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A new Assemblage of Mosasaurs from the Upper Cretaceous Savoy Pit,

Austin Chalk, Northeast Texas

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by

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Abstract

A new Assemblage of Mosasaurs from the Upper Cretaceous Savoy Pit, Austin Chalk, Northeast Texas

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The fossil assemblage at the Savoy Pit (Fannin County, Texas) was collected in 1940 by participants in the Works Progress Administration working alongside personnel from the Bureau of Economic Geology at The University of Texas at Austin. The locality is contained within the Ector Chalk (lower Coniacian), an argillaceous limestone, of the Austin Group. Previously published taxa from the site include the bird *Ichthyornis* and fish such as *Belonostomus* and *Laminospondylus transversus*; several types of shark teeth and invertebrates (e.g., crustaceans, asteroids, and bivalves) also have been found. Several mosasaur specimens are present at the site and include isolated elements and associated skeletons that have yet to be described.

My collaborator Joshua Lively and I scored the material from the Savoy Pit using published and novel morphological characters and compared our results to about 250 mosasaur specimens from North America and Sweden. We then ran a phylogenetic

analysis using maximum parsimony to hypothesize the taxonomic composition of the mosasaur assemblage. At least three taxa are identified: a russellosaurine represented by a frontal resembling *Russellosaurus coheni*, an undetermined basal mosasaurine represented by a partial skull and vertebrae, and *Tylosaurus nepaeolicus* based on a premaxilla and quadrate. The mosasaurine possesses a unique combination of characters including synapomorphies of both Mosasaurinae (e.g., striated quadrate tympanic rim, dorsally constricted suprastapedial process) and Russellosaurina (e.g., short premaxilla-maxilla suture, low surangular coronoid buttress). In our phylogenetic analysis, we recovered this specimen as a basal mosasaurine that does not align with any published genus, and we recognize it as a new taxon. The russellosaurine synapomorphies possessed by the new taxon may represent the plesiomorphic state of Mosasaurinae; some of those characters are shared with *Kourisodon puntledgensis*.

The presence of a russellosaurine resembling *Russellosaurus coheni* may extend the range of this species into the Coniacian. The new taxon helps to fill a stratigraphic gap of approximately six million years between the earliest known mosasaurine, *Dallasaurus turneri*, and '*Clidastes liodontus*.' Identification of *Tylosaurus nepaeolicus* at the Savoy Pit extends the lineage into the Early Coniacian and represents one of the earliest occurrences of that genus.

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INTRODUCTION

During the Late Cretaceous, a shallow epicontinental sea known as the Western Interior Seaway (WIS) covered much of North America as a north-south trough just east of the Rocky Mountains, at times connecting the regions analogous to the Arctic Ocean and the Labrador Sea/Hudson Bay (occasionally) with the Gulf of Mexico (e.g., Kauffmann, 1984). Throughout its history, the WIS was marked by numerous marine transgressions and regressions before the seaway disappeared by the end of the Cretaceous (Hancock and Kauffman, 1984; Young, 1986). During the Early Coniacian, a marine transgression that began in the Late Turonian flooded North America with the second-highest sea levels of the Late Cretaceous, falling short of the Early Turonian transgressive event (Kauffman, 1984). The WIS during the Early Coniacian was home to a variety of sea animals including the bird *Ichthyornis*, a number of fish such as *Cretoxyrhina mantelli* and *Xiphactinus*, ammonites, inoceramids, and a variety of marine reptiles. Among the latter category were the mosasaurs, a group of primarily marine squamates (*Pannoniasaurus inexpectatus*, described in Makádi et al., 2012, is an exception) that are traditionally aligned with the varanoid lizards (e.g., deBraga and Carroll, 1993; Conrad, 2008), but other authors (e.g., Lee, 1997; Reeder et al., 2015) suggested these reptiles may have higher phylogenetic affinities with snakes.

During the Great Depression, the Works Progress Administration (WPA) was launched as part of Franklin D. Roosevelt's New Deal Program. The WPA was created to provide jobs for the unemployed through federally-funded projects, some of which

centered on paleontological and mineralogical specimen collection. In Texas, the WPA was active from 1939 through to 1941 with 26 projects across the state including one at my study site, the Savoy Pit in Fannin County (worked March to September 1940; Evans, 1941). Lloyd J. Ryman served as the Project Superintendent in Fannin County and worked in conjunction with the Bureau of Economic Geology at The University of Texas at Austin (UT Austin). At least some of the collected specimens were taken to an exhibit in Dallas and eventually made their way into the collections housed at the Vertebrate Paleontology Laboratory (VPL) at UT Austin. A large portion of the fossils collected at the site remain unprepared and only a handful were ever published, namely the fish *Laminospondylus transversus* (new taxon named by Springer, 1957), *Belonostomus* (Bardack, 1968), *Apsopelix anglicus* (Teller-Marshall and Bardack, 1978), and *Saurodon leanus* (mentioned by Bardack and Sprinkle, 1969) and a specimen of the bird *Ichthyornis* dispar (Parris and Echols, 1992). Apart from the preparation of some individual elements and a tentative identification, the mosasaurs (isolated elements and associated skeletons) were largely ignored since their collection in 1940. In this thesis, I describe several of the specimens of mosasaur from the site but exclude some prepared isolated teeth, a russellosaurine vertebra, a mosasaurine dentary, an eroded mosasaur vertebral centrum (collected in January 2018), and an incompletely prepared partial skull of *Tylosaurus* sp.

GEOLOGIC CONTEXT AND LOCALITY INFORMATION

The Savoy Pit study site is located in Fannin County in northeast Texas, about seventy-two miles north/northeast of Dallas using US-75 N and TX-160 N (Figure 1). This locality (TMM 31051) derives its namesake from its position south of the city of Savoy. The Austin Group is not as well studied in Fannin County as it is in the type area near Austin. In Fannin County, it is mostly known from exploratory petroleum wells drilled in the 1960s (e.g., Lokke & Brent, 1966). The pit itself exists within the Ector Chalk, first described by Stephenson (1919) as the Ector Tongue (near the city of Ector) within the Austin Chalk. Its stratigraphic rank was debated with some authors designating the unit as a formation (e.g., McNulty Jr., 1954; Lokke & Brent, 1966; Bardack, 1968) while others described the Ector Chalk as a member or unit within the Atco Formation of the Austin Group (e.g., Young, 1963; AlShuaibi, 2006, 2011). The Ector Chalk was interpreted to be in the lower Coniacian (~89-90 Ma according to Ogg et al., 2012) by Young (1963) due to a tentative correlation with the lower portion of his unit "A" that showed the presence of the ammonite *Peroniceras haasi*. This designation for unit "A" was later questioned by Klinger and Kennedy (1984) who identified the European equivalent of the lower Coniacian as the *Barroisiceras petrocoriense* zone, a view subsequently followed by Young (1985, 1986). Those publications do not address the age of the Ector Chalk and authors of some subsequent publications and dissertations maintained the view of a lower Coniacian unit (Parris and Echols, 1992; AlShuaibi, 2006). In a paper following his dissertation, AlShuaibi (2011) confirmed the age as lower

Coniacian through foraminiferal analyses that verified the presence of *Pessagnoites ectorensis*.

The Ector Chalk was likely deposited at a subtidal water depth, potentially within the fairweather wave-base, owing to the presence of abundant mottling from bioturbation and frequent disarticulation of specimens from the Savoy Pit. Notes on the Savoy Pit excavation from the State-Wide Paleontologic-Mineralogic Survey for Texas (Evans, 1941) described the locality stratigraphy as follows

> Blue Eagle Ford shale forms the floor of the Savoy Pit. For ten feet above the shale, the walls consist of blue-gray argillaceous limestone cut by numerous vertical joints. Above this are two to three feet of thin- bedded limestone overlain by up to three feet of black clayey soil. Nodules of pyrite are widely scattered throughout the matrix. (Evans, 1941, pp. 52-53)

The clayey soil formed as the result of weathering (Evans, 1941). My examination of samples collected in 1940 and during a visit to the locality in January 2018 confirmed the presence of the two subunits (Figure 2) though the 'upper' subunit is created through weathering and bioturbation. The lowermost consists of a clay-rich or argillaceous bivalve packstone with a medium light gray coloration (Munsell color N6; Figure 2a and b). Bivalve shell fragments (usually ≤ 1 mm) are abundant and are either cemented together by calcite or enclosed by mud. A gradational contact separates the two subunits and represents the extent of weathering and bioturbation effects on the normally gray

chalk (Figure 2a; Evans, 1941). The 'upper' subunit (Figures 2a, 2c-e, and 5) is very pale orange (10YR 8/2) and often weakly lithified, massive, and displays pale yellowish orange (Munsell color 10YR 8/6; coloration from oxidation) mottling similar to in structure to *Thalassinoides* burrows. The 'upper' chalk fractures into thin flakes or irregular blocks and contains lenses of the original medium light gray limestone (Figure 2c-e).

The Savoy Pit has been filled with sandstone from a smaller nearby pit (see next paragraph) and transformed into a cattle pond (larger pond in Figure 3a). Most of the rock around the pit has been broken up by landscaping activities, but some patches of in-situ limestone (Figure 3b) are present in what is otherwise a minor surficial exposure (Figure 3c). A proper stratigraphic section in the pit, non-existent from the original excavation, is rendered nearly impossible by these changes.

A smaller pit (upper left of Figure 3a) found slightly over 100 m northwest of and stratigraphically underlying the Ector Chalk of the Savoy Pit contains quartz-rich sandstone. The unit is light olive gray (Munsell color 5Y 5/2) to moderate yellowish brown (Munsell color 10YR 5/4) when fresh and weathers to dark yellowish brown (Munsell color 10YR 4/2) to dusky yellowish brown (Munsell color 10YR 2/2). Oysters (e.g., *Gryphaea*) and bivalve shell fragments are abundant and certain portions are full of anastomosing *Planolites* burrows (Figure 4c). Two partial ammonites were found during the 2018 site visit and may belong to the genus *Prionocyclus* (Figure 4a and b). This sandy unit is likely the Bells Sandstone or possibly the overlying Maribel Shale that

becomes sandier as the unit loses its identity and transitions into the Bells Sandstone underneath the Ector Chalk (McNulty Jr., 1966).

The locality preserves an abundance of fish fossils in the Ector Chalk (some articulated) such as *Saurodon leanus*, *Belonostomus*, *Laminospondylus transversus*, *Xiphactinus*, *Apsopelix anglicus*, and shark teeth including those of *Ptychodus mortoni* (Evans, 1941; Springer, 1957; Bardack, 1968; Bardack and Sprinkle; 1969; Teller-Marshall and Bardack, 1978). The invertebrate assemblage includes the lobster *Enoploclytia* (incorrectly identified as a crab by Evans, 1941), starfish, inoceramids, and oysters (Evans, 1941). Other vertebrates include *Ichthyornis dispar* and bones from plesiosaurs and mosasaurs (Evans, 1941; Parris and Echols, 1992). The mosasaur specimen TMM 31051-84 was preserved in the 'uppermost' subunit of the Savoy Pit; other specimens came from the 'lower' subunit.

