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Description and histology of a small-bodied elasmosaur and discription of mortuneria seyemourensis postcranium

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DESCRIPTION AND HISTOLOGY OF A SMALL-BODIED ELASMOSAUR AND DISCRIPTION OF MORTUNERIA SEYEMOURENSIS POSTCRANIUM

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
Elizabeth Lester
Approved by
Dr. F. Robin O'Keefe, Committee Chairperson
Dr. Suzanne Strait
Dr. Anne Axel

Marshall University
May 2019

APPROVAL OF THESIS

We, the faculty supervising the work of Elizabeth Lester, affirm that the thesis *Description and histology of a small-bodied elasmosaur and Discription of Mortuneria seyemourensis postcranium* 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 7, 2019

Dr. F. Robin O'Keefe, Department of Biological Sciences Committee Chairperson Date

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ABSTRACT

Elasmosauridae is a monophyletic group of plesiosaurs that evolved in the Early Cretaceous and radiated to achieve a cosmopolitan distribution by the end of the Cretaceous. They were a highly successful group of deep sea predators with long necks, small heads, and stout four flippered bodies. Here we describe four postcranial elasmosaurs skeletons that were collected from the shallow marine Lopez de Bertodano formation located on Seymour Island of the Antarctic Peninsula. One specimen is a small-bodied elasmosaurs. Despite its small size it has several advanced ontogenetic character states including the fusion of neural spines to the vertebral centra. The individual was considered to be sub-adult in age. Histological samples were taken of the right femur that showed a moderate amount of remodeling while still preserving much of the fiber lamellar bone associated with fast growing juveniles. Together these features confirm a late juvenile to sub-adult ontogenetic stage for the specimen. Two of the other specimens are moderate sized elasmosaurs with unusual characteristics sometimes attributed to the clade Aristonectinae. We use their characters along with other WBP (Weddelian Biogeographic Provinance) and Pacific elasmosaurs taxa to better understand the relationships among basal Aristonectine elasmosaurs and evaluate characters attributed to them. The final specimen is the post cranial material from the holotype for *Mortuneria seymourensis*. Using this taxa we can better understand potential apomorphic characters and its relationship to closely related aristonectines. This paper aims to better understand these unusual elasmosaurs and the relationships of WBP elasmosaurs.

CHAPTER 1

BACKGROUND

Introduction

Sauropterygia is a clade of secondarily marine reptiles spanning from the Lower Triassic to the Cretaceous-Paleogene boundary. The clade is a result of the Late Permian- Early Triassic radiation of diapsid reptiles that has led to poorly resolved early relationships and controversy within stem diapsids (Schoch & Sues, 2015). Currently, sauroptergians are defined as a sister taxon to Pan-Testudines and Lepidosauriformes (Schoch & Sues, 2015). Sauroptergians are considered euryapsids and lack the lower temporal opening of their diapsid ancestors, maintaining only the upper temporal fenestra (Storrs, 1993). From their early diapsid precursers their evolution is marked by a trend to a deeper marine environment leading to an abandonment of terrestrial locomotion. Several main groups evolved from the diapsid ancestors; Placondontia, Nothosauroidea, Pistosauriodea, and Plesiosauria (Rieppel, 2000; Sato, Hasegawa, Manabe, 2006). Sauropterygia is united by the synapomorphies: a single upper temporal fenestra, pterygoids cover the braincase creating a closed palate, and coracoid bones, a small ilium, and fenestra in the pectoral girdle (Ketchum & Benson, 2010). Each of the main groups showed adaptations towards a greater dependency on marine life. Placodonts were small and heavy-bodied, and most likely exploited a shallow water environment. The term Eusauropterigia contains the forms more derived than Placodontia. Early lineages within Eusauropterigia, pachypleurosaurs, nothosaurs and pistosaurs, show some levels of hyperphalangy—increasing limb flexibility. Nothosaurs had several adaptations for a more aquatic life including possible viviparity (Griebeler & Klein, 2019) and decreased bone mass (Klein, Sander, Krahl, Scheyer & Houssaye, 2016). Later representatives of the clade evolved rigid trunks that inhibited undulation and relied on para-axial movement through the water (Storrs, 1993).

By the late Triassic the plesiosaurs evolved. The group, the sister group to pistosaurs, was the most derived to an aquatic lifestyle (Sato et al., 2006; Wintrich, Hayashi, Houssaye, Nakajima, & Sander, 2017). Plesiosaurs inhabited fully aquatic deep marine environments permissible by the evolution of hydrofoil flippers and viviparity (O’Keefe & Chiappe, 2011). Within the crown group of plesiosaurs evolved short- necked and long-necked lineages. The family of elasmosaurs took this lengthening to an extreme; *Albertonectes* (Kubo, Mitchell, & Henderson, 2012) reached over 18m and had a neck length of 7m containing 75 cervical vertebrae. Elasmosauridae is a monophyletic group of plesiosaurs that evolved in the Early Cretaceous and radiated to achieve a cosmopolitan distribution by the end of the Cretaceous. Elasmosaurs were a highly successful group of deep sea predators with long necks, small heads, and a stout four-flippered body.

Evolution of Sauropterygia

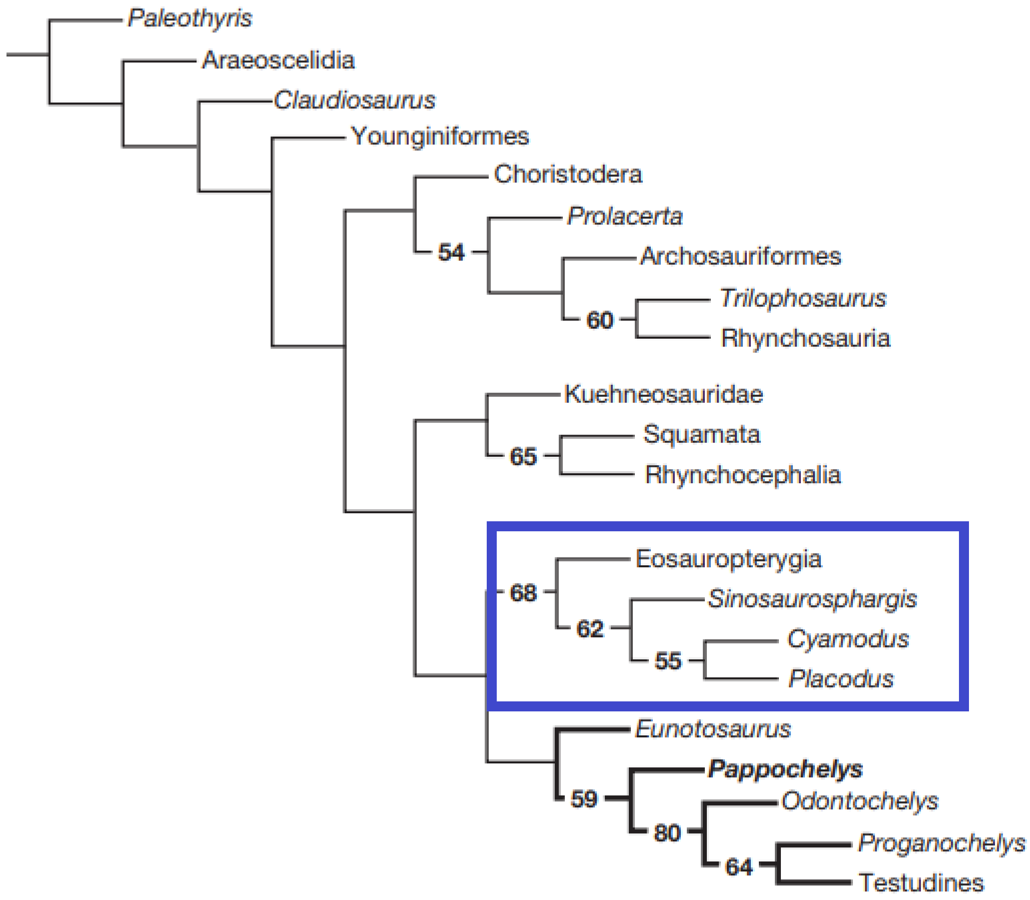

Figure 1. Early phylogenetic relationship within diapsida. Modified from Schoch and Sues 2015.

Placodontia

Placodonts represent a very basal sauropterygian lineage. The group had wide skulls with a single supratemporal fenestra. The most basal placodont evolved in the Western Tethys and lacked lacrimal bones (Neenan & Scheyer, 2012). Other similarities that tie placodonts to sauroptergians are the clavicles are located medial to the scapula, and reduction of the carpels (Motani, 2009). The palate was broad with short, squared pterygoids. Later evolutionary change saw elongate palates and specialized dentition for durphagy (Neenan, et al., 2014). Teeth occurred not only on the premaxilla, maxilla, and dentary, but also the palate. Two main lineages evolved; placodontoids that lacked armor and Cymodontoidae which had dermal armor. The braincase was robust and the skull reinforced to withstand the crushing bite resulting from their specialized diet of hard shelled organisms (Neenan et al., 2014). Stout and heavy in body, placodonts were likely shallow water animals and inhabited the Tethys Ocean of the early Triassic. Post-cranially the group was fairly unspecialized for an aquatic lifestyle. The fingers were distinct and the limbs robust. Dermal amour in Cymodontoidia would have hindered axial swimming, but even the non-armored lineage had a robust thoracic region that may have helped the organism by acting like a ballast to help placodonts maintain proper buoyancy for foraging (Storrs, 1993).

Pachypleurosauria

Pachypleurosaurs are a monophyletic group that evolved in the Tethyan Ocean during the mid-Triassic (Liu et al., 2011). They are considered the most basal eusauropteyrigians (Rieppel, 1994, 1998, 2000). The group has also been placed as basal Nothosaurs (Rieppel & Hagdorn, 1997; Holmes, Cheng, & Wu, 2008). The name pachypleurosaurs refers to their thick ribs; the increased rigidity of the ribs may support some para-axial propulsion. Their presacral to caudal length proportions are similar to other marine reptiles, and they likely relied on axial movement through the water. In addition they have elaboration of the coracoids suggesting the use of the anterior limbs while swimming (Carroll & Gaskill, 1985). The distal limbs still resemble the ancestral terrestrial condition and there was only slight hyperphalangea in *Keichousaururus* (Holmes et al., 2008). The cranium shows a reduction of bones: the epipterygoid is lost and the pterygoids broaden and close dorsally over the brain case. The ectopterygoid is elongate. The nasal bones are large and touch the frontal. Like the preceding members of the clade, pachypleurosaurs have a relatively small temporal opening and overall small to moderate body size. The group inhabited near shore coastal environments and was common in the Triassic (Klein, 2012). Pachypleurosaurs are the earliest known sauropterygian to give live birth. They are well represented in the fossil record allowing for studies on ontogenetic and intraspecific variation including sexual dimorphism in the propodial and pelvic elements (Rieppel, 1989; Cheng, Wu, & Ji, 2004; Xue et al., 2015). The growth rates of pachypleurosars were comparable with extant reptiles, but they matured faster (Klein & Griebeler, 2018).

Nothosauroidea

Nothosaurs were a mid-Triassic, partially aquatic, marine group that has been found in North America, Europe, and China. Specimens of nothosaurs are found almost exclusively in shallow near-shore environments. They may have lived in a similar manner to modern seals. Their tails were long and the group likely maintained axial movement. The limbs and pectoral girdle show some modification for aquatic life such as limited hyperphalangy, a curved humerus, ossified ribs, and gastralia which may have compensated for buoyancy in the water column (Storrs, 1993). The skull of nothosaurids became more triangular in shape and also showed an elongation of the post orbital region with an increase in the upper temporal fenestra size. An early species *Nothosaurus marchicus*, showed a broad skull and numerous heterodont teeth--large heterodont teeth remained common in the clade. They had large pterygoids that lack an interpterygoid vacuity (Klein & Albers, 2009). *Cymatosaurus* maintained openly constructed occiput that was closed and plate-like in other Nothosaurids, but occurs in the later taxa Plesiosaurs (Rieppel, 1998; Maisch, 2014). Nothosaur grade taxa studies of the life history has found at least some more advanced nothosaurs were viviparous (Griebeler & Klein, 2019). Nothosaurs grew and matured quickly compared to modern reptiles (Klein et al., 2016).

Pistosauroidea

A contemporary of nothosaurs and pachypleurosaurs, pistosaurs show many adaptations towards a fully marine habitat and therefore closely resemble the more derived plesiosaurs. They evolved necks with 30 or more cervical vertebrae and had an increased growth rate compared to more basal eosauropterygians (Wintrich et al., 2017). *Corosaurus alcovensis* is the most basal pistosaur known from the upper most Early Triassic (Rieppel, Martin, & Storrs, 2002) The pterygoids begin to open posteriorly, exposing the parasphenoid. The quadrojugal and coracoid foremina are lost (O'Keefe, 2001). Pistosaurs and plesiosaurs have keeled sagittal crest, narrowing parietals; the pineal foramen moves forward (O'Keefe, 2001). The jugal becomes separate from the orbital margin (Rieppel et al., 2002). The limbs are large and express hyperphalangy. The coracoids are large forming a long median symphysis (Sues, 1987), suggesting anterior para-axial propulsion. The caudal region was shortened as the limbs likely became the dominate form of locomotion. A reduced number of caudal vertebrae and flipper-like limbs are shared with plesiosaurs, and likely represent the sauroptyrigian's progression to the deep marine environments where plesiosaurs later radiated (Storrs, 1993).

Plesiosauria

Plesiosauria is the crown group in the lineage Sauropterygia. They evolved in the late Triassic and were medium to large, fully aquatic carnivores. Early plesiosaurs had robust thoracic regions with heavily ossified gastralia and thick ribs, potentially to help maintain balance in the water column (Storrs, 1993). The basicranium shows some more primitive characters, particularly involving the reduction of the pterygoids (O'Keefe, 2006). Several post cranial synapomorphies include: coracoids that become expanded and a large ventral puboischiadic plate (Sues, 1987). The limbs exhibit increased hyperphalangy and taper distally.

Propodials are shortened, but broad, expanded, and curved distally. The epipodials are shortened and widened to become broader than long. Together these form four broad, paddle-like limbs that were used in para-axial propulsion (O'Keefe, 2001). Their tails were reduced. Their evolution is concurrent with an increased metabolism; studies involving their cortical growth rates and periosteal deposition demonstrate plesiosaurs grow faster than basal sauropsids, likely accompanied by an increased body temperature, compared to predecessors (Fleischle, Wintrich, & Sander, 2018). An elevated metabolism may have facilitated their success at exploiting open waters and surviving the Triassic/ Jurassic boundary (Wintrich et al., 2017).

