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Locomotion and skeletal morphology of Late Cretaceous mosasaur, *Tylosaurus proriger*

An Honors Thesis submitted in partial fulfillment of the requirements for Honors in the Geology and Geography Department.

By
Jesse A. Carpenter

Under the mentorship of Dr. Katy Smith

ABSTRACT

Mosasaur (Reptilia: Squamata) are apex marine predators from the Late Cretaceous (Turonian to Maastrichtian) epicontinental seas of North America, Africa, Europe, and Asia. From previous studies, it has been suggested that this group trends towards increased rib compactness, lengthening and increased posterior inclination of neural spines of intermediate and terminal caudal vertebrae to support a caudal fluke, and a transition from anguilliform to carangiform locomotion, closer to thunniform in pelagic adapted species. This study examined multiple *Tylosaurus* specimens using centrum length/width (CL/CW) and width/height (CW/CH) ratios along with neural spine height and angle of posterior inclination to (1) describe the vertebral column of GSM-1, a previously undescribed *Tylosaurus proriger* and (2) assess the viability that *Tylosaurus* used carangiform locomotion and had a hypocercal caudal fluke. CW/CH and CL/CW showed that *Tylosaurus* had a neck with an increased range of motion relative to pelagic mosasaurs like *Plotosaurus bennisoni*, a mostly restricted dorsal region, and that pygals and caudals allow for increased range of motion relative to the dorsals and cervicals with the exception of those interpreted to be supporting the fluke. These trends are consistent with known fluked and/or carangiform swimmers and suggest that *Tylosaurus* also employed this mode of locomotion. A single juvenile specimen suggested that younger *T. proriger* had more restricted cervicals and dorsals with greater mobility in the tail, possibly similar to the locomotion of pelagic mosasaurs, though more research will need to be conducted.

Thesis
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INTRODUCTION

In North America, Europa, and Africa, the breakup of Pangea resulted in the formation of subtropical epicontinental seas where some members of Reptilia transitioned from fully terrestrial to fully aquatic lifestyle. In North America, this epicontinental sea was called the Western Interior Seaway and the early Gulf Coast (Figs. 1-2; Russel, 1967; Blakey, 2014). This new group of marine reptiles, the mosasaurs, would become some of the top marine predators of the Cretaceous until their extinction 66 Ma during the K/Pg mass extinction event (Russel, 1967; Bell, 1997).

Tylosaurus (Reptilia: Squamata), the mosasaur genus examined in this study, are members of the superfamily Mosasauoidea and have been found on almost every continent (Fig. 3; Russell, 1967; Bell, 1997, Polcyn and Bell 2005). They are one of the most

common and among the largest of the mosasaurs, first described by Osborn (1899), and are closely related to *Ectenosaurus*, *Hainosaurus*, and *Platecarpus* (Fig. 3). Like most mosasaurs, *Tylosaurus* was thought to be an anguilliform swimmer, an organism with a long snake-like body that swims via undulating serpentine motions of the entire axial column much like an eel (Osborn, 1899). Given the general snake-like shape of the group and their close relation to snakes, such an assumption was, at the time, a reasonable one (see Lee, 1997). However, recent studies have shown that this is not the case in most, if any mosasaur species. Many specimens, including close relative of *Tylosaurus*, are subcarangiform to carangiform swimmers, those in which the posterior vertebral column and tail generate the largest propulsive force. This swimming style typically has somewhat mobile cervical vertebrae, restricted anterior dorsals, and a posterior increase in lateral mobility from the more posterior dorsals, pygals, and caudals. (Lindgren et al., 2010; Lindgren et al., 2011; Konishi et al., 2012; LeBlanc et al., 2013).

Thunniform methods, where the tail is the sole source of propulsion, are employed by ichthyosaurs and many fish species. Here one sees that cervicals, dorsals, and pygals are generally restricted and almost all lateral mobility is concentrated in the caudals. Some mosasaurs, namely *Plotosaurus bennisoni*, began to encroach on deep marine habitats, growing significantly closer to thunniform locomotion (though still remaining carangiform) than other species (Lindgren et al. 2007). Similarly, many mosasaur species evolved a hypocercal (i.e. bottom lobe is larger than the top lobe) tail fluke that served as a hydrofoil, generating thrust perpendicular to the plane that contains the fluke, here meaning that the thrust is generated from lateral movement of the fluke in a horizontal

plane, unlike the dorsoventral movement of cetacean flukes in a vertical plane (Fig. 4; Lindgren et al., 2007; Konishi et al., 2012).

Within the axial skeleton, numerous studies (e.g., Lindgren et al., 2007; Lindgren et al., 2010; Lindgren et al., 2011; Konishi et al., 2012; LeBlanc et al., 2013) have shown that morphological changes in the vertebral column reflect the locomotive mode and body shape. These changes include (1) an increase in neural spine height (NH) and posterior angle of inclination (AI) when there is an increase in muscle or connective tissue (i.e. cartilage) attachment, the latter in the case of supporting a fluke, (2) decrease in centrum length versus width ratios (CL/CW) to accommodate increased lateral movement or increasing to restrict said movement, (3) increase in centrum width versus height ratios (CW/CH) and decrease in CL/CW ratios when supporting a fluke or restricting lateral movement or increasing CL/CW and decreasing CW/CH for increasing lateral range of motion, and (4) increase in zygapophyseal orientation to restrict lateral movement, decreasing for more unrestricted movement (Lindgren et al., 2007).

These evolutionary changes to the axial skeletal morphology are not the only evidence of caudal flukes and carangiform locomotion as soft tissues and impressions of soft tissues, preserved in *Ectenosaurus*, *Plotosaurus*, and *Platecarpus*, among others, give direct evidence for the presence of a caudal fluke (Lindgren et al., 2007; Lindgren et al., 2010; Lindgren et al., 2011; LeBlanc et al., 2013). Similarly, histological studies indicate an increase in rib compactness (Houssaye and Bardet, 2012; Houssaye 2013, D'Emic et al., 2015) and widespread development of strong costal musculature (D'Emic et al., 2015), trends expected during carangiform and thunniform locomotion where the dorsal region must be stable but capable of producing the forces necessary for swimming.