MATERIALS AND METHODS

Mechanical preparation was performed on the mosasaur specimen TMM 31051-84, preserved in a block of chalky limestone (Figure 5), using an air scribe, pin vise, toothbrush and water, and air abrasion. Specimens TMM 31051-59, TMM 31051-64, and several bones from TMM 31051-84 were already prepared before this project began. Measurements of the specimens (in millimeters) were completed via calipers. Photographs of the individual fossil elements were taken with Nikon and Canon cameras using focus image-stacking on a black canvas background and constructed in Adobe

Bridge CC, Adobe Photoshop CS6 and Helicon Remote. A bone map (Figure 6), a chronostratigraphic diagram (Figure 27), and figure labels were constructed using Adobe Illustrator CS6 and a graphic drawing tablet.

Institutional Abbreviations: AMNH – American Museum of Natural History, New York; CDM – Courtenay and District Museum and Palaeontology Centre, British Columbia, Canada; FMNH – Field Museum of Natural History, Chicago, Illinois; MSC – McWane Science Center, Birmingham, Alabama; SMU – Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; TMM – Texas Memorial Museum, The University of Texas at Austin, Austin, Texas.

SYSTEMATIC PALEONTOLOGY AND DESCRIPTIONS

SQUAMATA Oppel, 1811

MOSASAUROIDEA Camp, 1923

MOSASAURIDAE Gervais, 1853

MOSASAURINAE Williston, 1897

New taxon

Holotype – TMM 31051-84 (Figures 5-22), disarticulated partial skull including maxillae, left prefrontal, partial jugals, squamosals, squamosal rami of the postorbitofrontals, partial right pterygoid, partial right palatine, right and partial left quadrate, left and partial right surangular, partial left coronoid, partial left angular, atlas (lacking intercentrum),

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cervical vertebrae, trunk vertebrae, and ribs. TMM 31051-85 (the label on some bones) belongs to the same individual and has been synonymized with TMM 31051-84.

Type locality, horizon, and age – TMM locality 31051, Savoy Pit, Fannin County, Texas; Ector Chalk, at least ten feet above the contact with the Eagle Ford Group; Early Coniacian

Diagnosis

Autapomorphies are followed by *, synapomorphies of Mosasaurinae by $^\theta$, and synapomorphies of Russellosaurina by $^\blacklozenge$.

Maxilla: Short premaxilla-maxilla suture$^\blacklozenge$ ending above the third tooth, premaxilla-maxilla suture rises dorsally before running posterodorsally, smooth tooth surface without medial striations$^\theta$ and surface structures, 15 tooth positions, pleurodont dentition, excavation for external naris, ventrally descending groove anterior to suture with palatine

Prefrontal: Concavity on anterior projection, incipient supraorbital process*, prefrontal contributes to margin of external naris

Squamosal: Facet on dorsomedial surface of posterior squamosal body for articulation with the squamosal ramus of the parietal, minor posterodorsal process, suture with supratemporal extends anterodorsally onto postorbitofrontal ramus, short facet for contacting the cephalic condyle of the quadrate

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Pterygoid: Tooth row does not extend ventrally below the main body◆

Quadrate: Striated margin of the quadrate tympanic ala$^\theta$, dorsally constricted suprastapedial process of the quadrate$^\theta$, weak ridge on cephalic condyle, anterior deflection of mandibular condyle, concave ventral margin

Coronoid: Short dorsal extension of posterodorsal process◆, slight ventral extent of lateral wing to parallel anterior horizontal portion

Surangular: Low coronoid buttress◆, ventral border shift from low rise below articular fossa to rapid posterodorsal curve

Vertebrae: Short atlantal synapophyses◆, cervical synapophyses do not extend below ventral border of centrum, anterior trunk vertebral condyles without dorsoventral constriction$^\theta$

DESCRIPTION

SKULL

Maxilla

A nearly complete right and partial left maxilla are preserved from the new taxon (Figure 9). The left maxilla is missing the portion anterior to the seventh tooth position, and the alveoli in the sixth and fifteenth positions are only partially preserved. Most of the preserved teeth on the right maxilla are incomplete whereas the left maxilla has three

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nearly complete teeth out of five. Both maxillae are crushed along their posterodorsal lamina. The posterior margins of the laminae are missing.

Overall, the maxilla is narrow and elongate. Numerous foramina are present the along anterolateral half of the maxilla with those lying above the tooth row likely serving as exit points for the *superior alveolar nerve*, a subdivision of the trigeminal (maxillary) nerve (Bahl, 1937; Oelrich, 1956; Russell, 1967).

The suture with the premaxilla rises dorsally on the anteriormost portion of the maxilla before running posterodorsally to terminate above the third tooth. A short premaxilla-maxilla suture (i.e. above or anterior to the fourth maxillary tooth) is normally observed in russellosaurines but also appears in the mosasaurine *Kourisodon puntledgensis* (ending upon reaching the fourth tooth position in the maxilla; Nicholls and Meckert, 2002). In contrast, mosasaurines tend to possess longer sutures ending above or posterior to the fourth tooth position while halisaurines possess longer sutures terminating above or posterior to the sixth maxillary tooth position. The dorsal surface in the maxilla of the new taxon plateaus before dipping slightly in the nasal embayment with the deepest segment above the fifth tooth position. There is a gentle rise to the top of the thin posterodorsal lamina that covers the anterior fourth of the prefrontal and most of its ventrolateral surface (Figure 10c). This suture does not exclude the prefrontal from the margin of the external naris where a length of approximately 1 cm of the prefrontal is exposed. The prefrontal prevents the lamina from contacting the frontal (the latter is not preserved). Deep grooves along the posterior end of the lateral surface just above the tooth row indicate the site of jugal attachment.

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The maxilla possesses fifteen tooth positions. The tooth crowns taper throughout their length, lacking the basal inflation observed in some species of *Prognathodon* and *Globidens* (the latter taxon was described as possessing "bulbous" teeth by Gilmore, 1912; Schulp et al., 2008; Konishi et al, 2011). Mediolateral flattening, fluting, and faceting do not appear in the conical teeth from either maxilla. No carinae are present. All teeth are equivalent in size except for the smaller final three teeth. The enamel surfaces are smooth and lack striations but show fine cracks from taphonomy. The maxilla lacks the prominent medial parapet that descends from the main ramus in mosasaurines with the exclusion of *Kourisodon puntledgensis* that shares a pleurodont dentition with the new taxon. An edentulous process extends posteriorly underneath the orbit and tapers, possibly to a point. Although the exact number of suborbital teeth is unknown, there are likely at least two based on the position of the process on the left maxilla relative to the prefrontal orbital margin.

The suture with the palatine terminates on the maxillary ramus anteriorly above the eleventh tooth position and posteriorly at the fourteenth tooth position as indicated by deep grooves and a dorsoventrally constricted maxillary ramus. Just anterior to the palatine suture is a ventrally-descending groove that probably formed a foramen with the palatine. The feature may have provided passage for the trigeminal nerve through the maxilla and palatine to the foramina lining the lateral surface above the tooth base. (Bahl, 1937; Russell, 1967). This maxilla-palatine foramen (as ascribed by Bahl, 1937) does not appear in *Tylosaurus*, *Clidastes*, and *Platecarpus* (Russell, 1967).

Prefrontal

The left prefrontal of TMM 31051-84 (Figure 10) appears complete but the posteroventral portion of the prefrontal is smashed dorsally, distorting the orientation of the smooth triangular edge contributing to the orbital margin and the articulation surface for the palatine.

A rounded flange extends anteriorly and contacts the posterodorsal lamina of the maxilla dorsolaterally. This projection is concave on its ventral surface. As in other early-diverging mosasaurines such as *Clidastes propython*, the prefrontal contributes to the posterolateral margin of the external naris (Russell, 1967, pers. obs. from photographs). In *Kourisodon puntledgensis*, it is unknown if the prefrontal would have formed part of the external naris (Nicholls and Meckert, 2002). A slight depression on the posteromedial edge of the dorsal surface would have contacted the frontal ventrally. The suture hints at a frontal lateral margin that curves slightly anteromedially before continuing a linear path. Only a small, incipient supraorbital process is present on the posterolateral margin of the element, contrasting with the large triangular protrusion typical of mosasaurines including *Mosasaurus hoffmannii* (Street and Caldwell, 2016). That process possesses a rough surface. The presence and state of the supraorbital process is variable within the Russellosaurina and Halisaurinae and include no lateral projection as seen in *Russellosaurus coheni* and *Eonatator sternbergii*, incipient processes in *Phosphorosaurus ponpetelegans* and species of *Latoplatecarpus*, and minor supraorbital wings in *Platecarpus tympaniticus* and the halisaurine *Phosphorosaurus ortliebi* (Dollo,

1889; Bardet & Suberbiola, 2001; Polcyn & Bell, 2005; Konishi & Caldwell, 2009, 2011; Konishi et al., 2012; Polcyn et al., 2012; Konishi et al., 2016).

Jugal

The partial left jugal of TMM 31051-84 (Figure 11) consists of the nearly right-angled intersection between the infraorbital and postorbitofrontal rami. Most of both rami are missing and the postorbitofrontal ramus is crushed dorsally. A fragment of the right jugal is present but consists merely of a partial bulge on the posterior surface, muscle striations, and a groove that rotates from the lateral surface to the posterior edge, moving dorsally. The lateral surface is largely intact. but the medial face is eroded. A separate, partially crushed piece of bone may represent part of the anterior ramus of the right jugal but that segment is not described here. Otherwise, no additional portions are preserved.

The shallow trough-like contact for the ectopterygoid on the medial surface of the infraorbital ramus starts near the middle of the curved dorsal margin and descends anteroventrally for a centimeter before continuing anteriorly. Unlike the ventromedially directed ectopterygoid contact in *Clidastes* (pers. obs.), the groove is oriented somewhat dorsomedially in the new taxon due to less medial extension and ventral rotation of the dorsal surface. *Kourisodon puntledgensis* and *Platecarpus tympaniticus* possess an orientation for the ectopterygoid groove similar to that in the new taxon though they appear slightly more medially oriented.

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A short triangular process is present posteroventrally, extending posteriorly with a rounded tip. This process is not present in *Clidastes* and forms a small protrusion in *Kourisodon puntledgensis* (Russell, 1967; Nicholls and Meckert, 2002). The protrusion is positioned nearly level with the ventral surface of the infraorbital ramus unlike *Platecarpus tympaniticus* which has a process with a more dorsal position on the posterior edge of the jugal. The latter taxon also possesses a more pointed protrusion than that of TMM 31051-84. The posterior surface of the jugal from the new taxon bulges slightly above that projection before narrowing at the base of the postorbitofrontal ramus. A narrow groove begins on the lateral face at the dorsal end of the bulge and twists around to the posterior margin as it continues dorsally. Muscle striations are present ventral to the groove and extend partway onto the medial surface of the jugal.

Squamosal

The squamosals of the new taxon (Figure 12) are nearly complete. Both elements have postorbitofrontal rami that were mediolaterally smashed postmortem, preventing proper articulation with the left squamosal ramus of the postorbitofrontal. The anteriormost portion of each ramus is missing. There is slight crushing on the expanded posterior of the right squamosal. The left squamosal is missing both the posterior parietal process and a dorsomedial portion of the anterior ramus.

