

THE ONTOGENY OF THE SHOULDER IN *POLYCOTYLUS LATIPINNUS* (PLESIOSAURIA: POLYCOTYLIDAE) AND ITS BEARING ON PLESIOSAUR VIVIPARITY

F. Robin O'Keefe and Christina J. Byrd

Department of Biological Sciences, Marshall University, One John Marshall Drive, Huntington, West Virginia 25755
okeefef@marshall.edu

ABSTRACT

Delayed ossification and associated morphological change in the pectoral and pelvic girdles are a common feature of plesiosaur ontogeny, and the ability of this variation to mislead the unwary in taxonomic assignments has been acknowledged for decades. Understanding ontogenetic change in girdle morphology is particularly important given the recent discovery of a gravid plesiosaur, a late Cretaceous polycotylid (*Polycotylus latipinnus*), that provided the first evidence for viviparity in plesiosaurs. The fetal material associated with this adult includes most of the major girdle elements. One main supporting argument for viviparity in this fossil was the taxonomic identity of the adult and fetus based on humeral morphology. Comparison of the fetal material with another juvenile polycotylid from a closely related taxon demonstrates that the elements identified as fetal humeri are in fact scapulae, and that the fetal clavicles were misidentified as the scapulae. In this paper we compare the scapulae and clavicles of the fetus with the juvenile polycotylid specimen, as well as with adult material of *Dolichorhynchops osborni*. The scapulae of the fetus and juvenile possess ossifications that resemble the scapulae of more basal sauropterygians. As polycotylid growth continues, progressive ossification produces scapular ossification similar to adult basal plesiosaurs, such as *Plesiosaurus*. At full adulthood the scapula assumes its fully derived form, with a large and well-ossified anterior process of the ventral ramus. Therefore, the ontogeny of the scapula recapitulates its sauropterygian phylogenetic history. The morphology of the scapula is too ontogenetically variable for reliable classification of the fetus; however, the triradiate morphology and concavities of the clavicles are diagnostic to Polycotylidae. Further research has also determined that the fetal ilium was originally misidentified as the femur. Traits of this element, and of the ilium of the adult, are diagnostic to *Polycotylus*. Therefore, the taxonomic identity of the fetus continues to support an *in utero* relationship with the adult *Polycotylus*.

INTRODUCTION

Background—Plesiosauria is a group of extinct, marine reptiles that evolved at or near the Triassic-Jurassic boundary and disappeared at the end-Cretaceous mass extinction (Benson et al., 2012). The clade is characterized by a set of highly derived locomotor adaptations comprising a rigid trunk propelled by both fore and hind limbs. Both sets of limbs were hydrofoil-shaped with non-functional elbows and knees (Caldwell, 1997). The transition from nothosaur-grade sauropterygians to plesiosaurs is well-represented in the fossil record, and documents a rather gradual transition from axial propulsion with plesiomorphic, drag-based limbs to lift-based, appendicular-dominated propulsion (Storrs, 1993; Caldwell, 1997; Sato et al., 2010). The acquisition of the characteristically plesiosaurian suite of locomotor adaptations is correlated with a large increase in body size (O'Keefe, 2002; Benson et al., 2012), leading to long-standing speculation concerning the ability of large plesiosaurs to leave the water, and the possible life history constraints imposed by an obligatory aquatic lifestyle. Viviparity seemed a logical inference for plesiosaurs, and was given circumstantial support

by the discovery of gravid nothosaur-grade sauropterygians (Cheng et al., 2004). However, the long-standing and puzzling lack of evidence for plesiosaur viviparity was rectified only in 2011 (O'Keefe and Chiappe, 2011) with the description of the first gravid plesiosaur, a large, late Cretaceous polycotylid (*Polycotylus latipinnus*) from Kansas (LACM 129639a (adult) and LACM 129639b (fetus)).

Polycotylidae is a large Cretaceous family of short-necked plesiosaurs with a global distribution, long thought to be related to the short-necked Jurassic plesiosaurs. However, there is emerging consensus that the plesiosauromorph features found in polycotylids are convergently evolved, and that plesiosaur body shape evolution is much more complex than previously imagined (O'Keefe, 2001, 2002; Ketchum and Benson, 2012; Benson et al. 2012; the analysis of Druckenmiller and Russell, 2008, does not recover this grouping, but the taxon sampling in this analysis has been criticized (Ketchum and Benson, 2010)). While O'Keefe and Chiappe's (2011) paper on plesiosaur viviparity described the LACM adult and fetus in general terms, many questions remain concerning the detailed anatomy of the fetus and the ontogenetic trajectory between it and the adult. The purpose of this

paper is to focus on one of these questions, the ontogeny of the shoulder girdle.

The morphologies of the scapula and clavicle are critical because further research shows that the bones described as fetal humeri and scapulae by O'Keefe and Chiappe (2011) were incorrectly identified; the misidentifications can be demonstrated by reference to another, very juvenile but postnatal polycotylid specimen described below (The 'Wallace Ranch juvenile'). This skeleton is from the same formation and geological age as the gravid plesiosaur, although it is probably not referable to *Polycotylus*. O'Keefe (2008) suggested a referral to the genus *Dolichorhynchops*, although this was not firm, and the alpha-level taxonomy of the Late Cretaceous polycotylids is a very difficult problem even in adults (see Discussion). However, all other skeletons referable to *Polycotylus* are adult, and the Wallace Ranch juvenile is the best comparative data currently available. Additionally, associated skeletons of young juvenile plesiosaurs are rare, and this skeleton comprises all girdle elements save the interclavicle, and includes three propodials and other flipper bones, and a partial skull.