This study focuses on characterizing the vertebral morphology of *Tylosaurus*, with specific focus on a nearly complete specimen of *Tylosaurus proriger*. This research marks the first morphological description and morphometric analysis of the vertebral column *Tylosaurus proriger* held by the Georgia Southern University Museum, GSM-1. Two hypotheses were tested: (1) *Tylosaurus proriger* primarily uses carangiform locomotion and (2) possessed a hypocercal tail fluke. This study highlights how *Tylosaurus* compares with other mosasaurs in terms of locomotion and morphology.

MATERIALS AND METHODS

Materials

This study examined eight specimens of *Tylosaurus sp.* and *Tylosaurus proriger* from Georgia Southern University Museum (GSM), the McWane Science Center (MSC), and the University of Alabama (UA) Collections. Specimens that had vertebrae numbered to indicate their position in the vertebral column were classified as “in sequence” (Table 1).

GSM-1, from GSM, is an 8 m long largely complete subadult *Tylosaurus proriger* with poorly preserved pygals, many neural spines missing, and a crushed skull. UA provided 3 *Tylosaurus* specimens, a largely complete subadult (PV1993.0001.0001) with many neural spines and terminal caudal vertebrae missing, a highly weathered dorsal sequence of vertebrae (unnumbered), and a very deformed series of intermediate caudal vertebrae (PV1985.0020), the latter of which was not used due to its deformation. MSC provided 5 *Tylosaurus* specimens. One specimen (RMM5610) was a juvenile with some pyrite oxidation that only affected certain measurements. The other four specimens

(RMM2475, RMM3371, RMM3253, RMM1913) were from specimens of numerous sizes and states of preservation (see Table 1 for preservation notes).

Vertebral classification

Each vertebra was classified as cervical, dorsal, pygal, intermediate caudal, or terminal caudal (Fig. 5). Cervical vertebrae are anterior to the shoulder girdle and may or may not have lateral facets for rib articulation (Polcyn and Everhart, 2008). These vertebrae also have prominent and blade-like hypapophysis. Dorsal vertebrae have short transverse processes with lateral facets for rib articulation (Lindgren et al., 2007; Polcyn and Everhart, 2008; Lindgren et al., 2010). Pygal vertebrae have blade-like transverse processes and lack chevrons. Intermediate caudal vertebrae have blade-like transverse processes and ventral chevrons. Terminal caudal vertebrae lack transverse processes and have ventral chevrons (Lindgren et al., 2007 and Lindgren et al., 2010). All vertebrae were labeled with an abbreviation (C, D, P, I, and T) followed by a number that represents its position in series when available.

Vertebral measurements

Measurements of centrum length (CL), height (CH), width (CW), neural spine height (NH), and anterior-posterior angle of inclination (AI) (Fig. 6) were made on each specimen and recorded in millimeters (mm). CL was measured on the both the left and right lateral surfaces from the anterior-most articulation surface to the posterior-most and averaged. Centrum length (CL) averages for each specimen were summed for the total length (TL) when the correct order of vertebrae in the column was known. Centrum height (CH) and CW were measured on the condyle. In the case of fused vertebrae, Centrum

height (CH) and CW was taken as close to the condyle as possible, which was possible on all vertebrae examined in this study except for those that had fractured or pyrite oxidized condyles. In specimens where this fracturing or oxidation occurred, not all measurements were affected. The affected dimensions were ignored or not taken. Neural spine height (NH) was measured from the top of the neural canal to the distal-most end of the neural spine. Angle of inclination (AI) was measured in reference to a horizontal line corresponding to the top of the centrum and a line corresponding to the long axis of the neural spine. The angle was taken from the posterior-most side of the vertebra using lateral view photographs in ImageJ. If the angle was greater than 90°, the spine was anteriorly inclined (procumbent) and if it was less than 90° the spine was posteriorly inclined (recumbent). CW/CH and CL/CW were plotted against fraction of postcranial length for GSM-1 and PV1993.0001.0001.

RESULTS

CW/CH and CL/CW vs. Fraction of Postcranial Length and Neural Spine Inclination

GSM-1 and PV1993.0001.0001 have cervical vertebrae that are dorsoventrally tall and long. Their dorsal vertebrae are wider and anteroposteriorly longer but are shorter when approaching the pygal region of the vertebral column (Fig. 8). Unlike the deformed pygals of GSM-1, PV1993.0001.0001 showed a rapid decrease in CW/CH and CL/CW in this region. This decrease in ratios continues through to the intermediate caudal vertebrae of both GSM-1 and PV1993.0001.0001 until I15 in GSM-1 and I9 in PV1993.0001.0001. This decrease indicates these vertebrae become relatively taller, shorter in length, and wider than their preceding counterparts. Beginning at T2 in GSM-1 and T6 in

PV1993.0001.0001, terminals show a stark transition to wider vertebrae reflected by an increase in CW/CH and a decrease in CL/CW.

For RMM 2475, RMM3371, RMM3253, and RMM1913, vertebrae follow the patterns indicated by GSM-1 and PV1992.0001.0001. In the juvenile RMM5610, the cervical vertebrae and dorsal vertebrae are of a similar shape and have higher restriction of lateral movement than in the adult specimens. Intermediate caudal vertebrae show a decrease in CL/CW relative to the other vertebrae in the specimen, and are longer than they are wide. Neural spines of GSM-1 and PV1993.0001.0001 show recumbent (posteriorly inclined) or vertical dorsal vertebrae. The pygal vertebrae become more recumbent than the dorsals. In the intermediate caudal and terminal vertebrae, specifically T2-T16 in GSM-1 and T1-T10 in PV1993.0001.0001, there is a shift from recumbent to procumbent (anteriorly inclined) and back to recumbent neural spines. Procumbent spines in this region are consistently over 100°. In GSM-1, additional terminal vertebrae show a transition back to procumbent neural spines.