Most of the length of the squamosal consists of the postorbitofrontal ramus, a narrow process that projects anteriorly from its contact with the parietal and

supratemporal. That process possesses a U-shaped trough along the dorsal surface that sutures with the squamosal ramus of the postorbitofrontal. Near the posterior end of the element (the final one-sixth of the total length), the squamosal expands ventrally. On the ventromedial face, the squamosal would contact the supratemporal along a largely flat ovoid surface split anterodorsally by a medial shelf, indicating an interdigitating suture with the supratemporal. Several foramina are present along this surface. The suture with the supratemporal becomes linear underneath the shelf and extends anterodorsally for ~4 cm. A second shelf forms the ventral border of the anterodorsal extension of the supratemporal sutural surface and would have divided this surface from the facet contacting the quadrate. The supratemporal would have overlapped the dorsomedial surface of the squamosal via a facet-like suture in the form of an elongate ovoid (Figure 12d). This facet terminates in a point anteriorly when it contacts the anterodorsally ascending ventromedial suture for the supratemporal, at least one centimeter from the posterior end of the trough that accepts the squamosal ramus of the postorbitofrontal. Posteriorly, the facet has a wider termination. The facet appears in the same proportions on both squamosals indicating this feature was not created by taphonomic alteration. The russellosaurine *Russellosaurus coheni* possesses a similar condition except the anterior termination in that taxon does not form the pointed tip of an ovoid but rather extends medially away from the squamosal ramus. The overall shape of the facet is triangular in *Russellosaurus coheni* with the apex pointing posteriorly. An overlapping supratemporal dorsomedial articulation on the squamosal is currently only known to occur in the new taxon and *Russellosaurus coheni* and may have indicated the plesiomorphic state in

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mosasaurs. Evaluation of the characteristic outside of Mosasauridae has been difficult due to the lack of squamosal preservation in 'aigialosaurs' and close relatives.

On the posterior dorsomedial surface, a short (3 mm high), rounded parietal process protrusion is present approximately 1 cm posteriorly from the posterior termination of the facet and it cannot be determined if the supratemporal would have abutted this projection. The parietal would likely have not reached the dorsal surface of the squamosal. Other mosasaurs possess variable states of the posterodorsal projection (if preserved) ranging from the absence of a process (e.g., *Russellosaurus coheni*) to moderate or well-developed (e.g., *Latoplatecarpus* and *Globidens dakotaensis*) and may or may not contact the suspensorial ramus of parietal (Russell, 1975; Polcyn and Bell, 2005; Konishi and Caldwell, 2009, 2011). Posteroventrally, the squamosal contacts the suprastapedial process of the quadrate with a longitudinally concave facet (1.5 cm in length).

Postorbitofrontal

Only the squamosal rami of the postorbitofrontals are preserved in TMM 31051-84. Both are somewhat crushed, and the left squamosal ramus may be crushed more extensively than its counterpart. Each element is missing the anterior end. The posterior termination of the left squamosal ramus is missing, and the posterior extent of the right squamosal ramus is concealed by ribs from posterior trunk vertebrae. Even with the preserved portions, there remains a possibility that some of the features described here were affected by taphonomic alteration.

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The dorsal surface is largely a flat face that becomes mediolaterally thinner moving posteriorly as the rounded ridge forming its lateral edge transitions into a thin vertically-oriented ridge. The medial face underneath the ridge is inclined at ~55° from the horizontal up to the posterior 2 cm of the preserved element where it twists to become approximately horizontal. On the medial side, a short ridge projects nearly ventrally and runs along the length of the ramus near the ventromedial border, forming a trench-like sulcus.

Palatine

The partial right palatine of TMM 31051-84 (Figure 13) preserves most of the articulation surface with the prefrontal although the nature of contact is distorted by crushing. The posterodorsal connection with the pterygoid is obscured except for the ventral portion of the articulation, which is preserved as a triangular trough. Most of the anterior and part of the medial side of the element are missing. The condition of the maxillary suture is indiscernible on the palatine where the posterior portion is present. At the articulation surface with the maxilla, the medial parapet is slightly dorsoventrally constricted, hinting at a palatine that would have enveloped the parapet as seen in mosasaurines (Joshua Lively pers. comm., 2017).

Pterygoid

The partial right pterygoid (Figure 14) appears to be substantially crushed. This created a trough in the medial surface of the quadrate ramus and rotated the dorsal sulcus approximately 90° medially. The number of tooth positions in the pterygoid cannot be assessed in the new taxon due to a posteriorly and anteriorly incomplete tooth row. The dorsomedial side of the tooth row experienced heavy erosion within a fossa. This same erosion also formed a hole through part of the tooth row. The palatine and basisphenoid processes are unknown. Only the origin of the ectopterygoid process is present, and most of the length of the quadrate process is preserved.

Of the four tooth positions preserved on the ventral surface of the pterygoid, only the middle two alveoli bear the basal enamel of the teeth and resorption pits. Whereas nothing can be said about the surface features and overall shape of the teeth, they were not mediolaterally flattened, and were smaller than the maxillary teeth based on the size of the preserved tooth roots. It is possible that the teeth could have become similar in size to the maxillary teeth anteriorly. As typically observed in russellosaurines, the teeth attach to the main body of the element, contrasting with the prominent descending ramus to which the pterygoid dentition of mosasaurines attaches (Palci et al., 2013; Joshua Lively pers. comm., 2016).

Dorsally, a shallow sulcus is located along the posterolateral surface of the ectopterygoid process and continues (partially interrupted by crushing) along the preserved length of the long and narrow quadrate ramus for the probable attachment of the *m. pterygoideus profundus* (Russell, 1967).

Quadrate

A nearly complete right quadrate and partial left are preserved in *the new taxon*. The right quadrate (Figure 15a-f) is well-preserved but is partly eroded along and at the distal tip of the suprastapedial process and the lateral region between the ascending tympanic rim and articular condyle. Some crushing is evident on the lateral face, distorting the ascending tympanic rim and infrastapedial process (if it was present), and on the more medial portion of the anterior face. The left quadrate (Figure 15g and h) only preserves the origin of the suprastapedial process, the upper half of the tympanic ala, the posterior cephalic condyle, and the dorsal segment of the stapedial pit. Several of those areas are eroded.

The quadrate possesses a C-shaped outline in lateral view. A shallowly depressed tympanic ala projects laterally from the main shaft. It is rimmed by a striated margin, a character shared by all known mosasaurines (Joshua Lively pers. comm., 2015), that extends slightly anterolaterally at the base of the vertically-oriented segment of the rim. There may be a minor stair-step ventrolateral margin in anterior view, but erosion makes the presence of this feature unclear. Dorsally, the margin of the tympanic ala possesses a higher degree of curvature than the rest of the rim.

The suprastapedial process emerges from the uppermost part of the main shaft and descends ventrally until about midheight, ending in a thick flange distally. As in all mosasaurines, the suprastapedial process is constricted mediolaterally on its dorsal surface (Palci et al., 2013; pers. obs.). It does not tightly surround the stapedial opening. The cephalic condyle is positioned dorsal to the suprastapedial process. An anterodorsal

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excavation is present between the tympanic ala and the anteromedial projection of the cephalic condyle, likely providing an attachment area for the dorsal segment of the *m. adductor mandibulae profundus* (Russell, 1967). A weak rounded ridge stretches distally from the anterodorsal excavation along the suprastapedial process for the articulation of the squamosal and supratemporal dorsolaterally and the paroccipital process of the otooccipital dorsomedially.

The ascending tympanic rim rises dorsally towards the distal end of the suprastapedial process but the posterodorsal end is distorted by crushing. A horn-like infrastapedial process projects posteromedially from the crushed mass on the posterior face. It does not contact the suprastapedial process and may be pathologic.

In medial view, the quadrate shaft is primarily vertical. The ovoid stapedial pit is elongate without medial constriction and is vertically oriented. A rounded ridge is present above the pit, extending a short distance posteriorly on the medial face of the suprastapedial process. A thin ridge begins anterior to the most ventral portion of the stapedial pit and travels ventrally to meet the mandibular condyle. There is a small dorsoventrally elongate foramen positioned posterior to the dorsal termination of the ridge.

The mandibular condyle possesses an ovoid outline in ventral view and is wider laterally because of an upward deflection of the condyle when viewed anteriorly. It features a saddle-like anteroposterior profile due to a concave ventral margin, a condition that is also found in *Russellosaurus coheni* (Polcyn and Bell, 2005). The condyle extends about 4 mm medially past the vertical edge of the quadrate shaft, similar to the condition

in *Platecarpus tympaniticus* and *Russellosaurus coheni*, but contrast to the straight medial margin seen in *Clidastes propython* (Joshua Lively pers. comm., 2016; pers. obs.). Anteriorly, the condyle deflection is rimmed by a shallow depression on the anterior face of the quadrate. A pair of small circular foramina are present dorsal to the deflection with one resting just within the depression. The *m. adductor mandibulae* probably attached to most of the anterior face (Russell, 1967). A thin ridge projects from the anterior face near the anteromedial margin of the quadrate. That ridge originates at about 1.8 cm below the dorsomedial corner of the cephalic condyle and transitions into a rounded ridge 1 cm ventrally, about the same point of origin for the ridge present on the medial face. Both of these ridges may serve as the quadrate origin of the *m. adductor mandibulae posterior* (Russell, 1967). A slight depression is present between the bifurcated ridges.

Coronoid

A partial left coronoid is preserved from TMM 31051-84 (Figure 16); it is missing the anterior portion. The element is slightly crushed as evidenced by a slight groove formed in the lateral surface, slight dorsal bending of the posterior medial wing, and the faint offset present within the ventral surface.

Overall, the coronoid appears saddle-shaped. The posterodorsal process ascends at approximately 45° above the horizontal base of the bone. Unlike the tall processes of *Clidastes propython* and other mosasaurines, the structure in the new taxon does not extend far dorsally and is poorly developed as typical of russellosaurines and also appears

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in *Kourisodon puntledgensis* (Nicholls and Meckert, 2002). The coronoid is laterally excavated underneath this process for the articulation of the coronoid buttress from the surangular along the lower portion and the probable attachment of the bodenaponeurosis dorsal to the suture with the surangular (Oelrich, 1956; Russell, 1967).

The ventral surface of the coronoid forms a shallow trough, oriented anteroposteriorly, for receiving the anteromedial shelf of the surangular. Lateral and medial wings would have formed on either side of the split created by a crest on the surangular. The coronoid sutural surface on the surangular hints at a short lateral wing remaining subparallel to the horizontal ventral margin underneath the posterodorsal process, a condition seen in *Russellosaurus coheni*. The ventral extent of the medial wing is less clear though it probably continued to descend anteriorly.

The posterodorsal process and the medial face are heavily striated along their posterior segments, likely from the attachment of the *m. adductor mandibulae externus superficialis* and *medialis*, and the *medius* muscles in life (Bahl, 1937; Oelrich, 1956; Russell, 1967).

Surangular

The left surangular of TMM 31051-84 (Figure 17) is mostly complete, missing two portions of the ventral body, the anterior shelf that dorsally overlaps the articular, the anteriormost dorsal coronoid suture, and a segment of the dorsal border near the anterior termination of the coronoid buttress. The partial right surangular of TMM 31051-84

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consists primarily of the coronoid suture; part of the dorsolateral flange along that suture is missing. Only the anteriormost coronoid buttress is intact on the right surangular with no bone preserved farther posteriorly. Erosion is evident on the right element. Both surangulars are slightly crushed, and the ridge along the midline of the coronoid suture is laterally bent on the right element. On the left element, the posterior medial shelf overlying the articular is compressed into a trough.

The surangular is a long and narrow bone. The dorsal surface (when the coronoid suture is oriented horizontally as in life) rises only about 5 mm to meet the coronoid relative to the lowest point on the dorsal surface just anterior to the articular fossa. This low coronoid buttress remaining essentially parallel to the main body of the element (rather than rapidly rising) is a characteristic observed in russellosaurines but is usually atypical of mosasaurines with the exception of *Kourisodon puntledgensis* (Nicholls and Meckert, 2002).