Early plesiosaurs had moderate neck length and head size, with a short preorbital region and a deeply embayed cheek (Storrs & Taylor, 1996). From early plesiosaurs, two main morphotypes evolved in response to different feeding strategies; large headed, small necked pliosaurmorphs and small headed, long necked plesiosaurmorphs (O'Keefe, 2002; O'Keefe & Carrano, 2005). Recent findings in Germany, uncovering a primitive plesiosaur from the Jurassic, suggest that diversification in plesiosaurs occurred very early in their history (Wintrich et al., 2017). The short necked variety may have fed on larger prey, like modern sharks, whereas the smaller head variety consumed fish with several species of fish found in their remains (Cicimurri & Everhart, 2001). Other features associated with each include; in pliosaurmorphs the femur is longer than the humerus with larger posterior limb (O'Keefe & Carrano, 2005). This condition is reversed in plesiosaurmorphs. The two main morphotypes are not monophyletic groups, but rather the pliosaurmorphs evolved independently at least twice and the long necked variety converged at least three times (O'Keefe, 2002).

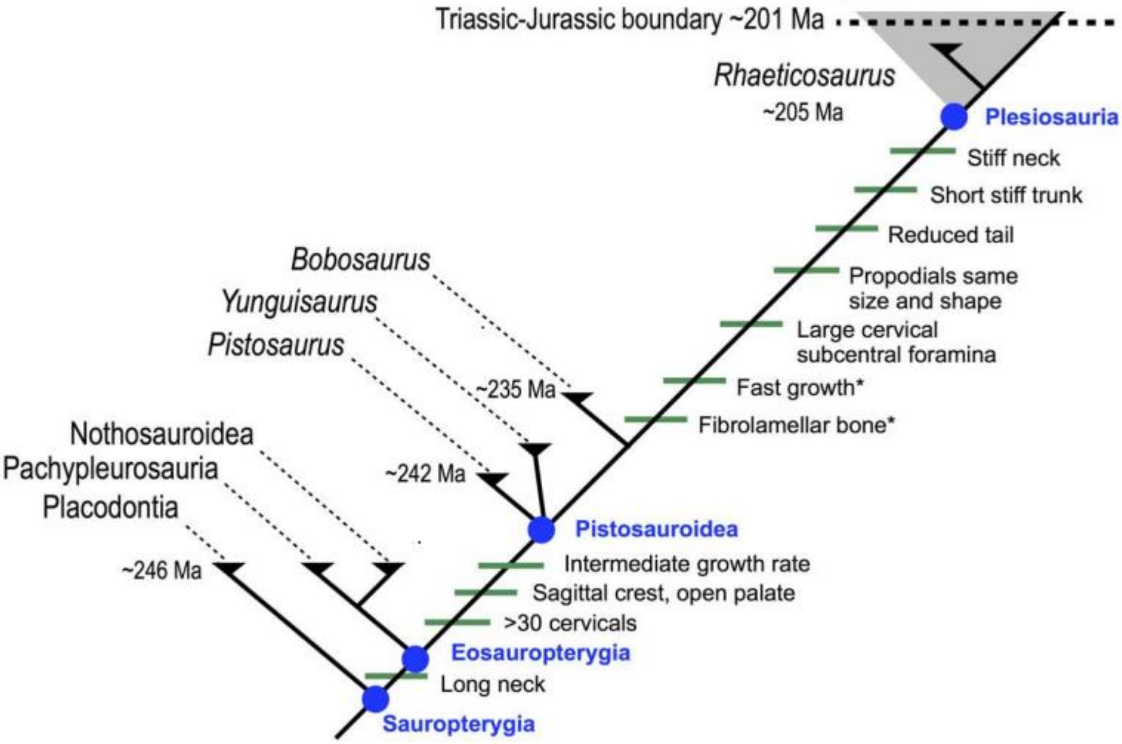

Figure 2. Phylogeny of Sauropterygia (modified from Wintrich et al., 2017).

Elasmosauridae

Elasmosaurs evolved in the Cretaceous as early as the Valanginian (O’Keefe, 2001; Benson, Evans, & Druckenmiller, 2012) and had a cosmopolitan distribution, with the Western Interior Seaway in the Northern hemisphere and the Weddelian sea in the Southern hemisphere containing a great many taxa (Welles, 1952; Brown, 1981; Carpenter, 1999; Fostowicz-Frelik & Gaździcki, 2001; O’Keefe, 2001, 2004; Ketchum & Benson, 2010; O’Gorman, Salgado, Olivero, & Marenssi, 2015; Serratos, Druckenmiller, & Benson, 2017). Cranial characteristics include continued opening of the pterygoids, a vomer extending posterior to the internal nares (O’Keefe, 2001) and the posterior extension of the premaxilla separates the frontals. The pineal opening was lost. Other characteristics of elasmosaurs include: a posterior interpterygoid vacuity, an occipital condyle composed only of the basioccipital and bilobed cervical vertebrae (Otero, Soto-Acuña, Vargas, et al., 2014), triangular heads, and a cardiform opening between the coracoids (Sachs & Kear, 2015). By the end of the Cretaceous elasmosaurs also had a distinctive fully open medial embayment of the coracoid (Otero, O'Gorman, Hiller, O'Keefe, & Fordyce, 2016). The post cranium is relatively conserved, but the family is known for very elongate gracile necks with a great increase in neck vertebrae from the ancestral condition of approximately 55 (Otero, Soto-Acuña, Salazar, & Oyarzún, 2015) to upwards of 72 in *Elasmosaurus* and 75 in *Albertonectes* (Sachs, Kear, & Everhart, 2013). The centra are dumbbell shaped and longer than high with the exception of *Aristonectes*, to be discussed.

Aristonectinae

The evolutionary history of aristonectine elasmosaurs, now known to be within Elasmosauridae, has been contentious since their first discovery in 1941 (Cabrera) due to their unusual morphology and what was, for many years, only fragmentary remains. They have been placed in Cryptocleididae (O'Keefe, 2001; Cruickshank & Fordyce, 2002) and in their own family Aristonectidae (O'Keefe & Street, 2009; Otero, Soto-Acuña, & Rubilar-Rogers, 2012). The first suggestion that they were Elasmosaurids came from Gasparini, Bardet, Martin, & Fernandez (2003) which was later supported in a phylogenetic analysis (Ketchum & Benson, 2011). They are known only from the Campanian-Maastrichian ages of the late Cretaceous (Sachs & Kear, 2015). Found in South America (O'Gorman Gasparini, & Salgado, 2013; Otero, Soto-Acuña, O'Keefe et al., 2014), Antarctica (Chatterjee & Small, 1989), New Zealand (Cruickshank & Fordyce, 2002), and Angola (Araújo et al., 2015) they are restricted to high latitude southern locations around the Weddellian Biogeographic Province (WBP, hereafter, Zinsmeister, 1979) with two potential exceptions from the Pacific in California and Japan (Sato et al., 2006; O’Gorman, 2016). Despite the preservation of several taxa, the phylogeny of the origin of the group is poorly understood. The subfamily is unique among other elasmosaurs in that they have relatively large heads and short necks. Their reduced neck is achieved through a reduced number of short, broad vertebrae. They have around 60-65 aveoli (Otero, Soto-Acuña, O’Keefe, 2014) in the maxillary and dentary, which is increased compared to other elasmosaurs and is achieved with smaller teeth. The mandibles have a large hoop-like appearance due to having increased transverse length between the mandibular symphysis and rostrum (O’Gorman et al., 2013). The mandibular symphysis is short and weak (O’Keefe et al., 2017). Another autopomorphic aristonectine feature includes the jaw articulation being placed beyond the basicranium due to a posterior extension of the quadrate flange (O’Keefe et al., 2017). The unique cranial adaptations have begged a morphological explanation (O’Gorman et al., 2013). A 2017 paper by O’Keefe et al. involved a unique member of Aristonectinea, *Mortuneria*, and explored a potential feeding strategy of filter feeding.

The current defining characters of aristonectine elasmosaurs has been restricted to the cranial and cerval elements. It has also been proposed that strongly octagonal caudal vertebrae may indicate an aristonectine. The shape of the caudal vertebrae has been used to place several postcranial remains into the subfamily Aristonectinae (Otero et al., 2015, O’Gorman, 2016).

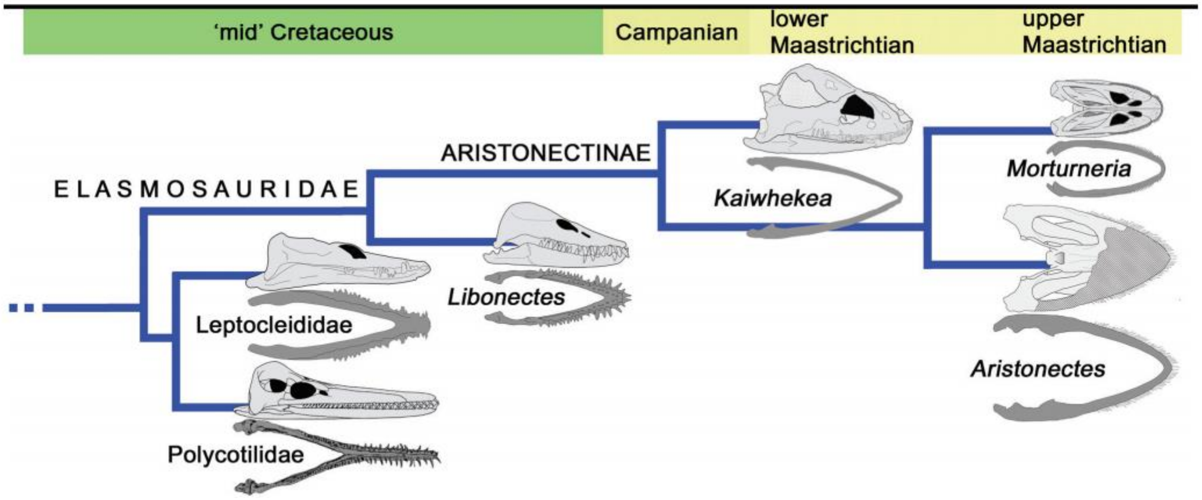

Figure 3. Phylogenetic relationships of the evolution of the subfamily Aristonectinae within Elasmosauridae. Figure modified from O'Keefe et al., 2017.

Neck Evolution

Elasmosauridae is considered a monophyletic clade, but the inter-relationships are poorly understood. One characteristic used to compare taxa are measurements of the vertebrae. The vertebral centra are measured in breadth, width, and length (Welles, 1943) and overall size is compared using ratios. Overall shape of the vertebrae can be compared using a vertebral length measurement (O'Keefe & Hiller, 2006, figure 4). This measurement gives the overall shape in one number without size bias, allowing for taxa of various sizes to be compared. There are three main morphotypes often used to group taxa based on the centrum proportions of the cervical vertebra with emphasis on the maximum length found in adult, mid cervical vertebrae. A non-elongate, also referred to as a plesiomorphic, condition contains taxa that have centra that are longer than high with vertebral length indices (VLIs) of approximately 100, and moderate vertebrata counts around 60 (O'Keefe & Hiller, 2006; O'Gorman, 2016). This group is represented by several taxa in the northern hemisphere, including *Libonectes* at 108 and *Aphrosaurus* sensu O'Keefe & Hiller (2006) and *Nakonectes* (Serratos et al., 2017). The

Southern hemisphere also includes non-elongate taxa through the Campanian-Maastrichtian, including *Vegasaurus* from Antarctica with average VLIs lower than 108 (O’Gorman, 2016). *Mauisaurus* from New Zealand and *Kawanectes* from South America had a maximum VLI of 110 (O’Gorman, 2016). The third group contains the Aristonectinae, with very low VLIs averaging near 80 (Otero, Soto-Acuña, O’Keefe et al., 2014) and with as few as 43 cervical vertebrae (Otero et al., 2015). The shorter necked group is currently only known from the Southern Hemisphere, and is found in deposits with the moderate-necked taxa.

$$VLI = 100\left(\frac{L}{(H+W).5}\right)$$

Figure 4. The equation to calculate vertebral length indices (VLI). L equals the length, H equals the height of the centrum, and W equals the width of the centrum along the articular surface. From O’Keefe and Hiller 2006.

A limitation of the VLI measurement is that elasmosaur cervical centra increase disproportionately through ontogeny. Length proportion can increase over 20% and continues to do so well into development (O’Keefe & Hiller, 2006). One also needs to know whether or not the centra is a central vertebra, which may be difficult if few vertebrae were found. Overall average VLIs have been used for comparison with southern taxa (O’Gorman, 2016; Otero et al., 2015) where, by the Maastrichtian, only non-elongate and shortened taxa are known (Otero et al., 2015).

Histology

Histology, the study of tissues, has a long history of being used to learn about the life style and ontogeny of fossil taxa (Padian & Lamm, 2013). Histology has been performed on plesiosaurs since 1883 (Kiprijanoff) and has since been used to study the clade's adaptations for a marine lifestyle (Wiffen, Buffrénil, Ricqlès, & Mazin, 1995; Klein et al. 2016; Klein & Griebeler, 2018), ontogeny (Wiffen et al., 1995; O'Keefe, Sander, Wintrich, & Werning, 2019), and the phylogeny of plesiosaurs (Wintrich et al., 2017). Secondarily aquatic amniotes show specializations for their mode of life that fall into two main categories: increasing or decreasing bone mass (Houssaye, Sander, & Klein, 2016). Slow moving species show pachyostotic, dense bone, such as manatees (Houssaye, 2009). The increased ossification acts as a ballast for the animal. Quick swimming animals lighten the bone to reduce inertia. Osteoporitic bone structure is beneficial for species with quick-moving prey (Wiffen et al., 1995) likely to resist the forces during propulsion through the water (Houssaye, 2008, 2013). Plesiosaurs show both dense bone, as juveniles, and osteoporotic bone density as adults.

Bone tissue can also indicate the metabolism of animals. Pachypleurosaurs had growth rates similar to modern reptiles, though they reached maturity younger. The first sauropterygian with elevated metabolism was in *Pistosaurus*, a taxa close to the origin of plesiosaurs. Pistosaurus still retained primary osteons, and there was no fibrolamellar bone tissue (Fabbri, Vecchia, & Cau, 2013; Wintrich et al., 2017). Haversion remodeling, which is unique to plesiosaurs among sauropterygians (O'Keefe et al., 2019), and fibrolamellar bone can indicate increased metabolic rates. Increased vascularization provides increased blood flow to supply a high metabolism, but may also be the result of large sizes.

Histology also allows us to determine the relative state of development of a fossil organism. Studies with homologous bones among juvenile and adult plesiosaurs have shown that plesiosaurs undergo Haversion remodeling. The fetal medullary center bone is compact, following birth juveniles show quick radial, lateral growth of cortical bone that appears in elongate fibers outward from the medullary region. The medullary and corticle bone are separated by Kastschenko's line (Klein & Griebeler, 2018). The endosteal cartilage narrows in the center of the propodial and expands towards the ends resulting in an hour glass shape. The periosteum wraps the endosteum and grows outward, visually separated due to a change in deposition referred to as the birth-line (Curtin, 1999). However in plesiosaurs it is unknown whether this line represents the sudden change in development as the organism is no longer provided with maternal nutrition or if this represents the end of the first year of life (Wintrich et al., 2017). The latter hypothesis is supported in part by the position of the line, which occurs at approximately 60% the total maximum shaft diameter. Wintrich et al. (2017) argue that 60% is too large to be natal size. A further complication of the interpretation of this separation between the cortex and periosteum being the birth line is that ribs sectioned show more lines than the propodials which may indicate that multiple years occur before the first line. The plesiosaur acquires further sequential lines with rapid-growing, radial fibrolamellar bone between. As the plesiosaur reaches adulthood, secondary replacement occurs and the bone develops a "porous" look due to the formation of secondary osteons.