DISCUSSION

Tylosaurus is expected to be more carangiform in its locomotor pattern, meaning that unlike more marine adapted mosasaurs, *Tylosaurus* has a more undulatory and eel-like locomotive pattern than that of pelagic mosasaurs, based on comparisons of data and descriptions of well described mosasaurs in literature and aquatic adaptations (i.e. Osborn, 1899; Lindgren et al., 2010; Lindgren et al., 2011; Konishi et al., 2012; LeBlanc et al., 2013). Data for GSM-1 and PV1993.0001.0001 indicate that cervical vertebrae are dorsoventrally tall and anteroposteriorly long, allowing for increased movement of the neck relative to the dorsal vertebrae but have recumbent neural spines for connection of

axial musculature, showing that while it is more mobile than derived species such as *Plotosaurus*, its movement is still restricted more so than other sections of the skeleton, particularly the pygals and caudals. Contrarily, the pelagic *Plotosaurus* has short, wide, and deep cervicals, restricting its movement and resulting in a general stiffness of the axial column (Lindgren et al., 2007). Furthermore, the shallow marine *Dallasaurus*, a more basal mosasaur species, has been shown to have cervicals that are much longer than that of *Plotosaurus* and *Tylosaurus*, indicating a much higher range of lateral motion in this region. Similarly, the terrestrial relative *Varanus exanthematicus*, a modern analog for the earliest common ancestor of mosasaurs and monitor lizards, has been shown to have even more lateral range of motion in its cervicals (Lindgren et al., 2011).

Tylosaurus dorsals are wider than they are long or subequal, indicating more restricted movement than the cervicals, pygals, and caudals. These are also the largest vertebrae in the vertebral column. Similar to those of *Plotosaurus*, dorsal vertebrae become taller and wider in the posterior section of the vertebral column where more movement would have been occurring during locomotion. In *Plotosaurus*, the tail stock, or base of the tail, and the displacement unit where the large majority of movement occurs are contained within the pygal region (see Fig. 3A, Lindgren et al., 2007). The same functional units in *Tylosaurus*, marked by a decrease in CW/CH and CL/CW , contain all (or most) of the pygals and many of the intermediate caudal vertebrae (P1-I15 in GSM-1 and P2-I9 in PV1993.0001.0001). Furthermore, these functional units in *Tylosaurus* are not as stark as those in *Plotosaurus*. This is likely a result of differing locomotive methods. *Plotosaurus*, a fusiform carangiform swimmer, concentrates its movement completely within the tail and would have a stiff hip preventing movement further up the vertebral column, and thus a

sharp drop in CW/CH and CL/CW. *Tylosaurus*, however, shows more flexible hip and gradual, nearly uniform change in ratios that would be consistent with movement more widely distributed through the vertebral column, typical for carangiform swimming.

In the intermediate caudals and terminal caudals, the shift in neural spines from recumbent to procumbent and back to recumbent (I24-TC31 in GSM-1 and I21-T8 in PV1993.0001.0001) form a broad fan shape (or half of the fan in the case of PV1993.0001.0001, as many of the terminal caudal vertebrae were not preserved) which is interpreted as the dorsal tail fluke, though it is not as pronounced in GSM-1 as seen in *Plotosaurus* (Fig. 9). This difference the distinction of the fan shape could be the result of varying locomotive styles between species. Similar patterns have been noted in *Plotosaurus*, ichthyosaurs, metriorhynchid crocodylomorphs, and preserved soft tissues or impressions of soft tissues (see Nicholls and Manabe, 1999; Fig. 5 in Lindgren et al., 2007, Fig. 5 in Young et al., 2010). For the fluke to function properly, as Lindgren et al. (2007) highlighted, the transition back to procumbent neural spines to support the fluke would be expected. These procumbent spines, peaking at high angles in T2-T16 for GSM-1 and T1-T10 for PV1993.0001.0001, are here interpreted to be the base of the tail fluke. Moreover, the vertebrae with these procumbent spines also have higher CW/CH ratios and lower CL/CW ratios and tend to be taller than adjacent vertebrae. Unlike the rest of the caudals described above, these vertebrae are overall much wider with taller neural spines than adjacent vertebrae to support the fluke (see Fig. 2A, Lindgren et al., 2007, Lindgren et al., 2010), have more areas for connective tissue attachment, and increase stability of the tail (Fig. 9). Similar trends are seen in *Plotosaurus*, *Platecarpus*, and other mosasaur species as well as sharks with heterocercal flukes, though mosasaurs and other marine reptiles

possess hypocercal flukes (see McGowan, C., 1992; Nicholls and Manabe, 1999; Little and Bemis, 2004; Lindgren et al., 2007; Lindgren et al., 2010; Lindgren et al., 2011, Konishi et al., 2012). However, for the basal *Dallasaurus*, this trend is far less noticeable, suggesting that the early mosasaurs lacked or had a substantially less pronounced fluke than that of their derived relatives. In *Varanus* this trend is no longer present at all, with laterally mobile vertebrae throughout the vertebral column with increased mobility posteriorly, an expected trend of an anguilliform, suggesting that the earliest mosasaur relatives were likely also anguilliforms (Lindgren et al., 2011).

RMM5610 shows a stark contrast to the adult specimens in that lateral mobility of the cervical and dorsal vertebrae is restricted but the intermediate caudals allow for a relatively higher range of motion (Fig. 10). This difference could be an indicator that while young, *Tylosaurus proriger* was adapted for faster, more tail-driven swimming, like the swimming mode of *Plotosaurus* (its CW/CH and CL/CW ratios show similar trends to those described by Lindgren et al., 2007). This would be an advantageous adaptation for predator evasion or prey capture in young mosasaurs, but as individuals grow older and larger, the need for predator evasion grows less important and the body would grow into the patterns seen in the larger specimens like GSM-1 and PV1993.0001.0001. Due to the incompleteness of this skeleton and lack of other juvenile specimens in the study, this hypothesis will require further research.