A low, rounded ridge descends anteroventrally on the smooth lateral surface from the articular fossa, merging into the main body around mid-length. In life, the dorsolateral surface likely served as the attachment for the *m. adductor mandibularis externus* which was thought by Russell (1967) to attach to the anteroventrally descending rounded ridge as the *superficialis* and *medialis* components (Oelrich, 1956). Multiple foramina are present on the lateral face near the dorsal margin.

The ventral border of the surangular rises continuously at a low angle until below the anterior lip of the articular fossa, where the curvature increases rapidly, ending at the posterior border of the surangular portion of the fossa. This condition is most similar to

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the russellosaurines *Tethysaurus nopcsai* and *Russellosaurus coheni* and (see Bardet et al., 2003, and Polcyn and Bell, 2005). Halisaurines have vertically or posteroventrally descending ventral borders near the articular fossa and most other mosasaurs have ventral borders that curve dorsally into the posterior margin of the surangular. The element thickens at the articular fossa which consists of two flanges: one projecting medially and the posterior flange forming the posterior-most portion of the lateral surface. Sutural grooves are present along the latter flange and continue partway down the ventral margin for the articulation of the articular. The surangular likely constituted half of the articular fossa.

Medially, a shelf, though somewhat taphonomically distorted, descends anteroventrally approximately parallel to the ventral margin. That shelf rests on top of the prearticular process of the articular and serves as the base of Meckel's canal that probably transported the mandibular artery (Bahl, 1937; Oelrich, 1956; Russell, 1967). The anterior termination of the basal shelf is unknown. A thick medial shelf begins anterodorsally, supporting the coronoid above and posteriorly forming the dorsal border of Meckel's canal. Grooves are present throughout the coronoid suture but are most apparent along the anteromedial face of the coronoid buttress. A crest of bone bifurcates the anterior half of the suture. The lateral section remains roughly horizontal while the medial portion descends approximately 4 mm relative to the posterior part of the suture. A foramen is visible on the anterior margin directly underneath the coronoid suture that was postulated by Russell (1967) to have allowed a branch of the mandibular nerve to enter the surangular.

The articular would have rested against the medial shelf just below the coronoid. The sutural surface includes grooves along the posterior surface present just dorsal to an anterodorsally rising groove that also housed part of the articular. The anterior suture is unclear past the groove, and the coronoid could have abutted or dorsomedially covered the articular.

Angular

The left angular (Figure 18) is partially preserved in the new taxon. Most of the medial and posterior sections are broken and missing with only a small portion of the lateral face remaining. The splenial-angular articulation surface is weathered and not diagnostically useful.

POST-CRANIAL SKELETON

The vertebrae are the only bones preserved posterior to the cranium and include most of the atlas, four post-axis cervicals, and eleven trunk vertebrae. No axis vertebra is preserved, and the exact length of the vertebral column and precise positions of the vertebrae cannot be determined. Without pygal and caudal vertebrae, it is unknown if the new taxon possessed a downturned tail. Limb elements are not preserved in TMM 31051-84 though a number of ribs across the cervical and trunk vertebrae are preserved, many as partial elements.

Atlas

The atlas, the first of the cervical vertebrae, consists of four bones in mosasaurs, namely the atlantal intercentrum, atlantal centrum (also referred to as the odontoid), and a pair of contralaterally positioned atlantal neural arches. Of those, the latter three are preserved in TMM 31051-84. Both neural arches (Figure 19a-e) are nearly complete except for a small portion of the posterodorsal surfaces and some of the margin of the dorsal process. The anterior surface is sub-rectangular for articulation with the occipital condyle of the skull. No ventral process occurs on the atlantal neural arch, but the rounded ventromedial surface would contact the intercentrum. Short synapophyses extend posteriorly in a state similar to Russellosaurina but unlike the elongate and sometimes pedunculate condition seen in *Clidastes propython*, *Kourisodon puntledgensis*, and other taxa within Mosasaurinae (Bell 1993; Bell and Polcyn, 2005).

The dorsal process is marginally posterior to the anterior condylar surface (by ~2 mm). This growth features an anteriorly concave margin and is mediolaterally flattened with a rugose tip. Several fragments of vertebral neural spines are attached by matrix, obscuring the medial face of the left neural arch process. The dorsal neural spines likely touched in life. Medially, the atlantal neural arch possesses a saddle-shaped condylar surface. The posterior end near the synapophysis would articulate with the axis vertebra while the anterior half accepts the centrum.

The atlas centrum (Figure 19f and g) is a squat bone that becomes anteroposteriorly thicker moving dorsally, forming an anterior lip. That protrusion is rounded with a slightly projected middle unlike the semicircular outline seen in *Clidastes*

propython. The dorsal face is shallowly excavated but largely flattened overall to serve as the floor of the spinal cord. The posterior surface articulates with the centrum of the axis posteriorly and possesses a rectangular outline that is divided in two by a rounded ridge running dorsoventrally. This ridge is more pronounced in the new taxon than in *Clidastes propython*. Ventrally, the articulation surface for the atlantal intercentrum forms a slight excavation as an elongate ovoid. Erosion has damaged the ventral, posterior, and dorsal faces. There is evidence of light compression on the lateral edges that did not distort the overall shape of the centrum.

Post-atlas vertebrae

All vertebrae have experienced some degree of crushing that has flattened the neural arches and/or the transverse processes, distorting the shape of the synapophyses (rib articulation surfaces on the transverse processes). As in all mosasaurs, the centra of the vertebrae are procoelous (Russell, 1967). Zygapophyses are present in all preserved vertebrae, including far into the trunk series as in the majority of mosasauroids (Bell, 1993; Bell and Polcyn, 2005). Prominent zygosphenes and zygantra appear well into the trunk vertebrae, a plesiomorphic character according to Bell and Polcyn (2005). These structures are missing on several elements due to taphonomic alteration. Neural spine bases are preserved in some cervical and trunk vertebrae, but only three trunk vertebrae have associated mediolaterally flattened neural spines. Of these, one is largely intact and

in place, one flattened by crushing, and the third consists of fragments. Other isolated fragments of these dorsal projections were also recovered.

Cervical vertebrae (Example shown in Figure 20)

The transverse processes are completely missing from the one of the anterior preserved cervicals. Of those preserved, many are crushed and the synapophyses eroded. Two of the vertebrae preserve postzygapophyses projecting posteriorly off the neural arch though the second posteriormost preserved cervical is missing the right-lateral side. Only the latter element preserves prezygapophyses though crushing has slightly distorted their orientation so that the facets are facing more medially. The centra are largely intact but show evidence of minor crushing on several of the cervical vertebrae.

The centra of the cervicals are distinctly shorter than the most anteroposteriorly elongate trunk vertebra, contrasting the synapomorphy present within *Plotosaurus bennisoni* and species of *Mosasaurus* (Bell, 1993; Bell & Polcyn, 2005). Both the anterior cotyles and posterior condyles of the centra are smooth surfaces that articulate into the previous and next vertebrae, respectively. The condyles are slightly wider than tall. A pedunculate process projects posteroventrally near the ventral surface of the condyle, ending in a narrow ovoid facet for articulation with the hypapophysis. All preserved cervicals would have possessed a hypapophysis, as shown by ventral facets, but only one hypapophysis is preserved. Moving posteriorly, the hypapophyseal facet

decreases in size and is not present within the preserved trunk vertebrae though without the full vertebral series, the last occurrence of the hypapophysis is unknown.

Transverse processes project laterally from the centrum on each side, somewhat closer to the cotyle than the condyle. The synapophyseal facet present on the distal end serves as an articulation surface for ribs. A discernible pattern of dorsoventral lengthening of the synapophyses is evident moving posteriorly down the neck, but they do not extend beyond the ventral margin of the centrum, whereas the synapophyseal facet extends underneath the ventral margin in *Dallasaurus turneri* (Bell and Polcyn, 2005).

The dorsal surface of the cervical vertebrae consists of a dorsally-projecting neural arch that forms the upper and lateral boundaries of a channel through which the spinal cord would have passed. From the base of the neural arch above the cotyle, paired prezygapophyses project anteriorly with dorsomedially oriented facets running along their length. These facets would have articulated with the ventrolaterally oriented facets on the postzygapophyses of the previous vertebra. The latter processes project posteriorly from the neural arch above the condyle and slightly dorsal to the position of the prezygapophyses. A tall, mediolaterally flattened neural spine would have ornamented the top of the neural arch.

Trunk vertebrae (Example in Figure 21)

All of the cotyles of the trunk vertebral series are affected by crushing with only the element preserving an intact neural spine preserving the nearly circular outline. The

condyle on the posterior ends of these elements are largely well-preserved, but some vertebrae display signs of dorsoventral crushing. One of the vertebrae is lacking transverse processes because of taphonomic alteration and three others have only one process remaining. Most of the trunk vertebrae preserve a neural arch that is crushed; the exception of three anterior trunk vertebrae. Most vertebrae preserve zygapophyses, zygosphenes, and zygantra.

Anteriorly, the synapophyses are dorsoventrally elongate, taller than wide, and sub-rectangular in outline. The transverse processes extend farther laterally and the synapophyses appear to shrink in both height and width moving posteriorly down the trunk series. The exact transition in form down the spine is somewhat obscured by crushing. Anterior condyles lack dorsoventral compression, resulting in an almost circular surface. Compression of more posterior vertebrae is unknown due to postmortem crushing. Like the cervical vertebrae, the prezygapophyses and postzygapophyses of all trunk vertebrae possess ovoid facets oriented dorsomedially and ventrolaterally, respectively.

Ribs

At least 13 ribs are partially preserved based on the preserved heads that would have attached to the vertebral synapophyses in life. The other portions of ribs are isolated from their attachment sites. The ribs of the new taxon range in size and position in the vertebral column from the longer anterior ribs (largest preserved is roughly 15 cm in

length along its curvature but it is distally incomplete [Figure 22]) to the posterior, almost tooth-like ribs (lengths of ~4 cm or smaller). All are anteroposteriorly flattened and all except for the more posterior ribs possess compressed midlines forming a groove along the anterior and posterior faces. None of the ribs are articulated with vertebrae, many are cracked, and several are crushed.

RUSSELLOSAURINA Polcyn and Bell, 2005

TYLOSAURINAE Williston, 1897

TYLOSAURUS Marsh, 1872

TYLOSAURUS NEPAEOLICUS Cope, 1874

Holotype – AMNH 1565

Diagnosis – See Jiménez-Huidobro et al. (2016)

Referred specimen – TMM 31051-64, partial premaxilla and left quadrate

DESCRIPTION

Premaxilla

The premaxilla of TMM 31051-64 (Figure 23) is missing most of the internarial bar (including the ventral keel), the anterior tip of the predental rostrum, the second left lateral tooth, and the distal ends of the anterior two teeth. Some minor crushing is evident

along the dorsal surface of the anterior internarial bar. The intermaxillary bar is smashed toward the right lateral side and is missing the posterior distal portion.

TMM 31051-64 possesses a large predental rostrum with a sub-rectangular outline anterior to the first two teeth. Elongate foramina of variable size are scattered (rather than evenly distributed or aligned) across the dorsal and lateral surfaces of the preserved premaxilla but are not present beyond the anterior margin of the posterior teeth. Most are concentrated on the predental rostrum. These openings likely provided passage for "ophthalmic ramus of the fifth nerve" (Bahl, 1937; Russell, 1967). What appears to be a weak medial ridge on the dorsal surface may be the result of taphonomic crushing evident on the anterior internarial bar. The internarial bar originates from the tooth-bearing segment of the premaxilla in a sub-rectangular base.