The identification errors in O'Keefe and Chiappe (2011) have important repercussions, because a primary piece of evidence supporting the argument for viviparity was the taxonomic identity of the adult and fetus, an attribution resting primarily on 'humeral' morphology. Below we describe the scapulae and clavicles of the fetus in detail, comparing the fetus to the adult. We also compare the fetus to an adult of *Dolichorhynchops osborni* (Williston, 1903) as well as the Wallace Ranch juvenile. We conclude that the fetal scapulae were misidentified as humeri and that the fetal clavicles were misidentified as scapulae by O'Keefe and Chiappe (2011). However, the fetal clavicles are diagnostic to Polycotylidae, and the fetus is very large given its ossification state. We can therefore state unequivocally that the fetus belongs to a large polycotylid. Also, the element originally described as the fetal femur by O'Keefe and Chiappe (2011) is in fact the ilium. This element has a curved shaft, which is an autapomorphy of *Polycotylus* within Polycotylidae. The attribution of the fetus to the same taxon as the adult therefore appears reasonably secure, with the fetus diagnostic to the generic level. Alpha-taxonomic assessment of the LACM fetus is complicated further by challenges inherent in polycotylid taxonomy, a complex problem that has resisted definitive resolution despite several concerted attempts (Shumacher, 2007, O'Keefe, 2008, Schmeisser McKean, 2012).

Shoulder Girdle Phylogeny—One key morphological transition occurring at or near the origin of the clade Plesiosauria is a fundamental rearrangement of

the anterior pectoral girdle (Figure 1). In all sauropterygians, the ventral aspect of the pectoral girdle is emphasized and its lateral aspect is reduced. Therefore all nothosaur-grade sauropterygians have a reduced dorsal scapular blade (termed the dorsal process) and a robust, ventrally-oriented coracoid with a posterior median symphysis (Storrs, 1993; Rieppel, 2000; see discussion in Benson et al., 2012). The ventral elaboration of the scapula is modest, being restricted to the area around the glenoid and lacking significant anterior or medial processes (Figure 1). The anterior and medial portions of the pectoral girdle consist of a robust clavicular arch, comprising heavy clavicles that reach the midline, while the interclavicle is often reduced with a short posterior process (Lin and Rieppel, 1998; Rieppel, 2000). The sister clade to Plesiosauria is the Pistosauria, a clade that may contain the lineage directly antecedent to plesiosaurs. In this clade, further ventral elaboration of the coracoid occurs, and it loses its plesiomorphic mid-element constriction and becomes a flat plate with a median symphysis along its entire median margin (condition in *Corosaurus*; Storrs, 1991; Figure 1). However, in *Corosaurus* and in *Yunguisaurus*, perhaps the most plesiosaur-like of all basal sauropterygians, the scapula remains a lateral element without strong antero-medial elaboration ventrally, and the anterior pectoral girdle still consists of a robust clavicular arch (Sato et al., 2010). Furthermore, the material of *Yunguisaurus* described to date has been juvenile, and adult morphology may differ.

Plesiosaurs are characterized by the loss of this robust clavicular arch, and its replacement by an antero-medial elaboration of the scapula, hereafter termed the ventral ramus. In archaic plesiosaurs the clavicular elements remain relatively large, such as in *Plesiosaurus* (Storrs, 1997) or *Westphaliasaurus* (Schwemann and Sander, 2011), although there is also significant development of a scapular ventral ramus that trends medially and contacts a neomorphic antero-medial process of the coracoid. The most plesiomorphic plesiosaur shoulder girdle known is that of *Westphaliasaurus* (Figure 1). In this taxon, both clavicle and interclavicle are large elements, but there is still significant anteromedial expansion of the scapula and the neomorphic contact with the coracoid as seen in *Plesiosaurus*. In the later evolution of Plesiosauria, there is a trend toward extreme reduction of the clavicular arch and the repeated evolution of a neomorphic contact of the scapulae on the ventral midline. The presence or absence of a midline symphysis of the scapula is a taxonomically variable character, evolving independently in Elasmosauridae (Cretaceous) and Cryptoclididae (late Jurassic) (Williston, 1906; Watson, 1924). The midline symphysis is absent in the more derived clades