CONCLUSIONS AND SUMMARY

Tylosaurus proriger has cervical centra that are anteroposteriorly long, wide, and dorsoventrally short, equipped for slight lateral movement but generally restricted, though not to the extent of more derived mosasaurs. The anterior dorsals resemble the cervicals in

all respects with the exception that they are larger and have taller neural spines for muscle and connective tissue attachment. Posterior dorsals are dorsoventrally taller and wider than their anterior counterparts, allowing for a slight increase in mobility. From the pygals through the intermediate caudals and ending with the terminal caudals, centra grow anteroposteriorly shorter, relatively dorsoventrally taller, and relatively narrow, indicating an increase in mobility in the posterior most regions of the body, a trend further supported by the low number of pygals and high number of intermediate caudals. Intermediate caudals and terminal caudals show neural spines shifting from recumbent, procumbent, and then back to recumbent alongside sections where centra increase in width. These patterns are consistent with the hypothesis that *Tylosaurus* was a carangiform swimmer that used its tail and corresponding hypocercal fluke as its primary locomotive source and propulsive surface respectively.

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APPENDIX

TABLE 1.

Specimen	Origin	Organism	Age	Notes
GSM-1	Pierre Shale, Southern Black Hills, South Dakota	<i>Tylosauru s proriger</i>	Campanian	Pygals badly deformed, vertebrae in sequence
PV1993.0001.0001	Tombigbee River, Green County, Alabama	<i>Tylosauru s proriger</i>		Vertebrae in sequence
Unnumbered		<i>Tylosauru s proriger</i>		Numbered vertebrae – inconsistencies in numbering make sequencing uncertain
RMM5610	Mooreville Chalk, Hale County, Alabama	<i>Tylosauru s proriger (juvenile)</i>	Campanian	Pyrite oxidation on many vertebrae; vertebrae not in sequence
RMM2475	Tombigbee Sand Member, Eutaw Formation, Montgomery County, Alabama	<i>Tylosauru s sp.</i>	Santonian	Highly weathered; vertebrae not in sequence
RMM3371	Lower Mooreville Chalk, Greene County, Alabama	<i>Tylosauru s sp.</i>	Campanian	Vertebrae not in sequence
RMM3253	Lower Mooreville Chalk, Greene County, Alabama	<i>Tylosauru s proriger</i>	Campanian	Many vertebrae deformed; vertebrae not in sequence
RMM1913	Lower Mooreville Chalk, Hale County, Alabama	<i>Tylosauru s proriger</i>	Campanian	Laterally deformed; vertebrae not in sequence

TABLE 1. Specimens examined in this study. Where there are no locations or ages listed, said information is unknown.



FIGURE 1. Mid Cretaceous (105 Ma) map of North America. Note the Western Interior Seaway and Gulf Coast. (Modified from Blakey, 2014).



FIGURE 2. Late Cretaceous (85 Ma) map of North America. Note the Western Interior Seaway and Gulf Coast. (modified from Blakey, 2014)

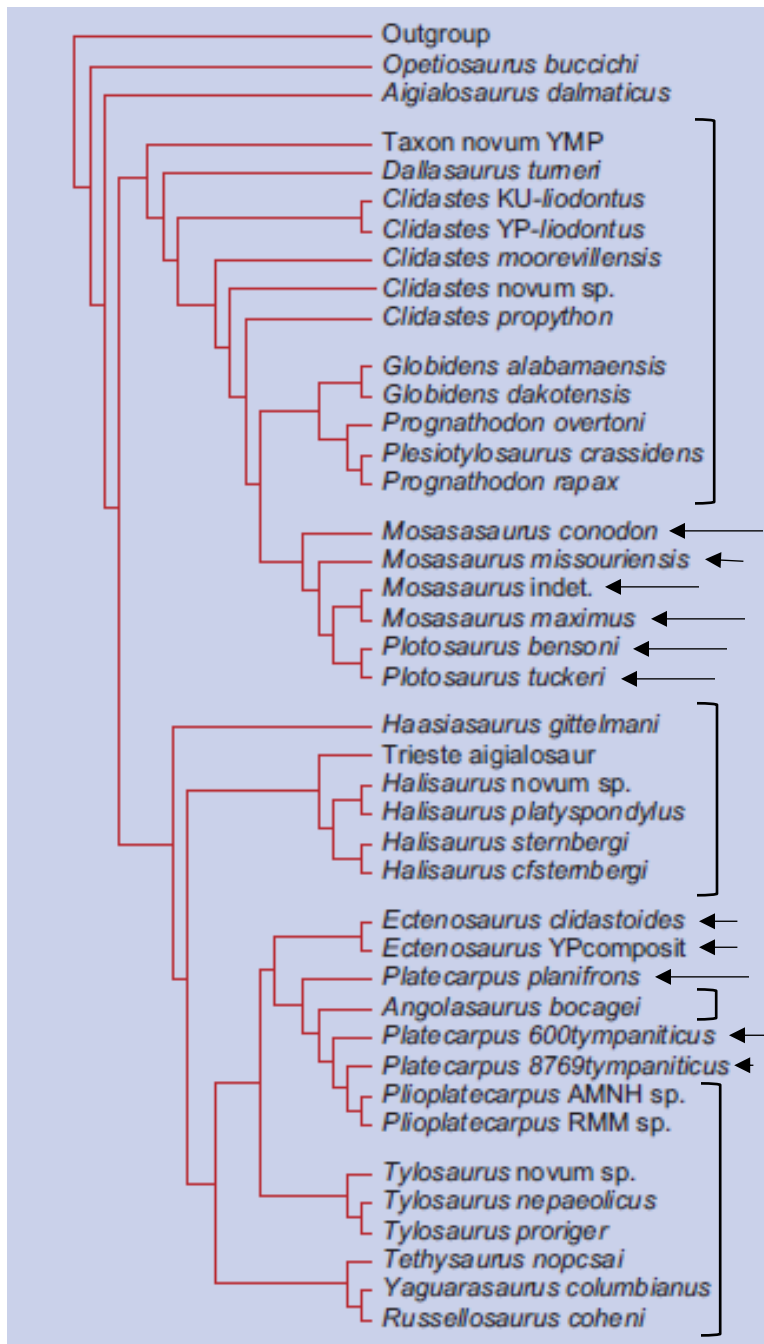


FIGURE 3. Mosasauoidea phylogenetic relationships, one of three equally parsimonious trees described by Polcyn and Bell (2005) (Fig. 8). Arrows point to a few of the species presumed to have some degree carangiform locomotion (see Lindgren et al., 2010; Lindgren et al., 2011; LeBlanc et al., 2013, D'Emic et al., 2015). Brackets indicate species

likely to have sub-carangiform to carangiform locomotion based on the most parsimonious origin of this locomotive style (modified from Fig. 8, Polcyn and Bell, 2005).