The intermaxillary bar begins between the anterior two teeth and projects posteriorly and slightly ventrally, forming a structure separate from the internarial bar. Along the ventral surface of the predental rostrum just anterior to the first pair of teeth are two faint bulges that Russell (1967) hypothesized as marking the gum line in *Tylosaurus*. The teeth taper distally from their base and lack faceting, fluting, inflation, and mediolateral compression. Heavy striations are present across the enamel. No posterior carinae were present but there may have been weak anterior carinae based on the posterior right tooth. From examination of the tooth bases, all four teeth appear to have been equidimensional.

The premaxilla alone does not confirm the taxonomic identity of this specimen and the element along with the associated quadrate are reported by Everhart (2005b) to

"have similar characteristics to the Kansas specimens [*Tylosaurus kansasensis*] but require further study." Its large and inflated predental rostrum is found within all tylosaurines though only *Tylosaurus nepaeolicus*, *Tylosaurus* 'kansasensis,' and *Tylosaurus proriger* are found chronostratigraphically near the early Coniacian. This element is not referable to *Tylosaurus* 'kansasensis' because it has a sub-rectangular base of the internarial bar (*Tylosaurus* 'kansasensis' possesses the shape of an inverted triangle), but it is possible the shape of the base could vary through ontogeny or intraspecifically (Everhart, 2005b; Palci et al., 2013). The sub-rectangular predental rostrum also supports the hypothesis that the specimen is not referable to *Tylosaurus* 'kansasensis,' whose predental rostrum is rounded (Everhart 2005b), but the difference in shape is contentious because Jiménez-Huidobro et al. (2016) claimed both states show intraspecific variation within *Tylosaurus nepaeolicus*.

Quadrate

The right quadrate (Figure 24) is 81 mm tall when measured from the base of the shaft to the highest point of the suprastapedial ridge. The suprastapedial process is longer than midheight by ~12 mm. An extension of the suprastapedial process from approximately midheight to two-thirds down was described for *Tylosaurus kansasensis* while *Tylosaurus nepaeolicus* was said to "[reach] one-third to the midheight of the shaft in Jiménez-Huidobro et al. (2016: p. 74). Examination of suprastapedial process lengths in that article and the character state scorings by Bell and Polcyn (2005) and Bullard

(2006) reveal that both taxa display processes of 'moderate length' around midheight. This may indicate intraspecific or ontogenetic variation if these two taxa are synonymous as suggested by Jiménez-Huidobro et al. (2016). *Tylosaurus proriger*, in contrast, always displays a short process "well above midheight" (Palci et al., 2013: p. 10, supplemental data matrix). The suprastapedial process of TMM 31051-64 is not deflected medially as it extends ventrally and ends in a downward-oriented triangular bulge. The suprastapedial process forms a stapedial notch that is dorsoventrally elongated and widely spaced. A medial protrusion is present on the suprastapedial process for the articulation of the supratemporal. No fusion exists between the suprastapedial process and the poorly developed infrastapedial process. The laterally extending tympanic ala is thick with a shallow concavity, unlike the thin, deeply bowled tympanic ala possessed by *Tylosaurus proriger* (Palci et al., 2013; Jiménez-Huidobro et al., 2016; pers. obs.). Dorsally, the tympanic margin is more tightly curved. The ascending tympanic rim comes close to contacting the mandibular condyle and does not rise medially towards the infrastapedial. Pores appear along the tympanic margin, providing evidence of minor erosion.

The dorsal surface features a cephalic condyle that is excavated anteriorly, forming a wide curve between the tympanic ala and the dorsomedial edge. This concave surface likely formed the attachment site for the dorsal part of the *m. adductor mandibulae externus profundus* that originates from the anterior face of the quadrate (Russell, 1967). A pronounced rounded crest is present along the length of the suprastapedial process. The squamosal and supratemporal would have articulated dorsolaterally along the ridge while the paraoccipital process attached on the medial side.

A porous erosional texture is prevalent on the dorsal surface and is concentrated anterolaterally and in a few areas along the suprastapedial.

On the vertical medial face of the quadrate, the stapedial pit appears as an elongate ovoid with a constricted midpoint and slight expansion dorsally on the suprastapedial. A short, rounded ridge stretches dorsoventrally above the pit. Ventral and slightly anterior to the stapedial pit, a narrow elongate foramen is present. A rounded ridge descends from the dorsal surface and continues ventrally along the anteromedial margin to meet the mandibular condyle, transforming into a thin ridge at midheight. It is possible that the ridge served as the anchor for the *m. adductor mandibulae posterior* (Russell, 1967). The ridge does not bifurcate as it descends ventrally unlike the condition in *Tylosaurus* '*kansasensis*' (Bell and Polcyn, 2005; Everhart, 2005b).

The mandibular condyle is ovoid in shape and slightly wider on the lateral side. The articulation surface lacks extensions beyond medial or lateral surfaces of the quadrate. Anteriorly, the condyle is deflected dorsally and surrounded by a shallow depression. The mandibular condyle is slightly concave in posterior and anterior views though a large portion of the condyle is convex.

YAGUARASAURINAE Palci et al., 2013

YAGUARASAURINAE CF. *RUSSELLOSAURUS COHENI* Polcyn and Bell,

2005

Holotype – SMU 73056

Diagnosis – See Polcyn and Bell (2005)

Referred specimen – TMM 31051-59, partial frontal

DESCRIPTION

Frontal

The frontal (Figure 25) is mostly complete but is missing the anterior portion of
the bone that would have contacted the internarial bar from the premaxilla. Material is
missing from the tips of the posterolateral processes and the descending processes on the
ventral surface. The lateral margin along the orbits and the posterolateral projections are
intact but become jagged by taphonomy along the flanges overlapping the prefrontals.
Minor crushing is visible on the posterodorsal surface. A diagonal crack spans the width
of the frontal around the mid-length of the element. No material is missing and the two
'halves' were properly realigned by a previous researcher (identity unknown). Pitted
erosion is evident on most of the dorsal and ventral surfaces. The posterior margin is also
somewhat eroded, but the overall structure of the contact with the parietal is intact.

The element is a roughly triangular bone with mediolateral constriction above the orbits; the strongest constriction is present lateral to the anterior edge of the postorbitofrontal suture. Anteriorly, the frontal laterally expands slightly until the sutural surface with the prefrontal beyond which the element continuously decreases in width. The frontal is widest just across the posterolateral processes that taper to a point along the frontoparietal edge. Tylosaurines and plioplatecarpines (except for *Latoplatecarpus willistoni*), in contrast, possess broader and more rounded alae (Bell, 1997; Bullard, 2006; Konishi and Caldwell, 2011; Palci et al., 2013). It may be said that the frontal is 'sinusoidal' along its lateral margins, but that condition appears to be highly variable among mosasaurs, even within the same species, grading from curvy edges to nearly straight borders.

A nearly straight and vertical posterior margin hints at a transverse suture with the parietal with a slight invasion of the frontal by the parietal just lateral to either side of the midline. The frontal would not have invaded the parietal with overlapping flanges as seen in the plioplatecarpines and tylosaurines (Palci et al., 2013 data matrix).

No dorsal median ridge is present. Posteroventrally, the postorbitofrontal would have articulated with the frontal along the bottom of the posterolateral processes, ending anteriorly in a semicircular depression. The postorbitofrontal is separated from the prefrontal by about 16 mm. At the point of prefrontal articulation, the frontal forms a thin lateral flange that overlaps the prefrontal dorsally. This sutural surface decreases in width anteriorly and ends in a semicircular depression posteriorly. A ventral triangular boss is positioned along the frontal midline near the posterior border, demarked on either side by

an elongate ovoid sulcus (the left sulcus is slightly distorted by crushing). Descending processes (as named by Polcyn and Bell, 2005) extend posteriorly and anteriorly to form the medial margins of the postorbitofrontal and prefrontal sutures, respectively. The processes connect laterally to the slight ventral extension of the frontal separating the prefrontal and postorbitofrontal. It is unknown if they would have nearly blocked what is interpreted as the olfactory canal as is seen in *Russellosaurus coheni*; the incomplete medial allow for that interpretation (Polcyn and Bell, 2005).

Several characteristics distinguish this frontal from the Tethysaurinae (*Pannoniasaurus inexpectatus* and *Tethysaurus nopcsai*) and other yaguarasaurines (*Romeosaurus* and *Yaguarasaurus columbianus*; definitions of Tethysaurinae and Yaguarasaurinae follow Palci et al., 2013). The frontals of *Tethysaurus nopcsai* and *Romeosaurus sorbinii* lack an embrasured or a nearly closed olfactory canal and the latter taxon does not possess an emarginated supraorbital region nor separated prefrontal and postorbitofrontal sutures (Bardet et al., 2003; Palci et al., 2013). Another difference from *Tethysaurus nopcsai* is the lack of a dorsal median ridge that, while not described by Bardet et al. (2003; the state may be visible in their Figure 2A), was scored as low by Palci et al., 2013. The frontal of *Romeosaurus fumanensis* is poorly preserved and only visible in dorsal view whereas in *Pannoniasaurus inexpectatus* the element is unknown (Makádi et al., 2012; Palci et al., 2013, Figure 5). *Russellosaurus coheni* and *Yaguarasaurus columbianus* share similar frontal morphology. *Yaguarasaurus columbianus* possesses "greater emargination [anteriorly] of the frontal by the external nares" and a wider frontal than the condition seen in *Russellosaurus coheni* (Polcyn and

Bell, 2005: p. 331). The missing anterior portion of TMM 31051-59 cannot be utilized for evaluation of narial emargination or the suture with the premaxilla, but the element displays a frontal width proportional to that of *Russellosaurus coheni*.

PHYLOGENETIC ANALYSIS

My collaborator Joshua Lively gathered data and photographs from approximately 250 mosasaur specimens from museums in North America and Sweden. We scored TMM 31051-84 and other mosasaurines using 121 characters (77 cranial and 44 post-cranial), both novel discrete characters and those previously published by Russell (1967), Bell (1993, 1997), Bell and Polcyn (2005), and Konishi and Caldwell (2011). The outgroup was set as two russellosaurine taxa: *Plesioplatecarpus planifrons*, and *Russellosaurus coheni*. The character matrix for 26 terminal taxa was organized in Mesquite v. 3.40 and we ran a maximum parsimony analysis using a traditional heuristic search with tree bisection-reconnection and 1000 random addition search replicates in TNT v. 1.1 (Goloboff et al., 2008).

From the analyses, 12 most-parsimonious trees were found, each with a step length of 215, a consistency index (CI) of 0.526, and a retention index (RI) of 0.753. The strict consensus tree is shown in Figure 26. The new taxon was recovered as the basal-most member of Mosasaurinae, sister to all other known taxa of that clade. The unique combination of characters (see diagnosis) warrants the erection of a new species. A

comparison of the characters found on specimen TMM 31051-84 against other mosasaurs documents that this animal also does not align easily with any known genus.