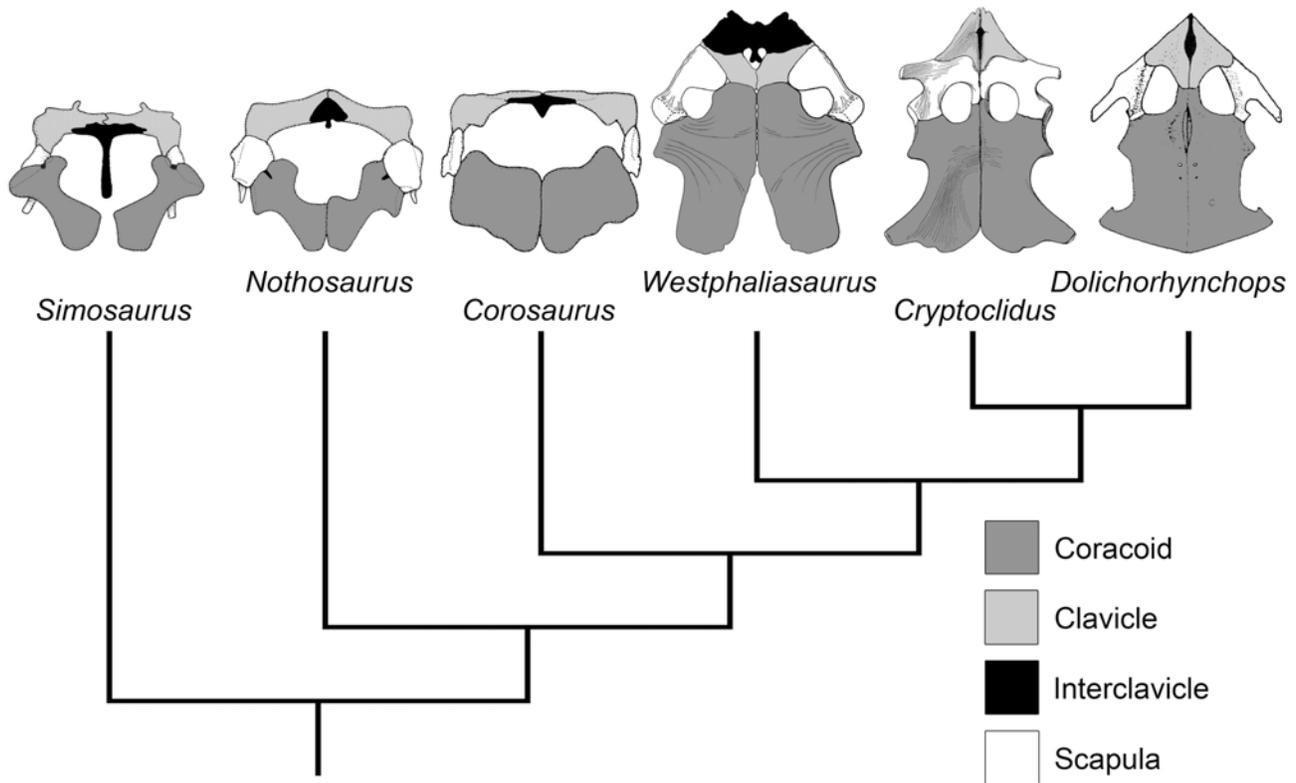


FIGURE 1. Summary of pectoral girdle evolution within Sauropterygia. The basal topology (*Simosaurus*-*Corosaurus*) is derived from Liu et al., (2011); ingroup plesiosaur relationships (*Westphaliasaurus*-*Dolichorhynchops*) are based on Benson et al., (2012). Note hypertrophy of the coracoid, which first loses its waisting to become plate-like, and then extends far posteriorly in more derived taxa. The scapula transitions from a primarily lateral element with modest ventral elaboration in 'nothosaur' grade taxa to a ventro-lateral element with a significant anterior process on the ventrum in plesiosaurs. The extent of this anterior process varies both ontogenetically and phylogenetically in plesiosaurs. The dermal elements (clavicle and interclavicle) comprise the major part of the anterior aspect of the girdle in 'nothosaur' grade sauropterygians, but are supplanted by the scapula and relatively unimportant in most plesiosaurs. The girdles of *Cryptoclidus* and *Dolichorhynchops* are shown in visceral (dorsal) view, while the other taxa are in superficial (ventral) view, because the dermal elements are largely hidden by the anterior processes of the scapula in most derived plesiosaurs.

Leptocleididae (early Cretaceous) and Polycotyliidae (late Cretaceous) (Williston, 1906; Ketchum and Benson, 2010; Kear and Barrett, 2011). In polycotyliids at least this may be a secondary loss linked to posterior hypertrophy of the locomotor apparatus correlated with large prey size (O'Keefe and Carrano, 2005). However, marked anteromedial elaboration of the scapula is characteristic of all plesiosaurs in contrast to all more basal, nothosaur-grade sauropterygians, and the clavicle is correspondingly reduced and underlain broadly by the scapula. Morphology of the adult scapula, clavicle and interclavicle is extremely variable in Plesiosauria, and therefore taxonomically useful. However, as discussed first by Brown (1981), the shapes of all endochondral girdle elements change radically over ontogeny, and ossification is delayed in plesiosaurs as in other fully aquatic tetrapods. Extreme care is therefore necessary when scoring the girdle elements taxonomically, because juveniles often display different states than adults.

In derived polycotyliid taxa such as *Dolichorhynchops osborni*, the adult scapulae have a robust glenoid ramus carrying the anterior half of the glenoid as well as the ventral ramus (termed 'ventral plate' by Tarlo 1957; Figure 3) with significant antero-medial expansion. The scapular ridge runs ventrally from the glenoid process anteriorly along the medial edge of the ventral ramus, and divides the lateral and ventral portions of the scapula. The dorsal process, or scapular blade, extends posterodorsally, and is long and well-developed, unlike the condition in elasmosaurs where it is often reduced (Hiller and Mannering, 2005). The clavicle is situated on the dorsal, or visceral, surface of the scapula, is large by plesiosaurian standards, and possesses a characteristic triradiate morphology with a thickened anterolateral border. The medial edge is irregular and thin and is dished into a shallow fossa that accepts the interclavicle. The interclavicle is known only in adults, and is small with a prominent