Purpose of Study

The purpose of this study is to reevaluate four specimens collected by a team from Texas Tech University and originally described in 1989. Since their original description, great strides have been made in our understanding of elasmosaur ontogenetic states and evolution. In this paper we use histology to determine the ontological state of the small elasmosaur MTTU 9218. MTTU 9219, fragmentary postcranial remains from the holotype *Mortuneria seymourensis* and MTTU 9217 likely represent the same taxon. Previously this material has only been described under the genus *Aristonectes*. This is the first paper describing it as *Mortuneria*. Considering its characters as a separate genus we can better understand potential apomorphic characters and their relationship to closely related aristonectines. This paper aims to better understand these unusual elasmosaurs and the relationships of WBP elasmosaurs.

CHAPTER 2

DESCRIPTION OF THE POSTCRANIUM OF *MORTUNERIA*

Introduction

Antarctica has revealed many unique marine reptiles that inhabited its near-polar seas during the end of the Cretaceous. The plesiosaur remains from the Antarctic peninsula have been at times puzzling including the Aristonectines, whose unusual morphology lead them to be originally placed in Cryptocleididae (Chatterjee & Small, 1989; Cruikshank & Fordyce, 2002) then later into their own family Aristonectidae, then finally their own subfamily within elasmosauridae Aristonectinae (O'Keefe & Street, 2009; Otero et al., 2012). Our understanding of aristonectines has been limited to cranial characters and proposed postcranial characters, but these have at times been dubious with what were considered aristonectine characters appearing in taxa without the shortened cervical centra (Fostowicz−Frelik & Gaździcki, 2001); see chapter 3. Currently the affinities within Elasmosauridae are not well understood. However morphological characters between Weddelian Biogeographic Province (WBP) taxa and Aristonectines may unite the two groups, and morphologies between WBP taxa and Pacific Late Cretaceous elasmosaurs may suggest a close evolutionary relationship. In this chapter we re-evaluate two specimens collected in 1989, MTTU 9217, and MTTU 9219, the former being the holotype of *Mortuneria seymourensis* (O'Keefe et al., 2017); MTTU 9217 is referred to as *Mortuneria* from cervical vertebrae and size.

Geologic Location

The Lopez de Bertodano Formation, where specimens MTTU 9217, MTTU 9218, and MTTU 9219 were collected, is exposed in the northeastern peninsula of Antarctica on the Seymour and Snow Hill Islands. It is the upper member within the Marambio group which is comprised of Santa Marta, Snow Hill Island, Haslum Crag and Lopez de Bertodano formations (O’Gorman, Olivero, & Cabrera, 2012). The upper Campanian-Maastrichtian aged formation overlies the Snow Hill Island Formation and is overlain by the Sobral Formation. The Lopez de Bertodano consists primarily of poorly consolidated sandy siltstone and calcareous concretions and is interpreted as a near shore environment in a transgressive-regressive cycle (Macellari, 1988; Olivero, Ponce, & Martinioni, 2007; Witts et al., 2015). The formation was separated into 10 informal units; the lower stratigraphic units 1-6 are informally termed the Rotularia units and the upper 7-10 are the Molluscan units (Macellari, 1988). The K-Pg boundary is interpreted as lying between units 9 and 10 due to the disappearance of ammonite fossils (Macellari, 1988) and evidence of high fish mortality (Zinmeister, 1998). The formation includes invertebrates such as echinoids, bivalves, and ammonites. Vertebrates found in the formation include aves (Chatterjee, 2002), sharks, teleost fish (Grande & Chatterjee, 1987), mosasaurs (Chatterjee & Small, 1989) and plesiosaurs (Chatterjee & Small 1989; Fostowicz-Frelik & Gaździcki 2001).

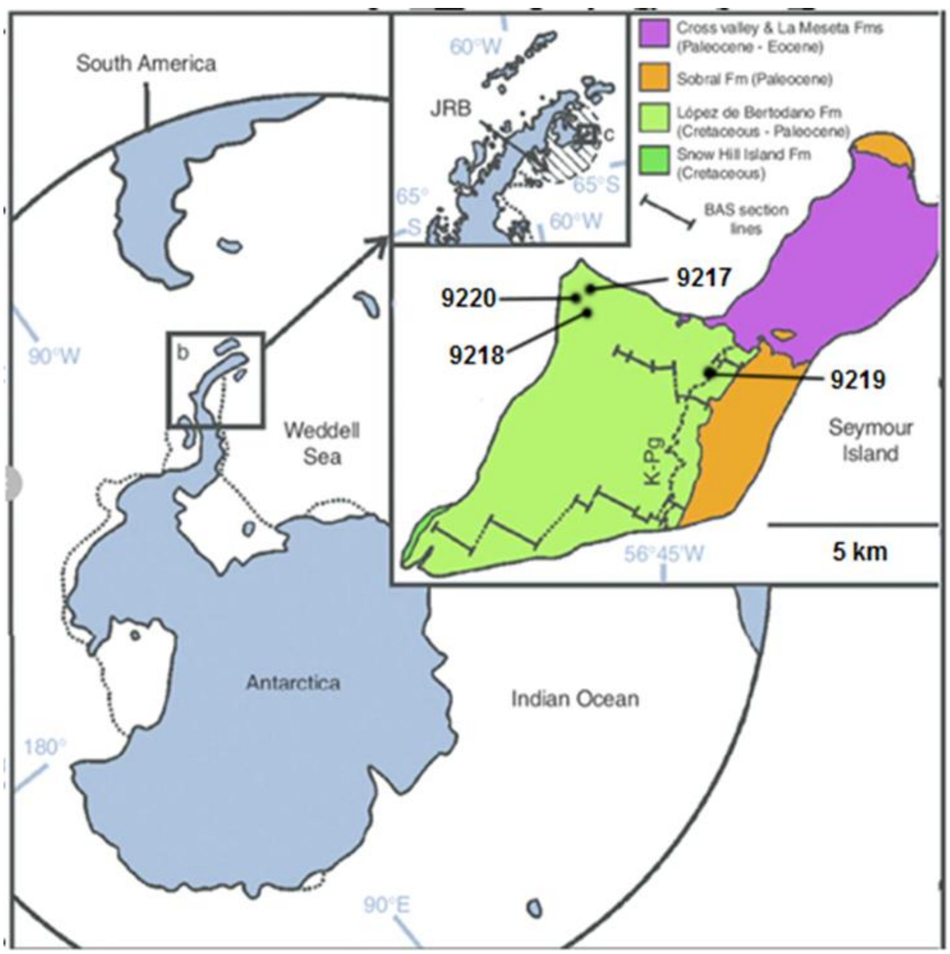

Figure 5. Seymour Island and location of the collection site of MTTU 9218. Dotted line represents the K/Pg boundry. Modified from Witts et al. 2016.

Institutional Abbreviations: CM.Zfr, Canterbury Museum, Christchurch, New Zealand; MTTU, Museum of Texas Tech University, Lubbock, Texas, U.S.A.; UCMP, University of California Museum of Paleontology; ZPAL, Polish Geological Institute, Warszawa, Poland

Anatomic Abbreviations: **act**, acetabulum; **actf**, acetabular foramen; **atna**, atlantal neural arch; **atr**, atlas rib; **axna**, axis neural arch; **cap**, capitulum; **ce**, centrale; **dc1**, distal carpal 1; **dc2+3**, distal carpal 2+3; **dc4**, distal carpal 4; **epf**, epipodial foramen; **f**, fibula; **ff**, fibular facet; **hf**, hemal facet; **isf**, ischiadic face; **nc**, neural canal; **pao**, postaxial ossicle; **par**, parapophysis; **pf**, pedicellar facet; **r**, radius; **rf**, radial facet; **tub**, tubercle; **u**, ulna; **uf**, ulnar facet; **un**, ulnare; **vf**, ventral foramen.

Materials

These specimens were collected below the Cretaceous/Paleogene boundary from the upper Maastrichtian of Seymour Island, Antarctica, by teams from Texas Tech University in the early 1980s. They were each collected from the Lopez de Bertodano Formation. Specimen MTTU 9217,was collected from units 5-6. MTTU 9219 was collected between units 9-10.

Systematic Paleontology

Order PLESIOSAURIA Blainville, 1835

Family ELASMOSAURIDAE Cope, 1869

Subfamily ARISTONECTINAE O'Keefe & Street, 2009 (sensu Otero, Soto-Acuna, & Rubilar-Rogers, 2012)

Genus *Morturneria* (Chatterjee & Small, 1989)

Type Species—*Morturneria seymourensis* (Chatterjee & Small, 1989).

Results

Type specimen MTTU 9219. Cranial elements for this specimen were described in O'Keefe et al. (2017). The specimen's post-cranium consists of five complete cervical vertebrae, a cervical fragment, two rib fragments, a capitulum (humoral head?), a fragment of an epipodial, a mesopodial, and 3 phalanges. Referred specimen MTTU 9217: Specimen includes posterior cervical vertebrae, the complete right humerus, distal end of left humerus, radius, ulna, mesopodials, phalanges and the nearly complete left femur.

Axial Skeleton

The atlas-axis complex of MTTU 9219 is a single anatomical feature with clear sutures. The atlas-axis complex is longer than broad and broader than tall (Figure 6). Its proportions are similar to *A. parvidens*, but not as long (Gasparini et al., 2003; O'Gorman, 2016) and much shorter than *Vegasaurus* and *A. quiriquinesis* (O'Gorman et al., 2015). The ventral surface lacks a ventral keel and any visible foramen. The axial ribs are broken off with part of the centrum so length and breadth are not known. The atlas neural arch contacts the axial neural arch, unlike *Vegasaurus* and *Tuarangisaurus keyesi*, leaving a foramen.

Five complete cervical centra were preserved and one fragment of MTTU 9219. The centra are "binocular-shaped," having greater concavity on the ventral surface than the dorsal surface. The centra are higher than long and broader than high. Two of the centra have neural spines, but show clear suture lines (Figure 7). The rest of the preserved cervicals had completely unfused neural arches with no clear rugosity. A few fragmented posterior cervicals show typical elasmosaur dumbbell shape and typical aristonectine shortening. The neural arches are shorter than the centra. The articular surfaces for the neural arches on the unfused centra are nearly round, with some rugosity towards what is estimated to be the posterior face. The neural spines are broken off. The rib articulations are smooth, showing little development towards fusing. Each centra has two near equal, rounded ventral foramina.

Appendicular Skeleton

There is one capitulum unarticulated to a propodial. It is highly convex and circular. The single mesopodial may represent the centrale. The edges are poorly ossified and the thin periosteum layer preserved on the ventral or dorsal side is flaking. The three preserved phalanges are short and only slightly spindle-shaped. Their edges are poorly ossified. One phalanx is broken parallel to the long axis. It shows a periosteal cone with the periosteal thickest in the center and thinning outward.

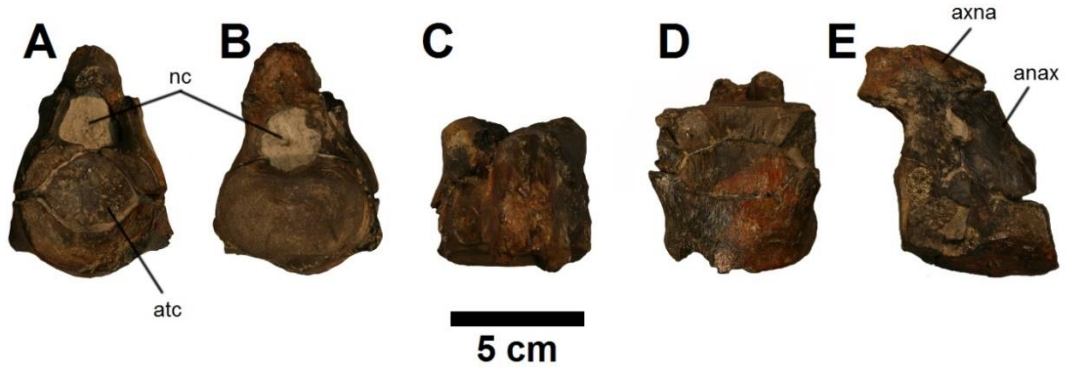

Figure 6. Atlas-axis complex of MTTU 9219. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view.

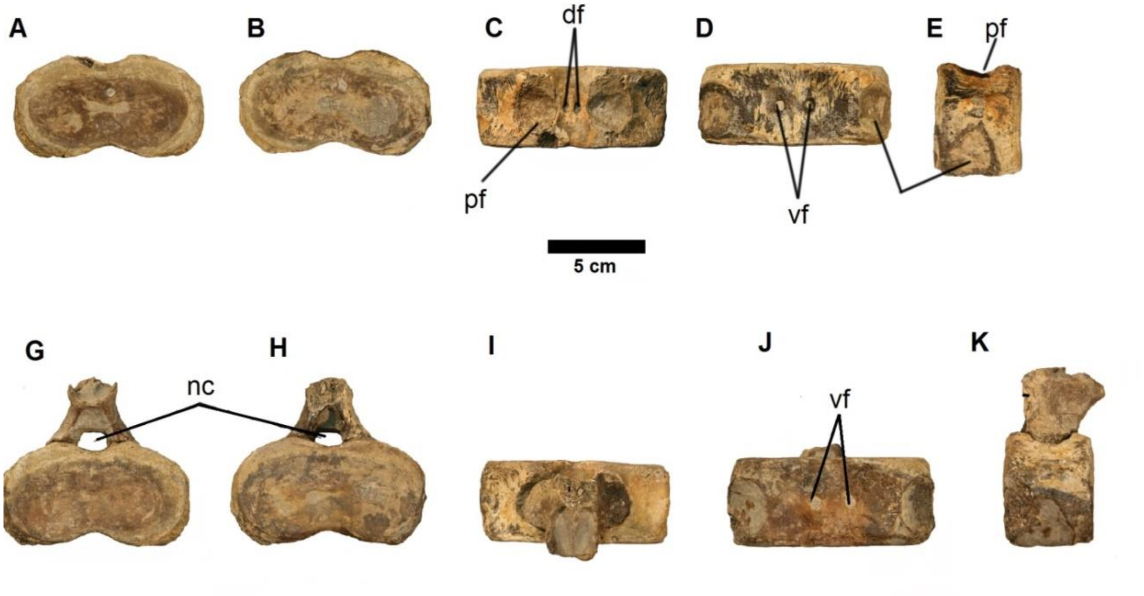

Figure 7. Cervical vertebrae of MTTU 9219. A-E cervical without preserved neural arch. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view G-K, preserved with poorly fused neural arch; G, anterior view; H, posterior view; I, dorsal view; J, ventral view; K, lateral view.

