. haasi* does not feature an anterior interpterygoid vacuity, and featured the anteriorly broad pterygoids, like a leptocleidid. The rostrum of *P. haasi* is elongated in comparison to overall skull size, like the more derived polycotylids of the late Cretaceous, and unlike *E. muddi*, and *P. wellesi*. Unlike the other 3 basal polycotylids, which form a clade, *P. haasi* and the rest of the more derived polycotylids feature an occipital condyle with the presence of a notochordal pit, the ventral surface of the cervical centra feature a sharp keel dividing two depressions, the absence of longitudinal trough on the posterior half of the lateral surface of the dentary, and the premaxilla and maxilla sutures oriented directly posterirorly and thus parallel for most of their length.

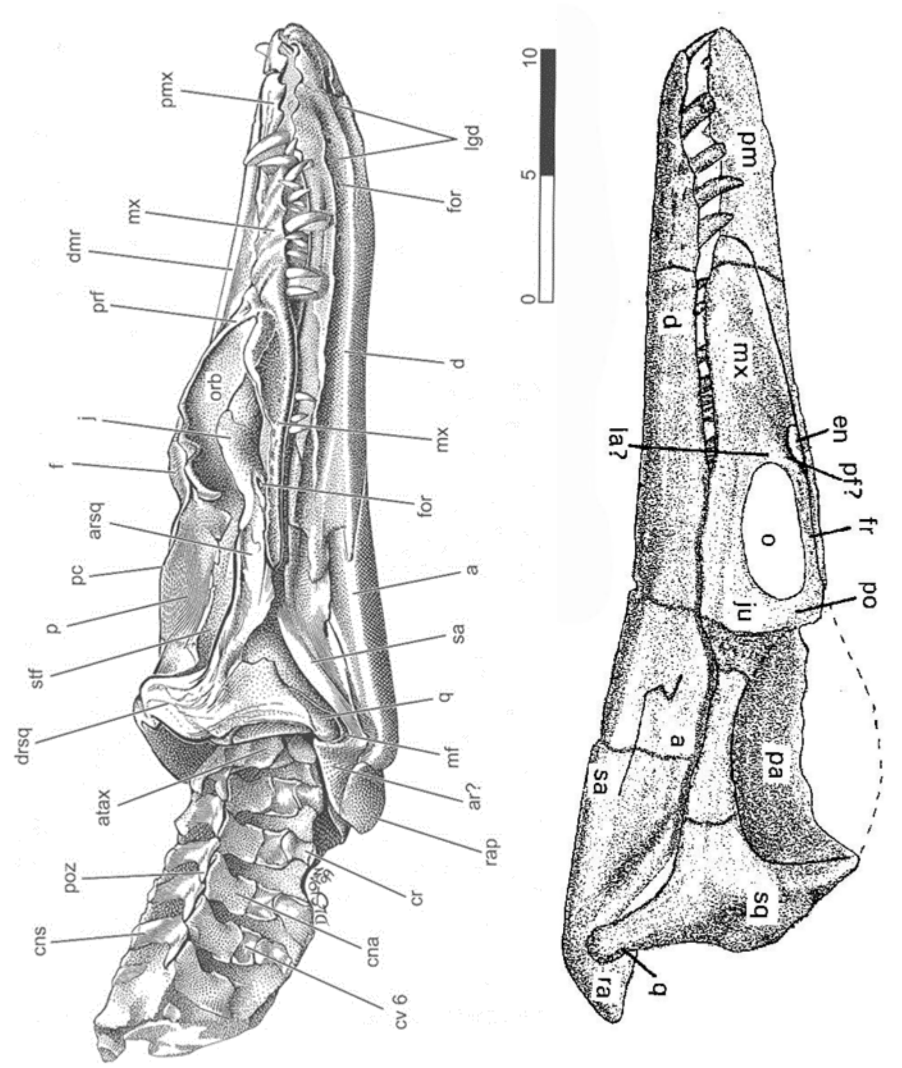

Figure 10 Comparison of the Lateral View *P. wellesi* and *N. borealis*. Both of the skulls lack the elongated rostrum seen in later polycotylids and share similar features of the articulation of the lower jaw and the dorsally tall surangular. Figure adapted from Carpenter (1996) and Druckenmiller and Russell (2008)

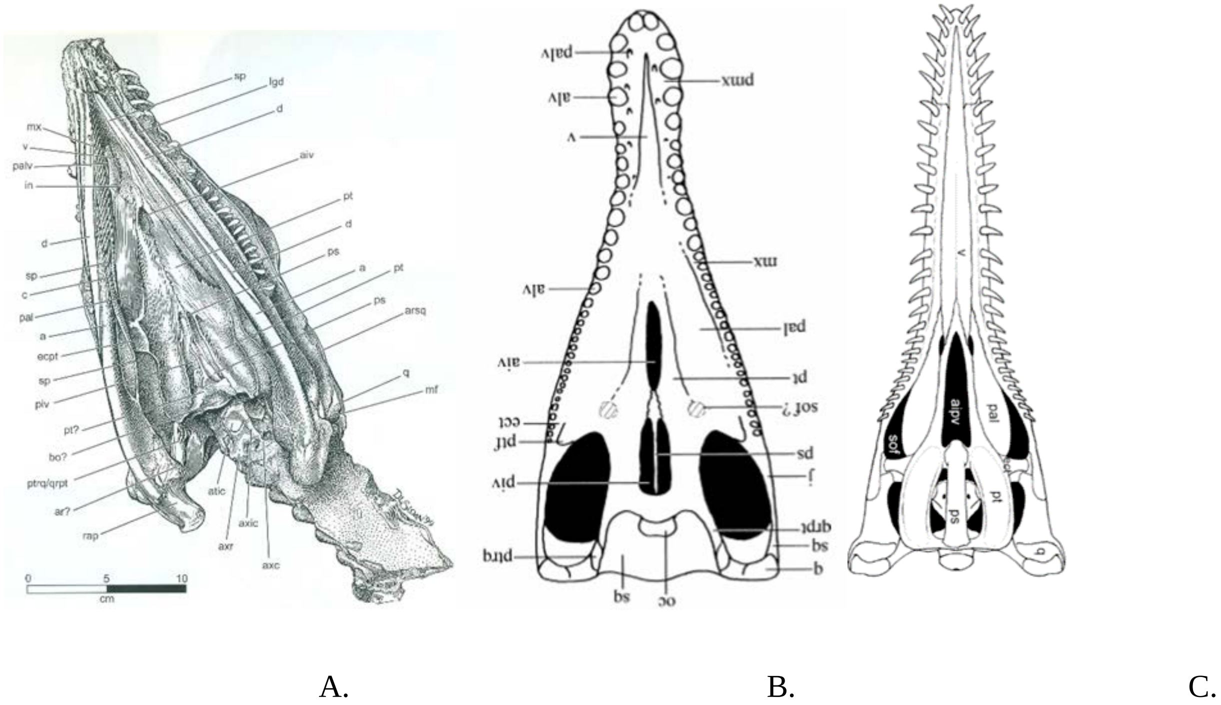

Figure 11 Evolution of the Polycotylid Palate. The Palate of *N. borealis* is on the left (**A.**) which is a derived Leptocleidid, and is considered to be one of the sister taxon to the Polycotylids. (**B.)** The palate view of a primitive Polycotylid *E. muddi*, which appears as an intermediate between Leptocleidid and Polycotylid state of the palate. (**C.)** The palatal view of a derived Polycotylid *D. osborni*. Figure adapted from Druckenmiller and Russell (2008), Druckenmiller (2002), and O'Keefe (2004).

Position of the African Polycotylids.

The two described species from Africa, *Thililua longicolis* and *Manemergus anguirostris*, are both from Turonian age sediments from Morocco (Bardet et al. 2003; Buchy et al. 2005). The skulls of both species feature an elongated rostrum and a low-profile skull with a short sagittal crest. The palates of neither species are well preserved, but the posterior portion of the posterior interpterygoid vacuity is preserved in *M. anguirostris*. The pterygoids resemble the condition seen in *E. muddi*, rather than *D. osborni* or *T. bentonianum*, with straight and narrow pterygoids and a slender parasphenoid bridging the gap of the posterior interpterygoid vacuity. Despite the similarities seen in *T. longicolis* and *M. anguirostris*, the phylogenetic analysis did not support a clade consisting of these two species. *M. anguirostris* is more closely related to the more derived polycotylids than *T. longicolis*. Unlike all of the other polycotylids, in *M. anguirostris* the external naris is not bordered by the premaxilla. Ketchum and Benson (2010) found this to be one of the synapomorphies of the polycotylid clade, but was later corrected in Benson et al. (2012b). *M. anguirostris* does feature two derived charcteristics with all of the other derived polycotlyids, which are not seen in *T. longicolis*. These characters are the participation of the frontal in the external naris, and the parietal extending the to the orbital midlength, which is unlike the condition seen in more basal polycotylids, where the parietal extends only to the level of the temporal bar (Benson et al. 2012b).

Non-Monophyletic *Dolichorhynchops*.

The phylogenetic analysis did not support a monophyletic genus *Dolichorhynchops*. The differentiation of *D. osborni* from *T. bentonianum* has been contested for the last century (Carpenter 1996; 1997; O’Keefe 2004; 2008; Sato 2005). Figure 12 exemplifies the similarities and differences between the skulls of *D. osborni* and *T. bentonianum*, and overall the skulls do appear quite similar. Since the erection of the genus *Dolichorhynchops* by Williston (1902), three additional species have been added to the genus, *D. bonneri*, *D. herschelensis*, and *D. tropicensis*. Only *D. bonneri* has had previous phylogenetic support for placement into the genus (O'Keefe 2008). Other species were erected based solely on whether the specimen featured more characteristics similar to *D. osborni* or *T. bentonainum* (O'Keefe 2008). However, assigning taxa to a genus without first reconstructing the evolutionary history of that group of organisms can lead to the creation of false relationships based on homoplastic characterstics that arise from convergence rather than from common descent (Baum and Smith 2013).

The main characteristics differentiating *D. osborni* from *T. bentonainum* are found in Table 2.1. However, many of these cranial characteristics are variable within the present genus *Dolichorhynchops*. One character, the presence or absence of a cultiform process of the parashpenoid projecting into the anterior interpterygoid vacuity, is found in *D. herschelensis* but not *D. bonneri* and *D. tropicensis*. Therefore the generic boundaries for *Dolichorhynchops* and *Trinacromerum* need to be reevaluated. This analysis finds that the Wallace Ranch specimens, along with *D. tropicensis* and *D. bonneri* are more closely related to *T. bentonainum* than to *D. osborni*. The unambiguous synapomorphies that unite the *Trinacromerum* clade are: the posteromedial extension of the maxilla posterior to the external naris, the ratio of the height of the dentary midway along the mandible versus the height of the dentary at the coronoid process, femoral length versus width ratio, presence of wedge shaped caudal vertebrae, posterior extension of the pterygoid plate extends far behind the posterior interpterygoid vacuity, the absence of a frontal foramen, the posteriorly orientated squamosal, and an ectopterygoid orientation that is not horizontal to the pterygoid plates.

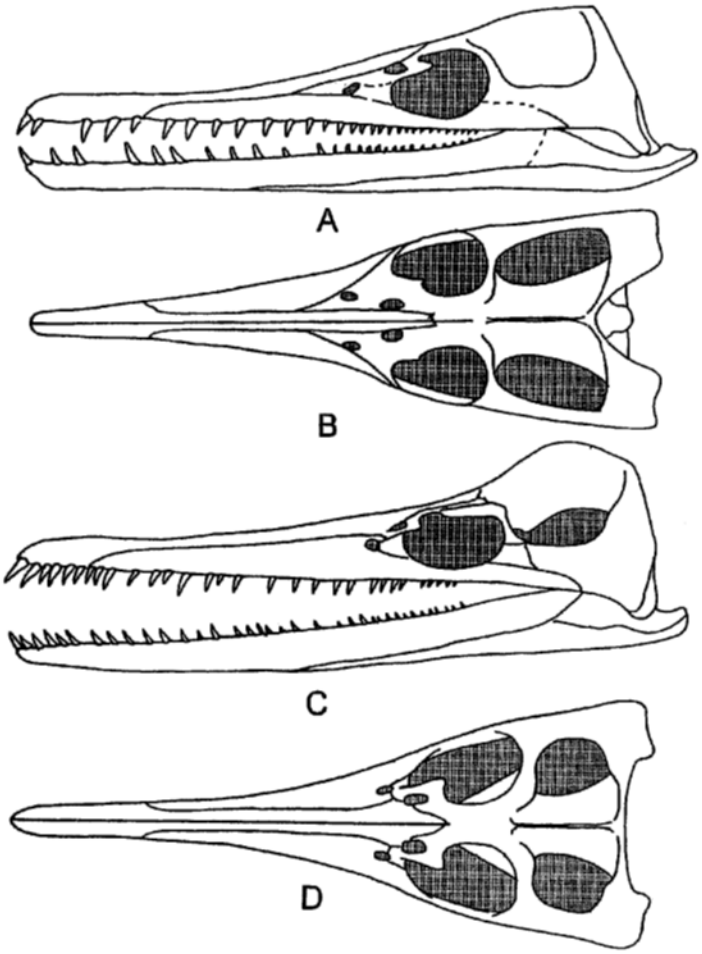

Figure 12 Comparison of *T. bentonainum* and *D. osborni* skulls. *T. bentonainum* (**A.** and **B.**) and *D. osborni* (**C.** and **D.**). Figure is from Carpenter (1996).

Character	***Dolichorhynchops osborni***	***Trinacromerum bentonainum***
Temporal fenestra	short anteroposteriorly and broad temporal fenestra	long and narrow temporal fenestrae
Sagittal crest	short and high sagittal crest	long and low sagittal crest
lateral margin of the posteriorly dished pterygoid	Curved/rounded	Straight
Termination of pterygoid plates behind the posterior interpterygoid vacuity	do not extend posteriorly far past the interpterygoid vacuity	extend posteriorly far past the interpterygoid vacuity
Quadrate flange of the pterygoid	short quadrate flange	long quadrate flange
Ventral exposure of the basisphenoid	basisphenoid is exposed on the ventral margin of the posterior interpterygoid vacuity	basisphenoid is completely covered by the parasphenoid
Ectopterygoid projection	ectopterygoid extends straight laterally from the pterygoid plates	ectopterygoid trends posterolaterally from the pterygoid plates
Parasphenoid projection into the anterior interpterygoid vacuity	projection of the parasphenoid into the anterior interpterygoid vacuity	parashenoid that does not project into the anterior interpterygoid vacuity
Length of mandibular symphysis	long mandibular symphysis	short mandibular symphysis
Number of cervical vertebrae	19	20
Vertebral centra	Lateral and ventral constriction of the centra	No lateral or ventral constriction of the centra

Table 1 Character Comparisons. Comparing the distinguishing character states between *D. osborni* and *T. bentonainum*. Data for characters and states are composited from Cragin (1888), Williston (1908), Carpenter (1996), O’Keefe (2004 and 2008), Sato (2005), and McKean (2012)

Monophyly of *Polycotylus*.

The species *Polycotylus latipinnis* was first described by Cope in (1869) from the Niobrara formation of Kansas. The holotype material for *P. latipinnis* is fragmentary, thus making it a wildcard taxon in recent phylogenetic analysis. However, three other specimens were designated to the *P. latipinnis* species, LACM 129639 (adult and fetus), PR 187 and SDSM 23020 (O'Keefe 2004; O'Keefe and Chiape 2011; Schumacher and Martin 2015). However, no one has phylogenetically checked to ensure that these three specimens, including the recently described complete skeleton by Schumacher and Martin (2015), actually represent one species. In this analysis, the position of the holotype material for *P. latipinnis* was trimmed out of the analysis, as the taxon again proved to be a wildcard taxon in the study, with variable placements within the polycotylidae. The other three specimens attributed to the *P. latipinnis* species were recovered together in a polytomy. The formation of a polytomy between the three purposed *P. latipinnis* specimens supports the idea that the individual specimens belong to the same species, as they phylogenetically could not be conclusively differentiated from one another. All of the *P. latipinnis* specimens feature strongly amphocelous vertebrae, propodials with four distinct epipodail facets, and an elongated posterior process of the coracoids. The only specimen to feature a significant amount of cranial material is SDSM 23020. The head of *P. latipinnis* features long extensions of the frontals onto the rostrum along with the large squared pterygoids that extend behind the occipital condyles.