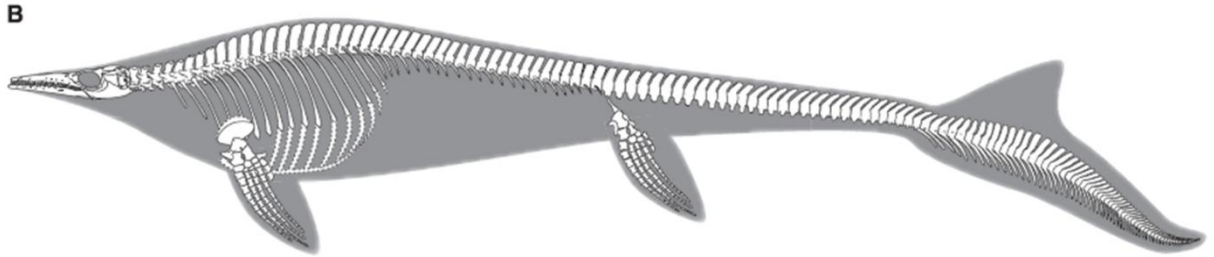


FIGURE 4. *Plotosaurus bennisoni* inferred body shape and skeleton. Note the hypocercal caudal tail fluke, a trait presumably shared to some extent with many other mosasaur species. (Fig. 3B, Lindgren et al., 2007).

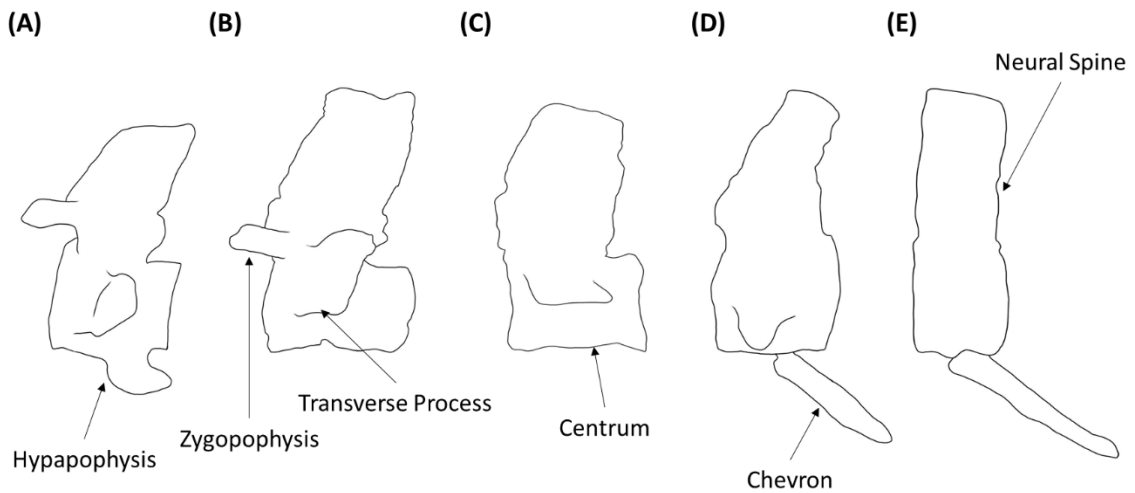


FIGURE 5. *Tylosaurus* vertebrae, not to scale. □A. Cervical vertebra with characteristic hypapophysis and transverse process. □B. Dorsal vertebra with characteristic transverse process with facet for rib articulation. □C. Pygal vertebra with characteristic blade-like transverse process. □D. Intermediate caudal with characteristic transverse process and chevron. □E. Terminal caudal vertebra with characteristic chevron.