The right humerus is complete. It is relatively slender compared to other Austral elasmosaurs such as *Vegasaurus* and CMZfr 145 (Hiller & Mannering, 2005; O'Gorman et al., 2015). The narrow diaphysis trends anteriorly then flares posteriorly approximately a fourth of the way from the distal end. The shaft is strongly bent towards the ventral surface of the organism from the capitulum. A similar, less exaggerated condition is observed in ZPAL R.8. The capitulum is semicircular and narrow with a rectangular, projecting tuberosity. The distal end becomes narrow and is rounded due to taphonomic compression. The shaft becomes very straight and narrow in lateral view towards the distal end due to the compression (Figure 8). The distal portion of the left humerus was preserved without the compression experienced by the right humerus. The left humerus does not narrow dorso-ventrally towards the distal end, and has a small ventral bend. The diaphysis is broken off at the point the distal posterior end flares to a posterior "knee" similar, but not as exaggerated as typical of some other WBP taxa (O'Gorman et al., 2015). The articular facets are present, but only moderately defined. The dorsal side of the humerus shows a greater concavity than the ventral side in distal view.

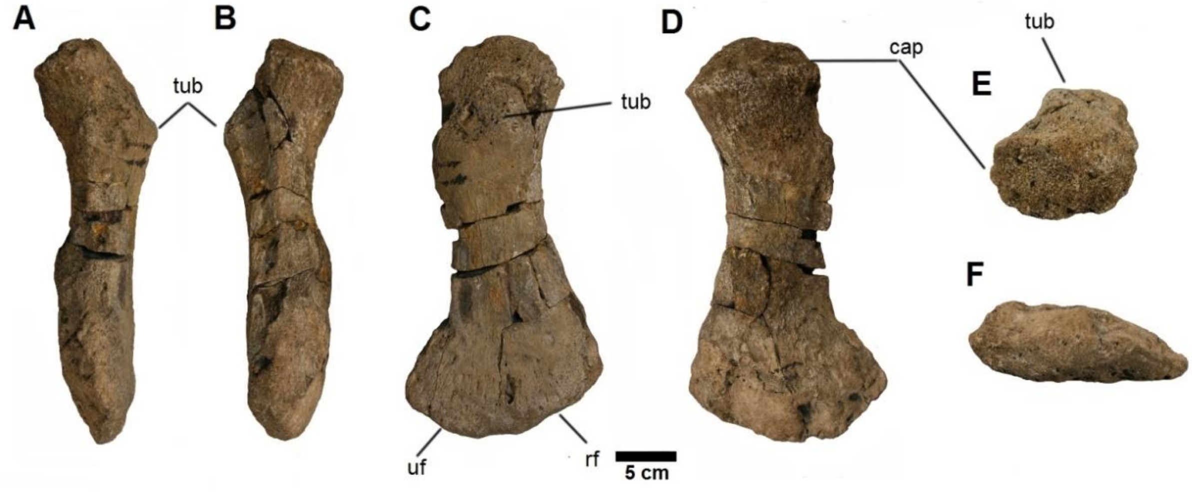

Figure 8. Right humerus of MTTU 9217. A, Right lateral; B, left lateral; C, ventral view; D, dorsal view; E, proximal view; F, distal view.

The left fore-paddle is nearly complete, apart from the proximal portion of the left humerus (Figure 9). The ulna is pentagonal with a short and angler articular facet for the centrale. The radius is broad and sub-rectangular. Mesopodials are well preserved with well-defined articular facets. The epipodial foramen of both the ulna and radius are small, circular, and positioned midway along the height of the element similar to CMZfr 145 (Hiller &

Mannering, 2005). The radius is rectangular and wider than tall. The ulnare is pentagonal and wider than long. The centrale is strongly pentagonal with the proximal side curving up along the inner edged of the epipodials, condensing their medial symphysis (Figure 10). The remaining mesopodials are shared with *A. parvidens* and similar in shape and proportion (Gasparini et al., 2003).

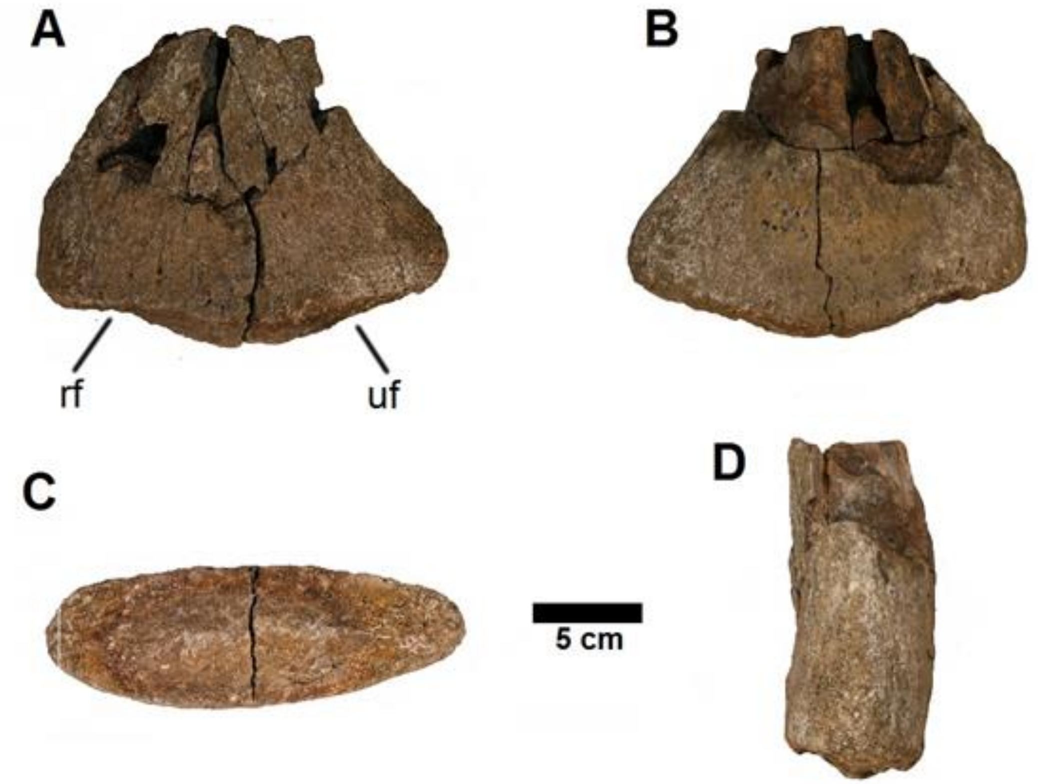

Figure 9. Left humerus of MTTU 9217. A, ventral view; B, dorsal view; C, distal view showing greater convex curvature on the dorsal side; D, lateral view.

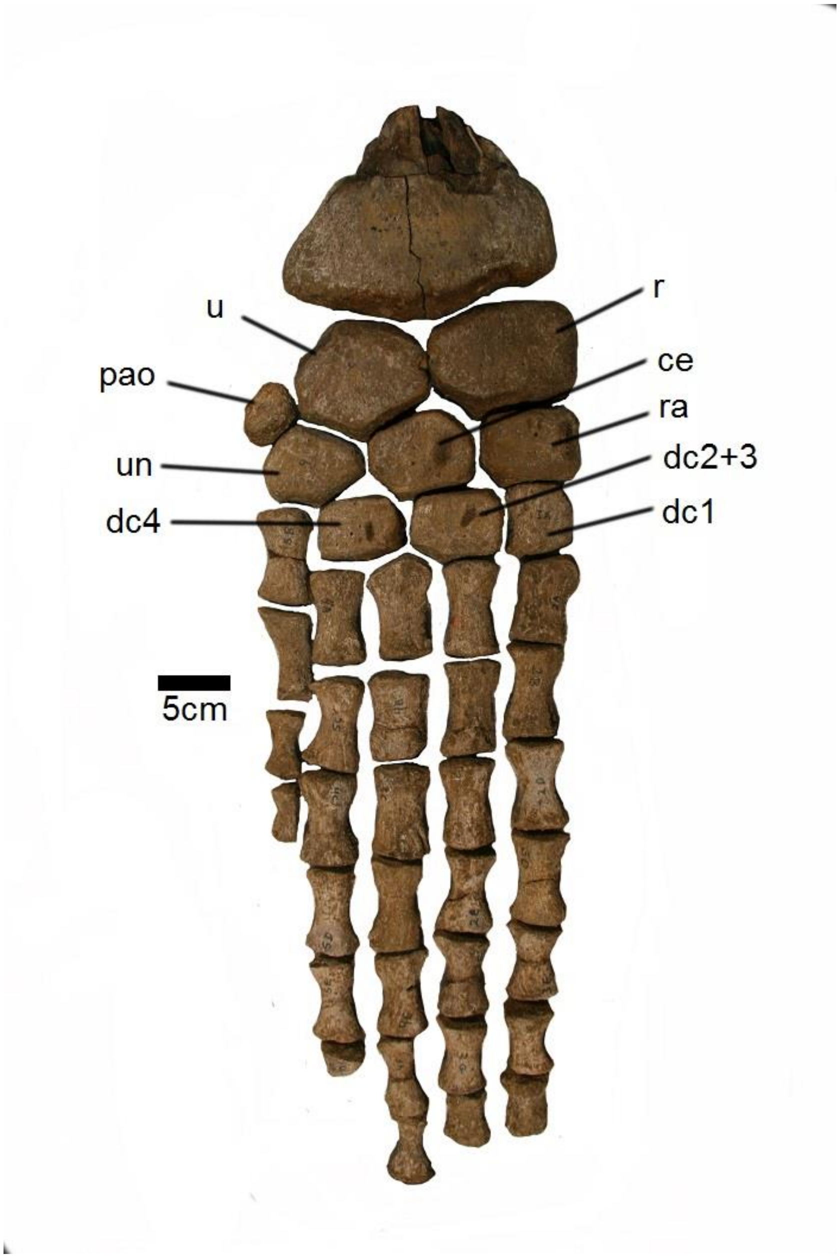

Figure 10. Left fore-limb of MTTU 9217 in ventral view.

The left femur is shorter than the humerus. The diaphysis is narrow and straight. The posterior muscle attachment is well developed and more exaggerated than in *A. quiriquinesis* (Otero et al., 2012). This feature seems to be unique to aristonectine specimens more derived than *Kaiwhekea* that, like other austral elasmosaurs, has a more rounded posterior distal end of the femur. There is what appears to be a third articular facet associated with this posterior extension (Figure 11) which may articulate to a supranumerary element that is not preserved. The ventral surface is slightly more convex than the dorsal surface, a condition shared by MTTU 9218, ZPAL R.8 and *A. quirquinensis* (Otero et al., 2012).

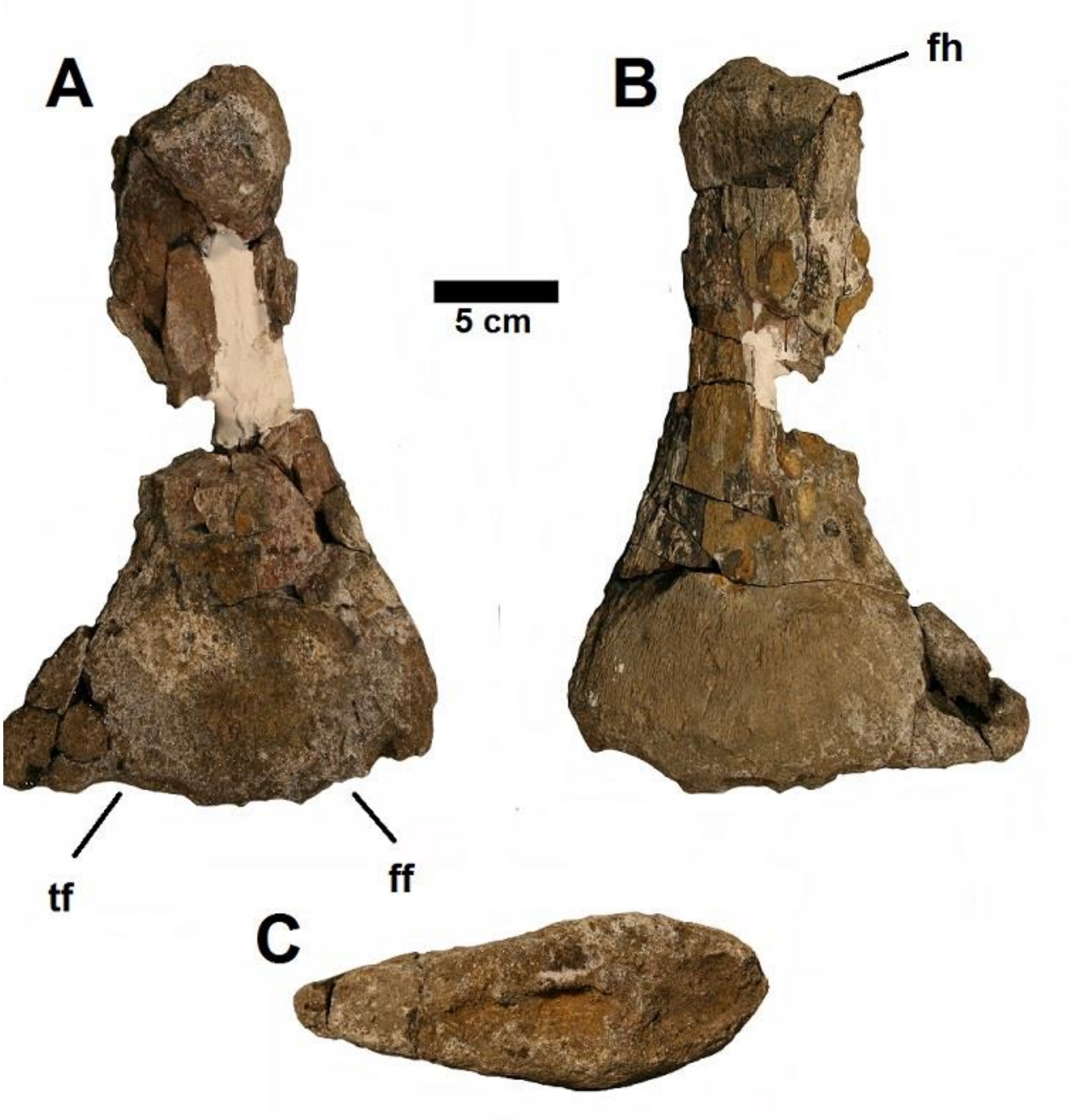

Figure 11. Right hind limb of MTTU 9217. A, dorsal view; B, ventral view; C, distal view.