Comparison with Other Contemporary Phylogenies of Polycotylidae

There are currently two other phylogenies of polycotylid plesiosaurs. The first is by Schumacher and Martin (2015), which is based on the phylogeny from Benson et al (2012b) with the recoding for *D. osborni*, *T. bentonianum*, *P. haasi*, and *P. latipinnis*. The other phylogeny is from Otero (2016), which features the most taxa for Polycotylidae, and is primarily based on the matrix from Benson and Druckenmiller (2014). Both analyses include an extensive number of characters (216 for Schumacher and Martin 2015) and (270 characters for Otero 2016). Both of the data sets have many overlapping characters, and the two matrices' main difference is that the Otero (2016) matrix does not include any ordered characters. The phylogeny from Schumacher and Martin (2015) lacked any test statics. The matrix for Otero (2016) was based entirely off of Benson and Druckenmiller (2014), and no continuous characters were scored quantitatively with gap coding. The reasoning Benson and Druckenmiller (2014) give for not using character ordering or the use of quantitative scoring of characters, was in the hope to generate a more user friendly matrix for future authors. However, Benson and Druckenmiller do warn that their matrix does present characters with subjective character boundaries and that the implications of these boundaries are unknown. The matrix from Benson and Druckenmiller (2014) were also focused on parsing out the differences among Jurassic plesiosaurs, with the inclusion of some Early Cretaceous plesiosaurs. Therefore, the data matrix for Otero (2016) may not be best suited for parsing out the relationships of Late Cretaceous polycotylids.

Comparison with Schumacher and Martin (2015).

The current analysis is based primarily on Schumacher and Martin's (2015) analysis with the addition of 22 novel characters to parse out polycotylid relationships. Both of these phylogenies found a basal polycotylid clade consisting of *P. wellesi* and QMF18041 (Figure 3). However, *E. muddi* was a more basal taxon than the clade of *P. wellesi* and QMF18041 in Schumacher and Martin (2015), but was found as a more derived member of the polycotylid clade in the current analysis. The two taxa *E. rankini* and *P. quadratus* were wildcard taxa in the current analysis due to their lack of character information. *P. quadratus* was found to be the basal most taxon in the current analysis while Schumacher and Martin (2015) found *P. quadratus* as a derived polycotylid, more closely related to the *E. rankini* and the members of the genus *Dolichorhynchops*. The position of the two African polycotylids *T. longicolis* and *M. anguirostris* are the same between the Schumacher and Martin (2015) phylogeny and the current analysis with *T. longicolis* being more basal than *M. anguirostris*. Schumacher and Martin (2015) also did not recover a monophyletic genus *Dolichorhynchops*, like the current study. *P. haasi* is positioned as a more derived polycotylid than the two African polycotlyids but less derived than the Campanian polycotylids, such as *D. osborni* and *T. bentonainum* in both analyses. The position of *D. herschelensis* as a more basal taxon than *D. osborni* is supported in both analyses. The position of the last three taxa in Schumacher and Martin (2015), *T. bentonainum*, *D. osborni*, and *P. latipinnis* differs between the current study, but both phylogenies support the position of these three taxa as more derived members of the polycotylid clade. In Schumacher and Martin (2015), *D. osborni* and *T. bentonainum* were recovered as sister taxa, and *P. latipinnis* was the more basal of the three taxa. In the current analysis, *T. bentonainum* and *P. latipinnis* were recovered as more closely related to one another, and *D. osborni* was the most basal of the three taxa. The similarity of the pterygoid plates and their termination are likely driving the relationship between *T. bentonainum* and *P. latipinnis* in the current analysis, and these characters highlighting the similarities in the palate were not present in the analysis by Schumacher and Martin (2015).

Comparison with Otero (2016).

The analysis from Otero (2016) contrast greatly from any of the other phylogenetic analyses of Polycotylidae systematics. The Otero (2016) analysis recovers *P. wellesi* as one of the most derived of all the polycotylids, and *D. osborni* and *T. bentonainum* as two of the most basal members of the polycotylid clade. The differentiation of derived Leptocleidida characters were not the main focus of the Benson and Druckenmiller (2014) analysis, from which the Otero (2016) analysis is based. Therefore, the relationships amongst the polycotylid taxa are questionable, and additional characters need to be introduced for the more derived Late Cretaceous Leptoleidida taxa. However, the analysis did include the most rigorous taxon sampling of any of polycotylid phylogeny to date, and the work should be expanded upon to see if the similar topologies between the Otero (2016) and the Schumacher and Martin (2015) phylogenies can be ascertained. One of the other major concerns with the Otero (2016) analysis is the subjectivity of the continuous characters used in the analysis. Unlike other analysis performed by Ketchum and Benson (2010) and Benson et al. (2013b) there were no ordered characters, weighting for quantitative characters, and no gap weighting for the continuous characters in the entire matrix.

Future Studies

This study has illustrated that the systematics of polycotylid plesiosaurs is in need of revision. The reassessment of the genera *Dolichorhynchops* and *Trinacromerum* are in need of re-description. All of the other skulls assigned to *D. osborni* from Carpenter (1996) need to be phylogenetically analyzed to see whether they are correctly assigned to the appropriate species. Also, *T. kirki*, *P. wellesi*, and QMF 10481 need re-descriptions so that they can as well be included in future phylogenetic analyses. Another priority will be to evaluate and incorporate the data matrix from Otero (2016) with the current analysis, and see if the differing phylogenies can be resolved with accurate character weighting and ordering of different character states. The goal for future research will be to evaluate every fairly complete polycotylid skeleton, especially the plethora assigned to *D. osborni,* and more accurately resolve the evolutionary history of the polycotylid plesiosaurs.

Proposed Formal Diagnoses for Polycotylidae taxa

Polycotylidae

-Cope (1869), modified definition from O'Keefe (2001, 2004, 2008)

Diagnosis: The following unique possession of the following characters denote the clade Polycotylidae: Neck length short, possessing a reduced number of cervical vertebrae; cervical vertebrae compressed anteriorly-dorsally; ischium longer than pubis; maxillary/squamosal suture present and formed by posterior expansion of maxilla; pterygoids with distinct medial processes that meets behind posterior interpterygoid vacuities; pterygoid plate present and dished; mandibular symphysis scoop-like or long; splenial included in mandibular symphysis; longitudenal pectoral bar present and formed by clavicle and coracoid; supernumerary ossifications in propodial and epipodial rows.

Proposed New Diagnosis: Shape of the dorsmedian ridge of the premaxilla is broad, coronoid participates in the mandibular symphysis, preaxial region of the radius is straight or convex, and the quantitative characters 1) C, 2) L, 112) H, 154) 9, 162) 5, 175) 8

The Genus *Dolichorhynchops*

-Williston (1903), modified definition from O'Keefe (2008)

Diagnosis: The following unique possession of the following characters denotes the genus *Dolichorhynchops*: Polycotylid plesiosaurs with 19 or 20 cervical vertebrae; 18-20 teeth in mandibular symphysis; short and very high sagittal crest; vertical suspensorium; temporal fenestra short antero-posteriorly and broad; orbits relatively large and round; scapula with distinct posterior bend at midshaft; epipodials shorter than broad and lacking antebrachial foramen; coracoid with lateral spur; haemal arch facets confined mainly to the posterior centrum face.

Proposed New Diagnoses: Genus is in need of revision, not recovered in current analysis as monophyletic.

Dolichorhynchops osborni

-Williston (1903), modified definition from O'Keefe (2008)

Diagnosis: The following unique combination of the following characters denotes the species: Small body size; angulars reach into symphysis but to not meet anterior to splenials; tooth crowns small and long relative to height; pineal foramen present; lateral plates of pterygoids wide with round lateral margins, ectopterygoid not carried on distinct pterygoid process, parasphenoid has well-developed anterior process projecting into anterior interpterygoid vacuity; anterior interpterygoid vacuity extends anteriorly between internal nares; dorsal vertebral centra not compressed; humerus sigmoid but long and gracile, with poorly defined facets for supernumerary ossifications; ilium with pointed proximal end, pubis possesses distinct lateral process.

Proposed New Diagnosis: Morphology of the posterior ramus of the pterygoid does not form a squared lappet, a straight ilium shaft, absence of anterolateral cornu of the pubis, presence of a large dorsomedian trough or rugosity of the prearticular, a rounded lateral margin of the pterygoid, a high sagittal crest, and vertebrae that are not amphocelous

Dolichorhynchops bonneri

-Adams (1997) (originally described as *Trinocromerum bonneri*), modified definition from O'Keefe (2008)

Diagnosis: The following unique combination of the following characters denotes the species: large body size; angulars reach forward to meet on the midline on the ventral surface of the mandible; teeth crowns large and broad relative to height; symphysis long; supraorbital mass present; anterior interpterygoid vacuity terminates posterior to internal nares; parasphenoid without anterior process projecting into anterior interpterygoid vacuity; pterygoid with lateral process carrying the ectopterygoid; lateral pterygoid plates narrow and not curved; dorsal vertebrae strongly compressed; humerus sigmoid but short and robust, with clear facets for supernumary ossifications; tongue-and-groove articulations between phalanges; ilium with a straight shaft and blunt proximal end; pubis lacks distinct lateral process.

Proposed New Diagnosis: Straight ilium shaft, pterygoid plate that terminates close to the posterior interpterygoid vacuity, and the quantitative character 154) 4.

Dolichorhynhops herschelensis

-Sato (2005)

Diagnosis: The following characteristics distinguish D. herschelensis from D. osborni: smaller size as an adult, sharp rise in front of parietal crest, and narrowed dorsal end of the ilium.

Proposed New Diagnosis: Prominent dorsomedian ridge of the premaxilla, combined width of the cervical zygopophyses are broader than the centrum, and a coracoid with long pointed posterior process.

Dolichorhynchops tropicensis

-McKean (2012)

Diagnosis: Small polycotylid, flat anterior margin of the paraspenoid, greater size range in teeth than other *Dolichorhynchops* species, moderately constricted dorsal vertebral centra, cheveron facets on anterior and posterior margins of caudal vertebrae, straight anterior margin and narrowed distal end of scapula, anterior process of coracoids divergent without meeting at midline, lack of clavicular notch on coracoids, curved ilium, sacral end of ilium broad and laterally flattened, well-defined facets for epipodials on propodials.

Proposed New Diagnosis: Shape of the squamosal in the temporal fenestration is broad and curved, two facets at the distal end of the femur, and vertebrae that are not strongly amphocelous.

Dolichorhynchops Skulls	Attributed Species	Skull Length	Geological Age
UCM 35059	*D. osborni*	45 cm	Early Campanian
MCZ 1064	*D. osborni*	47 cm	Early Campanian
FHSM VP-404	*D. osborni*	51.3 cm	Early Campanian
KUVP 1300	*D. osborni*	57 cm	Early Campanian
UNSM 50133	*D. osborni?*	61.8 cm	Early Campanian
UNSM 55810	*D. osborni?*	34 cm	Early Campanian
AMNH 5834	*D. osborni*	74.5 cm	Early Campanian
KUVP 40001	*D. bonneri*	98 cm	Campanian
KUVP 4002	*D. bonneri*	?	Campanian
ROM 29010	*D. bonneri*	70 cm	Campanian
RSM P2310.1	*D. herschelensis*	49 cm	Campanian-Maastrichtian
MNA V10046	*D. tropicensis*	56.7 cm	Turonian

Table 2 *Dolichorhynchops* Skulls. List of all the skulls assigned to the genus *Dolichorhynchops* with total skull length, and the age of corresponding geologic ages the specimens are from.

Trinocromerum bentonianum

-Cragin (1888), modified definition from O'Keefe (2008)

Diagnosis: The following unique combination of the following characters denotes the species: Large body size; teeth are robust with coarse striations like *Polycotylus lattipinnis* and unlike the slender teeth with fine striations of *Dolichorhynchops*. Temporal fenestra long and narrow, but are short and wide in *Dolichorhynchops*, suspensorium inclined posteriorly, not vertical as *D. osborni*. Pterygoid plates extend posteriorly beyond the posterior interpterygoid fenestra, pterygoid process of quadrate longer than *D. osborni*. 20 cervical vertebrae 3 pectoral, 23 dorsals. Centra without lateral and ventral construction as in *D. osborni* and *P. latipinnis*

Proposed New Diagnosis: Concavity of the articular face of the cervical vertebrae are gently concave, a straight ilium shaft, and a slender ventral projection of the quadrate

Trinacromerum bentonianum skulls	Skull length	Geological Age
USNM 10945	?	Turonian
USNM 10946	≈ 70 cm	Turonian
KUVP 1325	?	Turonian
KUVP 5070	74.5 cm	Turonian
YPM 1129	75 cm	Turonian
SM 3025	93 cm	Turonian

Figure 3 *Trinacromerum* Skulls. List of all the skulls assigned to the genus *Trinacromerum*, with the corresponding skull length, and the corresponding geologic age of each specimen.

Pahasapasaurus haasi

-Schumacher (2007)

Diagnosis: The following unique combination of the following characters denotes the species: Large body size; long rostrum; anterior interpterygoid vacuity absent; pterygoids united along midline anterior to parasphenoid; parasphenoid relatively robust element, possessing prominent ventral keel and sutured to dorsal surface of pterygoids; pineal foramen absent; temporal fenestra elongate (as in *Trinacromerum)*; symphysis elongate and including the splenial, encompassing the first 12 dentary teeth; teeth faintly striate on medial face; homodont dentition; teeth relatively robust; humerus sigmoidally curved; propodials bearing three distal facets and only a minor degree of posterodistal expansion; epipodials longer than wide, bearing distinct antebrachial foramen; phalanges rounded and elongate

Proposed New Diagnosis: prefrontal does not participate in the external naris, absence of the anterior interpterygoid vacuity, longitudinal medial crest of the mandible is present and weakly developed, 6 premaxillary teeth, concavity of the articular faces of the cervical centra are gently concave, preaxial margin of the humerus features a protuberance, the ulna postaxial margin is concave, and two facets at the distal end of the femur.

Polycotylus latipinnis

-Cope (1869), modified definitions from O'Keefe (2008), and Schumacher and Martin 92015)

Diagnosis: The following unique combination of the following characters denotes the species: Large body size; possessing 26 cervical vertebrae; ischia very long; humerus with pronounced sigmoid curvature and four distinct facets for articulation with ossification of epipodial row; robust, heavily-striated teeth; narrow central plate of pterygoid; low sagittal crest and robust epipterygoid; chevrons borne equally by adjacent caudal vertebrae; anterior edge of ilium posteriorly curved.

Proposed New Diagnosis: Scapula blade is postriodistally weakly inflected, ilium tubercle on the posterior surface around the midlength is present, a high sagittal crest, and the quantitative character 118) C.

Palmulasaurus quadtraus

-Albright et al. (2007)

Diagnosis: The following unique combination of the following characters denotes the species: Small body size; distinctly polygonal (i.e., nearly equi-dimensional) radius, ulna, tibia, and fibula, unlike short and broad epipodials of all other polycotylids exclusive of Palmulainae, subfamily. Four to seven pairs of premaxillary teeth (five in MNA V9442), no caniniform teeth, and a long mandibular symphysis.

Eopolycotylus rankini

-Albright et al. (2007)

Diagnosis: The following unique combination of the following characters denotes the species: Moderately sized polycotylid plesiosaur; resembles *P. latipinnis* in having stout and coarsely striated teeth unlike *D. osborni* which has slender teeth with fine striations and *T. bentonianum*, which has slender teeth with coarse striations; resembles *P. latipinnis* and *D. osborni*, but differs from *T. bentonianum*, in having non cylinder-like, but laterally and ventrally constricted vertebral centra; resembles *P. latipinnis*, but differs from *D. osborni* and *T. bentonianum*, in having some centra compressed anteroposteriorly, although not to the extent seen in *P. latipinnis*; resembles *T. bentonianum* in having lateral foramina on dorsal vertebrae; interclavicle, clavicle, scapula, and coracoid very similar to *Dolichorhynchops* and *Trinacromerum;* humerus resembles P. latipinnis in having four facets for articulation of epipodials, but differs in lacking greatly broadened distal end; humerus also differs from P. *latipinnis* and all other polycotylids in having short, broad, dorsoventrally compressed, less sigmoidal neck; femur differs from *P. latipinnis* in shorter neck and lack of greatly broadened distal end; ilium nearly identical to *P. latipinnis* in curvature and tapered sacral end, unlike the straight ilium with expanded sacral end of *T. bentonianum*; pubis very similar to *T. bentonianum* in lacking scalloped anterolateral edge seen in *T. kirki* and *P. latipinnis*; ischia very similar to *Trinacromerum*, not tapered posteriorly as in *P. latipinnis*, not as broad anteriorly as in *D. osborni*.