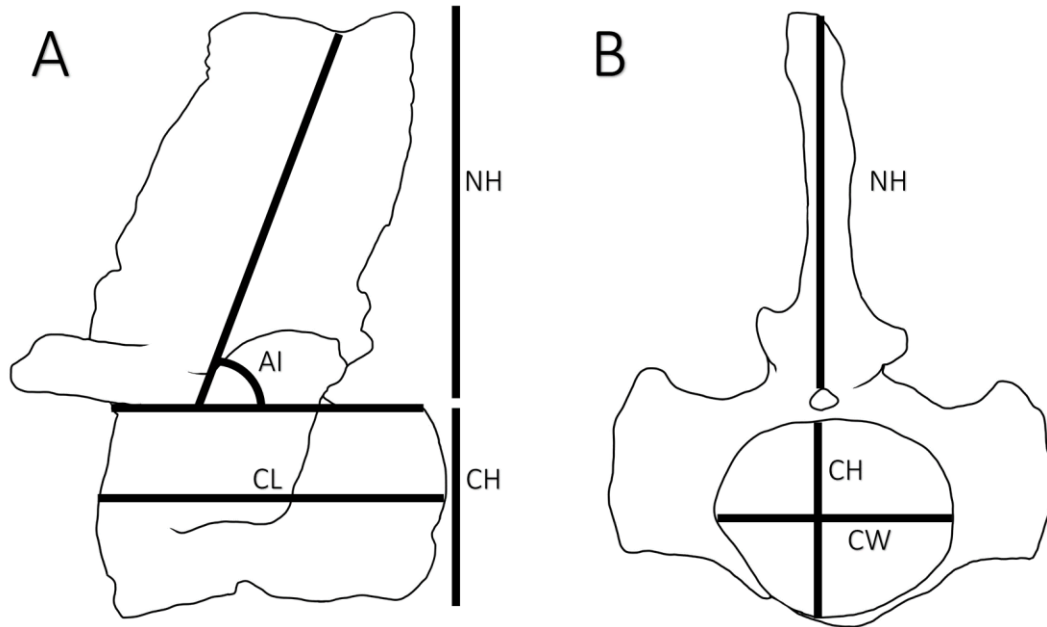
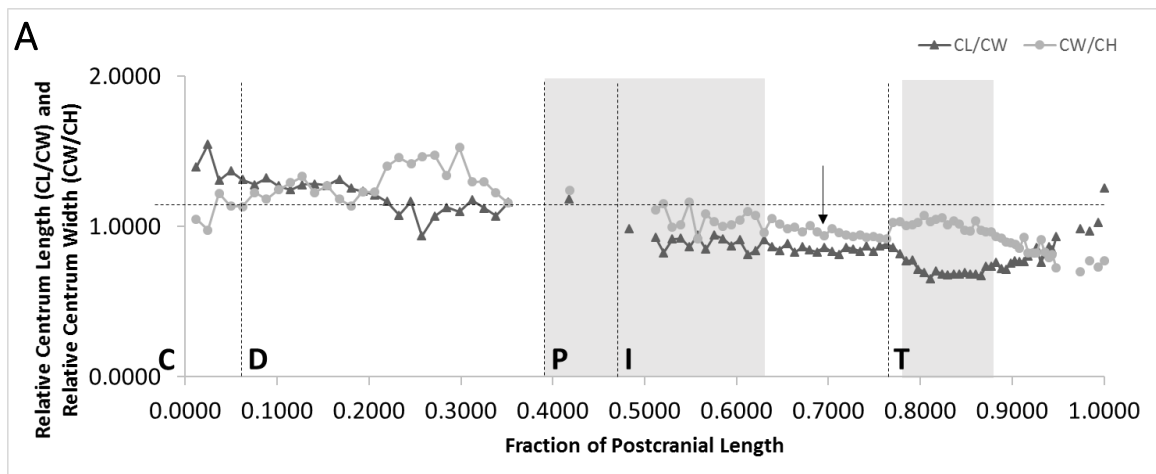


FIGURE 6. Tylosaurine dorsal vertebrae, A. lateral and B. posterior views with measurements in black. Abbreviations: AI, neural spine posterior angle of inclination, NH, neural spine height, CL, centrum length, CH, centrum height, CW, centrum width.



B

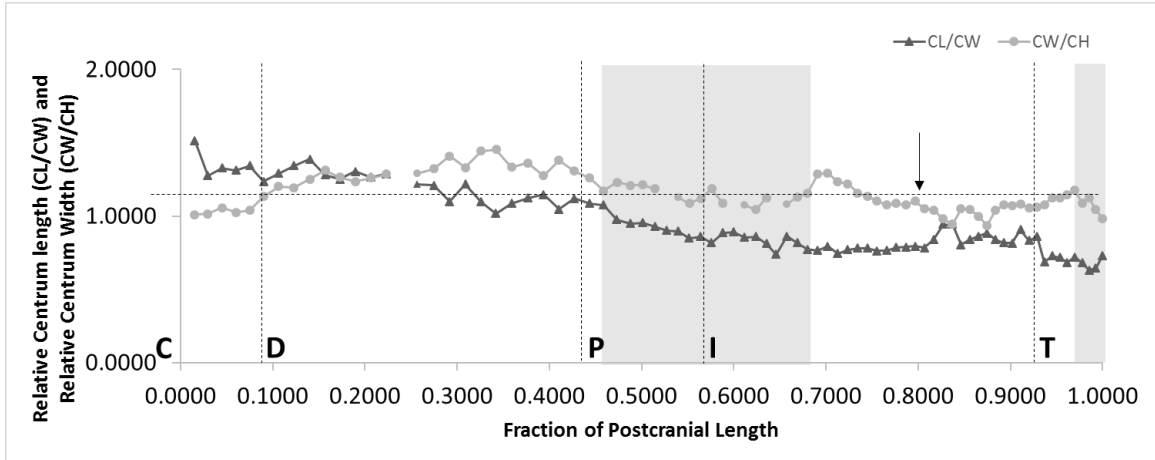


FIGURE 7. □A. Relative centrum dimensions and changes in centrum length based on GSM-1. □B. Relative centrum dimensions and changes in centrum length for PV1993.0001.0001. Note that PV1993.0001.0001 does not have as many terminal caudal vertebrae persevered and only shows parts of the expected trends. The arrows point to the interpreted beginning of the downward bend of the tail. The gray boxes over the pygals and intermediate caudals represent the base of the tail and subsequent displacement unit. The gray boxes over the terminal caudals represent the base supporting the majority of the tail fluke. Missing data points are those from deformed vertebrae whose measurements resulted in significant outliers and/or were not taken. Abbreviations: C, cervicals, D, dorsals, P, pygals, I, intermediate caudals, T, terminal caudals, CL, centrum length, CW, centrum width, CH, centrum height.

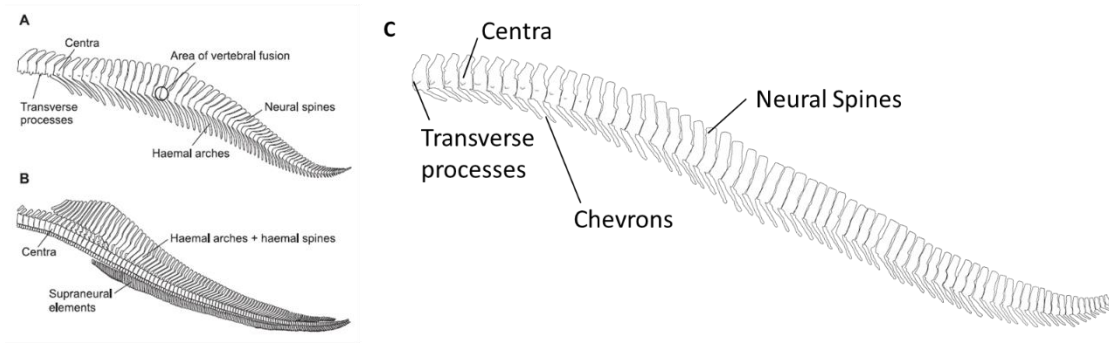


FIGURE 8. Distal portion of the tails of *Plotosaurus* (A), *Sphyrna lewini*, a living scalloped hammerhead (B), and GSM-1 (C). Note that in both the *Plotosaurus* and GSM-1 neural spines and the hammerhead haemal arches and spines shift recumbent, procumbent, and then to recumbent. a trend also seen in PV1993.0001.0001. Note that the neural spines of GSM-1 do not form as pronounced a fan shape as the other two specimens. (see main text for interpretation) (Modified from Fig. 5, Lindgren et al., 2007).