Plotosaurus bennisoni, *Mosasaurus*, and *Eremiasaurus heterodontus* formed one of the two most derived monophyletic groups, sister to the clade formed by *Prognathodon* and *Globidens*. *Prognathodon* was not recovered as monophyletic; '*Prognathodon*' *kianda* was hypothesized as the sister taxon to the clade of (*Globidens* (*Prognathodon* [except '*Prognathodon*' *kianda* and '*Prognathodon*' *stadtmani*])) and '*Prognathodon*' *stadtmani* was recovered as the sister taxon to that group. *Clidastes* also did not form a clade and is split between *Clidastes propython* and four other terminal taxa, one of which forms part of a polytomy with *Clidastes propython*, and the others forming the sister group to those taxa and the other mosasaurines. New Taxon #1 and New Taxon #2 correspond to unpublished specimens within the collections of the TMM, MSC, and FMNH, respectively.

The low CI and higher RI scores are likely driven by the lack of resolution in species of '*Clidastes*,' the two outlying taxa of '*Prognathodon*,' and possibly by the polytomy between *Mosasaurus*, *Plotosaurus*, and *Eremiasaurus*. *Dallasaurus turneri* (Bell and Polcyn, 2005), the oldest hypothesized member of the mosasaurines (~92 Ma), was excluded from the analysis due to its fragmentary condition. *Kourisodon puntledgensis* is not included with the evaluated taxa because specimen CDM 022 was not examined prior to conducting the phylogenetic analysis.

DISCUSSION

The following synapomorphies allow the placement of the new taxon into Mosasaurinae: smooth maxillary tooth surface without medial striations, striated margin of the quadrate tympanic ala, dorsally constricted suprastapedial process of the quadrate, and anterior trunk vertebral condyles without dorsoventral constriction. Strangely, the new taxon possesses several character states traditionally considered to be synapomorphies diagnosing the Russellosaurina. These include a short premaxilla-maxilla suture, a tooth row on the pterygoid that fails to extend ventrally past the main body of the element, a short posterodorsal process on the coronoid, a low and nearly horizontal coronoid buttress of the surangular, and short atlantal synapophyses. The mosasaurine *Kourisodon puntledgensis* is notable here for sharing with the new taxon a short premaxilla-maxilla suture, low coronoid buttress, and poorly developed posterodorsal process of the coronoid. These 'synapomorphic' character states may actually indicate the plesiomorphic state of Mosasaurinae along with the pleurodont dentition seen in the new taxon, *Kourisodon puntledgensis*, *Dallasaurus turneri*, *Russellosaurus coheni*, *Tethysaurus nopcsai*, both species of *Romeosaurus*, and the Halisaurinae; the state unidentifiable in current specimens of *Yaguarasaurus columbianus* and *Pannoniasaurus inexpectatus* (Bardet et al., 2003; Bell and Polcyn, 2005; Polcyn and Bell, 2005). Another potential ancestral state is the presence of a dorsomedial facet for the articulation of the squamosal process from the supratemporal that is, as of yet, only found in two taxa, namely the new taxon and *Russellosaurus*

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coheni though assessment of this feature in primitive mosasauroids has proven elusive due to the absence or poor preservation of the squamosal in *Dallasaurus turneri*, *Tethysaurus nopcsai*, most halisaurines except for *Halisaurus arambourgi* and *Phosphorosaurus ortliebi* (these taxa do not possess the facet), 'aigialosaurs,' and dolichosaurs (Dollo, 1889; Lingham-Soliar, 1996; Polcyn et al., 2012). The dorsomedial facet of the squamosal may be present in *Kourisodon puntledgensis* and *Yaguarasaurus columbianus* and future work will be required to evaluate this potential mosasaur plesiomorphy.

Although most of the skull of *Dallasaurus turneri* is fragmentary, the taxon is said to possess a pedunculate synapophysis on the atlantal neural arch typical of Mosasaurinae (Bell and Polcyn, 2005), unlike the short bump present in the new taxon. The partially preserved nature of the atlantal neural arch actually makes the character state unknown. A pedunculate synapophysis can also be found in *Kourisodon puntledgensis* and *Clidastes propython*. In contrast to the non-elevated row of pterygoid teeth in the new taxon, *Kourisodon puntledgensis* possesses teeth that rise from a ventral ridge like most mosasaurines including *Clidastes propython* (no pterygoid is known for *Dallasaurus turneri*). *Clidastes propython* coronoids possess a high posterodorsal process unlike those seen in *Kourisodon puntledgensis* and the new taxon. The state in *Dallasaurus turneri* is currently unknown. Both the new taxon and *Kourisodon puntledgensis* share a low coronoid buttress on the surangular as typically observed in russellosaurines while *Clidastes propython* possesses a rapidly rising coronoid buttress. *Dallasaurus turneri* is claimed by Bell and Polcyn (2005) to show a high coronoid

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buttress but this state cannot be assessed because the majority of the surangular including the dorsal border is missing. The information on these character states seems to indicate a step-wise evolution of mosasaurine synapomorphic characters.

The combination of character states considered synapomorphic of Mosasaurinae and Russellosaurina present in the new taxon serves to caution researchers to only tentatively assign taxonomic identity based on an isolated element. For instance, if the surangular or coronoid were found without the rest of TMM 31051-84, the bones would have been referred to the russellosaurines. Similarly, an isolated quadrate or anterior trunk vertebra would indicate the presence of a mosasaurine. More confident identification should be based on several associated elements (e.g., a quadrate and frontal) that together should provide a less ambiguous combination of diagnostic features and aide in describing potential synapomorphies, autapomorphies, and plesiomorphies.

The assemblage of mosasaurs from the Savoy Pit, specifically *Tylosaurus nepaeolicus*, Yaguarasaurinae cf. *Russellosaurus coheni*, and the new taxon has important implications for mosasaur evolution and biostratigraphy (Figure 27). Within Mosasaurinae, a chronostratigraphic gap of slightly more than six million years exists between the oldest and more lizard-like mosasaurine *Dallasaurus turneri* and the more derived members with paddle-like limbs with '*Clidastes liodontus*' as the first known example (initially occurring ~86.4 Ma; Everhart, 2001; Ogg et al., 2012). The new taxon of the Early Coniacian (~89 to 90 Ma) helps to fill this gap in knowledge. It is possible that the burst of diversity and disparity experienced by early mosasaurines was driven by a marine transgressive event in the Late Turonian and Early Coniacian, the extinction of

the ichthyosaurs 3 million years before the first mosasauroids, or the disappearance of the pliosaurid plesiosaurs following a brief overlap with the earliest mosasaurs that created openings for niche expansion, potentially as a combination of all three factors (Hancock and Kauffman, 1979; Kauffman, 1984; Haq et al., 1987; Schumacher, 2011; Fischer et al., 2016).

Prior to this study, the earliest recorded appearance of *Tylosaurus nepaeolicus* was the Late Coniacian and the occurrence of that species at the Savoy Pit (TMM 31051-64) extends the stratigraphic range back into the Early Coniacian. The quadrate and premaxilla represent one of the oldest known occurrences of the genus *Tylosaurus* along with *Tylosaurus* sp. from the Early Coniacian Fort Hays Limestone of Kansas described by Everhart, 2005a, and the Late Turonian specimens of *Tylosaurus iembeenses* reported by Mateus et al. (2012) and Atunes (1964; the latter was described as *Mosasaurus iembeenses* and referred to the genus *Tylosaurus* by Lingham-Soliar, 1992; this specimen was destroyed by fire according to Mateus et al., 2012).

If TMM 30151-59 belongs to *Russellosaurus coheni*, we would show a stratigraphic range extension for *Russellosaurus coheni*, like *Tylosaurus nepaeolicus*, into the Early Coniacian. Even with a match for every characteristic of *Russellosaurus coheni* on the nearly complete frontal, complete confidence in the taxonomic assignment to that taxon is lacking due to the missing anterior portion. The missing segment would have preserved the nature of the contact between the internarial bar of the premaxilla and the frontal in addition to any evidence of potential emargination by the external naris.
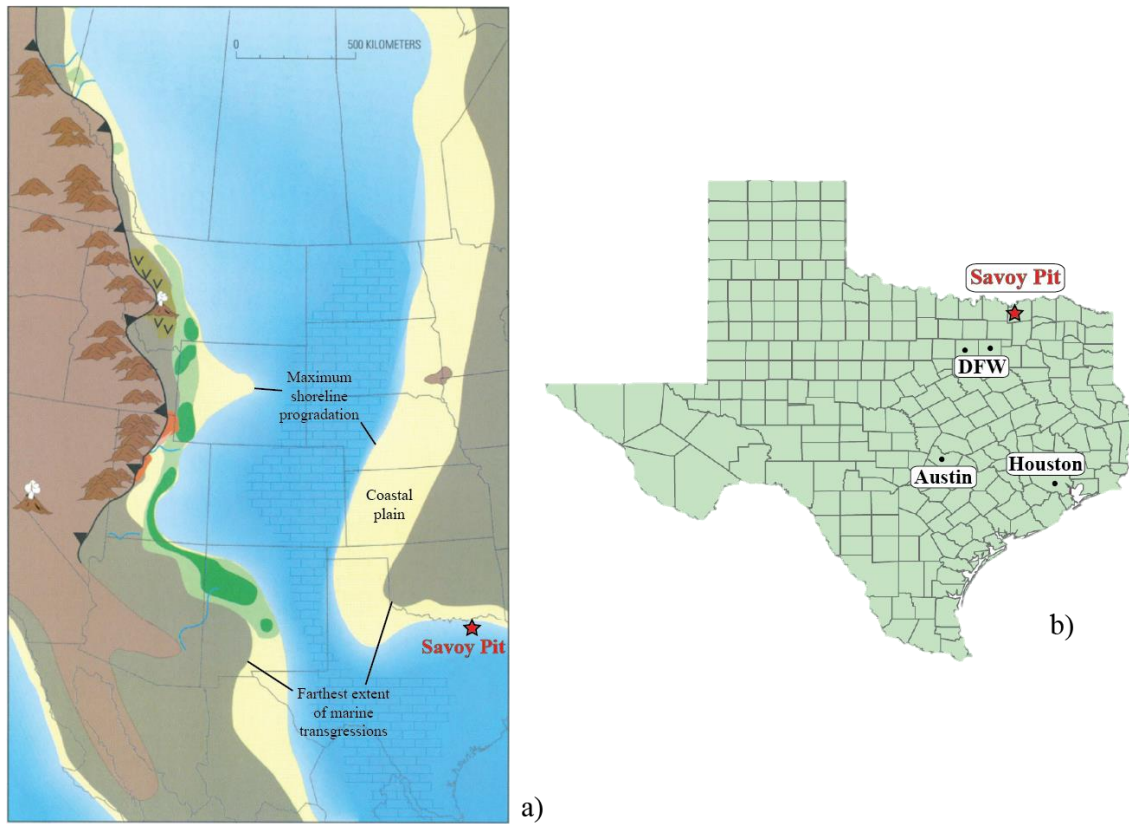
FIGURES