Edgarosaurus muddi

-Druckenmiller (2002)

Diagnosis: The following unique combination of the following characters denotes the species: Moderately sized (approximately 3.5 m in length), short-necked plesiosaur possessing the following suite of characters: pineal foramen present (absent in *Dolichorhynchops* and *Trinacromerum*); fenestra ovalis present (absent in *Dolichorhynchops*); suspensorium vertically oriented (angled posteriorly in *Plesiopleurodon* and *Dolichorhynchops*); six to seven premaxillary teeth (commonly five to six in *Dolichorhynchops*, five in *Trinacromerum bonneri*); caniniform teeth present (absent in *Dolichorhynchops* and *Trinacromerum*); relatively short mandibular symphysis bearing six pairs of dentary teeth (eight in *Plesiopleurodon*, 18–20 in *Dolichorhynchops*); 26 cervical vertebrae (19 in *Dolichorhynchops*, 20 in *Trinacromerum*); forelimb phalangeal formula 7-11-10-9-9

Proposed New Diagnosis: Squamosal oriented posteriorly trending posterior to the occipital condyle, a broad ventral projection of the quadrate, quantitative characters 155) 0, and 162) 0.

Thililua longicollis

-Bardet et al. (2003)

Diagnosis: The following unique combination of the following characters denotes the species: The premaxillae have swollen lateral processes between the external nares and the frontal foramina (absent at least in *Dolichorhynchops* and *Trinacromerum*; the orbits are regularly oval, without lateral processes (unlike *Dolichorhynchops* and *Trinacromerum*; the mandibular symphysis bears 15 pairs of teeth, much more than in Edgarosaurus (6) and less than in *Polycotylus* (20) and *Dolichorhynchops* (18 to 21); the dental formula includes five premaxillary, at least 22 maxillary and 29 dentary teeth (versus commonly 5–6/29/25–26 in *Dolichorhynchops*; 5–6/34/34 in *Trinacromerum*; ?/34/38 in Polycotylus;6 –7/26/29–31 in Edgarosaurus; unknown in *Sulcusuchus* and *Georgiasaurus*); the neck includes a relatively high number of cervical vertebrae (30), as compared to *Dolichorhynchops* (19), *Trinacromerum* (20), *Polycotylus* and *Edgarosaurus* (both 26); all the cervical centra but the anteriormost ones have a length more than 80% of the height, and are nearly as long as high between the cervical 19 to 22 (Table 2) (in other polycotylids, the mid-toposterior cervical centra are shorter and the ratio length/height does not exceed 0.75; the neck centra bear laterally a longitudinal ridge between the cervical 9 to 22, which is paired from the cervicals 19 to 22 (no lateral ridges are known in other polycotylids). The occurrence of lateral ridges on cervical vertebrae is convergently acquired by long-necked elasmosaurids. However, *Thililua* differs from elasmosaurids in that the number of cervical vertebrae is rather low (30 versus more than 40), the centra have rounded (versus oval or binocular) articular surfaces, whose length never exceeds the height.

Proposed New Diagnosis: Premaxilla participates in the external naris, lateral surface if anterior cervical centra feature a longitudinal ridge, the quantitative characters 2) N, and 118) E.

Manemergus anguirostris

-Buchy et al. (2005)

Diagnosis: The following unique combination of the following characters denotes the species: Rostrum represents 55% of the skull, rostrum is hemcylindrical over the rostral portion, the postorbital segment is subrectangular on dorsal view, the temporal bar is as high as the orbit, the suspensorium is vertical, the squamosal forms a dorsal shelf is overhanging the atlas and axis. A paired frontal foramen and lies level with the rostral margin of the orbits, it is bordered laterally by the prefrontal, the facial process of the premaxilla is regularly tapers caudally contacting the parietal level with the caudal margin of the external naris, teeth are slender and uniform in size, tooh formula: 5 premaxillary 10 maxillary 15 dentary including 9 symphysial teeth, 25 cervical 3 pectoral and 15 dorsal vertebrae, in the cranial portion the interclavicle is expanded laterally possessing wings that contact the clavicle, the interclavicle is restricted caudally to a rod-like median process

Proposed New Diagnosis: Premaxilla termination shallowly interdigitating suture with the frontal or parietal, pineal foramen located in the center of the temporal fenestra, an enlarged retroarticular process, the quantitative characters 1) 6, 111) 0, and 112) E.

Plesiopleurodon wellesi

-Carpenter (1996)

Diagnosis: The following unique combination of the following characters denotes the species: mandible with long symphysis bearing 8 pairs of large caniform teeth; teeth are circular in cross section and have a nearly smooth outer surface with except near the base (fine striations) cervical ribs are single-headed, coracoid with long, slender interpectoral bar; post glenoid margin of the coracoid is deeply notched.

Proposed New Diagnosis: Circumorbital margin is marked by a raised ridge, position of the mandibular glenoid fossa is coplanar with the occipital condyle, the quantitative characters 1) 5, and 112) D

Georgiasaurus penzensis

- Otschev (1976), Sato (2005), and Arkhangelsky, Averianov, and Pervushov (2007)

Diagnosis: A large polycotylid from the Santonian of the Penza region. Pictures and description of the material are scarce. Sato (2005) stated that it did feature a parasphenoid that projected into the anterior interpterygoid vacuity, and an elongated rostrum. Arkhangelsky et al. (2007) suggested that SGU 104a/37 from the Saratov Region, which is Campanian in age may be synonymous with the former. Both specimens are known for having an elongated mandibular symphysis. The SGU 104a/37 specimen, and possibly *Georgiasaurus*, also features splenials that reach the anterior end of the mandibular symphysis.

Sulchusuchus erraini

-Gasparini and Spalletti (1990), Gasparini, Casadio, Fernandez, and Salgado (2001), and O’Gorman and Gasparini (2013)

Diagnosis: Features anteriorly broad, dished pterygoids with a straight lateral edge, and a long rostrum in comparison to overall skull size.

CHAPTER 3

INTRODUCTION

This chapter focuses on the description of the axial osteology of the juvenile Wallace Ranch polycotylid (UNSM 55810). The primary focus is on the cranial osteology, as there are few preserved skulls of juvenile plesiosaurs (Vincent 2010). The state and patterns of the axial column ossification will be compared to other plesiosaurs, as well as to extant diapsids in an attempt to determine the ontogenetic stage of the UNSM 55180. The final part of the chapter focuses on the allometric growth patterns of the polycotylids, and some of the morphological trends of the clade.

General Polycotylid Cranial Anatomy

The general plan for the polycotylid skull is conserved throughout the family (Carpenter 1996; Druckenmiller 2002; O'Keefe 2004, 2008; Sato 2011). The skull of a polycotylid typically features an elongated rostrum and a fenestrated palate with large pterygoid plates. The rostral portion of the polycotylid skull is comprised medially of the premaxilla and laterally of the maxilla. As the maxilla extends anterior on the rostrum, it thins until it terminates, leaving the most anterior portion of the rostrum consisting solely of the premaxilla. In polycotylids, the premaxilla generally bares 5 to 6 teeth (Carpenter 1996; O'Keefe 2004, 2008; Sato 2011; McKean 2012; Schumacher and Martin 2015). The posterior portion of the premaxilla continues behind the rostrum and splits the frontal bones (Carpenter 1996; Druckenmiller 2002; O'Keefe 2004, 2008; Sato 2011; Schumacher and Martin 2015). In most polycotylids, the premaxilla terminate posteriorly in a suture with the parietal bone, however this is not seen in *E. muddi*, where the parietal meets the postfrontal (Carpenter 1996; Druckenmiller 2002; O'Keefe 2004, 2008). The maxilla in a polycotylid constitutes the ventral portion of the external naris; as well as, featuring a posterior projection that comprises the bottom of the orbit and sutures with the squamosal (O'Keefe 2004, 2008). The bones of the external naris vary in polycotylids. *E. muddi* features the external naris consisting of the maxilla posteriorly, and the prefrontal dorsally (Druckenmiller 2002). *P. wellesi* features the maxilla, premaxilla and frontal bones comprising the external naris (Carpenter 1996). The external naris of *T. longicolis* consists of the maxilla, premaxilla and prefrontal (Bardet et al 2003). While the derived polycotylids, such a *D. bonneri*, *D. osborni*, *D. tropicensis*, *T. bentonianum*, and *P. latipinnis* feature an external naris which is composed ventrally of the maxilla, dorsally by the frontal, and posteriorly by the prefrontal bone (Carpenter 1996; O'Keefe 2004, 2008; McKean 2012; Schumacher and Martin 2015). The orbit margin of a polycotylid has been illustrated by O'Keefe (2004, 2008) (Figure 14), with the orbit anteriorly consisting of the prefrontal bone anteriorly, the frontal bone and supraotbital dorsally, the posterior margin consisting of the postorbital superior to the jugal bone, and the bottom portion consisting of the maxilla. Posterior to the orbit is the temporal fenestra. The lateral margin of the temporal fenestra is comprised anteriorly by the postorbital, jugal, and the maxilla. Most of the lateral portion of the temporal fenestra consists of the squamosal and partially of the quadrate, which arches and unite at the posterior apex of the skull. The position of the arch also varies in the polycotylids, with some polycotylids like *T. bentonianum* and UNSM 50133 having the arched oriented posteriorly. The posterior orientation of the inferior portion of the squamosal arch allows for a jaw articulation posterior to the rest of the skull, possibly increasing the maximum gap of organism. In *D. osborni*, the position of the inferior portion of the squamosal arch is oriented vertically, so that the jaw articulation was flush with the posterior portion of the skull (Carpenter 1996). The medial portion of the skull, between the temporal fenestrae consists of the parietal bone. The parietal bears a sagittal crest in the polycotylid species, which has been utilized as a character marking species dissimilarities. *D. osborni*, *D. herschelensis*, *D. bonneri*, and *P. latipinnis* all feature a high sagittal crest, while *T. bentonianium* has a low crest (Williston 1903; Carpenter 1996; O'Keefe 2004, 2008; Sato 2005; Schumacher and Martin 2015).

The ventral view of a polycotylid skull displays their unique palate, see Figure (14). The typical polycotylid palate was described by Carpenter (1996) and O'Keefe (2004), and consists of: a fenestrated palate, dished pterygoids that unite posterior to the posterior interpterygoid vacuity, a parasphenoid that runs down the medial portion of the posterior interpterygoid vacuity, and the presence of anterior interpterygoid vacuity. The basal polycotylids, like *E. muddi*, do not feature a palate that is as fenestrated as derived polycotylids like *P. latippinis* or *D. osborni*, as the palatines are still covering most of the lateral surface of the palate (Druckenmiller 2002). *P. haasi* is claimed to not possess an anterior interpterygoid vacuity; however, the skull is dorso-ventrally crushed, the palate is poorly preserved (Schumacher 2007). The absence of the anterior interpterygoid in *P. haasi* seems unlikely, as all other polycotylids and leptocleidids, like *N. borealis*, possess one as well (O'Keefe 2004; Schumacher 2007; Druckenmiller and Russell 2008; Schumacher and Martin 2015). The pterygoid morphology is unique in polycotylids, as the pterygoids form dished plates at their posterior end and elongated rods in their anterior margins. At the posterior termination of the pterygoids, they possess a medial process that meet one another behind the posterior interpterygoid vacuity. On the lateral posterior ends of the pterygoid plates, the quadrate flange of the pterygoid is present. The quadrate flange of the pterygoid is reduced to a small projection in *D. osborni*, but is elongated in *T. bentonianum* (Carpenter 1996; O'Keefe 2004; Sato 2005).The parasphenoid in all polycotylids runs antero-posteriorly through the middle of the posterior interpterygoid vacuity. The width of the parasphenoid appears to increase as the polycotylids became more derived. *E. muddi*, *M.*

anguirostris, and *T. bentonianum* all feature slender parasphenoids, while D. osborni, *P. latipinnis*, *D. herschelensis*, and UNSM 50133 all possess wide parasphenoids. The participation of the paraspenoid in the anterior interpterygoid vacuity has also been utilized as a diagnostic character differentiating *D. osborni* from *T. bentonianum* (Williston 1903; Carpenter 1996; O'Keefe 2004; Sato 2005; 2011). *D. osborni* features a cultiform process of the parasphenoid that projects into the anterior interpterygoid vacuity, while *T. bentonianum* features a parasphenoid that does not project into the anterior interpterygoid vacuity (Figure 14) (Williston 1903; Carpenter 1996; O'Keefe 2004; Sato 2005; 2011).

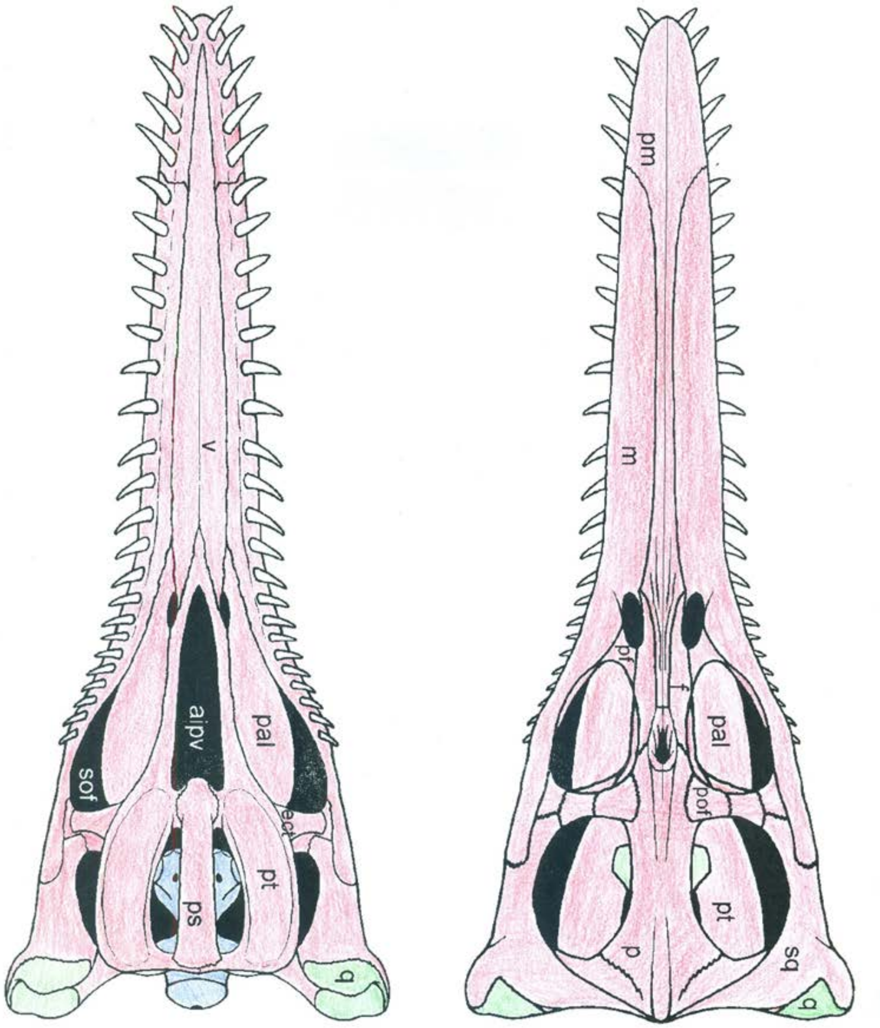

Figure 14 Illustration of *D. osborni*. An adapted illustration of the skull of D. osborni from O'Keefe (2004). The colors represent the different derivatives of the cranial bones. Red= dermatocranium, Blue= chondrocranium, Green= splanchnocranium. Dermal bones, which are the first to form in the skull do not have a cartilaginous precursor. This photo was adapted from O'Keefe (2004). V=vomers, aipv= anterior interpterygoid vacuity, pal= palatine, ps= parasphenoid, ect= ectopterygoid, pt= pterygoid, q= quadrate, f= frontal, sof= suborbital fenestra, pf= prefrontal, p= parietal, sq= squamosal, pof= postorbital

The general braincase anatomy of a polycotylid has been detailed thoroughly by Carpenter (1997), Druckenmiller (2002), O'Keefe (2004), and Sato (2011). The braincase is composed of the basioccipital, exocciptal/opisthotic, supraoccipital, prootic, basisphenoid, parasphenoid, epipterygoid, and pterygoids (Figure 15) (Carpenter 1997; O'Keefe 2004; Sato 2011). The occipital complex comprises the posterior portion of the braincase. The basiocciptial is the base of the skull and features the occipital condyle. The basiocciptial fuses anteriorly in the skull with the basisphenoid and together form the ventral basis of the braincase (Sato 2011). On the dorsal side of the basiocciptal bone, the two exoccipital/opisthotic bones fuse and form the bottom and part of the lateral portion of the foramen magnum. The exoccipital/opisthotic feature a lateral extension known as the paroccipital process, which fuses to the medial side of each quadrate to structurally support the posterior braincase elements (Carpenter 1997). At the base of the of the paroccipital process of the exoccipital/opisthotic, on the medial side, are the foramina for the cranial nerves vagus (X), accessory (XI), and hypoglossal (XII) (Carpenter 1997). The previous mention cranial nerve foramina are all posterior to the internal auditory meatus. Another cranial nerve, glossopharyngeal (IX), exits the exoccipital/opisthotic ventral to the foramina of (X) and (XI) on the medial side (Carpenter 1997). The posterior semicircular canal is contained mostly in the exoccipital/opisthotic, with the dorsal marigin extending into the supraocciptal. The horizontal semicircular canal is shared between the exoccipital/opisthotic posteriorly and the prootic in the anterior margin (Sato 2011). The prootic, which sits anterior to the exoccipital/opisthotic in the braincase, houses most of the fenestra ovalis on its ventral surface, which Carpenter (1997) claimed to be absent in *D. osborni*, but was later identified by Sato (2011). On the medial side of the prootic sits the anterior semicircular canal dorsally, above the extension of the horizontal semicircular canal (Carpenter 1997; Sato 2011). Inferior to the horizontal semicircular canal on the medial side of the prootic is the vestibule, and the foramen directly below the vestibule marks the exit of (VII), the facial nerve (Carpenter 1997 and Sato 2011). The ventral portion of the prootic also features a facet for articulation with the basisphenoid (Carpenter 1997; Sato 2011). One the anterior surface of the prootic, there is the presence of a groove that marks the exit of the trigeminal nerve (V) which exited the skull from the front side of the prootic (Carpenter 1997; Sato 2011). Both the prootic and the exoccipital/opisthotic articulate on their dorsal marigns with the supraocciptal, see Figure (15).