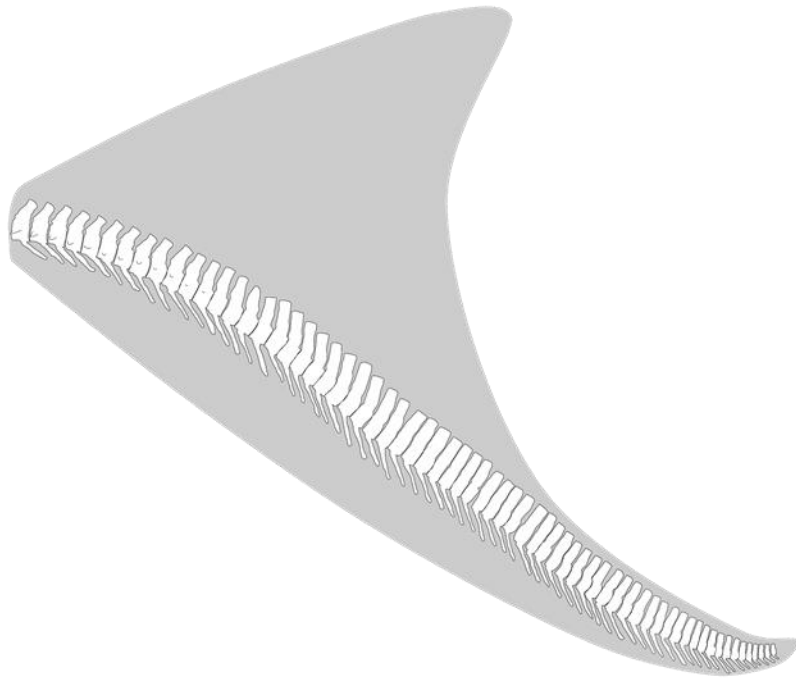


FIGURE 9. Caudal vertebrae reconstruction of GSM-1 (I24-END) with inferred fluke shape based on available vertebrae and mounted casts. Note the neural spine shift from recumbent, procumbent, to recumbent and changes in neural spine height at the base of the fluke.