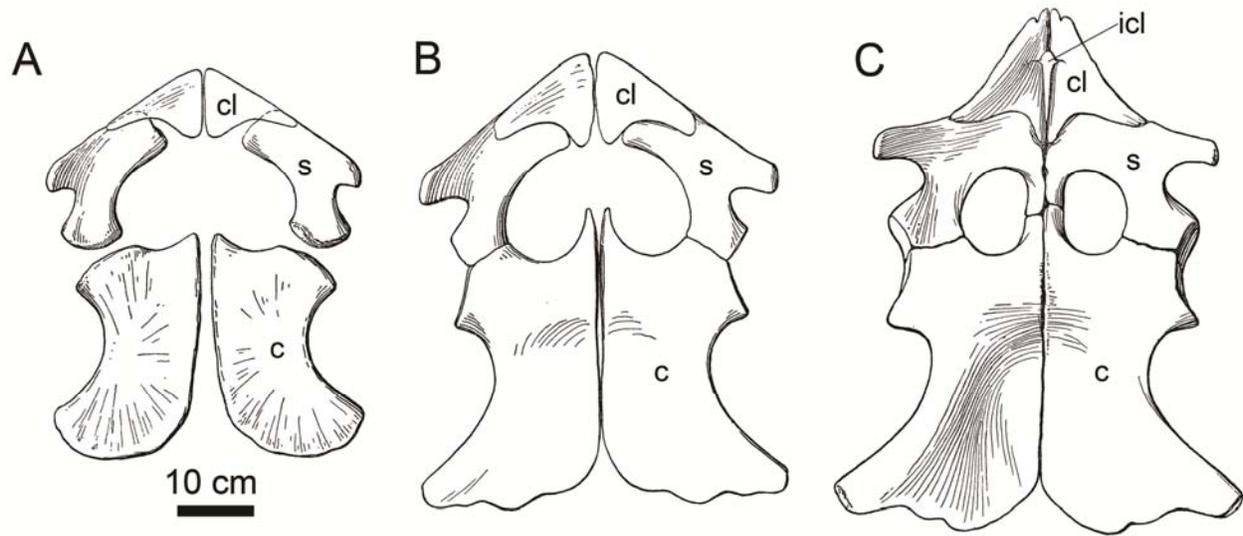


FIGURE 2. *Cryptoclidus oxoniensis* ontogenetic series: (A) juvenile, (B) subadult, and (C) adult. (Andrews, 1910; Schwermann and Sander, 2011). The scapulae of the juvenile and subadult *Cryptoclidus* have a morphology that resembles that of basal plesiosaurs such as *Plesiosaurus* and *Westphaliasaurus*. As *Cryptoclidus* ontogeny progresses, the ventral rami meet at the midline and growth continues posteriorly, forming a medial symphysis of the scapulae and contact with the coracoids. Abbreviations: c-coracoid, cl-clavicle, icl-interclavicle, s-scapula.

median fenestra, and often a separate anterior median cleft. In general, the anterior elaboration of the scapular ventral ramus and the clavicular arch are highly diagnostic in adult Polycotylidae, although *Cryptoclidus* also possesses triradiate clavicles enclosing the interclavicle, and *Muraenosaurus* possesses a fenestrate interclavicle (Andrews, 1910).

Pectoral Girdle Ontogeny—Knowledge of the ontogeny of the shoulder girdle in basal plesiosaurs is limited by available fossil evidence, but good post-natal data do exist for the common Oxford Clay taxon *Cryptoclidus*. *Cryptoclidus oxoniensis* is a plesiosauroid from the family Cryptocleididae with conservative neck and head anatomy (O'Keefe, 2002). Cryptocleididae is closely related phylogenetically to Polycotylidae, a relationship first proposed by O'Keefe (2001) and recently recovered by other authors (Ketchum and Benson, 2010; Otero et al., 2012). Figure 2 illustrates the ontogenetic series of the pectoral girdles from Andrews (1910) and demonstrates the variability in bone morphology that occurs during *Cryptoclidus* post-natal development. The juvenile *Cryptoclidus* scapula has morphological traits similar to those of archaic plesiosaur adult scapulae; i.e. the ventral ramus is poorly developed and does not meet its neighbor on the midline, and there is no medial contact between the coracoid and scapula.

However, as the scapula develops, the ventral ramus grows anteromedially until the two scapulae meet at the midline, and ossification continues posteriorly to contact the advancing coracoids. In adult *Cryptoclidus*, the scapulae have a long midline symphysis that completely hides the clavicular arch in ventral view, a feature reflected in the name of the taxon. The growth of the scapular ventral ramus is therefore an excellent example of ontogenetic recapitulation of a phylogenetic trend.

Some ontogenetic data is also available for the polycotylid *Dolichorhynchops* from Carpenter (1996). The pectoral ontogenetic series figured in this source lacks detail, but the general pattern of recapitulation is similar. Early in ontogeny the scapula resembles the primitive plesiosaurian condition with a relatively modest ventral ramus and a lack of medial contact with the coracoid or neighboring scapula, while later in ontogeny the ventral ramus ossifies anteriorly and medially to contact a ventral process of the coracoid. Unlike cryptocleidids, the scapulae have no midline symphysis in adult Polycotylidae, although they do continue to contact the antero-medial processes of the coracoids in the adults of at least some taxa (e.g. *Trinacromerum*; Williston, 1908).

Institution Abbreviations—KUV, Kansas University Museum of Natural History, Lawrence,