The supraoccipital also partially houses part of the posterior semicircular canal, and is responsible for the key-hole like appearance of the foramen magnum in polycotlyids (Sato 2011). The anterior ventral surface of the braincase is composed of the basisphenoid, which articulated posteriorly with the basioccipital (Sato 2011). The top of the basisphenoid features the dorsum sellae, which is posterior to the pituitary fossa. The pituitary fossa also feature the paired internal carotid foramina. The lateral extensions of the baspheniod feature plate like facets, which serve as the articulation site for the prootic. Carpenter (1997) also placed cranial nerve (VI) abducens exiting the dorsal surface of the basisphenoid; however, Sato (2011) could not conclusively identify the foramina on the dorsal surface of the basphenoid in ROM 29010. The ventral portion of the basisphenoid articulates with the parasphenoid, which runs medial in an I-bar shape (Carpenter 1997; O'Keefe 2004; Sato 2011). The anterior-lateral projections of the basiphenoid, the basipterygoid tubers, articulate with the medial anterior portion of the pterygoid plates (Sato 2011). From the on the anterior-dorsal portion of the pterygoid plates, near the border of the pterygoid and basisphenoid suture sits the epipterygoid (Carpenter 1997; Sato 2011). Carpenter (1997) describes the epipterygoid of *D. osborni* to rod-like in shape, but other polycotylids, like *P. latipinnis*, possess a more triangular shape epipterygoid (Schumacher and

Martin 2015). After observing the speciemen KUVP 5070, it is apparent that *T. bentonianum* also has a rod-like epipterygoid, and KUVP 4001, *D. bonneri*, appears to have an intermediate epipterygoid that is between the rod and triangular shape. This might indicate that the morphology of the epipterygoid is influenced by skull size, and maybe feeding ecology, to better support the skull against mechanical stress during biting.

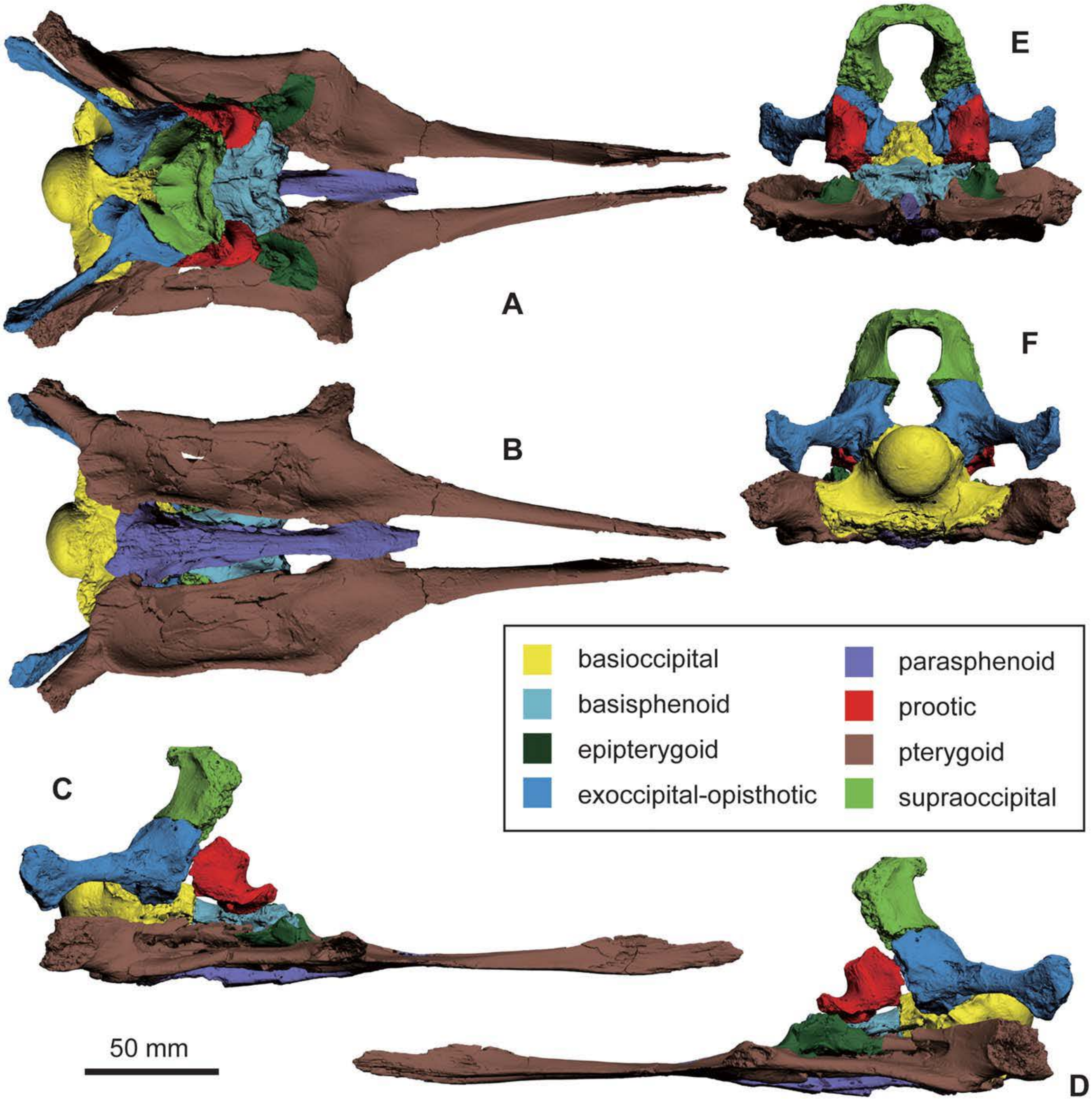

Figure 15 Braincase of the Polycotylid Plesiosaur ROM 29010. A) ventral view, B) right lateral view, C) left lateral view, D) anterior view, E) posterior view with the partial removal of the basioccipital and exocciptal-opsithotic, F) general posterior view. Notice the unique key-hole shape of the foramen magnum. This figure was taken from Sato (2011).

The typical lower jaw of a polycotylid was most recently described by O’Keefe (2008) and McKean (2012). The mandible consists of 7 bones: the angular, articular, coronoid, dentary, prearticular, splenial, and the surangular. Most of the lower jaw consists of the dentary which exposed on the lateral surface of the mandible. The teeth are housed in the dentary for most of the lower jaw, and the posterior teeth of the mandible are situated between the dentary and the coronoid (O’Keefe 2008). The mandibular symphysis consists of the following bones for all known polycotylids: dentary, coronoid, angular, and splenial (O’Keefe 2008). The presence of the angular in the symphysis was original not thought to be present in *D. osborni*, but later analysis by Sato (2005), O’Keefe (2008), and McKean (2012) confirmed that the angulars do enter the mandibular symphysis in *D. osborni*, and all other polycotylids.

The length of the mandibular symphysis has been previously utilized in differentiating polycotylid evolutionary relationships, with longer mandibular symphyses being the state in *D. osborni* and shorter symphysis in *T. bentonianum* (O’Keefe 2008; McKean 2012). The mandibular symphysis of *D. osborni* and *D. bonneri* comprise 19 tooth positions, while there are only 12 tooth positions present in the symphysis of *T. bentonianum* (O’Keefe 2008). The number of teeth in the mandibular symphysis appears to vary within the Polycotylidae, with the more basal condition being a shorter mandibular symphysis length, with fewer tooth positions. *E. rankini* possesses 14 or 15, *D. tropicensis* with 17, *P. haasi* with 12, *P. latipinnis* with approximately 14, *E. muddi* with 6, and *P. wellesi* possessing 8 teeth in the symphysis (Carpenter 1996; Druckenmiller 2002; O’Keefe 2004, 2008; Sato 2005; Schumacher 2007; Albright et al. 2007; McKean 2012; Schumacher and Martin 2015). The posterior portion of the mandible on the dorsal side consists of the dentary, until it posteriorly terminates with a suture with the surangular and the angular. The surangular is superior to the angular and comprises the lateral surface of the coronoid process of the mandible. Both the surangular and the angular continue posteriorly on the lateral surface of the mandible until the reach the articular. The articular comprises the articulation with the quadrate of the upper jaw. In all polycotylids, there is the presence of a retroarticular process of the articular bone the projects posteriorly from the articulation facet. Most polycotylids do not feature an elongated retroarticular process; however, *T. bentonianum*, UNSM 50133, AMNH 5834, and *M. anguirostris* feature an elongated retroartciular process that extends far posterior to the occipital condyle (Buchy et al. 2005). On the medial side of the mandible, posterior to the mandibular symphysis, are found the coronoid superiorly, the splenial in the middle, and angular comprising the inferior portion (O'Keefe 2008). The coronoid and splenial are posteriorly split about midway down the medial side of the mandible posterior to the mandibular symphysis, by the prearticular bone (O'Keefe 2008). The prearticular bone widens, as it moves posterior on the mandible, forcing the coronoid dorsally, creating the coronoid process (O'Keefe 2008). The coronoid then posteriorly sutures with the surangular (O'Keefe 2008). With the surangular superior to the prearticular, both bones meet the articular bone (O'Keefe 2008). The dorsal portion of the articular also sutures with the angular medially, before the formation of the articular facet of the articular bone (O'Keefe 2008). This pattern of the mandible is seen in other polycotylids, and is most likely conserved within the family (Sato 2005; O'Keefe 2008; McKean 2012).

UNSM 55810 Skull

The skull of UNSM 55180 is partially complete, and a total skull length can be calculated from the remains, which is approximately 403 mm. The skull of UNSM 55810 was originally attributed to the species *Dolichorhynchops osborni*; however, the skulls of the juvenile *D. osborni* specimens UCM 35059, MCZ 1064, and FHSM VP-404 are different morphologically from UNSM 55810. The rostrum of UNSM 55810 is much longer in proportion to overall skull length than any of the other juvenile specimens of *D. osborn*i. More characters of the rostrum and palate differ from *D. osborni,* and support a possible new species designation for both UNSM 55810 and UNSM 50013. The following sections discusses the preserved axial elements of UNSM 55810 and compares them to other known polycotylids.

Rostrum and Orbit.

A partial rostrum is preserved for UNSM 55810, which includes most of the premaxilla, fragments of the maxilla, and a portion of the frontal and prefrontal. There appears to only be four teeth in the premaxilla of the UNSM 55810, which is less than most other polycotylids which have 5-6; however it may not be complete (O'Keefe 2008). The premaxilla is accompanied for most of its length running parallel with the maxilla, most of the maxilla is not preserved for UNSM 55810, and therefore, a maximum tooth count was not ascertainable. One unique feature of the rostrum of UNSM 55810 is an enlongated process of the frontal anterior to the external naris, splitting the suture between the maxilla and premaxilla on the rostrum. This is unlike the condition in *D. osborni*, and *D. bonneri*, where the frontal do not feature a narrow anterior process of the frontal bone that extends far beyond the external naris onto the rostrum (O'Keefe 2004; 2008). This anterior slender projection of the frontal bone on the rostrum is similar to the condition seen in *T. bentonianum* and *P. latipinnis*, see Figure (16) (O'Keefe 2008; Schumacher and Martin 2015). The posterior border of the external naris is also preserved in UNSM 55810. The external naris in the posterior border is consists of the prefrontal laterally and the frontal bone in UNSM 55810, which is similar to the condition seen in all other derived polycotylids (Carpenter 1996; O'Keefe 2001, 2004, 2008; Sato 2005; Benson et al. 2012b; Schumacher and Martin 2015).

The anterior portion of the orbit sits posterior to the external naris. The external naris in UNSM 55810 and UNSM 50133 are positioned further back on the skull than other polycotylid taxa, and seem to facilitate the passage of air behind the orbit, see Figure (16). This feature would seem to be advantageous in comparison to the external naris position of *D. osborni*, which could possibly lead to the presence of air bubbles going over the eye and possibly impeding vision. The dorsal anterior portion of the right orbit is preserved in UNSM 55810. The most anterior portion of the orbit is composed of the prefrontal bone. The portion of the prefrontal bone which is preserved is slender and comes to a lap suture underneath the frontal bone posterior to the external naris (Figure 16). The frontal bone makes up the dorsal portion of the orbit. The orbit appears large in UNSM 55810, which is expected for a juvenile individual (Everhart 2004). The frontal bone also features a lateral flange of the frontal bone that forms a rim above the orbit. This feature was first interpreted by Carpenter (1996) to be the supraorbital that consists of this lateral ridge in *T. bentonianum* and *D. osborni*, and was later identified by O'Keefe (2008) in *D. bonneri*. O'Keefe (2008) hypothesized that this ridge did not just consist of the supraorbital bone, but also featured contributions from the frontal and the postorbital bone. UNSM 55810 allows for a unique look inside the superior lateral ridge of the orbit of the polycotylids in a young juvenile individual, where the sutures between the bones comprising the ridge are not ossified/indistinguishable. UNSM 55810 verifies the hypothesis by O'Keeefe (2008) that the anterior portion of the superior lateral ridge of the orbit does feature a contribution from the frontal bone in the anterior portion (Figure 16). None of the supraorbital bone is preserved, but there is a clear indentation in the frontal bone in the portion that makes up the superior lateral ridge of the orbit, indicating that the supraorbital bone sat on top of the frontal bone forming a lap suture above the orbit. None of the posterior orbit margin is preserved in UNSM 55810, and therefore inhibits further interpretation of the orbit margin.