Figure 1. The location of the Savoy Pit: a) paleogeographic map of the Western Interior Seaway during the Coniacian and Santonian epochs of the Late Cretaceous (modified from Roberts and Kirschbaum (1995, Figure 13); b) unprojected map of Texas counties created in ArcMap v. 10.5.1 with feature layer data (USA Counties (Generalized)), featuring select major cities.
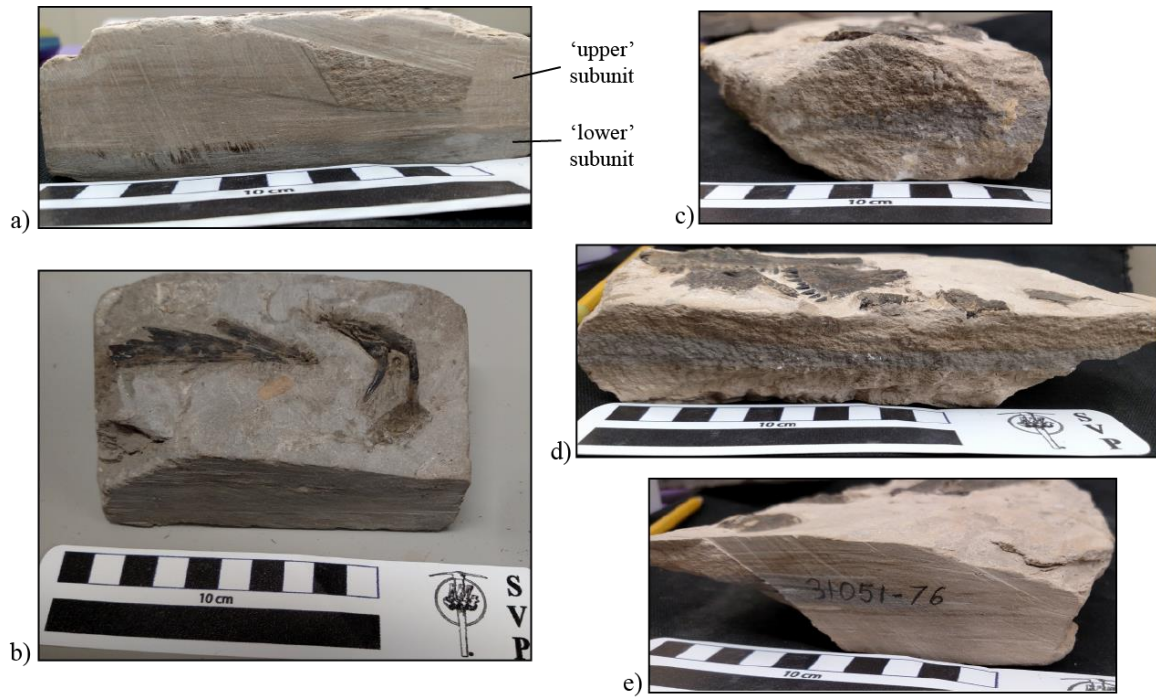
Figure 2. Rock samples collected from the Savoy Pit in 1940. Photograph a) shows a gradational contact between the 'lower' gray limestone subunit and the 'upper' chalkier subunit that represents the extent of weathering; b) shows a block of the 'lower' subunit containing parts of *Belonostomus* (TMM 31051-23); c), d, and e) depict three views of a lens of gray limestone within a block of the bioturbated 'upper' subunit (containing a partial fish, TMM 31051-76) with the lens pinching out in c) and e).
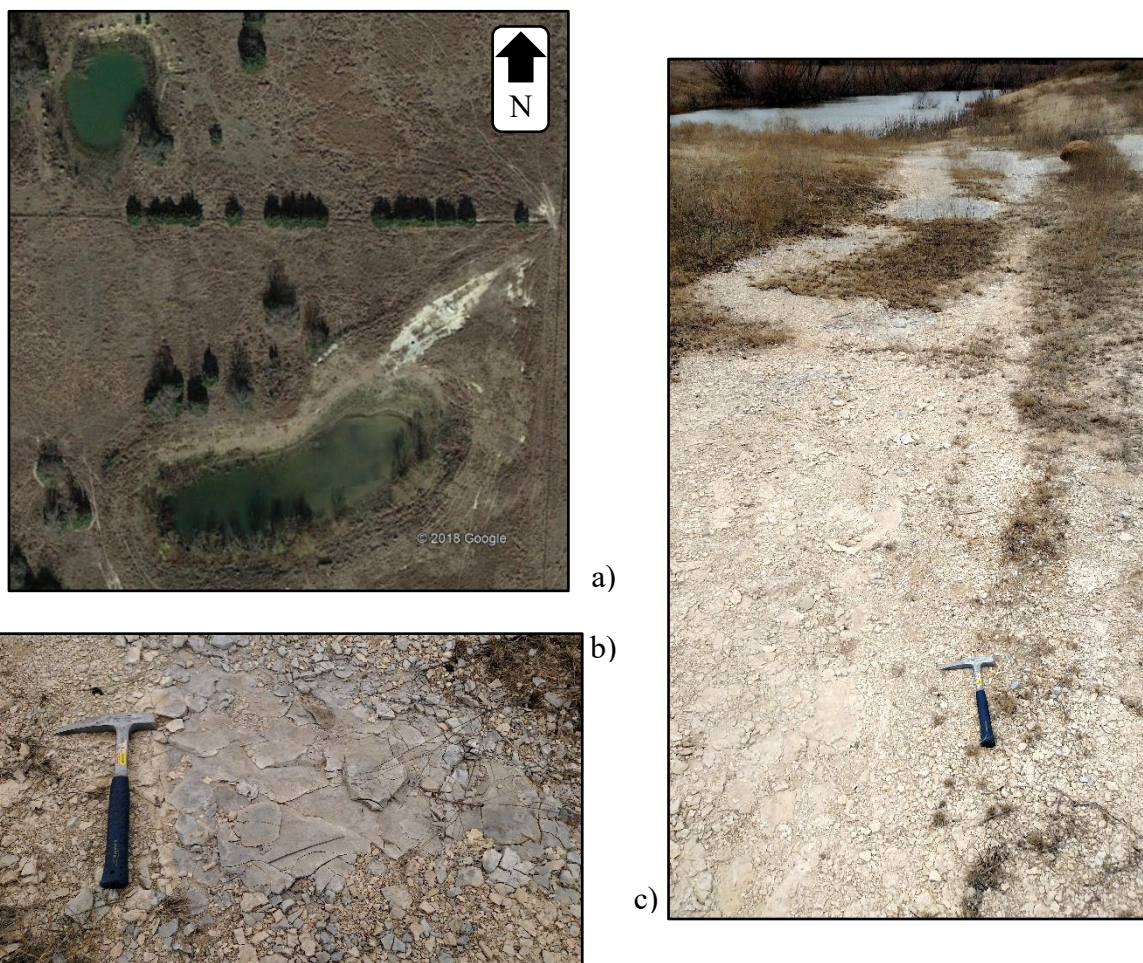
Figure 3. The Savoy Pit in the present day. As seen from above, a), the Savoy Pit has been filled with water and sediment from a neighboring pit (top left), leaving only a small outcrop exposure (top right of the photograph, Figure 3c; Google Earth Pro, 2017). A small portion of outcrop, b), along the surficial exposure has remained intact throughout landscaping activities and shows the surficial weathering effects on the gray packstone. Figure 3c) presents half of the broken-up exposure with the photograph oriented toward the southwest. The Savoy Pit is visible in the background.
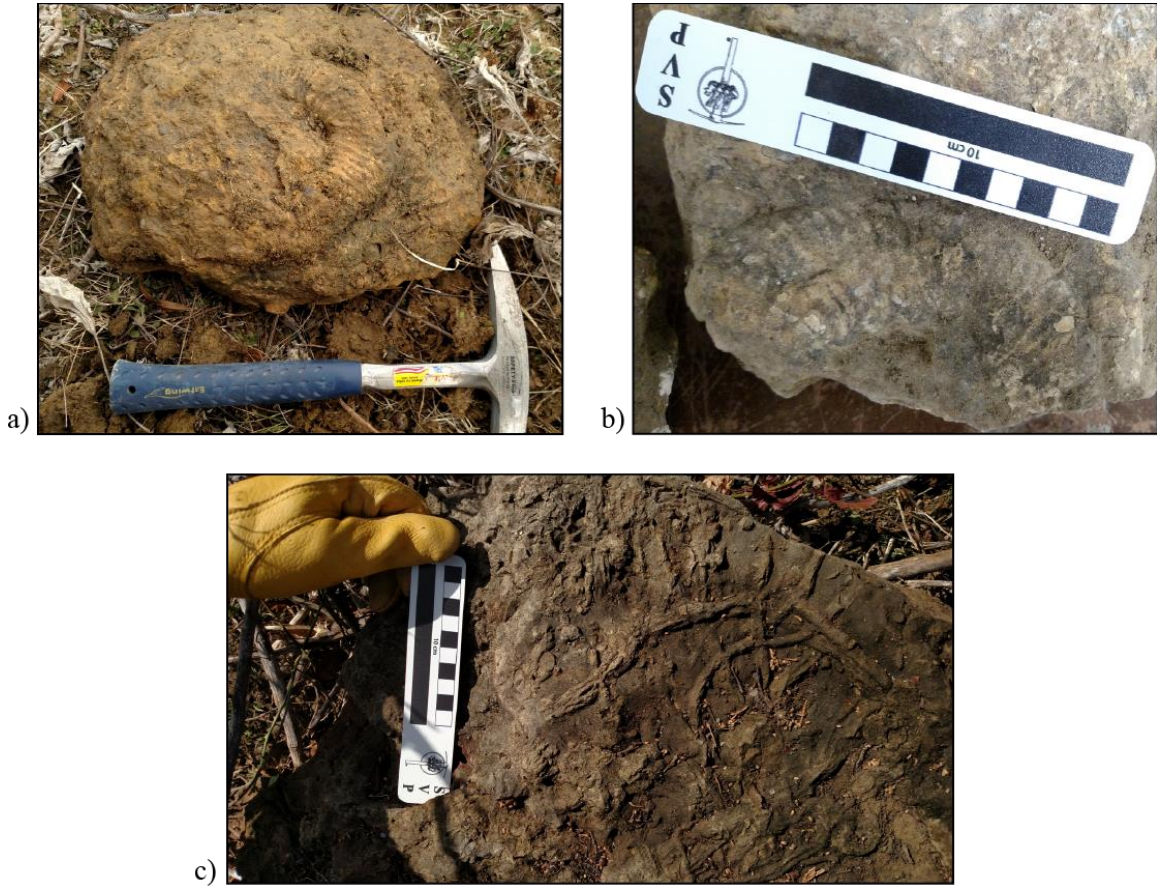
Figure 4. Select fossils observed during a trip to the Savoy Pit in January 2018. Two ammonites, a) and b), were collected from a sandstone unit (likely the Bell Sandstone) underlying the Ector Chalk and tentatively identified as *Prionocyclus*. Numerous sets of burrows, including c), are present within the same sandstone unit and consist of the trace fossil *Planolites*. No burrows were collected from the site.

a)

b)

c)