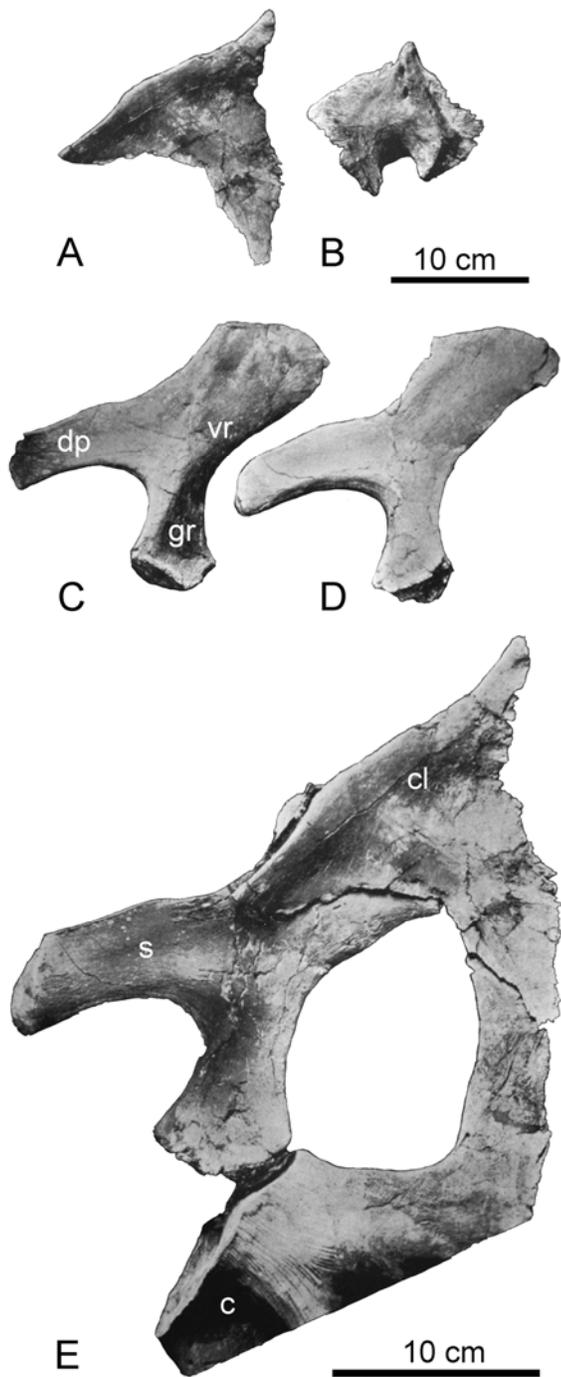


FIGURE 3. *Dolichorhynchops osborni* (KUV 1300) pectoral girdle elements disarticulated and articulated. A-D are the left clavicle and interclavicle in visceral view and the right ventral and left visceral views of the left scapulae, respectively. E demonstrates the articulated positions of the clavicle, scapula and left coracoid in visceral view (Williston, 1903). *D. osborni* has a triradiate clavicle that is situated on the visceral surface of the scapula. Abbreviations: c-coracoid; cl-clavicle; dp-dorsal process of scapula; gr-glenoid ramus; s-scapula; vr-ventral ramus.

Kansas; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; UNSM, University of Nebraska State Museum, Lincoln, Nebraska.

MATERIAL AND DESCRIPTION

The gravid specimen of *Polycotylus latipinnus* discussed here (LACM 129639) is from the Bonner Ranch in Logan County, Kansas, found in the Sharon Springs Member of the Pierre Shale Formation (middle Campanian). The stratigraphy of this formation is extensively reviewed and revised by Martin et al. 2007; those authors propose elevating the Sharon Springs to formation status, and designating the lower, vertebrate-bearing beds as the Burning Brule Formation. We follow the traditional stratigraphy here. The material of *Dolichorhynchops osborni* illustrated here is the holotype (KUV 1300), and was originally figured by Williston (1903). The holotype is an almost complete and well-preserved young adult from the Smokey Hill Chalk Member (*Hesperornis* zone, lower Campanian; Carpenter, 2003) of the Niobrara Formation, Logan County, Kansas. The pectoral girdle is complete, as is the clavicular arch, including the rarely preserved interclavicle. These elements are shown individually and in articulation in Figure 3. The juvenile skeleton, UNSM 55810, is from the Wallace Ranch Locality of South Dakota, and was found in the Sharon Springs Member of the Pierre Shale. This skeleton comprises most girdle elements, parts of all four paddles, and a partial skull, but no vertebral column. Its taxonomic status was discussed thoroughly by O'Keefe (2008). The Wallace Ranch skeleton is certainly a polycotyloid and was tentatively referred to *Dolichorhynchops*, but a firm identification is impossible due to the lack of ossification of the skeleton. The skeleton is relatively small, however, and may be referable to *Dolichorhynchops osborni*, rather than either of the large-bodied polycotyloids currently known from the Pierre Shale (*Dolichorhynchops bonneri* and *Polycotylus latipinnus*; O'Keefe, 2008; O'Keefe and Chiappe, 2011). The Wallace Ranch juvenile is a constructive source of comparison because it is a young juvenile from a taxon closely related to *Polycotylus*, and illustrates juvenile characters intermediate between polycotyloid adults and the fetus.

Scapula—Both scapulae of the fetus (LACM 129639b) are preserved, and were originally described as humeri by O'Keefe and Chiappe (2011). Superficially, the scapulae resemble adult humeri much more than adult scapulae (Figure 4a; the left scapula is figured and described here because the right is relatively poorly ossified and preserved). However, the juvenile skeleton (UNSM 55810) possesses both scapulae and one humerus, and the humerus consists

almost solely of the diaphysis with a poorly ossified proximal end and undifferentiated capitulum (humeral head) and dorsal tuberosity. The distal end is also poorly ossified, with modest antero-posterior expansion and a complete lack of the well-defined epipodial facets characteristic of polycotyliids (O'Keefe, 2004, 2008; lack of distal ossification in the propodials is a well-known feature of plesiosaur ontogeny (Brown 1981)). The fetal elements bear no resemblance to this humerus, but are very similar to the Wallace Ranch scapulae in both shape and size (Figure 4b). The scapula of the fetus lacks any anterior elaboration of the ventral ramus, and the anterior edge of the dorsal process is confluent with the anterior edge of the ventral body of the scapula, reminiscent of the condition in nothosaur-grade sauropterygians rather than plesiosaurs. The dorsal process has a thickened posterior edge and extends posterolaterally, but is short and poorly developed. The scapular ridge is also poorly developed, but does possess thickened bone on the ventral face of the scapula. The glenoid ramus is the best-developed portion of the fetal scapula, comprising a robust process terminating posteriorly in a large, rugose mass comprising the anterior portion of the glenoid fossa. The length of the scapula was measured from the anterior-most point of the ventral ramus to the posterior-most point of the glenoid process, parallel to the sagittal plane. The scapulae measure 95 mm for the right and 98 mm for the left. Scapular width from the most medial point of the ventral ramus to the most distal point of the dorsal process measures 84 mm for the right and 88 mm for the left.

The scapula of the Wallace Ranch juvenile (UNSM 55810; Figure 4B) is very similar to that of the fetus and differs from that of the adult (Figure 3C). There is little anterior ossification of the ventral ramus, although the dorsal process is significantly longer and more blade-like. The scapular ridge is well developed along the border of the ventral ramus and the glenoid ramus is identical to the fetal condition. Scapulae lengths are 101.5 mm for the right and 104.5 mm for the left. Widths of the scapulae are 107 mm for the right and 105.5 mm for the left.