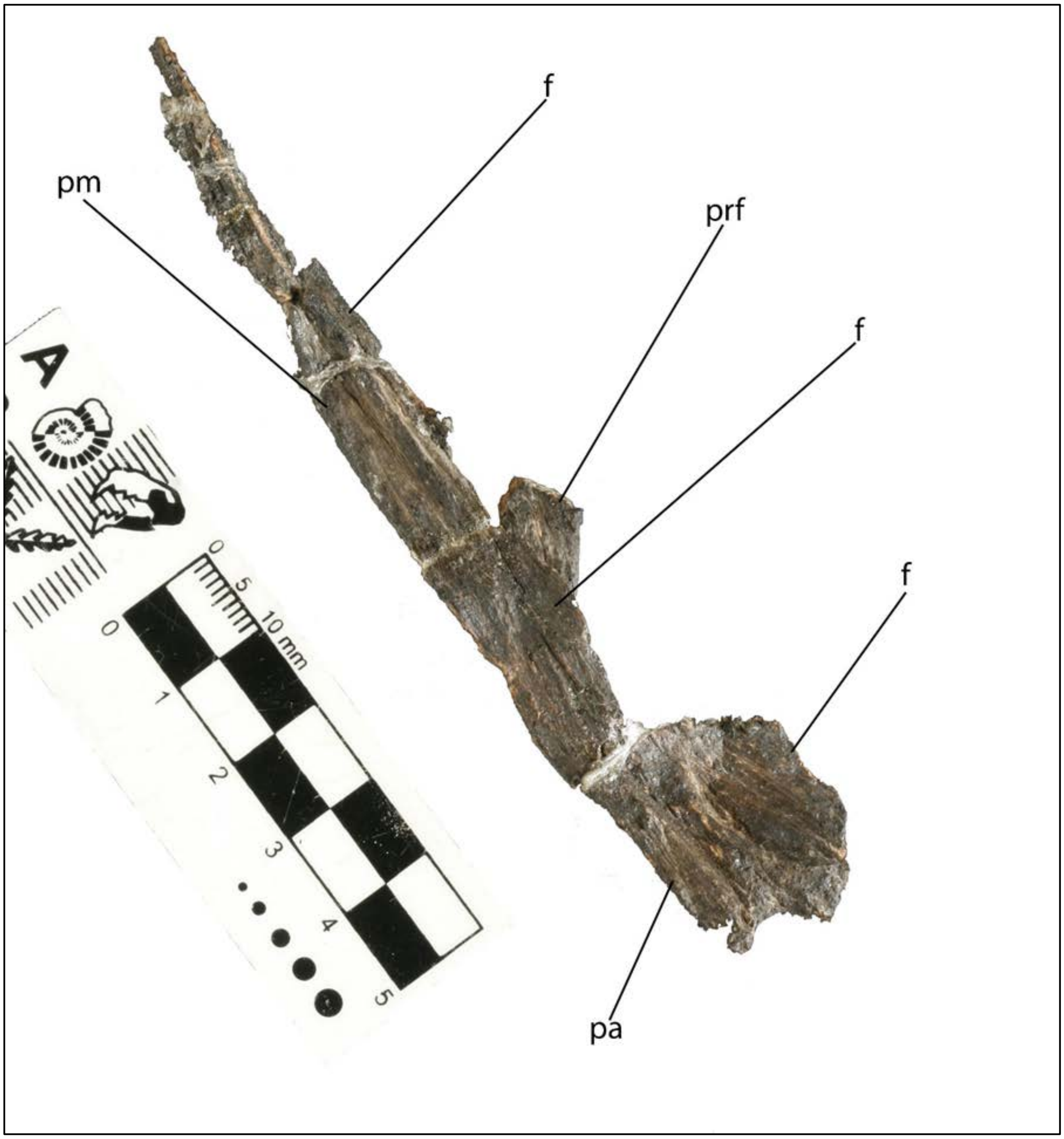

Figure 16 Rostrum of UNSM 55180. Preserved part of the right posterior portion of the rostrum of UNSM 55180 with the external naris and the anterior part of the orbit present. Notice the anterior extension of the frontal onto the rostrum, similar to *P. latipinnis.* The anterior portion of the orbit also features a portion of the frontal flange, which underlay the supraorbital in life. f= frontal, pm= premaxilla, pa= parietal, prf= prefrontal

Skull Roof.

The top portion of the skull roof in polycotylid plesiosaurs is composed of the parietal bones in the anterior portion and the meeting of the two arched squamosal bones in the posterior portion of the skull. The parietal of all polycotylids directly contacts the premaxilla, meaning that the frontals are completely split into left and right halves on the skull. The contact between the parietals and the premaxilla can be faintly distinguished in UNSM 55810, see Figure (17). The premaxilla features a distinctive midline ridge the runs the entire length of the premaxilla. The end of the midline premaxillary ridge can be seen between the anterior portion of the orbit, as the premaxilla meets with the parietals and forms a shallow interdigitating suture. The shallow interdigitating suture of the premaxilla and parietal is a feature seen in derived polycotylids, and is unlike the deep interdigitating suture found in primitive polycotylids, such as *E. muddi* (Druckenmiller 2002; Benson et al. 2012b; Schumacher and Martin 2015). The suture appears to be a flat border with the parietal, similar to *T. bentonianum*, *D. bonneri*, and *P. latipinnis*, and unlike the tapering premaxilla seen in *D. osborni* (Carpenter 1996; O’Keefe 2008; Schumacher and Martin 2015).

The suture between the squamosal and the parietal bones is usually obliterated in adult specimens as the suture lines are not visible in adult polycotylids (Carpenter 1996; O’Keefe 2008). UNSM 55810 provides unique insights into the suturing of the two squamosal bones to the parietal. The squamosal features a broad overlap onto the parietal anterior to the squamosal arch, but does reach to the point of the sagittal crest, which is composed entirely of the parietal bone. The suture between the parietal and the squamosal is a lap suture, with the squamosal overlying the parietal, see Figure (17). The squamosal arch of UNSM 55810 is narrow and is recurved, like the squamosal arch seen in *T. bentonianum*. The height of the sagittal crest cannot be inferred from the skull, as it appears that the crest was partially broken. The sagittal crest in polycotylids have been previously suggested to be sexually dimorphic, and similar to the nuchal crests seen in marine iguanas (Watkins 1998). However, this assertion has not been substantiated, as the only known female polycotylid LACM 129639 did not feature any cranial material. The adult specimen from the Wallace Ranch UNSM 50133 did feature a high sagittal crest similar to that of *D. osborni*, unlike the short crest seen in *T. bentonianum* (Carpenter 1996). The presence of a knob at the union of the two squamosal arches at the posterior apex of the skull cannot be determined in UNSM 55810, as this feature is seen in *D. herschelensis*. The arch of the squamosal is also oriented posteriorly, as in *T. bentonianum*, and unlike *D. osborni*, which features the two squamosal arches oriented straight vertically and not oriented posteriorly (Carpenter 1996; Sato 2005). On the ventral and medial side of the squamosal, is the articulation site with the quadrate. The quadrate is not preserved in UNSM 55810, and it does not appear the quadrate was broken off, but rather, that the ossification of the suture between the squamosal and the quadrate was not formed. The quadrate, unlike the squamosal, is not dermally derived, and is part of the splanchnocranium, which is first present as a cartilaginous precursor and ossifies as the organism develops (Rieppel 1992, 1993a, 1993b). The sutures of the splachnocranium elements and the dermal elements of the skull occur after the fusion of the dermal bones to one another (Rieppel 1992; Vincent 2010).

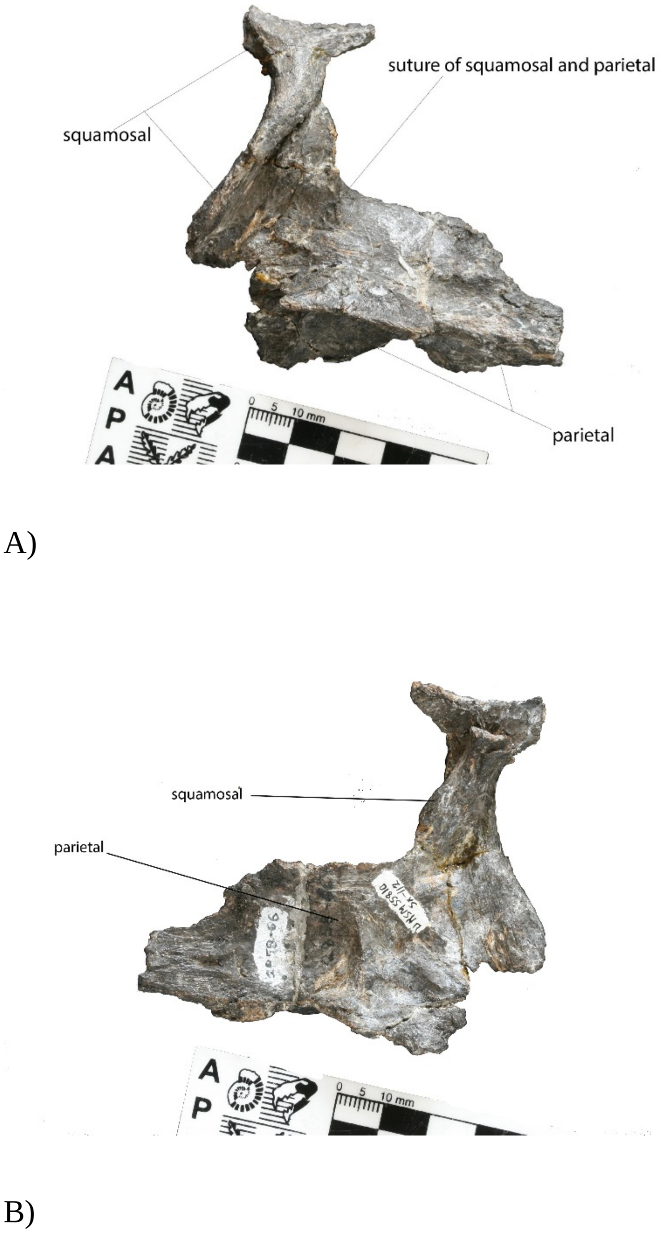

Figure 17 Skull Roof of UNSM 55180. A) Dorsal view of the skull roof of UNSM 55180. The suture between the parietal and the squamosal is clearly evident. The fusion line between the parietal and squamosal is usually obliterated in adult polycotylids. The quadrate is also missing from the ventral portion of the squamosal, and it appears that the two elements were not fused during life in UNSM 55180. B) The ventral view of the skull roof, showing where the medial articulation of the quadrate and squamosal would occur.

Palate.

The palate of UNSM 55180 is similar to that of *Dolichorhynchops osborni*, in that it features large pterygoid plates with rounded lateral edges (Figure 18). The pterygoid plates are also more robust than that of *Trinacromerum bentonianium*, which exhibits thin pterygoid plates with a straight lateral edge (Carpenter 1996; O'Keefe 2004, 2008). The curvature of the lateral surface of the pterygoid plates is an autapomorphy of *D. osborni* and should be more closely examined (Carpenter 1996; O'Keefe 2004, 2008; Sato 2005, 2011; McKean 2012). The pterygoid plates of UNSM 55180 also exhibits a curved lateral edge, like that of *D. osborni*. The specimen that most clearly exhibits this condition is FH-VP-404, which like UNSM 55180, is a juvenile individual, and the character therefore might be ontogenetic, rather than taxonomically significant. The posterior termination of the pterygoids are not preserved in UNSM 55810, and the basioccipital, which makes up the foundation of the posterior palate is also missing.

The parasphenoid of UNSM 55180 is different from most other Polycotylids, as it is very robust and medio-laterally expanded, see Figure (18) (O'Keefe 2004; Sato 2011). This condition is also seen in the adult individual from the Wallace Ranch UNSM 50133. The parasphenoid in both the UNSM specimens fills most of the posterior interpterygoid vacuity; which is unlike any other polycotylid known. The cultiform process of the parasphenoid projects into the anterior interpterygoid vacuity. This condition is also seen in ROM 29010, *Dolichorhynchops herschelensis*, *D. osborni*, and SDSM 23020 (Carpenter 1996; O'Keefe 2004, 2008; Sato 2005, 2011; Shumacher and Martin 2015). Unlike *D. herschelensis* and *D. osborni* which have a small round projection that enters the anterior interptrygoid vacuity, UNSM 55180, UNSM 50133, and SDSM 23020 have large triangular projections of the cultiform process into the anterior interpterygoid vacuity (O'Keefe 2004, 2008; Sato 2005, 2011; Shumacher and Martin 2015).

The palatines of UNSM 55180 were partially preserved on the left side of the palate. The palatine is incorrectly glued to the ectopterygoid in the specimen, but the lateral edge is well preserved. The right ectopterygoid is well preserved in UNSM 55180, and is oriented anteriorly, which is unlike both *Dolichorhynchops osborni* and *Trinacromerum bentonainium,* see Figure (18) (Carpenter 1996; O'Keefe 2004, 2008). In *D. osborni,* the ectopterygoid stretches horizontally from the anterior portion of the pterygoid plate, and the ectopterygoids of *T. benatonainium* and *Polycotylus latipinnis* are oriented posteriorly (O'Keefe 2004). The condition in the adult specimen UNSM 50013 also appears to have an anterior orientation for the ectopterygoid. This condition for the ectopterygoid is unique to the Wallace Ranch specimens, and to AMNH 5834 and ROM 29010.

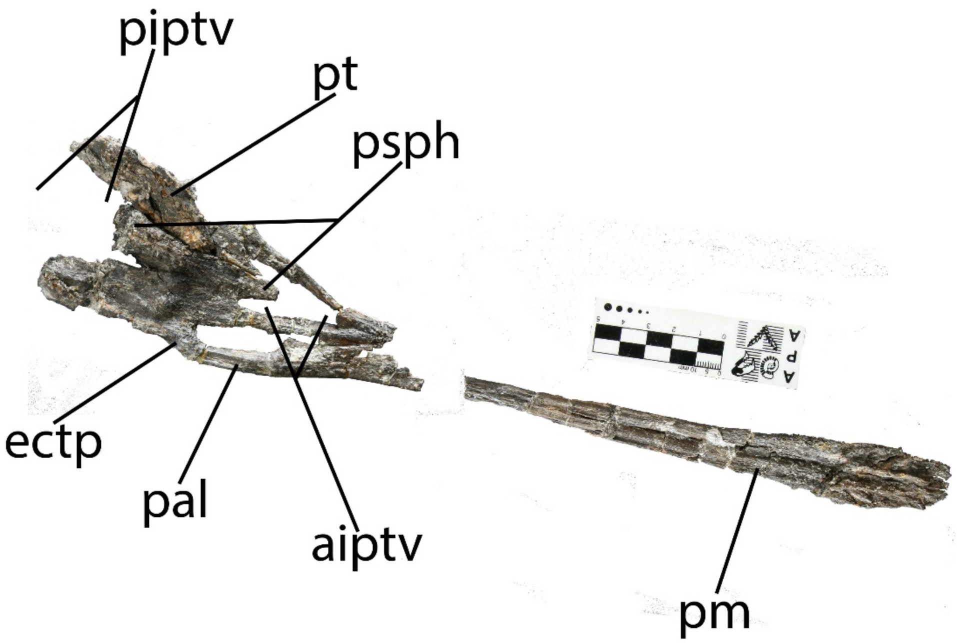

Figure 18 Ventral Palate of UNSM 55180. The palate features a well-developed parasphenoid that is posteriorly broad and features a triangular projection into the anterior interpterygoid vacuity. The ectopterygoids are also oriented anteriorly, which along with UNSM 50133 are the only taxa to feature this character state. The basioccipital, along with the posterior portions of the pterygoids plates are missing in UNSM 55180. aiptv= anterior interpterygoid vacuity, ectp= ectopterygoid, pal= palatine, piptv= posterior interpterygoid vacuity, pt= pterygoid, psph= parasphenoid, pm= premaxilla

Braincase.

The dorsal side of the palate features some of the braincase elements preserved in UNSM 58810, see Figure (19). The entire basisphenoid is present in dorsal view, but none of the occipital complex is preserved. On the lateral sides of the basiphenoid, which sit superior to the pterygoid plates, are the articulation facets for the prootic, which appear as semi-circular dishes (Figure 19). The sagittal suture running on the dorsal surface of the basphenoid is more pronounced in UNSM 55810 than that of ROM 29010. The dorsal surface of the basispenoid, the dorsum sellae, is also more rounded in the UNSM juvenile than is seen in ROM 29010. The anterior portion of the basisphenoid features two lateral lobes which project anteriorly, while the mid portion is horseshoe shaped and does not extend anteriorly like the two lateral lobes. The identity of this horseshoe shaped morphology of the anterior portion of the basisphenoid has been described as the sella tursica. Within the base of the sella tursica, are two paired foramina, which Sato (2011) identified as the two foramina as the internal carotids. In UNSM 55810, only the right internal carotid foramen is preserved. Sato (2011) also illustrated paired foramina on the lateral margins of the dorsal surface of the basphenoid, as the foramina for cranial nerve VI (abducens); however, this foramen is obscured in UNSM 55810. The left epipterygoid is partially preserved in UNSM 55810, and it sits anterior to the facet of the left prootic. The fusion of the left epipterygoid to the pterygoid displays well defined suture lines, and the right epipterygoid is completely missing, indicating a lack of complete fusion between the pterygoid and epipterygoid in UNSM 55810 (Figure 19). From the partial left epipterygoid, the epiterpterygoid appears cylindrical in shape, similar to the condition seen in UNSM 50013, *D. osborni*, and *T. bentonianum* (Carpenter 1997). O’Keefe (2004) described the braincase elements of *T. bentonianum* in a sagittal view. In *T. bentonianum*, there is a noticeable gap between the basioccipital and basisphenoid, which is not present in ROM 29010 (Figure 19) (Sato 2005). This feature is also not present in UNSM 55810, as the posterior portion of the basisphenoid is preserved. The posterior portion of the basisphenoid does feature a slight concavity in the medial posterior surface, but is does not appear to be as pronounced as *T. bentonianum*. In the dorsal view of the left pterygoids, there is an indentation that appears to mark the articulation of the quadrate ramus of the pterygoid. However, the quadrate ramus is not persevered, and not fused to the pterygoid in UNSM 55810. One of the key diagnostic character difference between *D. osborni* and *T. bentonianum* is the length of the quadrate ramus of the pterygoid. *D. osborni* features a short extension of the quadrate ramus, while *T. bentonianum* features an elongated quadrate ramus of the pterygoid.