Discussion

Mortuneria Postcranium

Using cranial apomorphies MTTU 9219 was placed in its own taxa *Mortuneria* *seymourensis* (O'Keefe et al., 2017). Typical elasmosaurs have well developed ventral keels on the atlas-axis centra (Kubo et al., 2012; Sachs & Kear 2015; O'Gorman et al., 2015). The aristonectine specimens also have a simplified region about the atlantal neural arch that closes off the intervertebral foramen unlike *Vegasaurus* (O'Gorman et al., 2015). If these combined traits are unique to derived aristonectines they may give further insight on the lifestyle driving this enigmatic, relatively short-necked clade of elasmosaurs. The atlas-axis complex of *Mortuneria* is very similar to *A. parvidens*, but it contrasts in appearance with *A. quiriquinesis*.

MTTU 9219 has poorly fused neural arches. When present the neural arches have a clear suture to the centrum. The ribs are unfused with rounded facets. Based on the criteria proposed by Brown (1981), MTTU 9219 represents a young organism due to these poorly fused elements. It was proposed in O'Gorman et al., (2015) that the sutures may close at a different ontogentic stage in *Aristonectes*. However as MTTU 9219 has very juvenile characters on all the preserved centra MTTU 9219 can give no insight into this character. The pedicular facets are broad and subelliptical pedicular facets of *Mortuneria* are similar to *A. parvidens* (Gasparini et al., 2003). Sub elliptical pedicular facets are suggested to be due to the juvenile state of the specimen. However there is reason to suspect that this sub elliptical pedicular facet is a feature of these aristonectine elasmosaurs. The unfused cervicals of MTTU 9218 (see chapter 3), the perinatal cervical found with MTTU 9218, and to an extent the young elasmosaurs MLP 15-I-7-6 (O'Gorman et al., 2018) have more elliptical pedicular facets. The facets of MTTU 9218 are fusing and more rugose on the posterior and anterior-most portions of the facets. The sub elliptical facets of MTTU 9219 are also rugose on the posterior and anterior-most portions.

MTTU 9217 offers more insight into the post cranium of *Mortuneria*. The well ossified elements and development of its articular facets place the specimen as ontogenetically older than

MTTU 9219, while still being much smaller than *Aristonectes* (Figure 12), supporting *Mortuneria* as a valid taxon. The most unique feature of MTTU 9217 are the propodials. They are strongly bent ventrally, so that they are convex in anterior view on the distal half. The typical elasmosaurs condition is a straight propodial in anterior view (Otero et al., 2016). Currently the only elasmosaur with a similar condition is ZPAL R.8 (Fostowicz−Frelik & Gaździcki, 2001). This smaller elasmosaurs has only a distal fragment of the humerus, which is very similar in shape, but the left femur is near complete and shows this bend. The femur of Z.PAL R.8 does not have the same strong posterior extension, however MTTU 9217 shares the fore flipper and femur with *A. quiriquinesis*. The fore flipper shares the typical WPB distal shape of the humerus with a projecting posterior end. Both specimens have long, relatively narrow diaphysis. The epipodials of MTTU 9217 are proximal-distally shorter than *A. quiriquinesis* and the mesopodials are shaped differently, particularly the centrale, which has more contact with the radius in MTTU 9217. The shape and position of the centrale gives the epipodials a narrower medial contact, causing the ulna to be pentagonal, with smaller epipodial foramen. The femur of MTTU 9217 shares the same distal shape with *A. quiriquinesis*. There is a strong posterior extension and the facets for the epipodals are nearly even giving a very flat, broad distal surface.

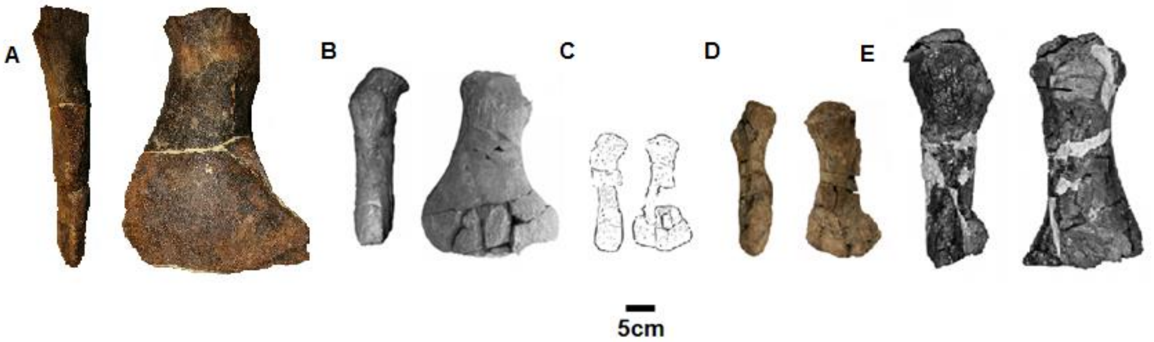

Figure 12. Comparison of propodials of WBP taxa. A, UCMP 38348 humerus in anterior and dorsal (mirrored) views; B, *Vegasaurus* (O'Gorman et al., 2015) humerus in anterior and dorsal view; C, femur of ZPAL R.8 in lateral, dorsal view (Fostowicz−Frelik and Gaździcki, 2001); D, humerus of MTTU 9217 in anterior, ventral; E, humerus of *Aristonectes quirquinesis* (Otero, Soto-Acuña, Vargas, et al., 2014).

Aristonectine Characters

The family the characters used to unite aristonectine elasmosaurs include cranial and cervical characters: rostrum relatively long, but unconstricted and wide anteriorly, with a narrow symphysis, paraoccipital process articulates only with the squamosal, numerous small teeth, greater than six premaxillary teeth, cervical vertebrae much wider than long that have poorly defined rims on the articular surfaces, and a less convex ventral surface that gives the vertebrae a binocular shape in anterior or posterior view (O'Keefe & Street, 2009). This description limits diagnosis of the family to cranial and cervical material. Other characters proposed through the literature in the ten years since the sub-family was erected include VLI, much below 100. This character is as of yet distinctive to the subfamily. Other features have included strongly octagonal anterior caudal vertebrae (Figure 13). Cranial material of non-aristonectes has also shared traits with *Aristonectes*. A non-aristonectine from the Snow Hill Formation on Vega island shares the cranial morphology of a posterior plate-like extension of the pterygoids and lacks an interpterygoid symphysis (O'Gorman et al., 2018). While the presence of these previously thought to be aristonectine traits in a non-aristonectine elasmosaur excludes these traits as being diagnostic to aristonectines, it does provide support to aristonectines evolving from plesiomorph-necked elasmosaurs of the WBP (O'Gorman et al., 2015; O'Gorman et al., 2018). While not aristonectine, elasmosaurs like MTTU 9218 (see Chapter 3), and ZPAL R.8 likely share an evolutionary relationship close to Aristonectines.

Figure 13. Comparison of caudal vertebrae between WBP taxa. A, *Vegasaurus* (O'Gorman et al., 2015); B, MTTU 9218; C, ZPAL R.8 (Fostowicz−Frelik and Gaździcki, 2001); D, Aristonectes parvidens (Gasparini et al., 2003); E, *A. quiriquinesis* (Otero, Soto-Acuña, O'Keefe et al., 2014). Not to scale.

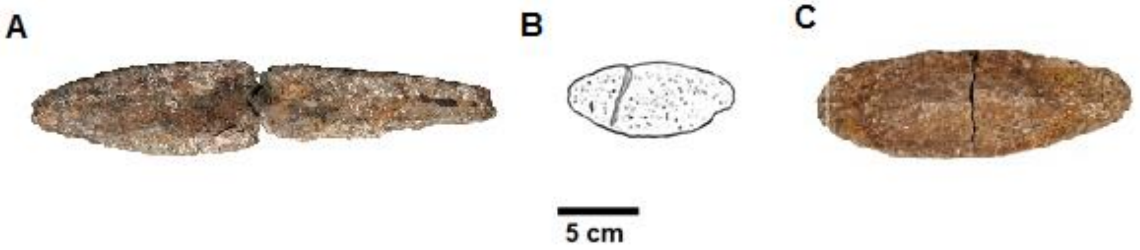

Figure 14. Comparison of the curvature between A, UCMP 58569; B, ZPAL R.8; C, MTTU 9217 with propodials in distal view.

Proposed Aristonectine Characters

The propodials of *Mortuneria* have other characters that also occur in aristonectines and non-aristonectine WBP elasmosaurs. Elasmosaurs typically have greater curvature on the ventral side of the propodial (Figure 14) or near equal curvature. In the aristonectines and some other Southern Hemisphere taxa the ventral surface is more convex. In taxa with this reversed curvature and complete, or near complete, propodials there is also a curve to the propodial in anterior view. The capitulum in these elasmosaurs, with bent midshafts and ventral curvature, is also at a strong angle to the propodial. This bent proximal end also occurs in *Vegasaurus,* whose midshaft is straight. The evolution of the bend occurs as early as *Alzadasaurus* of the early Maastrichtian (Figure 12), though the midshaft is straight and the proximal bend shallow. A long distal end of the femur with a potential third articulation is known only in *Mortuneria* and *A. quirquinesis* (Otero, Soto-Acuña, O'Keefe et al., 2014). *Kaiwhekea,* a more basal aristonectine, has a narrower distal end of the femur and is more similar in shape to ZPAL R.8 (Cruickshank & Fordyce, 2002). The long, flat distal femur may be a synapomorphy of advanced aristonectine elasmosaurs.

Conclusion

The post cranial materials of *Mortuneria,* along with other derived WBP taxa help shed light on the characters previously proposed to be aristonectine. The strongly octagonal caudal vertebrae previously suggested as an aristonectine trait is not restricted to aristonectines. The propodials of MTTU 9217 show curvature, including a more convex surface on the ventral side, a bend mid-shaft, and a strongly angled capitulum. These traits are not restricted to aristonectines, but may help define evolutionary relationships among Aristonectinae and other WBP elasmosaurs.

The femur of MTTU 9217 shows a long, flat distal end with a possible third articular surface similar to *Aristonectes*, but the large size difference, despite the ontogenetically advanced condition of MTTU 9217, and more angular epipodials and mesopodials further establish *Mortuneria* as a separate, valid taxa.

CHAPTER 3

DESCRIPTION OF A SMALL-BODIED ELASMOSAUR

Introduction

Indeterminate plesiosaur fossils have been collected from Antarctica since 1977 (del Valle, Medina, & Gasparini, 1977). Elasmosaurs have been identifiable from the area as early as the early Campanian (O’Gorman et al., 2012), but the late Maastrichtian has far more representatives (Chatterjee and Small 1989; Fostowicz-Frelic & Gaździcki, 2001; Martin, Sawyer, Reguero, & Case, 2007; O’Gorman et al., 2012). Seymour Island, off the Antarctic Peninsula, has produced several interesting Maastrichtian aged elasmosaurs including *Aristonectes* (O’Gorman et al., 2012), the filter feeding *Mortuneria* (O’Keefe et al., 2017), and several small, sub adult taxa.

Elasmosaurs are typically associated with large body sizes. *Albertonectes* (Kubo et al., 2012) reached over 18m and many others were in excess of 8m (Hiller & Mannering, 2005; Welles, 1952). In 1985 several small bodied plesiosaurs were found in Patagonia and attributed to polycotylids, later corrected to be members of Elasmosauridae (Gasparini & Salgado, 2000). In 1989 and 2001 small body plesiosaurs were described on Seymour Island in the Antarctic Peninsula (Chatterjee & Small, 1989; Fostowicz-Frelik & Gaździcki, 2001). In 2017 a contemporary of the small bodied austral elasmosaurs was described from North America (Serratos et al., 2017). Each specimen was found in deposits interpreted as shallow marine environments, hypothesized to be “nurseries” where elasmosaurs would give birth (Wiffen et al., 1995; O’Gorman, Coria, Reguero, & Mörs, 2017). However, these small elasmosaurs were each found to be ontogenetically sub adult or older due to the ossification of limb elements, fused vertebrae, or histological studies. However the possible interrelationships among these small bodied forms are unknown. In this chapter we describe a small bodied elasmosaur from the Antarctic Peninsula and compare the specimen to other small bodied, end-Cretaceous elasmosaurs.

Materials and Methods

MTTU 9218 includes postcranial material collected on Seymour Island of the Antarctic Peninsula from the Lopez de Bertodano Formation (Figure 5). The material was collected in unit 6 (Chatterjee & Small, 1989). The axial elements comprise 23 cervical centra, eight cervical vertebra fragments, and a single pectoral and caudal vertebra. The pelvic girdle is fragmented or missing aside from a single partial ischium and both distal ends of the ilia. The four propodials are incomplete, but elements of all four are present along with a radius, ulna, both fibulae, three mesopodials, and two phalanges. The vertebral measurements were taken with a mechanical caliper and include centra length measured along the dorsal side (L), the breadth of the posterior face (B), and height (H) from the center of the centrum to between the pedicles on the posterior face. Indices calculated are based on Welles (1952) and include: height index (height/length)*100, breadth index (width/length)*100, and breadth height index (width/height)*100. Vertebral length index introduced by Brown (1981) expresses the shape of the centra and allows for the comparison between different sized taxa (Figure 4).

Histology

We thin sectioned MTTU 9218 allowing us to better determine the biological age of the specimen. We used the most proximal portion that was preserved on the diaphysis of the right femur (Figure 20) for two reasons. (1) The propodials have a slower replacement, with the shaft having a slower growth than the ends, better allowing us to get a more reliable age estimation

(Wiffen et al., 1995). (2) The shape of the propodial fragment allowed for easy access to the mid shaft with minimal damage to the specimen. The mid-shaft of right femur was cut perpendicular to the long axis on an oil lubricated rock saw at Marshall University in Huntington, WV. The following preparations took place at Ohio University in Athens, Ohio. The three rough thin sections were cut on an IsoMet 1000 Precision Saw. The sections were then polished on a MetaServe 2000 Grinder-Polisher to width of approximately 80 μm. The images were viewed on a LEICA S8APO microscope and photographed by a Canon 60D camera through a LEICA 10445930 attachment.

Systematic Paleontology

Subclass SAUROPTERYGIA Owen, 1860

Order PLESIOSAUR Blainville, 1835

Superfamily PLESIOSAUROIDEA Welles, 1943

Family ELASMOSAURIDAE Cope, 1869

Results

Axial Skeleton

There are 23 mostly complete cervical centra and 8 fragments of separate centra identifiable as cervicals. The majority of the complete centra come from what is estimated to be the center to posterior of the column due to their size in proportion to the anterior centrum, and the dorsally migrating position of the cervical rib attachments. Many of the fragments appear to be similar in size to the posterior portion preserved. The centra are bilobate and are all longer than high and broader than long. The VLI measurements range from 68 to 108. The anterior cervicals are dorso-ventrally flattened and elongate. MTTU 9218 lacks a lateral longitudinal ridge similar to *Nakonanectes* (Serratos et al., 2017), which appears in Western Interior Seaway

(WIS) elasmosaurs. The rib facets are dorso-ventrally narrow, becoming dorso-ventrally wider and more elliptical through the series. The ribs are well fused without visible sutures. One posterior cervical rib is broken off at the centra with a smooth surface in the central portion of the rib articular surface and rugosity on the edges of the facet suggesting fusion was not complete despite the lack of visible sutures. Neural arches are fused in all but the anterior-most cervicals, with sutures visible at the base of the neural arches. Attachments to the neural arches are rounded laterally and extend almost the entire centra, slightly shifted posteriorly. Ventral foramina range from two to three, with three occurring only on the posterior most centra. The paired or tripled foramina are occasionally asymmetrical in size (Figure 15).