The scapula of the adult (LACM 129639a; Figure 4C) has significant anterior ossification of the ventral ramus, much like that of *Dolichorhynchops* (Figure 3) and other polycotyliids. The dorsal process has a wide root on the body of the scapula and narrows to a long, dorso-posteriorly directed process. The process lacks a bend at midshaft, a feature characteristic of *Dolichorhynchops* (see taxonomic discussion below); this trait contributes to the referral of the adult to *Polycotylus*. The length of the adult scapula is 330 mm and the width is 413.8 mm.

Clavicles—The bones interpreted as fetal scapulae by O'Keefe and Chiappe (2011) cannot be scapulae

based on the description above, and comparison with other material demonstrates that they are clavicles. Unlike the scapula, the shape of the clavicle is highly conserved through polycotyliid ontogeny. The clavicles used for comparison (LACM 129639b, UNSM 55810, and KUV 1300) share several morphological characteristics (Figure 5A-C). All of the clavicles possess the triradiate shape characteristic of Polycotyliidae and share a thickened anterolateral edge. A deep embayment is present on the posterolateral edge, and the midline carries a shallow fossa in all cases surrounding a concavity with a thin, irregular border. When the clavicles are paired together, the midline concavities form a foramen for acceptance of the interclavicle. In addition, they share irregular edges along the posterolateral border, and a shallow depression along the posterolateral concavity in visceral view.

Concerning the rest of the shoulder girdle, no interclavicle or coracoid could be identified from the fetal material in LACM 129639b. The adult *Polycotylus* (LACM 129639a) possesses both coracoids but no interclavicle (O'Keefe and Chiappe, 2011), and this is also the case with the Wallace Ranch juvenile (UNSM 55810). The coracoids are not described here because no coracoid was identified in the fetal remains, and the element is consequently not relevant to ontogenetic and phylogenetic discussion of the fetus.

DISCUSSION AND CONCLUSIONS

Misidentifications and Taxonomic Status—The bones identified as humeri in the fetal skeleton are here reinterpreted as scapulae based on their close similarity to those of the Wallace Ranch juvenile (UNSM 55810), and dissimilarity to the humeral material from that skeleton. The bones interpreted as scapulae in the fetus are clavicles, closely resembling the clavicle of the Wallace Ranch juvenile and of the adult *Dolichorhynchops osborni*. O'Keefe and Chiappe (2011) thereby joins a rather long list of publications containing misidentified plesiosaur girdle elements (reviewed in Smith, 2007). The correct identification of these elements raises two important questions. The first is the taxonomic status of the fetal skeleton associated with the LACM *Polycotylus* specimen, and the second is extreme shape change during the ontogeny of the scapula in polycotyliid plesiosaurs. We discuss the taxonomic status of the LACM fetus first, and then review the ontogeny of the scapula in the context of sauropteryian phylogenetic history.

The humeral characters used to assign the fetus to the taxon *Polycotylus latipinnus* are spurious, and the ontogenetic variation in scapular morphology makes it taxonomically useful in adults only. However, the

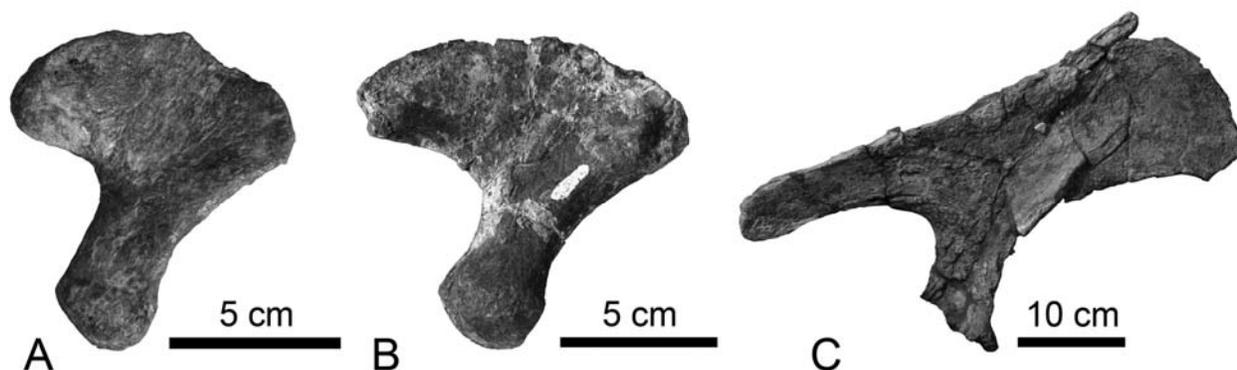


FIGURE 4. Comparison of scapulae of (A) the fetus (LACM 126396b), (B) juvenile (UNSM 55810), and (C) the adult (LACM 126396a). The fetus and juvenile have similar scapular morphologies and size. Both have a relatively well developed glenoid ramus when compared with the ossification of the ventral ramus and dorsal process. A scapular ridge is present on the ventral surface and runs anteriorly from the glenoid ramus along the medial edge of the ventral ramus. The overall morphology resembles that of basal sauropterygians, such as nothosaurs and pistosaurs. In the adult, the ventral ramus and dorsal process are more exaggerated and have a morphology that more closely resembles the scapular morphology of basal plesiosaurs.