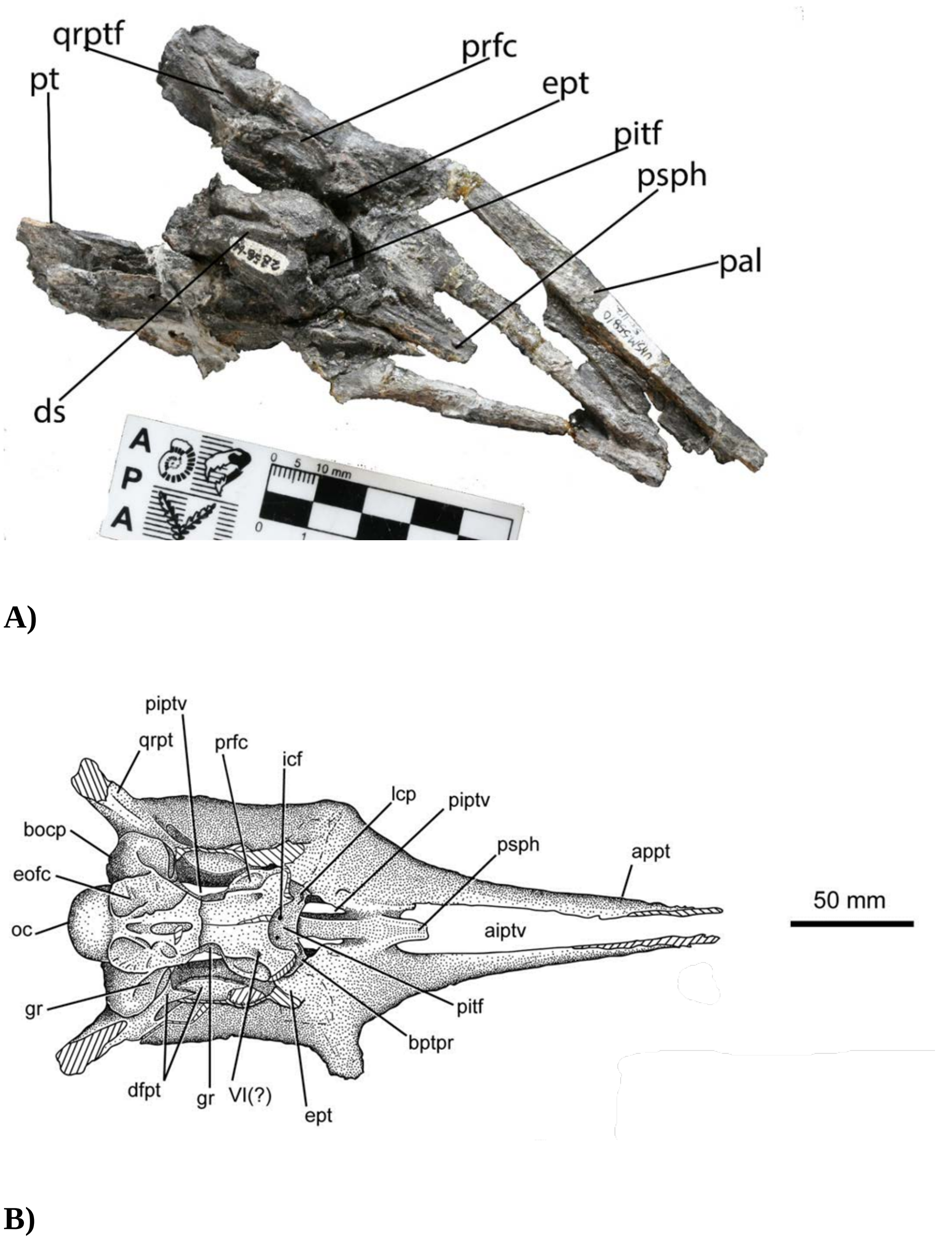

Figure 19 Dorsal Braincase of UNSM 55180. A) UNSM 55180. B) ROM 29010 (Sato 2011). The basisphenoid is well developed in UNSM 55180 and features a prominent pituitary fossa. The fusion of the basisphenoid and the basioccipital is observable in UNSM 55180, and the specimen resembles the condition seen in *D. osborni* rather than *T. bentonianum*. qrptf= quadrate ramus of the pterygoid fossa, pt= pterygoid, ds= dorsum sellae, prfc= prootic facet, pitf= pituitary fossa, pal= palatine, ept= epipterygoid, psph= parasphenoid

Disarticulated amongst the cranial material is part of the right prootic (Figure 20). The prootic is missing the ventral anterior projection which forms the notch for the trigeminal nerve (V). However, the depression for the vestibule on the medial surface of the prootic in UNSM 55810 is clearly defined, along with what Sato (2011) termed as the “facet for unossified median wall of otic capsule” is also present anterior to the vestibule (Figure 20). At the top of the right prootic on the medial side is the opening for the anterior semicircular canal. The portion of the prootic with the horizontal semicircle canal is well defined directly posterior to the position of the anterior semicircular canal. The missing elements of the right prootic of UNSM 55810 might have been at least partially cartilaginous in life, as there does not appear to be any breaks in the bone indicating that bone was broken during preservation.

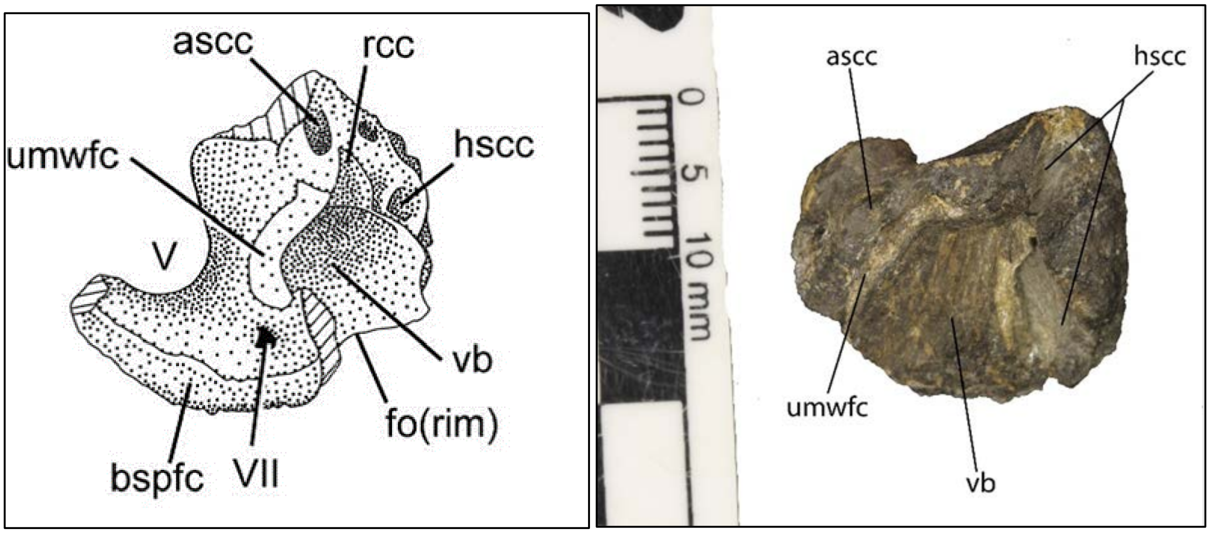

Figure 20 Prootic of UNSM 55180. Comparison of the prootics of ROM 29010 (left) and UNSM 55180 (right). The prootic from UNSM 51880 s missing the ventral and anterior portions of the bone. However, the vestibule and the ascending and horizontal semicircular canals are present in the specimen. ascc= anterior semicircular canal, umwfc= facet for unossified median wall of otic capsule, vb= vestibule, hscc= horizontal semicircular canal, fo= fenestra ovalis, rcc= recessus crus communis, bspfc= facet for the basisphenoid, V= trigeminal, VII= facial. The left image was adapted from Sato (2011).

Mandible.

The jaw of polycotylid plesiosaurs has been thoroughly described in O'Keefe (2008), and the morphology of the lower jaw of UNSM 55180 adheres to that description, see Figures (21 and 22). The dentary comprises the majority of the mandible, and well preserved in UNSM 55810. The exact location of the mandibular symphysis is difficult to locate in this specimen, as the mandible was crushed medio-laterally during fossilization. However, there are three distinct bones preserved for the mandible that participate in the symphysis; which include the dentary, coronoid, and the splenial (Figure 21). The angular would also participate in the mandibular symphysis, but the anterior extension of the angular not preserved in UNSM 55810. The coronoid runs along the dorsal side of the symphysis, while the splenial runs parallel with the coronoid ventrally. As the coronoid and splenial run anteriorly in the symphysis, the two bones begin to taper and run more deeply in the symphysis (O'Keefe 2008). As the coronoid and the angular taper, they are replaced by the splenials in the symphysis, which is clearly illustrated in UNSM 55810 (Figure 21) (O'Keefe 2008). The most anterior portion of the mandibular symphysis consists solely of the dentary, and this portion of the mandible is not preserved for either side of the lower jaw in UNSM 55810. This prevents the use of the left mandible fragment as a sole estimator of total skull length.

The teeth present in the dentary are slightly recurved, and feature fine serrations. Overall the teeth are uniform in size throughout the mandible, and don't seem to change with the position within the jaw. An overall mandibular tooth count cannot be attained from UNSM 55810, as the teeth do not have individual sockets within the jaw. The lack of individual tooth sockets in the jaw further suggests that UNSM 55810 is a juvenile individual, as the teeth of juvenile reptiles and even some mammals, such as odontocetes, feature tightly packed teeth in a trough, and as the animal grows in size, the jaw expands anterio-posteriorly and bone then encompasses each of the teeth into individual sockets (del Castillo et al. 2015). The posterior portion of the mandible for UNSM 58810 lacks the articular on either side, and therefore the state of the posterior projection of the articular remains speculative for UNSM 58810 (Figure 22). The location of the suture between the dentary and the angular appears to have been broken off and not preserved in UNSM 55810. The dentary sutures with the angular first, which is inferior to the surangular at its posterior termination. Only the angular is present on the lateral side of mandible, as the surangular appears to have not been fused to the rest of the mandible, leaving the coronoid exposed on the lateral surface of the jaw (Figure 22). The deep indentation in the lateral surface coronoid exhibits the extent to which the surangular reached superiorly on the mandible. Without the presence of both the coronoid and the suragnular, the height of the coronoid process cannot be assessed, as both elements comprise the coronoid process, with the surangular making up the most dorsal portion of the coronoid process. The posterior portion of the jaw is missing the articular. The posterior portion of the mandible preserved in UNSM 55810 only consists of the angular. In life, the articular would have covered the angular in the posterior margin of the mandible, creating a lap suture with the angular. One the medial side of the posterior portion of the left mandible, the prearticular is also missing, see Figure (23). With the absence of the articular bone on the mandible, the length of the retroarticular process of the mandible cannot be ascertained. The articular which is derived from Meckel’s cartilage, and the absence of the fusion between the dermally derived bones of the mandible and the splanchocranially derived bones, also suggest that UNSM 55810 is a juvenile individual.

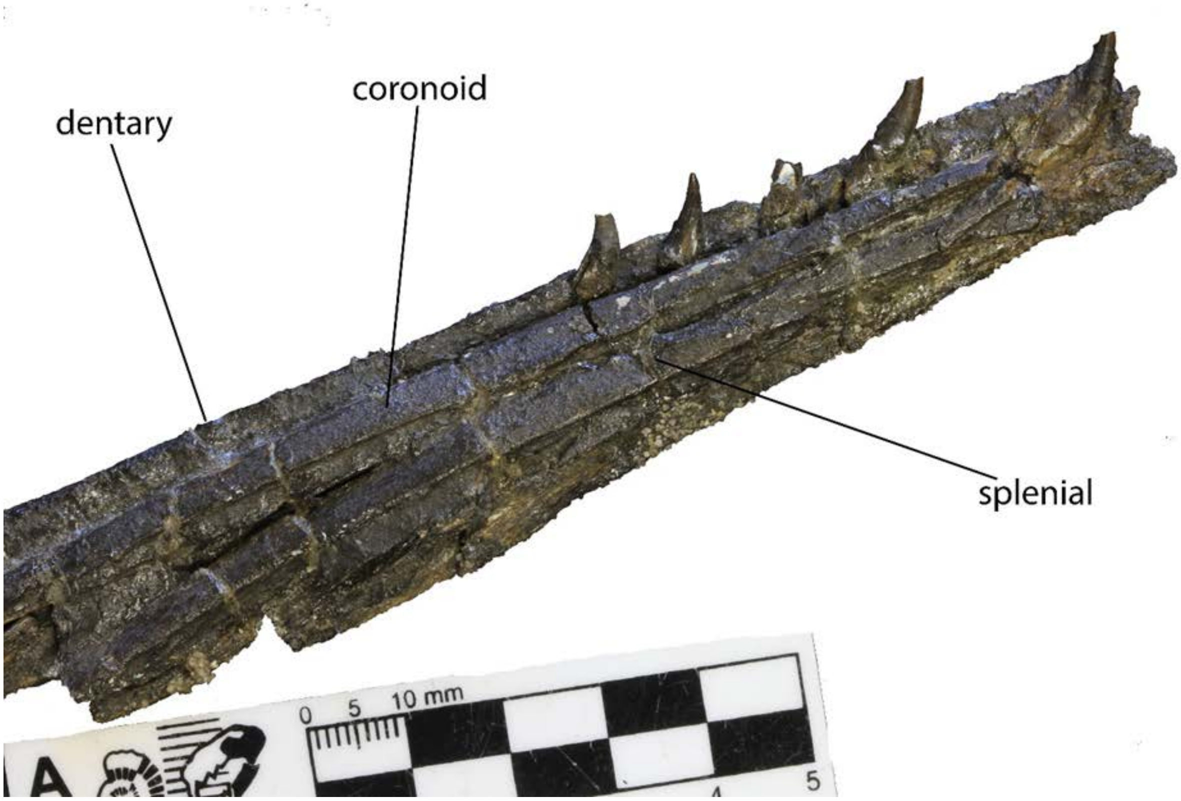

Figure 21 Medial mandible of UNSM 55180 in symphysis. Medial view of the anterior section of the left mandible of UNSM 55180. The angular is missing, which would lie ventral to the splenial. In the mandibular symphysis of polycotylids, the splenial, goes dorsal and surpasses the length of the coronoid anterior in the jaw.

Figure 22 Lateral View of UNSM 55180 Mandible**.** The left mandible of UNSM 55180 is the only well preserved element of the lower jaw. Notice the absence of the articular and the surangular in the mandible. The lack of fusion of the mandible indicates UNSM 55180 is a juvenile

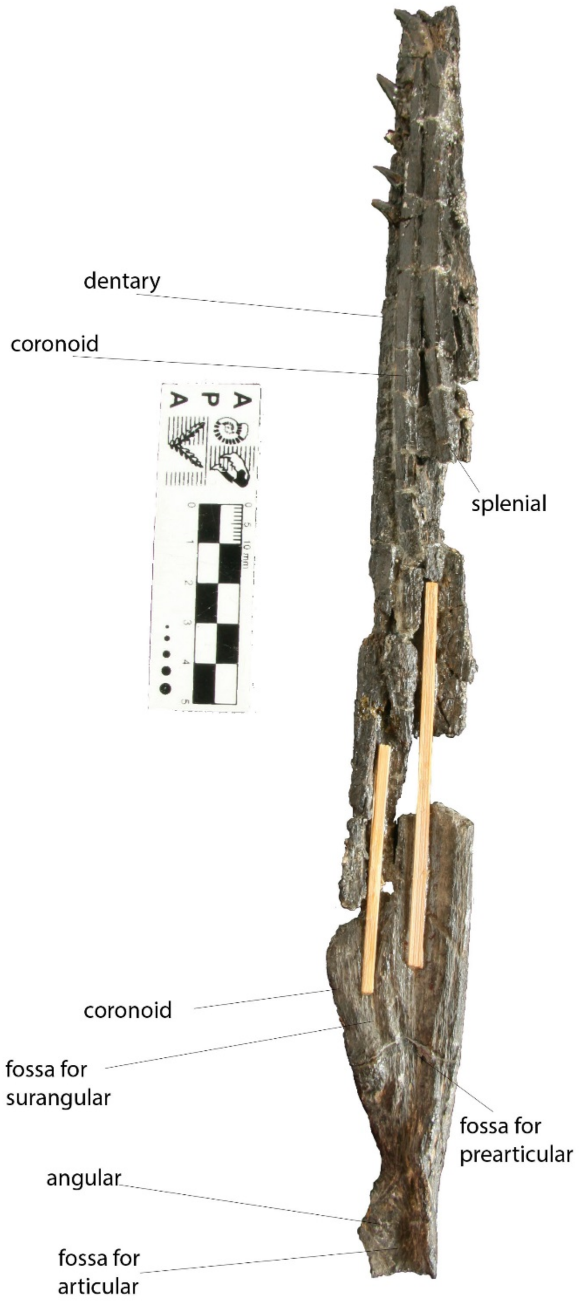

Figure 23 Medial View of UNSM 55180 Mandible. The absence of the articular, prearticular and surangular is evident in the medial view. Inferring the length of the retroaticular process is not possible for UNSM 55180 given the absence of the articular.