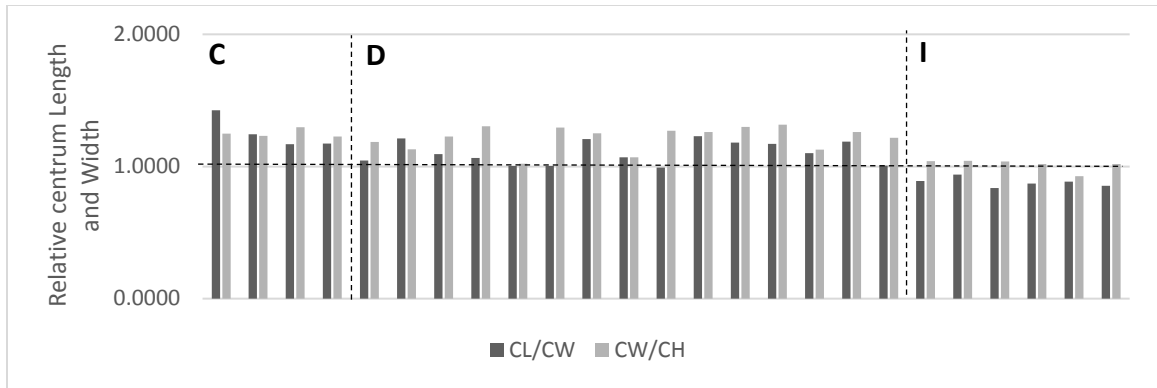
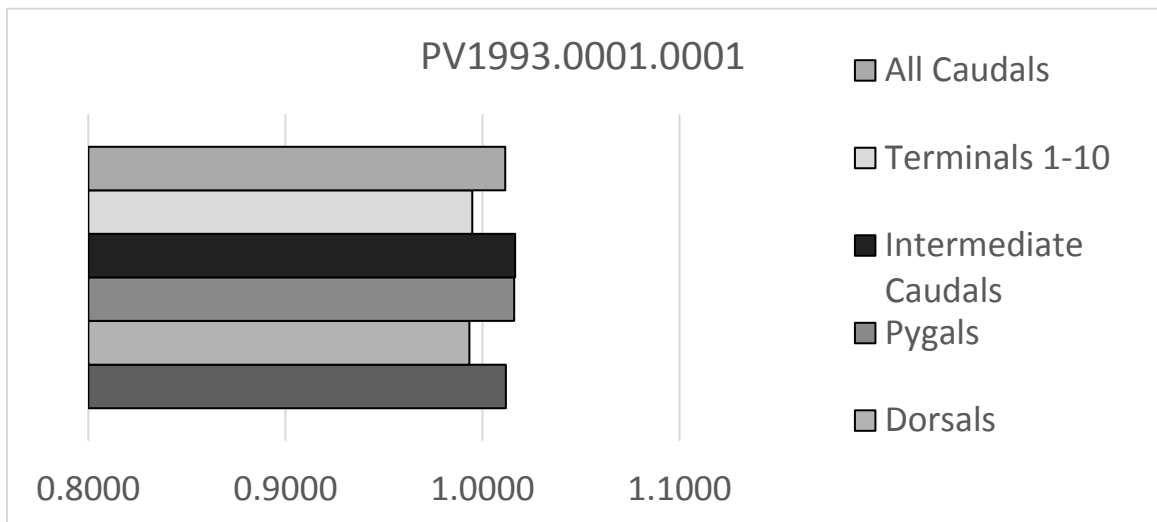
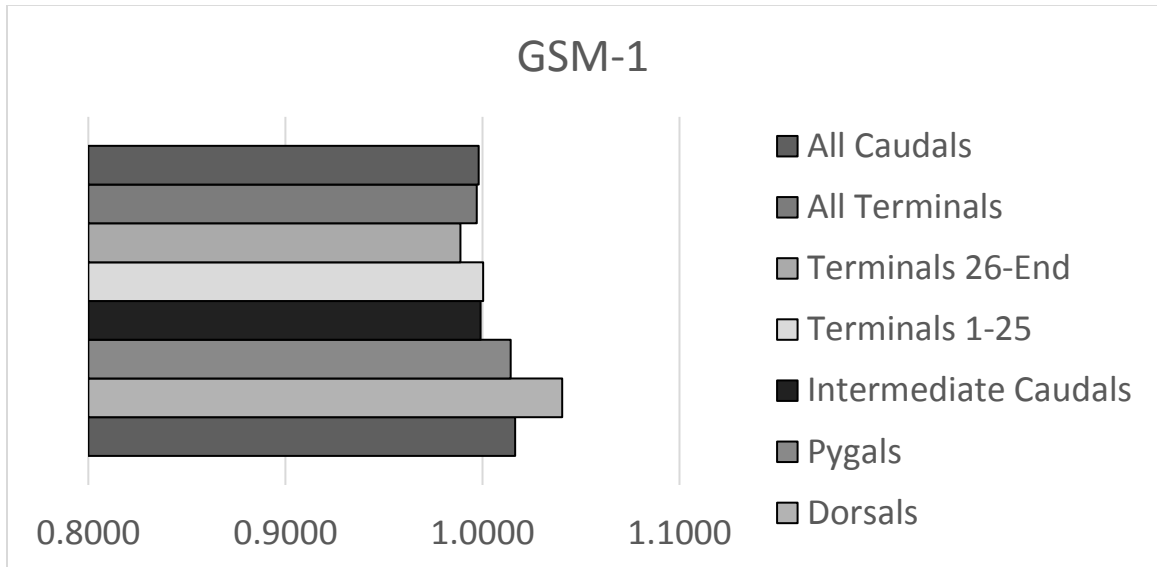
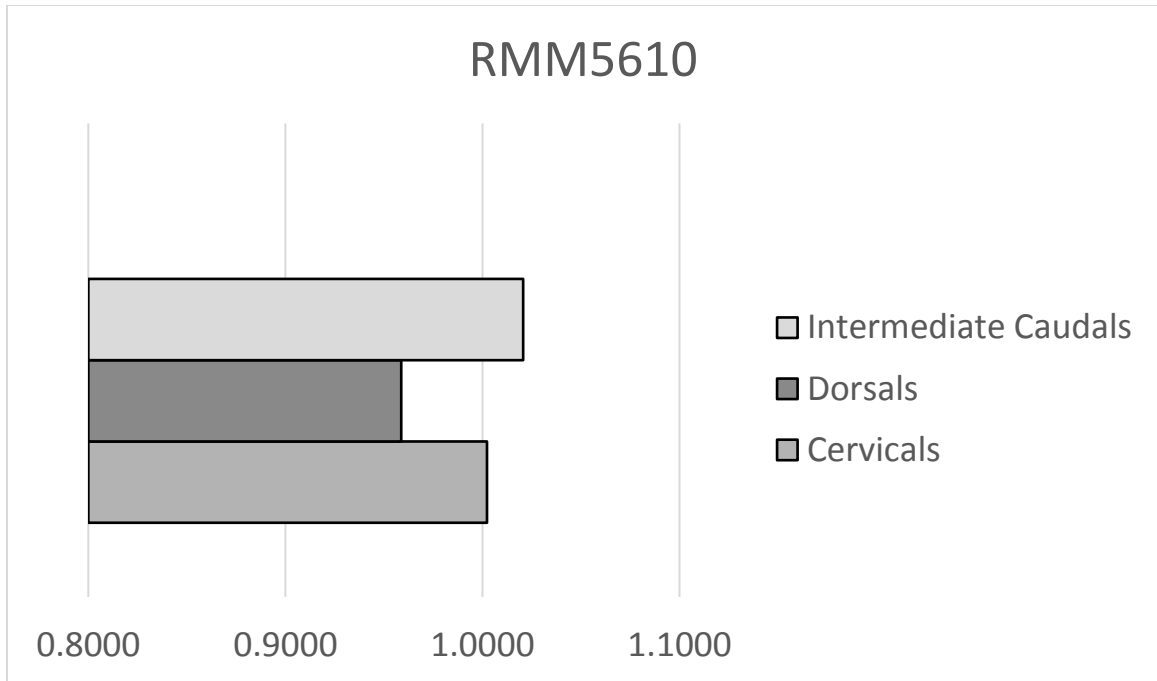


FIGURE 10. Relative centrum dimensions and changes in centrum length based on RMM5610. Unlike, Figure 8, values for RMM5610 are displayed as a bar chart because the position of vertebrae in the vertebral column was not known.

APPENDIX





APPENDIX 1. CL(left)/CL(right) ratios showing left to right deformation of vertebrae for GSM-1, PV1993.0001.0001, and RMM5610. These charts show the sections of the vertebral column of these three specimens and generally how deformed they were from their left to right sides. This is an average of a similar measurement taken for each vertebra of every examined specimen and was used to identify individual vertebrae or groups of vertebrae that were too deformed to use in the study. Similarly, outliers in centrum height and width were identified by strong separation from the trends of adjacent vertebrae in Figures 8 and 10. These were reexamined and remeasured to verify the deformation and rule out measurement error.