One of the cervical vertebrae with specimen MTTU 9218 does not belong to the same taxon as the rest of the material and represents a much younger individual with very smooth articular facets. The paired ventral foramen are large and widely spaced. This vertebra is marginally longer than high and binocular shaped like an anterior most cervical, but is much larger and yet younger ontogenetically.

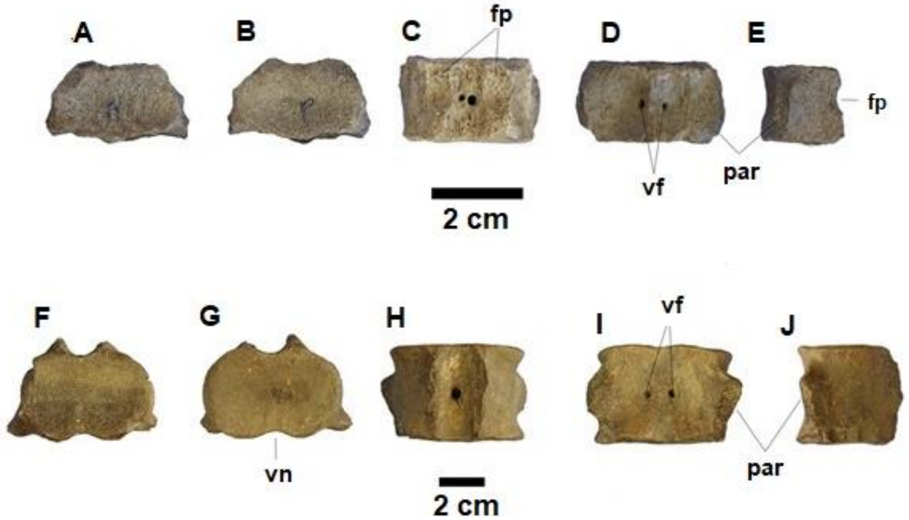

Figure 15.The anterior most preserved cervical vertebra and a posterior cervical vertebra. A-E shows the anterior most cervical preserved in A, anterior view; B, posterior view; C, dorsal view; D, ventral view; and E, left lateral; F-J show a posterior cervical vertebrae in F, anterior view; G, posterior view; H, dorsal view; I, ventral view; and J, left lateral.

preserved (Figure 16). The vertebra is higher than long and broader than high. There is one foraminen on the ventral surface. The articular facets are slightly convex. The pectoral ribs are broken off at the centrum with rough textured facets suggesting the ribs were beginning to fuse. The facet is sub-rounded and the rib dorso-ventrally flattened distally and curves posteriorly.

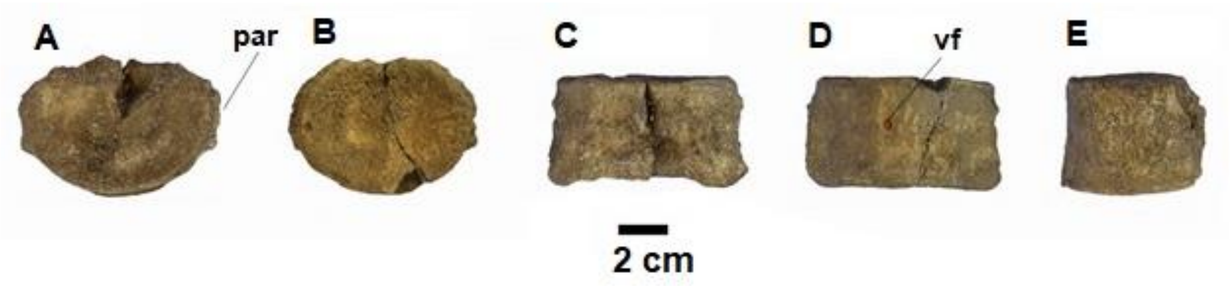

Figure 16. A pectoral vertebra of MTTU 9218. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; and E, left lateral.

The caudal region is represented by a single incomplete vertebra, likely from the anterior portion of the tail. The vertebra is higher than long and broader than high. The preserved articular rib facet is unfused, but roughly textured and laterally projected. The centrum has a slight concavity to both anterior and posterior surfaces, markedly more convex in the midsection compared to the pectoral vertebrae, creating a distinct “thumb sized” divot (Figure 17 A). Hemal arch articulations are present on the anterior ventral portion and are triangular in shape opening anteriorly (Figure 17) followed by a flat ventral region.

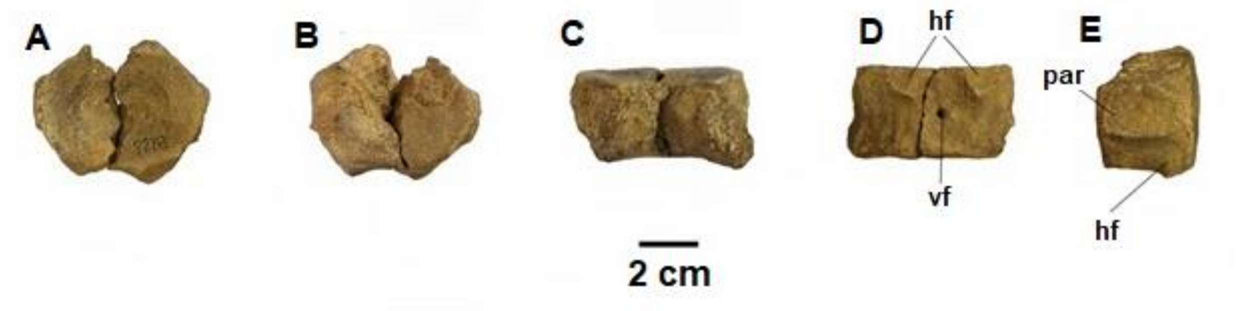

Figure 17. An anterior caudal vertebra of MTTU 9218. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; and E, left lateral.

No identifiable dorsal or sacral vertebrae were found among the available material. The rib fragments show that the ribs are nearly circular in cross section becoming sub-elliptical distally.

Appendicular Skeleton

The pectoral girdle was fragmentary with no identifiable elements. The specimen preserves fragmented ribs, including an articular head.

The central portion of the left humerus was preserved. Only a small portion of the anterior part of the distal end was preserved of the right humerus, and shows that the radial facet was not yet well developed (Figure 18). The capitulum of the right humerus was preserved and is spherical, contrasting with *Kawanectes* lunate capitulum. The capitulum was not preserved attached to the propodial so its articulated angle is unknown. The broken edge of the right humerus shows differentiation between the periosteum and endosteum. Both humeri possess a slightly more convex ventral surface in distal veiw, unlike the typical elasmosaur convex dorsal surface. This state is currently only known in one other austral elasmosaur, ZPAL R.8 (Fostowicz−Frelik & Gaździcki, 2001) and the aristonectines (see Chapter 2). The left radius and ulna are short and broad with a lateral width of 58mm and 63mm respectively and a proximal-distal height of 47mm and 49mm respectively. These forelimb epipodial elements are shorter and more elliptical in shape than *Vegasaurus*, *Nakonanectes*, or *Aristonectes quiriquinensis* (Otero, Soto-Acuña, O'Keefe et al., 2014; O'Gorman et al., 2015; Serratos et al., 2017) and are more similar in shape to *Terminonatator* (Sato, 2003). The epipodial foramen are situated relatively high on the elements compared to the mid-positioned epipodial foramen found in other WBP taxa.

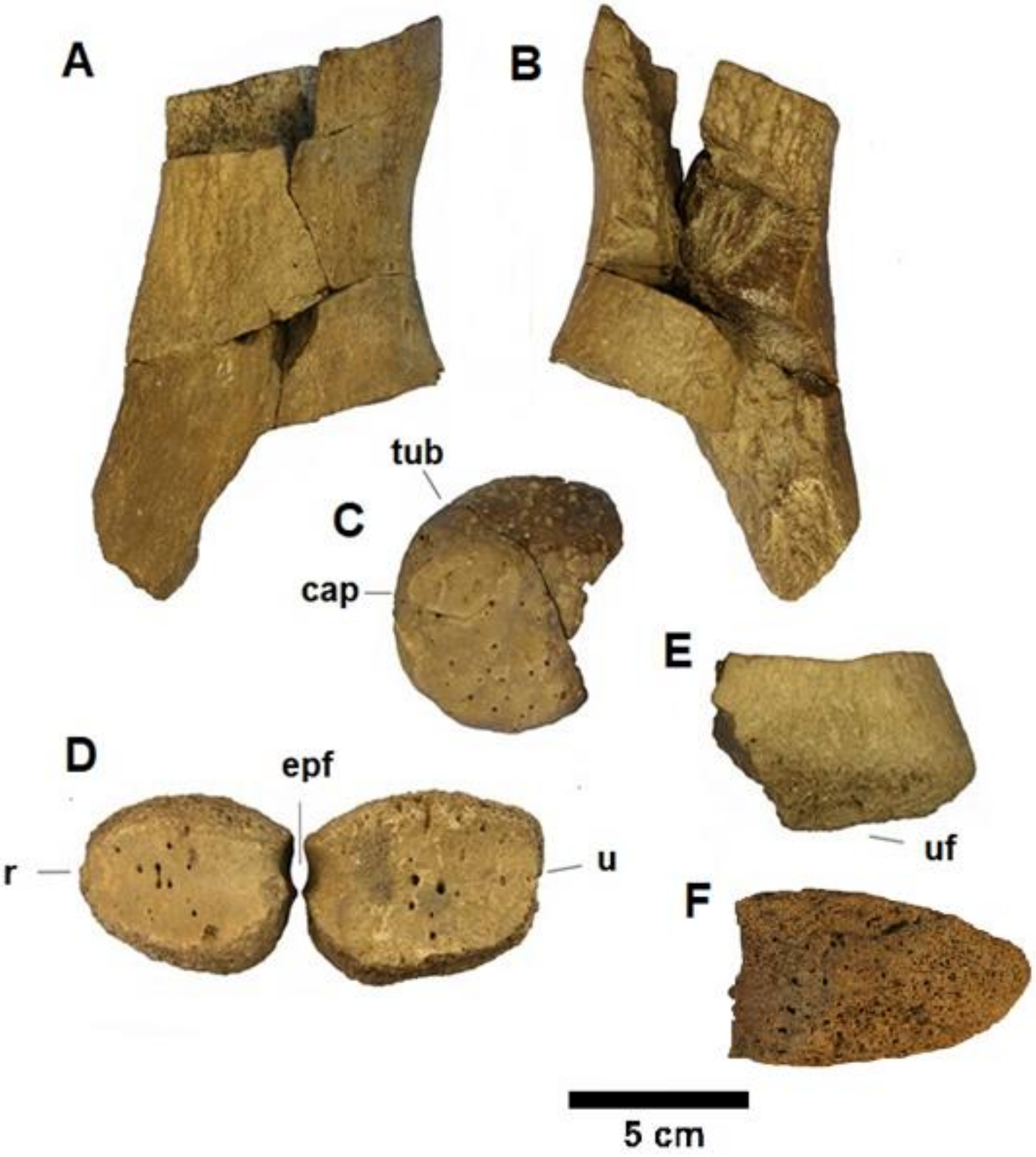

Figure 18. Left humerus of MTTU 9218. A, dorsal view; B, ventral view; C, capitulum; D, radius and ulna; E, right humerus.

The pelvic girdle was fragmentary, with only the right ischium and both proximal ends of the ilia preserved. The ilia are broad with rounded expansion (Figure 19) and a rugose surface. The ilia were large, especially given the small size of the specimen, with an articular surface of 58mm and two articular facets at a high angle creating a wide acetabulum. The proximal portion has a well-developed posterior knob similar to *Kawanectes* and *Vegasaurus*.

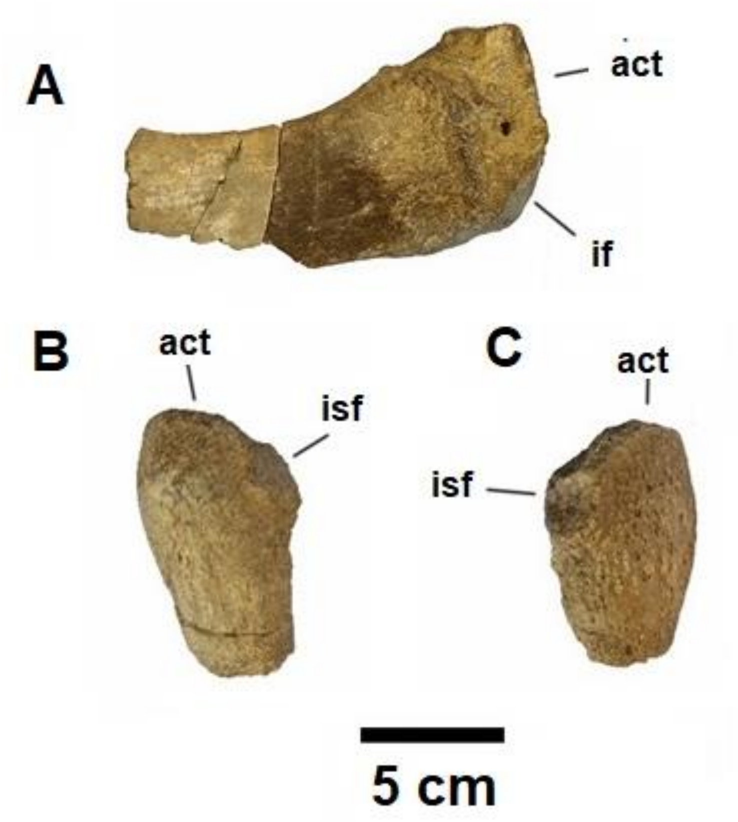

Figure 19. Preserved pelvic material of MTTU 9218. A, left ischium; B, left ilia; C, right ilia.

The mid shaft of the left femur and the distal end of the right femur were preserved. The midshaft is slender compared to the humerus. While the true ratio between the humerus and femur cannot be known due to incomplete preservation, the humerus does not appear to be significantly larger than the femur as in *Kawanectes*. Both fibulae of MTTU 9218 were preserved, but only one is complete. The complete tibia is pentagonal, unlike *Kawanectes'* square fibula, and very similar to that of ZPAL R.8 (Fostowicz–Frelik & Gaździcki, 2001) including a high epipodial foramen (Figure 20). The mesopodial facets are not well formed in MTTU 9218, but show the same angle as in ZPAL R.8. Both fibulae are flattened in comparison to the distal end of the femur. The right femur shows a greater convex curvature on the ventral side like the humeri.