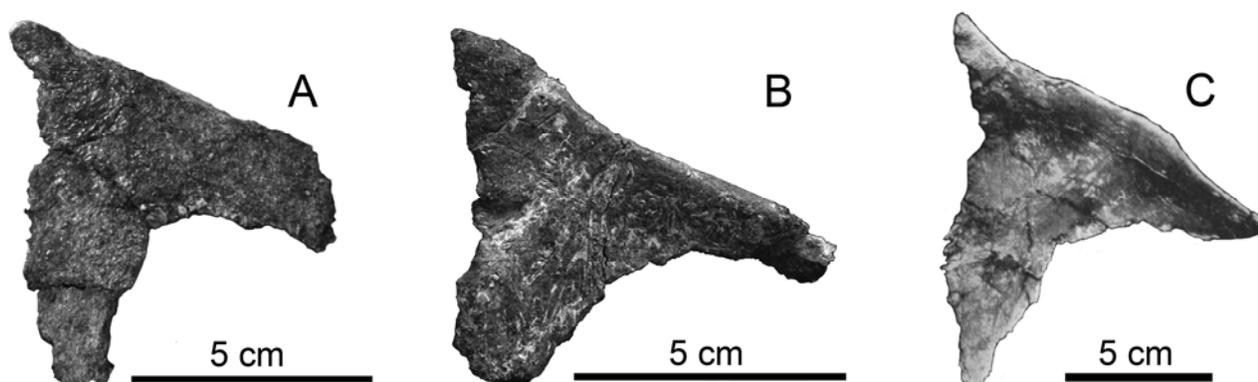


FIGURE 5. Comparison of clavicles for (A) the fetus (LACM 126396b), (B) juvenile (UNSM 55810), and (C) *D. osborni* (KUV 1300). All three clavicles share a similar triradiate shape with a thickened anterolateral border, posterolateral concavity, and smaller concavity along the midline border. The clavicles are less robust than those found in basal sauropterygians and even the basal plesiosaurs.

clavicles of the fetus are diagnostic; the polycotylid clavicle has a characteristic triradiate morphology with concavities along the midline and posterolateral border. Also, the morphology of the clavicle varies little ontogenetically.

The fetal clavicles are not diagnostic to the species level, but are diagnostic to the family Polycotylidae. Therefore, the fetus was certainly a polycotylid plesiosaur, and given its size and poor ossification state was probably a large one. Lastly, further research has determined that the element described as the fetal femur (O'Keefe and Chiappe, 2011) is in fact the ilium, depicted here in Figure 7. This ilium clearly shows a posterior bend or angle, a trait shared by several *Polycotylus* adults, including the mother (see below). Therefore, we can securely refer the fetus to the Polycotylidae based on the clavicle, and

further refer it to the genus *Polycotylus* based on the morphology of the ilium. This taxonomic attribution of the fetus continues to support its interpretation as *in utero* within a gravid mother.

The question of taxonomic assignment of the fetus touches on the larger problem of polycotylid alpha taxonomy. Homoplasy is rampant in the group, and stable diagnoses have proved very difficult to establish. As in most vertebrates the skull is highly diagnostic (O'Keefe, 2004), but the LACM adult lacks a skull, and the *Polycotylus* skull is known only from fragments in any case. O'Keefe and Chiappe (2011; Supplementary Online Information) referred the LACM adult to *Polycotylus* based on revised scoring for the cladistic matrix in O'Keefe (2008), and the balance of this evidence does support this attribution.

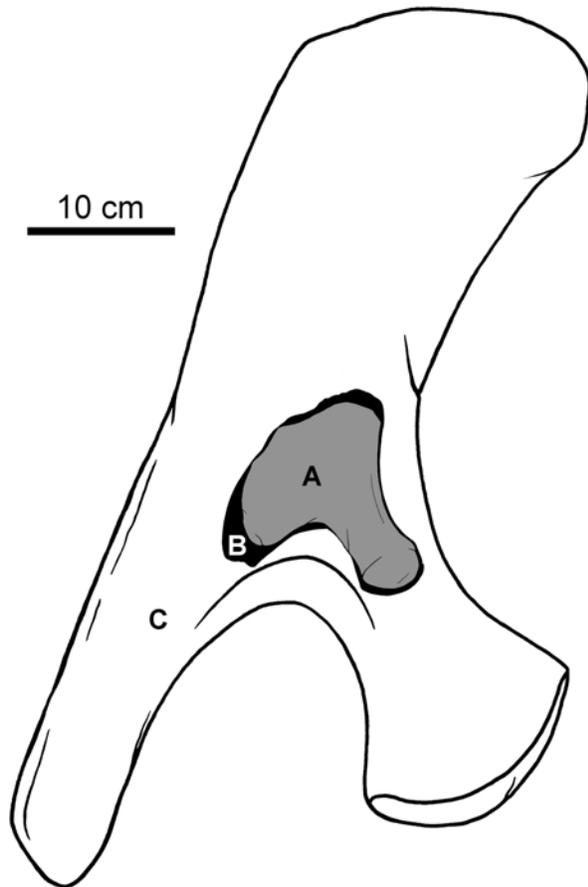


FIGURE 6. Scaled comparison of the (A) fetus, (B) juvenile, and (C) adult scapulae. Note the drastic difference in morphology from the fetus and juvenile to the adult stage, particularly the elongation of the ventral ramus into an anterior process, and lengthening of the dorsal process.