Postcranial axial skeleton

Vertebral centra shape varies throughout Plesiosauria. The polycotylid clade is known for having amphicoelous vertebrae, which contrasts with their sister taxon, the leptocleidids, which feature acoelous vertebral faces. The utility of having amphicoelous vertebrae remains uncertain in the polycotylids. Teleosts also feature amphicoelous centra, which resemble biconid hour glass cylinders in shape. Most polycotlyids, such as *D. oborni*, *P. latipinnis*, *D. herschelensis*, *D. bonneri*, and *D. tropicensis* feature concavity of the lateral surface of the centrum as well (Carpenter 1996; Sato and Storrs 2000; O'Keefe 2004, 2008; Sato 2005; McKean 2012; Schumacher and Martin 2015). *P. latipinnis* features the most drastic concavity of the lateral surface of the vertebrae (Sato and Storrs 2000; Schumacher and Martin 2015). *T. bentonianium* is the only polycotylid that does not feature lateral constriction of the centra, and only features slight constriction of the presacral vertebrae (Sato and Storrs 2000). The ventral surface of the centra also feature a medial keel that separates the ventral half of the centrum into left and right halves (Sato and Storrs 2000). In addition to the lateral constriction of the centrum, the vertebrae of polycotylids are anterio-posterioral short, and they lack the lateral ridge of the centrum (Sato and Storrs 2000).

UNSM 55810 has a total of 34 vertebrae preserved, with 13 cervicals, 3 pectorals, and 18 dorsals. Like all polycotylids, the centrum of the vertebrae are anterio-posteriorly short, and it does not appear to be due to compression during fossilization. The centra anterior and posterior cemtrum faces are not amphicoelus, see Figure (24). This condition of aceolous centra faces is not a typical polycotylid feature, and could be ontogenetic in nature (Schumacher and Martin 2015). This change from the aceolous to amphicoelous vertebrae is seen in LACM 129639, with the adult having strongly amphicoelous vertebrae, and the fetus featuring the aceolous condition

(O’Keefe and Chiappe 2011). The ventral portion of the vertebrae of UNSM 55810 do possess a ventral keel, and do feature paired nutrient foramina on either side of the keel. The lateral surfaces of the vertebral centra of UNSM 58810 are also compressed, as in most polycotylids (Figure 25) (Carpenter 1996; Sato and Storrs 2000; O’Keefe 2004, 2008; Sato 2005; McKean 2012; Schumacher and Martin 2015). Also on the lateral surfaces of the vertebrae, a distinctive layer of perichondral bone is present on the exterior surface. The amount of perichondral ossification on the vertebrae is greater than that seen on LACM 129639, which only feature a small ring of perichondral ossification (Figure 25) (O’Keefe and Chiappe 2011).

The neural arches for the entire vertebral column are not fused to the centrum in UNSM 55180. Most of the neural arches are present in two pieces, a right and a left half, which both unite together to form the spinous process (Figure 24). This feature is indicative of a juvenile individual, and is seen in other reptiles such as *Alligator mississippinis*, *Chelydva serpentina*, and *Lacerata vivipara* (Rieppel 1992, 1993a, 1993b). As the neural arches begin to form and develop around the developing spinal cord, two ossification centers on the left and the right of the spinal cord ossify and then suture with one another medially to form the spinous process (Rieppel 1992, 1993a, 1994b). The neural arches also form an ossification center with the dorsal margin of the centrum, which is also not fused in UNSM 55810. This is similar to the condition seen in the LACM 129639 embryo, in which the neural arches were in unfused and present in two bilateral arch elements (O’Keefe and Chiappe 2011). However, UNSM 55810 does have more neural arch fusion to than the LACM embryo, indicating that it was most likely at a more advanced developmental stage. Storrs (1993) and Vincent (2010), also used the fusion of the vertebral neural arches to assess whether an individual plesiosaur was a juvenile or an adult. Therefore, the use of the lack of fusion between the vertebral neural arches can be a reliable indicator for determining the relative age of a plesiosaur at the time of death. The ribs of UNSM 55810 are partially complete, and are poorly ossified (Figure 26). The vertebrae of UNSM 55810 are consistent with all other Plesiosauria, and only feature one articulation head with the centrum of the vertebrae (Ketchum and Benson 2010). The ribs also do not appear to be pachyostotic, like in cryptocleidid *Tatenectes laramiensis*, which is not a common condition in Plesiosauria (Street and O'Keefe 2010). No gastralia were preserved for UNSM 55810, and most of the ribs that were preserved were fragmentary, which could possibly indicate that the ribs were still poorly ossified, since they develop from two ossification centers, one from the proximal end and the other from the distal (Aoyama 2005).

Figure 24 Vertebrae From UNSM 55180. A) Cervical vertebrae from UNSM 55180. B) Dorsal vertebrae from UNSM 55180. Notice the lack of fusion between the neural arches to one another at the spinous process of the vertebrae, and the lack of fusion of the neural arches to the centrum. The vertebrae are not amphiceolous centra, but this feature may be ontogenetic in nature. C) Half of one of the cervical vertebrae neural arches, which was unfused in life, and had not developed zygopophyses yet.

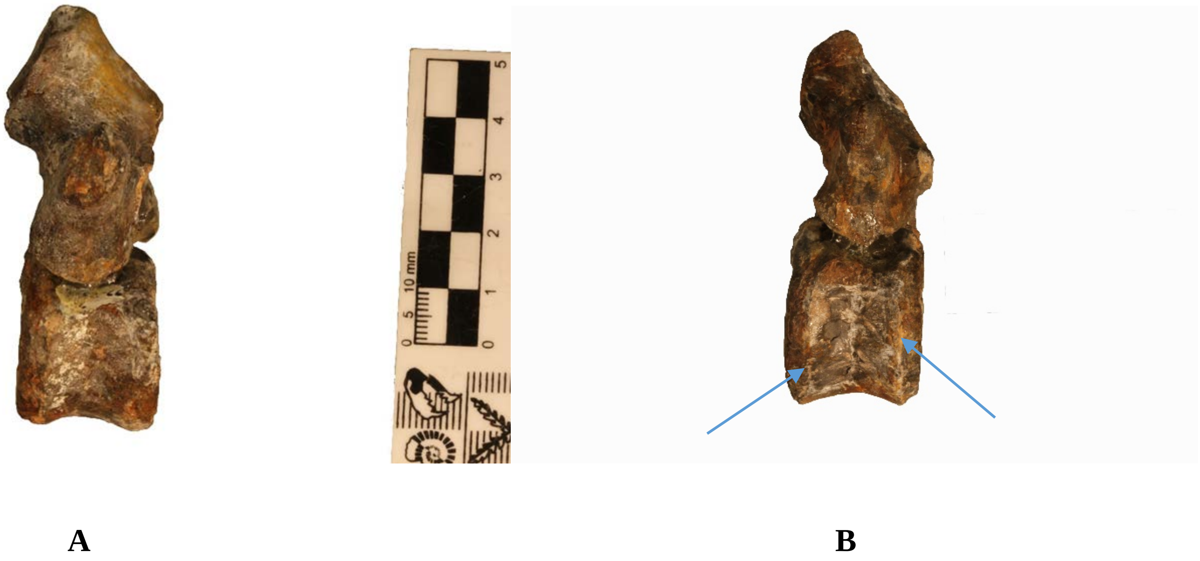

Figure 25 Vertebrae in Lateral View of UNSM 55180. A) Lateral view of a dorsal vertebrae of UNSM 55180. All the vertebrae of UNSM 55180 feature the lateral constriction of the centrum like most other polycotylids, except for *T. bentonianum*. B) Another cervical vertebrae that illustrates the partial covering of perichondral bone on the lateral surface of the centrum, as indicated by the arrows.

Figure 26 Ribs of UNSM 55180. Most of the ribs were poorly ossified. None of the gastralia was preserved with this skeleton

Discussion

The description of the axial osteology of UNSM 55810 indicates that the individual was a juvenile at the time of death. This conclusion is drawn from the lack of fusion of the cranial bones and of the neural arches of the vertebrae. Previous studies by Brown (1981), Storrs (1993), and Vincent (2010) have utilized the lack of fusion in the vertebral column, especially the degree to which the neural arches are fused to centra, to assess whether an individual was an adult or juvenile plesiosaur. To further bolster the placement of UNSM 55810 as a juvenile plesiosaur, the skull bones that are present are mainly from the dermatocranium, not the splanchnocranium or the chondrocranium (Figure 27). The only endochondrally derived bones present in the skull of UNSM 55810 were one partial epipterygoid, an isolated prootic, and the basisphenoid (Figure 27). The epipterygoid showed a well-defined suture with the pterygoid, indicating that the structure was not completely sutured together. The suture with the basiocciptal is also missing from UNSM 55810, and there does not seem to be any indication that the bone was broken off during fossilization, rather that the two elements were not totally fused during life. The well ossified basisphenoid might be a functional requirement of the skull for structural support, but this hypothesis would require further analysis. The prootic was not fused to the basisphenoid, and the facets for the prootic on the lateral dorsal surface of the basisphenoid are large and clearly indicate that the two elements were not completely fused during life in UNSM 55810. Rieppel (1992) found that the pterygoids are the first structure to ossify in the cranium for *Lacerata vivipara*. A similar pattern is seen in UNSM 55810, with the most heavily ossified bone of the specimen being the pterygoid plates.

Maisano (2001) found that viviparous squamates are born at a less ossified state than oviviparous squamates. In the vertebral column of viviparous squamates, the neural arch halves begin to fuse to one another shortly after birth, and the neurocentral suture also begins to close shortly after birth in the neonates (Maisano 2001, 2002). Maisano (2001) documented the clear posterior to anterior gradient in the fusion of neural arches in *Chalcides acellatus, Elgaria coerulea*, and the five xantusiid species that were analyzed. Therefore, the presence of unfused neural arches in a viviparous reptile, is indicative of the individual being neonatal in development. The posterior to anterior gradient in the ossification of the vertebral column seen in viviparous Lepidosauria, is also seen in UNSM 51880. Out of the 12 cervical vertebrae preserved with UNSM 51880, only 2 of them were preserved with neural arches intact, which were only partially fused. The dorsal vertebrae featured at least a partial neural arch, and none of the vertebrae featured completely fused neural arches or completely fused neurocentral sutures. Disarticulated neural arches are present from the cervical vertebrae, and some of the disarticulated neural arches did not have the formation of neural spine (Figure 24). For most of the cervical vertebrae, the anterior zygapophysis and posterior zygapophysis are not fully formed, and are just present in projections off of the neural arches (24 C). The amount of perichondral bone on the centrum has also been used to confirm of the fetal status of the LACM 129639 specimen. In the fetal specimen, the perichondral bone was limited to a small ring around the center of the lateral surface of each vertebrae. UNSM 51880 does feature more perichondral bone on its centra than the LACM fetus, but the ossification has not spread to envelop the entire outer surface of the vertebrae. As seen in (Figure 25 B) the lateral rim of the vertebrae features an outer surface that is mostly covered with perichondral bone, except at the anterior and posterior ends of the lateral surface of the vertebrae, where a distinct line can be seen which indicates the termination of the perichondral bone on the vertebrae.

However, as exemplified from Rieppel (2000), the timing of ossifications in reptiles can vary extensively. The sauropterigians as a clade feature delayed ossification during ontogeny (Klein and Scheyerm 2014). Sauropterygia are thought to feature paedomorphic skeletal ossification as an adaptation to a marine lifestyle (Klein and Scheyerm 2014). However, the paedomorphic skeletal ossification of the Sauropterygia might also be influenced by vivaparity, as seen in modern viviparous lizards (Maisano 2001). Overall, the axial skeletal osteology of UNSM 51880, when compared to modern saurians, indicates that the individual was most likely a neonate at the time of death. Further research is needed in the ossification patterns of the skeleton of polycotylid plesiosaurs throughout ontogeny, via looking at the histological growth of the bone.

Figure 27 Dorsal Skull Reconstruction of UNSM 55180. UNSM 55180 featured an elongated rostrum and a short posterior portion of the skull than what would be predicted for a juvenile polycotylid. Most of the preserved elements of the cranium are derived from the dermatocranium, not the chondrocranium or splanchnocranium.

Allometry of the Polycotylid Skull

The ontogenic growth series for the cranial anatomy of any group of plesiosaur remains highly speculative, due to the rare nature of the preservation of juvenile plesiosaur skulls. However, UNSM 55810 allows for a qualitative analysis of the allometry of polycotylid skull. Using the measurements from Carpenter's (1996) analysis, and comparing the dimensions of the adult UNSM 50133, found that the skull of UNSM 55810 is approximately 65% the size of the adult Wallace Ranch skull UNSM 50133 (Table 4). O'Keefe and Chiappe (2011) found that polycotlyid plesiosaurs are born at around the same size ratio as modern day cetaceans, with the infant being around 40% the size of the mother. The body size of UNSM 50133 was compared to the size of UNSM 55810 to see if it represents a mother and a newborn polycotylid. O'Keefe and Chiappe (2011) found that the humerus length scaled isometric with overall body size. Therefore, comparison of the humerus length between UNSM 51033 and UNSM 55810 could be used to estimate relative body sizes one another. O'Keefe and Chiappe (2011) calculated the total body length of the fetus by using the dimensions of the dorsal vertebrae. However, for this analysis, since both UNSM 55810 and UNSM 51033 featured well preserved humeri, the humerus length was used to predict overall body length. From the measurements of the humerus, UNSM 55810 was approximately 221.7 cm and UNSM 50133 was about 575.21 cm, indicating that UNSM 55810 was 38.5% the size of UNSM 50133. This ratio puts UNSM 55810 in the body size category of a neonate plesiosaur (O'Keefe 2011). When comparing skull lengths of the two Wallace Ranch specimens, UNSM 55810 was 238.6 cm and UNSM 50133 was 365.9 cm. This indicates that UNSM 55810 was around 65.2% of the size of UNSM 50133. The humerus length is most likely the best indicator of body size as the skull in vertebrates usually features negative allometry (Emerson and Bramble 1993).

Specimen	Skull length (mm)	Rostral length (mm)	(rostral)/(skull length) *100	(orbital)/(skull length) *100	(postorbital)/ (skull length) *100	(supratemporal fenestra length)/ (skull length) *100
UNSM 50133	618	375.126	60.7	-	-	18.6
UNSM 55180	403	259	64.3	-	-	-
SDSM 23020 *P. latipinnis*	938.45	603	64.3	10.9	24.8	-
ROM 29010	630.74	396.5	62.9	-	-	-
RSM P2310.1 *D. herschelensis*	409	243.5	59.5	-	-	-
SMNK-PAL 3861 *Manemergus anguirostris*	285	276.1	54.4	13	32.3	24.5
MNHGr.PA.11710 *Thililua longicollis*	660	382.8	58	13.7375	27.3	17
UCM 35059 *Dolichorhynchops osborni*	450	285	63.3	20.4	20.4	-
MCZ 1064 *Dolichorhynchops osborni*	470	269.78	57.4	23.4	17	-
FHSM VP 404 *Dolichorhynchops osborni*	513	319.6	62.3	20.4	17.5	16.6
KU VP 1300 *Dolichorhynchops osborni*	570	370	64.9	17.5	17.6	-
AMNH 5834 *Dolichorhynchops osborni*	745	464.88	62.4	21.5	22.1	18.8
KU VP 4001 *Dolichorhynchops bonneri*	980	569.38	58.1	14.7	20.1	20.4
KU VP 5070 *Trinacromerum bentonianum*	680	400	58.8	16.2	22.3	-
MOR 751 *Edgarosaurus muddi*	475	255.1	53.7	18.3	31.8	24.2
MNA V9431 *Dolichorhynchops tropicensis*	629.9	372.3	59.1	13.4	-	-
CM 2815 *Plesiopleurodon wellesi*	773	328.2	42.4	11.5	46.1	23.8
AMM 98.1.1 *Pahasapasaurus haasi*	799.66	472.2	59	14	27	-

Table 4 Linear Measurements and Skull Proportions for Specimens. The analysis here was expanded upon from Carpenter (1997) and Buchy et al. (2005).