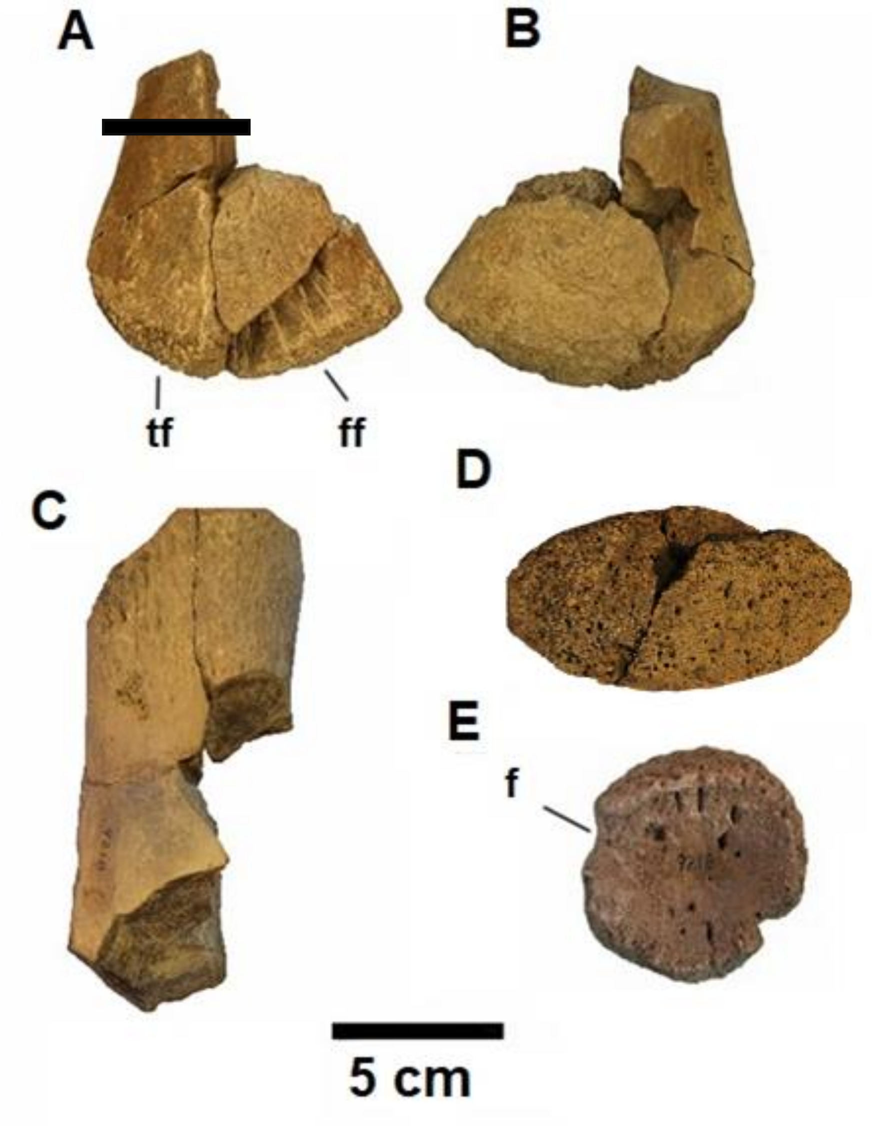

Figure 20. Femora and fibula of MTTU 9218. A, right femur in dorsal view; B, right femur in ventral view, black line indicates area of cut for thin section; C, left femur; D, distal end of the right femur; E, fibula.

Histology

The thin section showed the medullary region was dense and irregular. The endosteum and periosteum had a clear boundary, separated by a dense line that was paired in parts separated by vertical vascularization and the formation of secondary osteons (Figure 21). Following this line the bone grew with radially growing woven fiber bone. There was one other easily discernable line of arrested growth. There was a region at the edge of the periosteum where the tissue became denser suggesting a third LAG line. There is minor Haversion remodeling throughout. At the first LAG line there is a far greater number of secondary osteons.

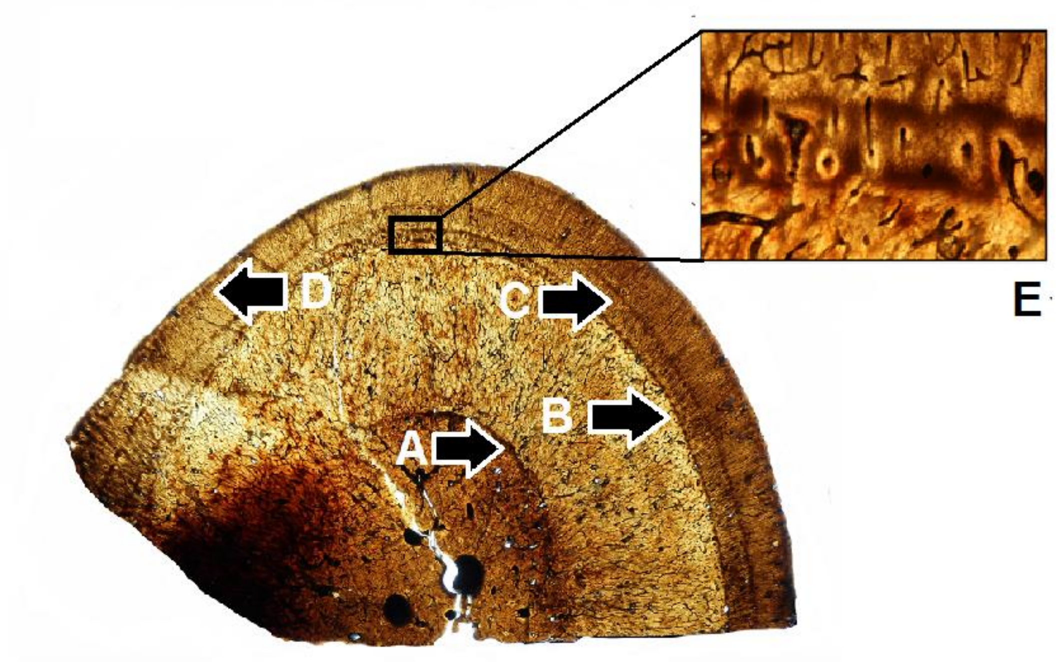

Figure 21. Histological thin section of the right femur. A, Kastschenko's line; B, the growth line; C, a close up of the birth line; D, shows the second line of arrested growth.

Discussion

Taxonomy

MTTU 9218 can be determined down to the family level of Elasmosauridae due to its dumbbell shaped cervical centra. Further identification is made difficult by the specimen's fragmentary preservation, but there are similarities between MTTU 9218 and other WBP Campianian-Maastrichtian elasmosaurs.

Neck Length

Cervical vertebrae are variable among elasmosaurs with three morphotypes being recognized based on relative neck lengths. An elongate group contains species with VLIs greater than 125-138 (O'Keefe & Hiller, 2006) and includes *Thalassomedon, Styxosaurus, Elasmosaurus,* and other Western Interior Seaway taxa (Welles, 1943, 1962; Sachs et al., 2013).

Central neck vertebrae are longer and may reach VLI of between 150 to 200. Along with a lengthening of the vertebrae these taxa also have elevated numbers of cervical vertebrae with *Albertonectes* having 72 (Kubo et al., 2012). The elongate group is restricted to taxa from the WIS (Otero et al., 2015). The non-elongate, or plesiomorphic group have VLIs averaging close to 100 with length still greater than height. These taxa include *Vegasaurus* and *Kawanectes,* that have about 55-65 cervical vertebrae (O'Gorman, 2016). They are not restricted geographically, with members in the WIS (Serratos et al., 2017) and WBP (Chatterjee & Small, 1989; O'Gorman et al., 2015), though most members are austral. A third, shortened vertebral group contains the monophyletic Aristonectinae. Aristonectines are, with the exclusion of the controversial *Futabasaurus* (Sato et al., 2006; O'Gorman et al., 2015), restricted to high latitudes in the southern hemisphere. MTTU 9218 can be considered in the non-elongate group; its VLI measurements range from 68 to 108. While the whole cervical region was not preserved the total count can be estimated to be approximately 55 as in other non-elongate taxa (O'Gorman et al., 2015). With the fusion of the neural arches it is likely that MTTU 9218 has attained near adult proportions and VLI numbers.

Histology/Ontogenetic Considerations

Elasmosaurs are typically associated with large body sizes. This along with the possibility of an elasmosaur having a single live young up to 40% of the adult's total body length (O'Keefe & Chiappe, 2011) led to the suggestion that the small individuals found in shallow marine environments are very young. It has been proposed that elasmosaurs give birth in shallow marine environments (Wiffen et al., 1995) where the young stay for a duration after birth. How long the young may stay in this environment, or whether all of the small bodied elasmosaurs are developing in nursery environments with the trajectory to develop into deep marine predators, is unknown. In order to answer the question as to the age of individuals found in these shallow marine environments, histology has been done on several small bodied elasmosaurs (Gasparini & Goñi, 1985; Palamarczuk & Landman, 2011). The histology of young individuals have a central, dense medullary area followed by a Kastschenko's line (Klein & Griebeler, 2018) then quick radial growth outwards. As the animal matures the bone become porous looking, "spongey," as the radial growth is remodeled. In MTTU 9218 we have reasonable cause to interpret the growth lines to be yearly indicators—particularly as, even with the Weddelian Sea in the Late Cretaceous being more temperate, it still would have been subject to a polar winter. The first growth line in MTTU 9218 is unique in appearance, having areas where the line is parted by vertical vascularization giving the appearance of a double line that is not consistent through its ring around the medullary region. The concentration of secondary osteons on this line and between the double portions of the first line suggests that the growth of these osteons is causing the double appearance of the line. The concentration of these osteons on this line suggests that Haversion remodeling begins at the endosteum/periosteum boundary and spreads through the rest of the bone from there. It is unknown whether the first growth line indicates the birth, the end of the first year, or even possibly conceals several years (Wintrich et al., 2017). However, there is a clear growth line superior to the division between the medullary region and cortex. The fibrous bone also becomes denser at the edge suggesting the organism died during conditions that would have otherwise lead to a second LAG. Due to these two LAGs we can interpret MTTU 9218 as being at least two years in age which accords with other ontogenetic indicators.

MTTU 9218 has several characteristics that place it as a late juvenile-young adult. The neural spines and ribs of the cervical vertebrae are fused in all preserved vertebrae posterior to the two anterior most cervicals. The ribs of the pectoral and caudal vertebrae did not fully fuse, but the facet surfaces are rugose, suggesting fusion was beginning. In elasmosaurs, very immature specimens have well rounded propodials with thin layers of periosteum that may break off on the ends giving an appearance similar to flaking (O'Gorman et al., 2018; O'Keefe et al., 2019). The bones are well ossified of MTTU 9218, with a periosteum layer thicker than would be found on a neonate and not flaking. The articular surfaces are not well defined, but the propodial ends are more developed than the rounded ends expected of a young juvenile.

Taxonomic Comparisons

Kawanectes

Austral specimens are also typically large like the WIS elasmosaurs, but several small near adult specimens are known (Palamarczuk & Landman, 2011; O'Gorman, 2016). Gasparini and Goñi (1985) originally ascribed three specimens to *Trinacromerum lafquenianum,* later amended as Elasmosauridae (Gasparini & Salgado, 2000) and later described as *Kawanectes* (O'Gorman, 2016). Estimated to be 3.8 meters in length, *Kawanectes* is a small elasmasaurid. It was found in the Pellegrini, middle section, of the Allen formation exposed in Patagonia. The formation age overlaps with the Lopez de Bertodano, but is considered middle Campanian to Early Maastrichtian (Dingus et al., 2000). The Allen formation is also considered to be shallow marine (Gasparini et al., 2015). The type specimen for *Kawanectes,* MLP 71-II-13-1, and MTTU 9218 share cervical vertebrae, caudal vertebrae, propodials, and ilia in preservation. The VLI measurements are similar between *Kawanectes* and MTTU 9218, with MTTU 9218 having slightly lower VLIs (Figure 22). The humeral cap of *Kawanectes* is more lunate, similar to *Nakonanectes,* compared to the nearly circular capitulum of MTTU 9218. The apomorphies of a posterior projection of the humerus and presence of pelvic bar cannot be compared to MTTU 9218 due to incomplete preservation. The humerus of MTTU 9218 does appear to be a larger, more robust element than the femur, as is typical for elasmosaurids, but the elements are incomplete, so whether MTTU 9218 shares the high aspect ratio of humerus to femur cannot be known, but the humerus does not appear to be significantly larger than the femur as in *Kawanectes*. The epipodials of *Kawanectes* are broader, with a large central epipodial foramen and a steep proximal curve to the fibula, unlike MTTU 9218 with a strongly pentagonal fibula and high epipodial foramen. The shape of the distal end of the femur and laterally projected parapophyses of the caudal vertebrae are shared between specimens. However the latter may not be a strong diagnostic tool, as *Nakonanectes* also shares this characteristic (Serratos et al., 2017).

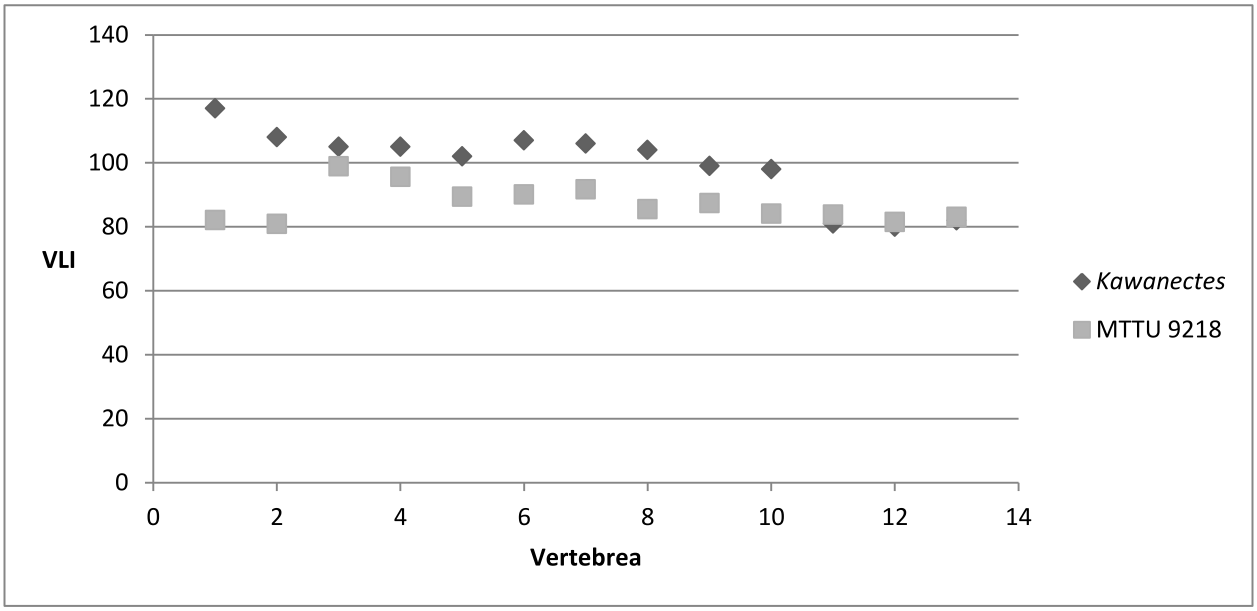

Figure 22. Vertebral measurement comparison of MTTU 9218 and *Kawanectes*.