However, character 16 is equivocal; the caudal facets for hemal arches are generally on the posterior vertebral centra as in *Dolichorhynchops*, not *Polycotylus* (Carpenter, 1996), although attachment varies significantly along the caudal series, and both states are present in LACM 129639a. Characters thought unequivocally diagnostic of *Polycotylus* included character 26, posterior extensions of coracoid are present; character 31: ischium length vs. width, the ischium is long posteriorly; and character 37: the dorsal scapular process is not bent. O'Keefe and Chiappe (2011) also listed a new character, a lateral expansion of the anterior part of the ventral ramus. To these features may be added a posteriorly angled ilium; the ilia of the LACM adult have apparently been lost, but historical photographs showing the elements were kindly provided by one of the reviewers (BAS) and they clearly show a posterior bend as noted in *Polycotylus* by Carpenter (1996). These five characters differentiate *Polycotylus* from all species of *Dolichorhynchops* then known (including the large-



FIGURE 7. Right ilium of fetus of *Polycotylus*, (LACM 126396b), lateral view on the left, medial on the right, with sacral end at top. This element was originally identified as the femur by O'Keefe and Chiappe, 2011. The bend to the shaft of the ilium is diagnostic to *Polycotylus* within Polycotylidae.

bodied *Dolichorhynchops bonneri*). However, a newly described, stratigraphically early taxon referred to *Dolichorhynchops* (Schmeisser McKean, 2012) also has an expanded scapular anterior ramus, has *Polycotylus*-like ischia, and possesses subtle posterior extensions on the coracoids. Posterior coracoid extensions may also be found in the long-necked cryptocleidid *Muraenosaurus*, from the Callovian Oxford Clay of England (Andrews, 1910). Also homoplastic is the humerus, where the narrow, constricted shaft with a strong sigmoid curvature was stated to be diagnostic of *Polycotylus* by O'Keefe and Chiappe (2011). The humerus of *Dolichorhynchops bonneri* is actually quite similar to that of *Polycotylus*, also possessing a strongly sigmoid shaft, and while it is not as constricted as that in *Polycotylus* the difference is subtle and may be due to postmortem compression (O'Keefe, 2008). The humeri of both taxa also have four distinct facets for ossifications in the epipodial row. In summary, the alpha taxonomy of the

Polycotyliidae is a difficult problem, with homoplasy common among supposedly diagnostic characters. There is a growing suspicion among polycotyliid workers that sexual dimorphism may contribute to this homoplasy, although the research to document this has yet to be done. Sexual dimorphism would be plausible, however, if polycotyliids did indeed live in social groupings as suggested by O'Keefe and Chiappe (2011).

Polycotyliid Shoulder Ontogeny—Early in polycotyliid ontogeny, the scapula appears to be more nothosaur-like than plesiosaur-like. A scapula possessing a broadened, well-developed glenoid ramus, a low, poorly-developed dorsal process, and lacking anterior elaboration of the ventral ramus is typical of adult nothosaurs and pistosaurs (Storrs, 1991; Sato et al., 2010; Figure 1). This condition is mirrored in the early ontogenetic stages of polycotyliids. As polycotyliids continue to grow, the ventral ramus ossifies anteriorly and the morphology comes to resemble that of basal plesiosaurs such as *Plesiosaurus* and *Westphaliasaurus*, while in the adult they closely approach the midline. The scapulae therefore recapitulate sauropterygian phylogenetic history during ontogeny.

The greatest difference between the juvenile polycotyliid scapulae and the scapulae of nothosaurs and pistosaurs is the anterior border of the ventral ramus. The border of the ventral ramus of the fetus and juvenile is thin and irregular, as opposed to the thickened and smooth edge found in basal sauropterygians. The irregular edge suggests incomplete ossification of the scapulae, which implies the presence of significant cartilage along the ventral ramus and anterior edge of the dorsal process. The extent to which the juvenile scapula was actually present in cartilage prior to delayed ossification over ontogeny is not known, but was probably significant. Early ossification of the scapulae is concentrated at the area of the glenoid process and its junction with the dorsal process, thereby providing skeletal strength near the joint capsule needed for swimming after birth. A similar pattern of glenoid ramus development can also be seen in juvenile *Cryptoclidus* (Figure 2). A cartilaginous ventral ramus would provide support for the anterior girdle elements until the ventral ramus and dorsal process are completely ossified.

When the scapulae of the fetus and Wallace Ranch juvenile are compared to those of the adult, we see a large amount of allometric growth occurring along the ventral ramus and dorsal process (Figure 6). When the ratio of scapular length and width is taken, we see that allometric growth is occurring in the width of the bone. The fetus has a scapular ratio (length/width) of 1.12, which shows that the scapula is longer than it is wide. The juvenile has a scapular ratio of 0.97 and the adult has a ratio of 0.8. These ratios



FIGURE 8. Left scapula of a young juvenile elasmosaur in superficial (top) and visceral (bottom) views (AMNH 5261). This specimen is the holotype of "*Leurospondylus ultimus*" (Brown, 1913), declared a *nomen dubium* by Sato and Wu, 2006, due to its immaturity and lack of diagnostic characters. The overall morphology is similar to that of the juvenile polycotyliids illustrated here, with a relatively well-ossified glenoid region but with truncated dorsal process and little anterior elaboration of the ventral process. The ventral ramus is comparatively broad medially, a feature found in adult elasmosaurs.

suggest that throughout ontogeny, the scapulae become wider. However, the orientation of the scapula is anteromedial, so increasing width of scapula is a

function of anteromedial growth of the ventral ramus and the lengthening of dorsal process.

Ontogenetic variation in the morphology of the polycotylid shoulder girdle complicates attempts to identify elements of the examined subadult specimens. However, the fetus, juvenile, and adult specimens discussed here provide an ontogenetic series of sorts, at least for the family Polycotylidae. The general pattern displayed here also seems applicable to other clades of plesiosaurs, given the growth series of *Cryptoclidus* illustrated above (Figure 2), and a postnatal elasmosaur scapula illustrated here for comparison (Figure 8). The juvenile elasmosaur scapula is notable for having a relatively wide ventral ramus, an adult elasmosaur feature that differentiates this poorly ossified element from those referable to Polycotylidae. However, the juvenile elasmosaur scapula lacks an ossified anterior process, as in *Cryptoclidus* and the polycotylids, so this ossification pattern may be general to plesiosaurs. Comparisons of pectoral girdle morphologies not only aid in correcting bone misidentifications, but illuminate ontogenetic shape change and allometric growth. Obviously, caution is needed in using the scapula as a source of taxonomic characters in juvenile material, a point made originally by Brown (1981).

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