UNSM 55810 is the developmentally youngest polycotylid with cranial material. The material was compared to that of other known juvenile polycotylids which belong to the species *D. osborni*, see Table (5). The two juveniles from D. osborni are UCM 35059 and MCZ 1064 (Table 5). Both UCM 35059 and MCZ 1064 are about the same size, even though they differ in some cranial proportions. MCZ 1064 features a larger orbit than UCM 35059, and MCZ 1064 also has a shorter rostrum in comparison to UCM 35059. Therefore, MCZ 1064 might not actually be a juvenile member of *D. osborni*, but maybe a juvenile of *D. bonneri*, due to the reduced premaxilla and larger orbit which are indicators of a young individual (Everhart 2004). UNSM 55810 features a long rostrum for a juvenile, which is similar to the condition seen in UCM 35059 (Table 4). The presence of a long rostrum at a young juvenile stage may represent parallelism with *Gavialis gangeticus.* Even as a new hatchling, *G. gangeticus*, features an elongated rostrum, which appears to be a functional adaption to a strictly piscivorous diet (Piras et al. 2010).

	UCM 35059	MCZ 1064	FHSM VP-404	KUVP 1300	UNSM 55810	UNSM 50133
Skull length	45	47	51.3	57	40.3	61.8
Posterior width of skull	15.3	14	19.4	-	-	23
Length of premaxilla	35.5	31	38	40	-	
Length of tooth bearing portion of the premaxilla	7	7	8.5	~8	-	7.3
Maximum diameter of the orbit	9.2	11	~10.5	~10	-	-
Orbit diameter/ skull length * 100	20.4	23.4	~20.5	~17.5	-	-
Length of retro-articular process	5	4	4.8	~4	-	7.5
Length of tip of premaxilla to orbit	28.5	27	32	~37	25.9	37.5
Length from back of skull to posterior edge of orbit	9.2	8	9	~11	-	-
Length of sagittal crest	8	~9	10	~11	~8.5	11.8
Length of lower jaw	49.5	49	56.2	60	-	73.5
Length of suture between dentarys		18	23.8	-	-	-

Table 5 *Dolichorhynchops* Growth Data. Expansion on Everhart (2004) comparing the growth series for *D. osborni* to that of the Wallace Ranch specimens. The differences between cranial proportion of UCM 35059 and MCZ 1064 differ from a lot from one another considering their similar size. These two specimens should be reevaluated to ensure that they are in fact both *D. osborni*. The rostral length in UNSM 55180 s large for its size and age, when compared to young individuals of *D. osborni*.

After expanding upon the work of Carpenter (1996) and Buchy et al. (2005), linear measurements on all of the known polycotylid skulls were ascertained to look for trends throughout the clades' evolution. One evident pattern that is seen in the data is that the percentage of the skull that consists of the postorbital region decreased as the polycotylids became more derived (Table 4.). Another assertion in the primary literature is that as the polycotylids became more derived, their percentage of skull consisting of rostrum increased as well (Buchy et al. 2004; Gasparini et al. 2001). However, these claims for rostral length increase in the Polycotylidae were never quantitatively analyzed. The polycotylids were separated into 3 categorical groups based on geologic time. The first group consisted of the basal polycotylids from the Aptian and Albian, the second category were the Turonian, and the third group featured the Campanian and Maastrichtian polycotylids. The (Figure 28) shows that there is an upward trend in the portion of the skull that was rostrum. When the categories were evaluated via a T-test between each of the groups, statistically, there is no difference between the three groups. However, the difference between the early polycotylid group and the latest polycotylid group were almost statistically significant, with a one-tailed T-test p-value equal to 0.097, see Figure (29). The category of the Albian and Cenomanian polycotylid skulls only included the measurements from three skulls, thus lowering the statistical power of the sample. More skulls from the Albian and Cenomanian are needed to evaluate whether there is a significant difference between the basal and more derived polycotylids in rostral length. One proposed hypothesis for this trend is that as the polycotylids became more derived in the late Cretaceous, they became more specialized piscivorous feeders, which led to the elongation of the rostrum paralleling the modern *Gavialis gangeticus*.

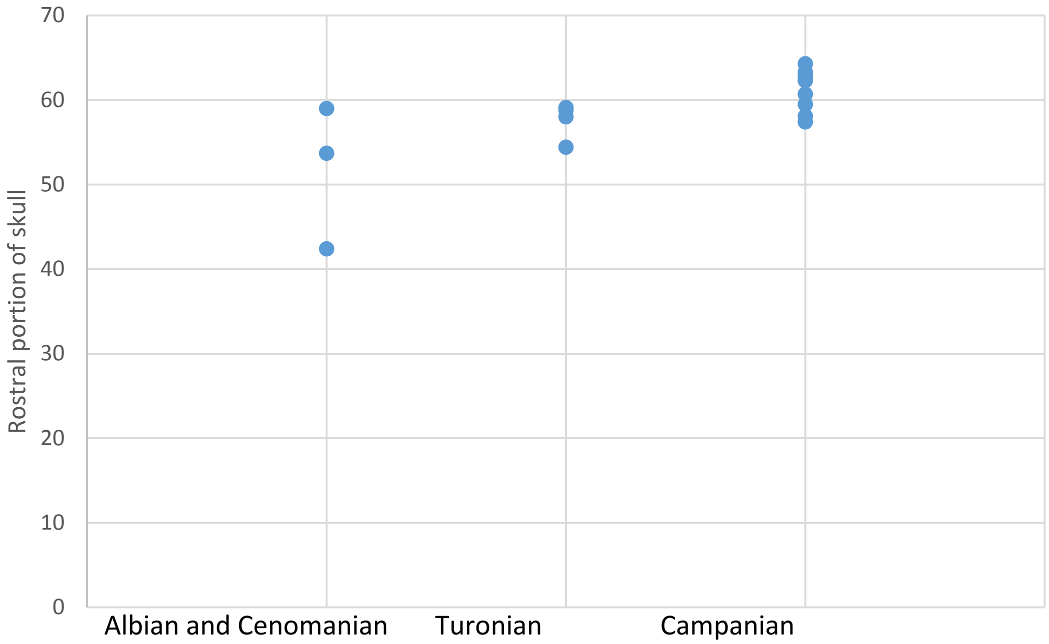

Figure 28 Rostrum Plots. Plotting the propotion of the skull that is equal to the rostrum for the Polycotylids throughout the Cretaceous period. There does seem to be a positive trend in rostrum length as the polycotylids became more derived. There are only three taxa from the

t-Test: Two-Sample Assuming Unequal Variances

	Variable 1	*Variable 2*
Mean	51.7	61.21111111
Variance	71.89	5.843611111
Observations	3	9
Hypothesized Mean Difference	0	
df	2	
t Stat	-1.91713	
P(T<=t) one-tail	0.097631	
t Critical one-tail	2.919986	
P(T<=t) two-tail	0.195263	
t Critical two-tail	4.302653	

Figure 29 T-test for Rostrum Length. T-test comparing the Albian-Cenomanian taxa to the Campanian taxa. The highlighted value is the p-value for 1-tailed T-test, which is not significant, but lack of significance could be due to the small sample size for the Albian-Cenomanian taxa.

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APPENDIX

SEXUAL DIMORPHISM OF THE ILIUM

Sexual dimorphism is present in almost every branch of Animalia, and it is not farfetched to think that sexual dimorphism was present throughout Plesiosauria as well (Shine 1989; Watkins 1998; Hone et al. 2012). The major problem with the Plesiosauria, since there are no living members of the clade, properly identifying structures that might be influenced by sexual selection can be difficult. More frequently, morphological sexual characters are often visual structures, which aid in either attracting or winning a mate (Hone et al. 2012). Therefore, characters hidden deep within the body of an animal that are not visible to other members of that organisms species are usually not under selective pressure via sexual selection. However, possible internal structures that deal with the reproductive tract could be under selective pressure. O'Keefe and Chiappe (2011), illustrated through the preservation of an immaculate fossil plesiosaur, that plesiosaurs actually gave live birth to young which were close to 40% the size of the mother. This is similar to the parturition size of modern cetaceans, which have taken over similar ecological roles in modern oceans as plesiosaurs once did in the Mesozoic era. Since plesiosaurs gave birth to such large young, the pelvic cavity of female plesiosaurs would need to be larger than that of males, to safely birth their young. The major bone in the pelvic girdle of polycotylids and all other plesiosaurs that limit the size of the pelvic cavity is the ilia bone. The ilium sits on top of the ischium and runs dorso-ventrally (vertical) until it attaches to the sacrum. Interestingly, in polycotylids, the ilia bones come in two distinct varieties: straight and robust, and narrow and anteriorly curved. These two varieties in ilia bones could mark sexually dimorphic states within polycotylids, with the males having the narrow and curved ilia that restrict the size of the pelvic cavity, and the females having the robust and straight ilia which maximize the space of the pelvic cavity (Schumacher and Martin 2015). In the O'Keefe and Chiappe (2011) paper, the pregnant plesiosaur mother featured robust and straight ilia. It is therefore predicted that female polycotylids would feature the straight robust ilium, while the males would have the curved and more gracile ilium. Data for this study were collected from personal photographs and from Shumacher and Matrin (2015). The linear measurements ascertained on the elements were: the width of the proximal head of the ilium, width of the distal head of the ilium, width of the midshaft of the ilium, total length of the ilium, and the angle of the medial side of the ilium for each specimen.

For the distribution of the ilia medial side angles, a histogram was generated for the data, and a Students T-test was ran to see if there were any differences between the shortest angled ilia and the rest of the sample (Figure 3.18). After collection of the linear data and the angle measurements, the data was then ran through a Spearman's Correlation Analysis in SAS. Spearman's Correlation Analysis allows for the analysis of correlation between different variables without requiring the data to fit a linear model. However, Spearman's Correlation Analysis does require that the relationship between the data be unidirectional. With Spearman's Correlation Analysis, the data are transformed into ranks and correlation is between variables are based upon the ranks, rather than the raw data (Pagano et al. 2000).

$T = \frac{\chi - \mu_0}{S/(\sqrt{n})} = \frac{147.5-164.3}{10.6066/(\sqrt{2})} = -2.24$
Df = (n-1) at $\alpha=0.05 = -6.314$
T (-2.24) $>$ $\alpha = 0.05$
Figure 30 T-test of the Smallest Angled Group of Ilia Against the Mean.

For the data points in the left most side of the histogram, which caused a skewing to the left for the distribution, I ran a Students T-test with the mean of that data against the sample mean to assess whether the points were statistically different from the mean. The results of this Test can be found in (Figure 30). The results of this analysis were not significant, and are probably a byproduct of a small sample size for the narrow angled ilia bones. Therefore, the null Hypothesis, which states that the ilia bone angles are not different from one another cannot be rejected.

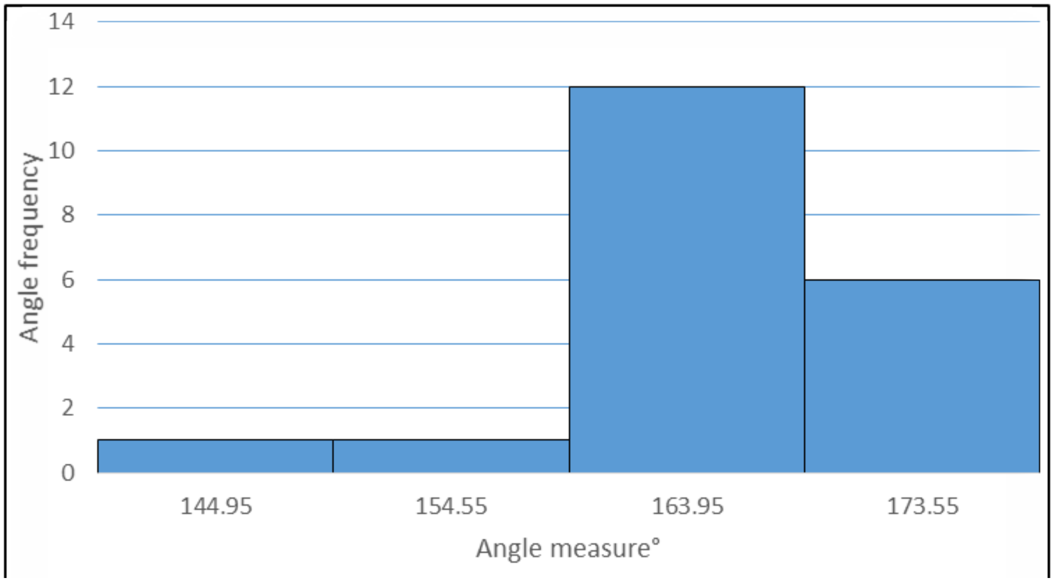

Figure 31 Histogram of Polycotylid Ilia Angles. Notice the skewing left of the data, this might indicate a possible bimodal distribution of the ilia

For the Spearman’s Correlation Analysis (Figure 3.19), all the measurement data is correlated with each other, except for the angle of the medial side of the ilia. For the angle of the ilia, there is no correlation with any of the other linear measurements, and therefore, the angle of the ilia cannot be predicted by any of the other variables that were collected in this research. Total length of the ilia featured a positive correlation with midshaft width, proximal width, and distal width. This trend indicates that as the total length of the ilia increases, the widths of the other elements are also increasing. The width of the ilia midshaft featured a positive correlation with total ilia length, proximal width, and distal width of the ilia. Therefore, as the midshaft width increases in size the width at both the proximal and distal ends also increases, along with an increase in total ilial length. The width at the proximal end is positively correlated with total ilia length, distal width, and midshaft width. Therefore, as the proximal end of the ilium increases in width, so does the distal end of the ilium, the midshaft width, and the total ilial length. The width at the distal end is positively correlated in the same way and has been explained with the rest of the variables above.

The SAS System

The CORR Procedure

5 Variables: totallength midshaftwidth withproximal widthdistal angleshaft

Simple Statistics

Variable	N	Mean	Std Dev	Median	Minimum	Maximum
totallength	20	21.18650	5.74457	21.86500	11.30000	33.70000
midshaftwidth	20	3.94500	1.37782	3.70000	2.10000	6.00000
withproximal	20	4.02500	1.56032	3.65000	2.00000	6.90000
widthdistal	20	6.54500	1.96749	6.30000	3.40000	11.20000
angleshaft	20	164.30000	7.90802	165.00000	140.00000	178.00000

Spearman Correlation Coefficients, N = 20
Prob > |r| under H0: Rho=0

	totallength	midshaftwidth	withproximal	widthdistal	angleshaft
totallength	1.00000	0.77619 <.0001	0.76555 <.0001	0.86177 <.0001	-0.24339 0.3011
midshaftwidth	0.77619 <.0001	1.00000	0.77707 <.0001	0.80814 <.0001	-0.06392 0.7889
withproximal	0.76555 <.0001	0.77707 <.0001	1.00000	0.80091 <.0001	-0.17367 0.4640
widthdistal	0.86177 <.0001	0.80814 <.0001	0.80091 <.0001	1.00000	-0.27524 0.2402
angleshaft	-0.24339 0.3011	-0.06392 0.7889	-0.17367 0.4640	-0.27524 0.2402	1.00000

Figure 32 Spearman's Correlation Analysis for the Ilia Bone Measurements
The top values indicate the Spearman's Correlation Coefficient and the bottom are the p-values.

The hypothesis that male and female polycotylids feature sexually dimorphic ilia bones is not supported by this study (Figures 30, 31). However, the angle of the ilia histogram is skewed left, indicating that there might be a bimodal distribution of the ilia bone angles. To verify this claim, more ilia bones are required, and all known polycotylid ilia bones were used in this study, and until more specimens are found, the question of whether the ilia bones are sexually dimorphic cannot be ascertained. When the small data points were analyzed via a Students T-test to the mean of the population for polycotylid ilia bone angles, the p-value was not significant. The null hypothesis, stating that there is not a difference between the ilia bone angle cannot be rejected. With the Spearman's Correlation Analysis, the angle of the ilia was not correlated with any of the other measurements that were collected. Therefore, the angle of the ilia cannot be predicted from random bone fragments of ilia in museum collections. The lack of correlation between the angle of the ilia and other measurements also suggests that the prediction that females would have a more robust ilia, with larger distal and proximal ends is not supported by this research as well. The other elements of the ilia such as all of the width and the total length measurements are positively correlated with one another (Figure 32). This indicates that the longer the ilia, the larger that other portions of the ilia, like distal and proximal width, and midshaft width will be. The total length of the ilia and the distal end of the ilia have the strongest positive relationship equal to 0.86177. The width of the distal end of the ilia might be a way to estimate the total length of broken ilia in fossil collections for polycotylid plesiosaurs. In conclusion, this study does not support the hypothesis that female polycotylids would have an ilia bone with a measurement closer to 180° and more robust than males. However, there was evidence of skewing to the left in the angle of the ilia distribution, so further research is needed in collecting more ilia bones for polycotylids.

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Office of Research Integrity

April 29, 2016

Donald Morgan
M.S. Candidate
Department of Biological Sciences

Dear Mr. Morgan:

This letter is in response to the submitted thesis abstract entitled *"Revision of Polycotylid Plesiosaur Systematics (Sauropterygia Plesiosauria) and Description of the Axial Osteology of a Juvenile Polycotylid."* 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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