ZPAL R.8

Another small bodied-elasmosaur was found on Seymour Island in a lower stratigraphic position of the Lopez De Bertodano formation, unit 2, and was described in 2001 (Fostowicz−Frelik & Gaździcki, 2001). There is reason to suggest that ZPAL R.8 and MTTU 9218 are from the same taxon. Both specimens have preserved cervical vertebrae, anterior caudals, distal portions of the humeri, femora, and fibulae. The caudal vertebrae of ZPAL R.8 share laterally projected parapophyses with MTTU 9218, *Kawanecte*s and *Nakonanectes*. The size of the elements preserved suggests a slightly smaller individual than MTTU 9218, but ZPAL R.8 seems to show more development in the epipodial facets of the humerus, a distinction difficult to make due to MTTU 9218 having poor preservation and being more juvenile specimen. The femur of MTTU 9218 has the same distal posterior “knee,” common to WBP taxa (O’Gorman et al., 2015), but with the same angle in both MTTU 9218 and ZPAL R.8 (Figure 23). The fibulae of both specimens are medio- laterally flattened with a pentagonal shape and high positioned epipodial facet.

ZPAL R.8 is fragmentary, but its propodials share distinctive features with aristonectines. So far only aristonectines have strongly recurved propodials (Otero, Soto-Acuña, O’Keefe et al., 2014) with a sharp bend to the ventral side at the capitulum, then a gentle dorsal curve to the proximal end. MTTU 9218 does not possess enough proximal shaft to determine a curve. A feature ZPAL R.8 shares with MTTU 9218 is a greater curvature on the ventral side of the propodials (Figure 23). *Aristonectes quiriquinesis* and *Mortuneria* (see Chapter 2) are the only other known taxa with this reversed convex curvature on the propodials (Otero, Soto-Acuña, O’Keefe et al., 2014); all other known elasmosaurs have greater curvature on the dorsal side. Sharing these two traits unique to artistinectines indicates a possible relationship with ZPAL R.8 whose poorly preserved cervical vertebrae resemble the “plesiomorphic” neck morphotype. Furthermore, ZPAL R.8 has a close affinity to MTTU 9218, whose vertebral column is over half complete and displays a clear “plesiomorphic” morphotype. It is not the objective of this paper to do a phylogenetic study; however, this supports the hypothesis of an austral evolution of aristonectines as put forth by O’Gorman et al. (2015).

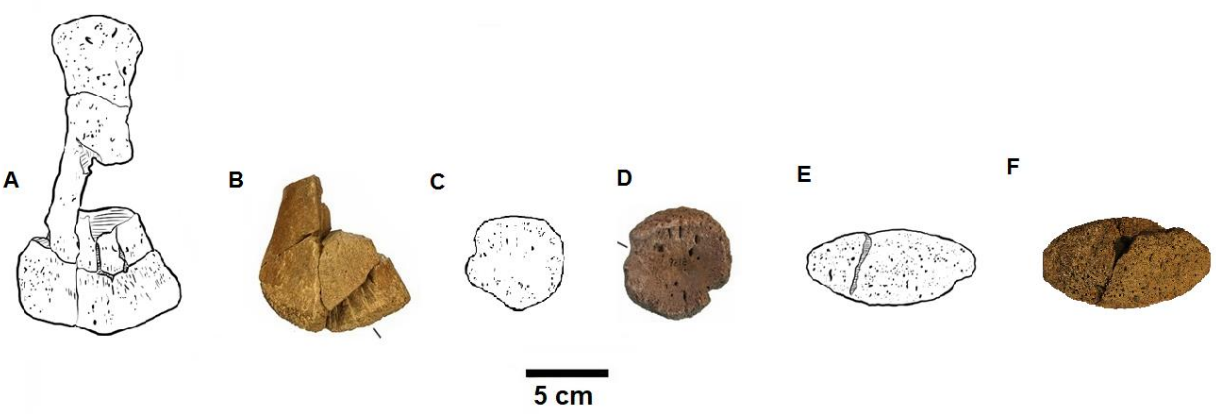

Figure 23. A comparison of the shared elements between MTTU 9218 and ZPAL R.8 (right). A, Posterior view of Z PAL R.8 left femur; B, Anterior view of MTTU 9218 right femur; C, Z PAL R.8 fibula; D, MTTU 9218 fibula (mirrored); E, Z PAL R.8 distal view of left femur; F, distal view of right femur.

Nakonanectes

Nakonanectes is a small bodied elasmosaur from the WIS described in 2017 (Serratos et al., 2017). It was found in the Campanian-Maastrichtian aged Bearpaw shale, interpreted as a shallow marine environment with potentially low saline water due to the presence of fresh water algae and dinoflagulates (Palamarczuk & Landman, 2011). The specimen itself was found to be of early Maastrichian age (Serratos et al., 2017). *Nakonanectes* shares in preservation with MTTU 9218 the presence of anterior cervical vertebrae, caudal vertebrae, humeri, radius, ulna, femura, and ilia. The caudal vertebrae share rounded rib facets with a lateral projection. However MTTU 9218 lacks the strong chevron facets on the articular surface of the caudal centra. The ilia are broad at the proximal end like MTTU 9218, but lack the same rounded dorsal expansion. The femur and fibula are markedly different between the two taxa. The femur in *Nakonanectes* curves downward on both sides of the distal edge. This curvature is unlike the southern elasmosaurs, including MTTU 9218, that have a posterior extension that forms an angle upward. While MTTU 9218 lacks the preservation of the skull material and intercoracoid vacuity that are diagnostic for *Nakonanectes*, the elements that they share suggest that MTTU 9218 is not a specimen of *Nakonanectes*.

Dwarf Aristonectines

Previously the concept of "dwarf *Aristonectes*" was proposed by Otero et al. (2015). In this category he includes ZPAL R.8. The cervical region of ZPAL R.8 is very poorly preserved with single fragmentary vertebrae from the neck. MTTU 9218 has strong affinities for ZPAL R.8 and a more complete cervical region with plesiomorphic VLIs. It is unlikely that ZPAL R.8 represents a true aristonectine, but the characters shared by the small elasmosaurs from Antarctica display a potential relation to aristonectines. They share curved propodials, stronger convex of the dorsal side of the propodial in distal view, and a strongly octagonal outline of the caudal vertebrae. The presence of these small bodied elasmosaurs suggests that aristonectine appendicular adaptations preceded the cervical shortening. These features shared may not be diagnostic for the subfamily Aristonectinae, but may be valuable for determining the lineage and evolutionary history of Aristonectinae and WBP elasmosaurs (Table 1; Figure 24).

	Cervical centrum length	Capitulum angular	Propodial bent dorsal-ventrally	Propodial reversed curvature	Third articulation on the distal end of the femur	Anterior caudal strongly octagonal
Kawanectes	Moderate	N/A	No	No	No	No
Vegasaurus	Moderate	Yes	Yes	No	No	N/A
MTTU 9218	Moderate	N/A	N/A	Yes	No	Yes
ZPAL R.8	N/A (likely moderate)	Yes	Yes	Yes	No	Yes
Mortuneria	Short	Yes	Yes	Yes	Yes	N/A
A. quiriquinesis	Short	Yes	Yes	Yes	Yes	Yes

Table 1. Appearance of aristonectine-like character states in southern taxa.

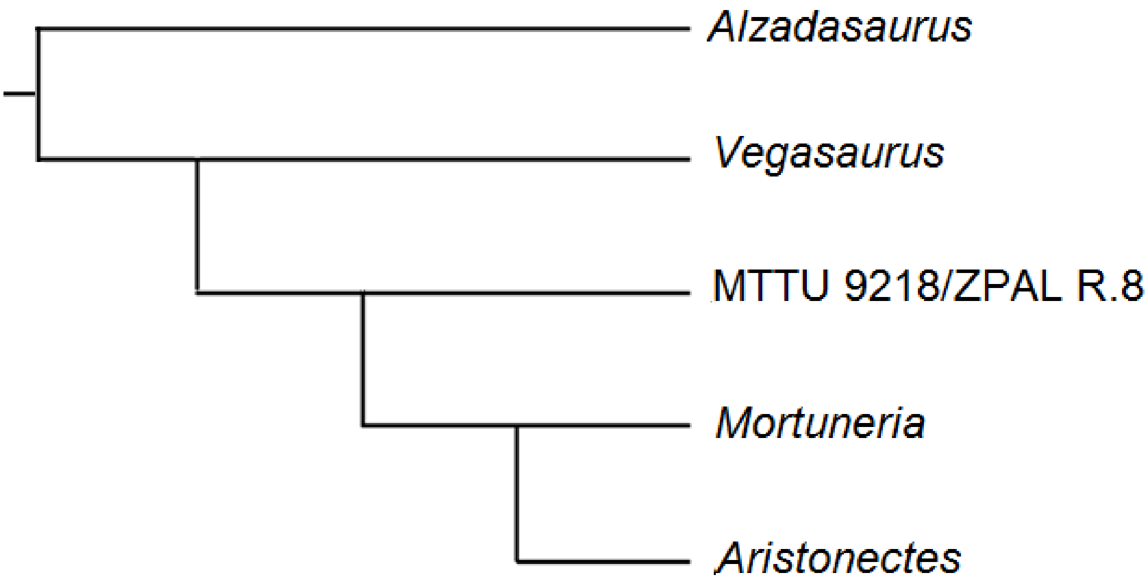

Figure 24. Phylogenetic hypothesis of the relationship between elasmosaurs with aristonectine-like affinities.

Conclusion

The fusion of neural arches and ossification of the elements in MTTU 9218 are intermediate between neonate and adult elasmosaurs. The histology, containing little remodeling, showed significant growth after the first growth line suggesting the specimen was at least two years old at death. The overall size and age indicates that MTTU 9218, of approximately 3-4 meters total length, was a small bodied elasmosaurid and would have grown up to be smaller than typically associated with elasmosaurs. The taxonomic position could not be identified due to fragmentary remains, but the specimen most closely resembles ZPAL R.8, another small bodied elasmosaur with postcranial attributes shared by *Mortuneria*. While there was no cranial material preserved it is probable that the cranial material reflects this intermediate position between WBP elasmosaurs and aristonectines. The cranial skeleton may have some aristonectine characters such as *Alexandronectes* (Otero et al., 2016). The description of MTTU 9218 is significant, adding to the knowledge of the uncommon small bodied plesiosaurs, information on the potentially near aristonectine Weddellian taxa, and examines the histology of a young, austral plesiosaur.

The combination of characters between MTTU 9218 and ZPAL R.8 in comparison with Pacific plesiosaurs and aristonectine characters provide support in the link WBP Aristonectines and Pacific plesiosaurs that has been suggested by O’Gorman (2016).

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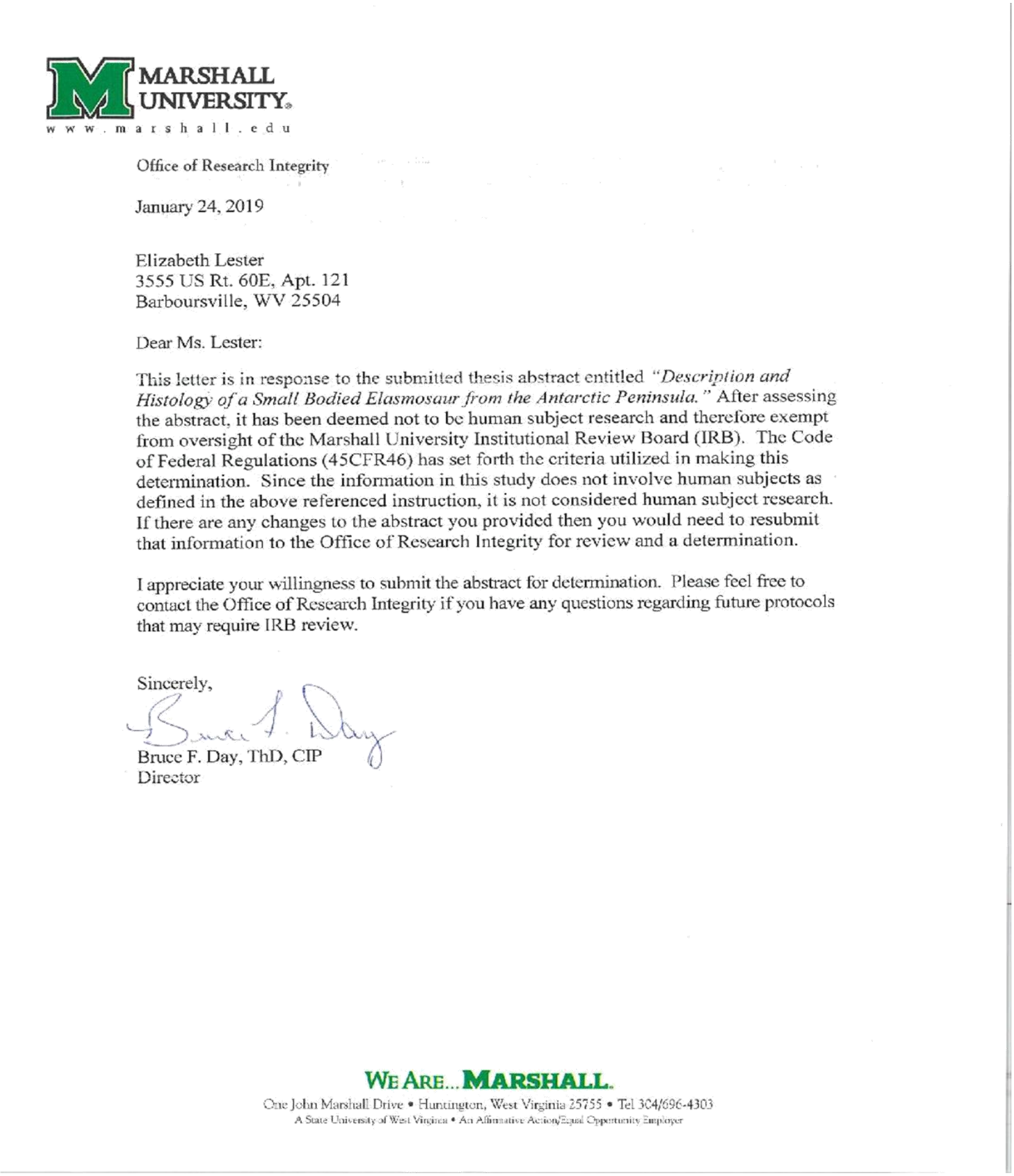
APPENDIX A: IRB LETTER



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Office of Research Integrity

January 24, 2019

Elizabeth Lester
3555 US Rt. 60E, Apt. 121
Barboursville, WV 25504

Dear Ms. Lester:

This letter is in response to the submitted thesis abstract entitled *"Description and Histology of a Small Bodied Elasmosaur from the Antarctic Peninsula."* 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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