Figure 5. One of two fossil blocks containing material from TMM 31051-84 within the 'upper' subunit. The box is approximately 66 cm by 41 cm and was unprepared at the start of the project. a) shows the block in February 2016, b) in September 2016, and c) in January 2017.
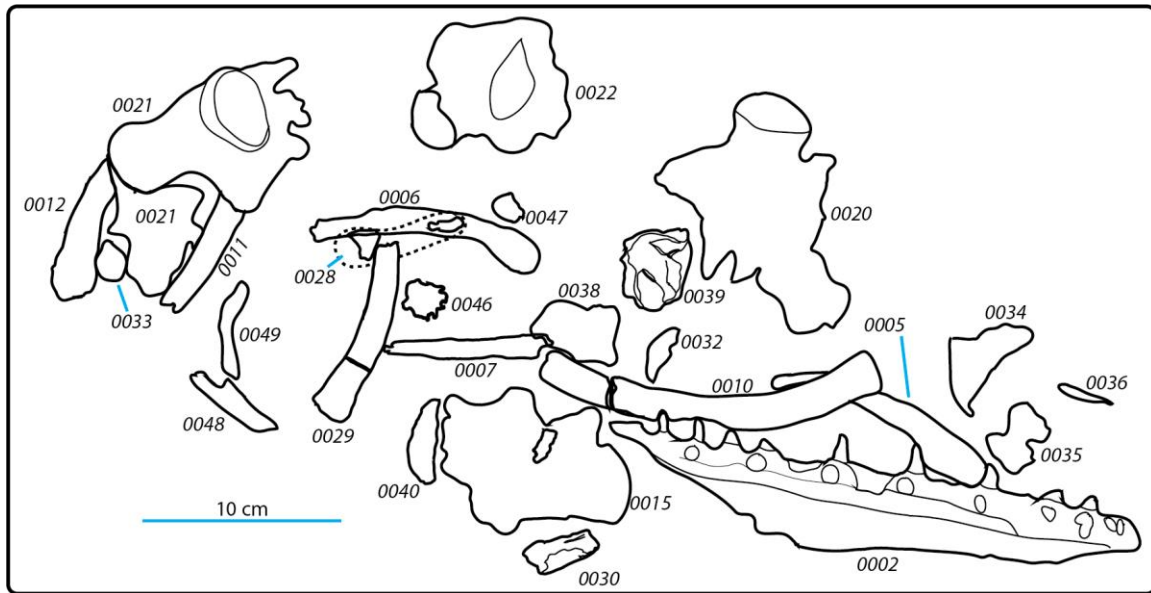
Figure 6. Bone map of the block shown in Figure 5. All elements have been removed and may be identified by the following numerical labels: 0002 (R maxilla); 0005 (R squamosal); 0006 (L squamosal); 0007 (squamosal ramus of the L postorbitofrontal); 0010-0012 and 0029 (ribs); 0020 and 0021 (trunk vertebrae); 0015 and 0022 (trunk vertebrae); 0028, 0030, 0039, and 0040 (unknown; 0040 may belong to a fish); 0032 (atlantal centrum); 0033 (hypapophysis of a cervical vertebra), 0034 (inoceramid fragment); 0035 and 0036 (unknown); 0038 (R atlantal neural arch); 0046 and 0047 (fish scales); 0048 and 0049 (posterior ribs covering the squamosal ramus of the R postorbitofrontal).
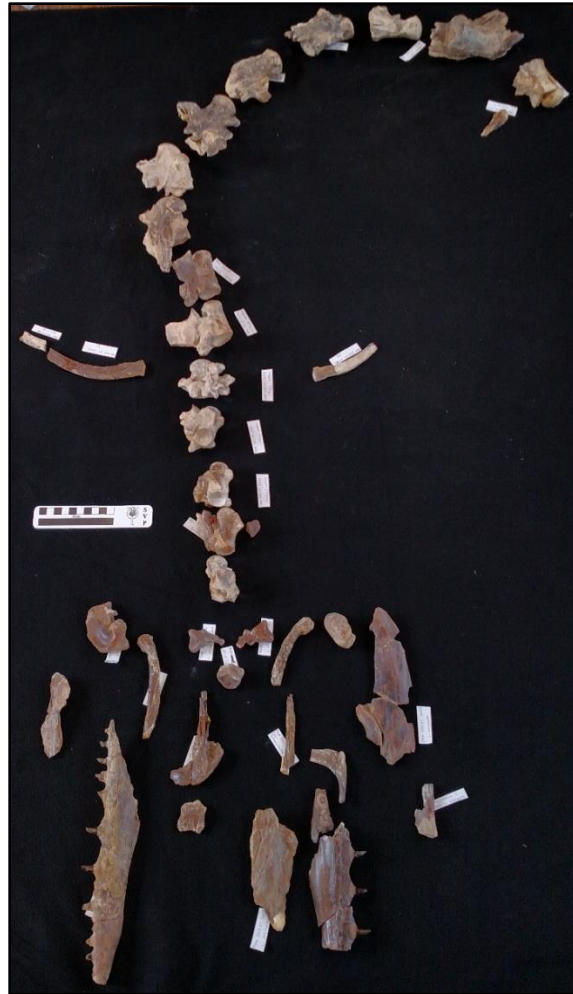
Figure 7. Nearly the entire skeleton of TMM 31051-84, the new taxon, in dorsal view, looking posteriorly. The vertebrae are placed in relative order, the squamosal ramus of the right postorbitofrontal is not shown, and not all preserved ribs are placed owing to their uncertain position. The entire scale bar in the photograph is ~16 cm in length.
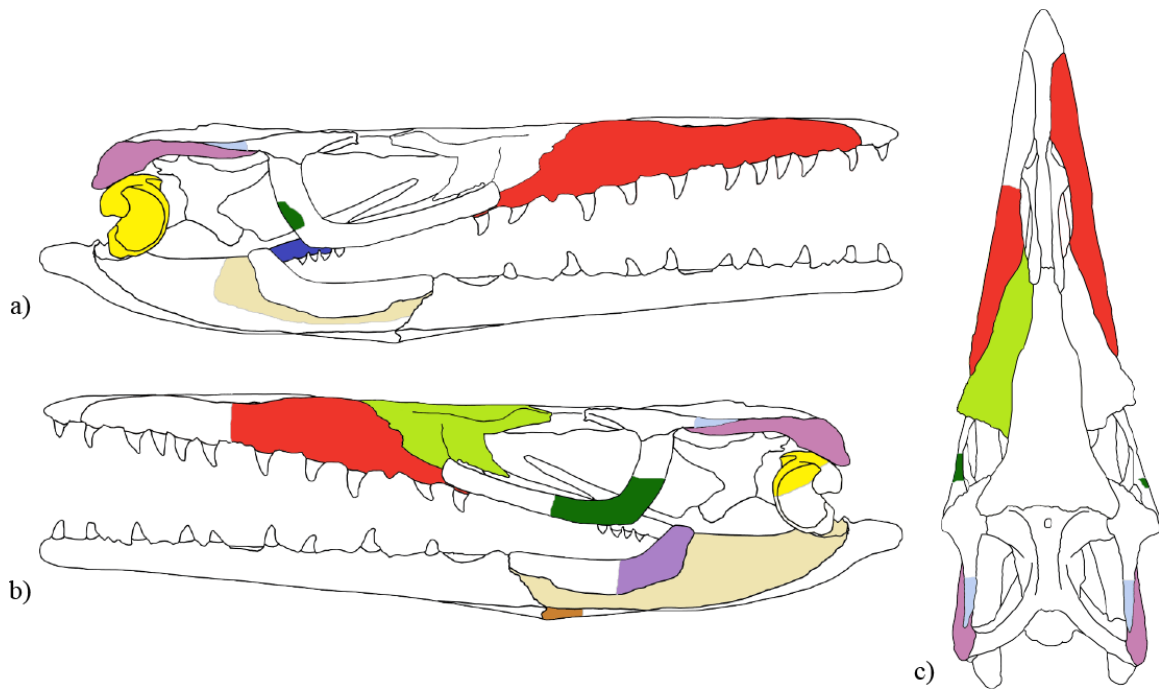
Figure 8. Preserved cranial elements of the new taxon depicted on a generalized mosasaur skull (sketched by Joshua Lively) in a) right lateral, b) left lateral, and c) dorsal views.
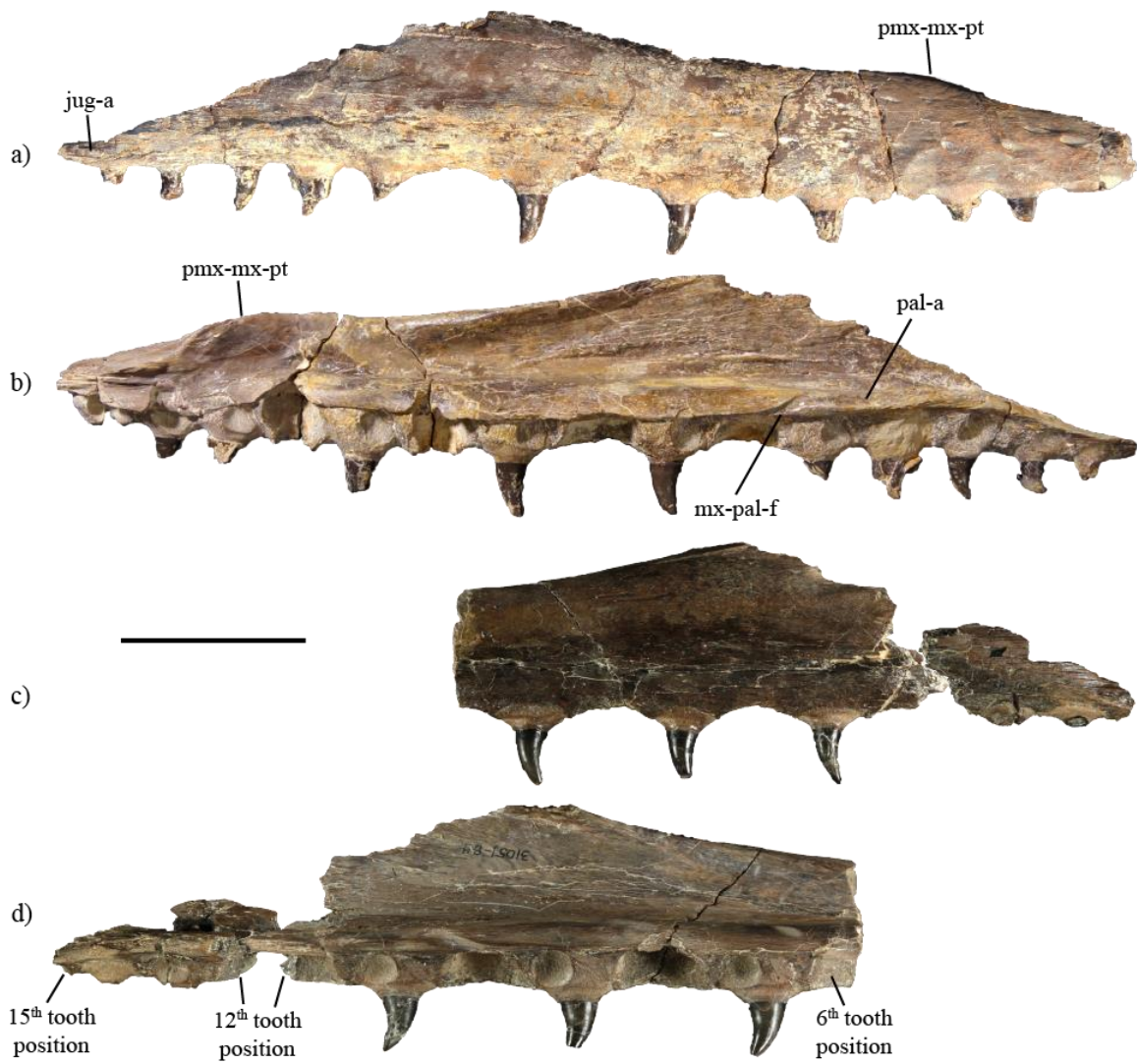
Figure 9. Maxillae of the new taxon. Right maxilla in a) lateral and b) medial views; partial left maxilla in c) lateral and d) medial views. Anatomical abbreviations: jug-a: articulation with the jugal; mx-pal-f: maxilla-palatine foramen; pmx-mx-pt: premaxilla-maxilla suture posterior termination; pal-a: possible articulation surface with the palatine. Scale bar = 5 cm.
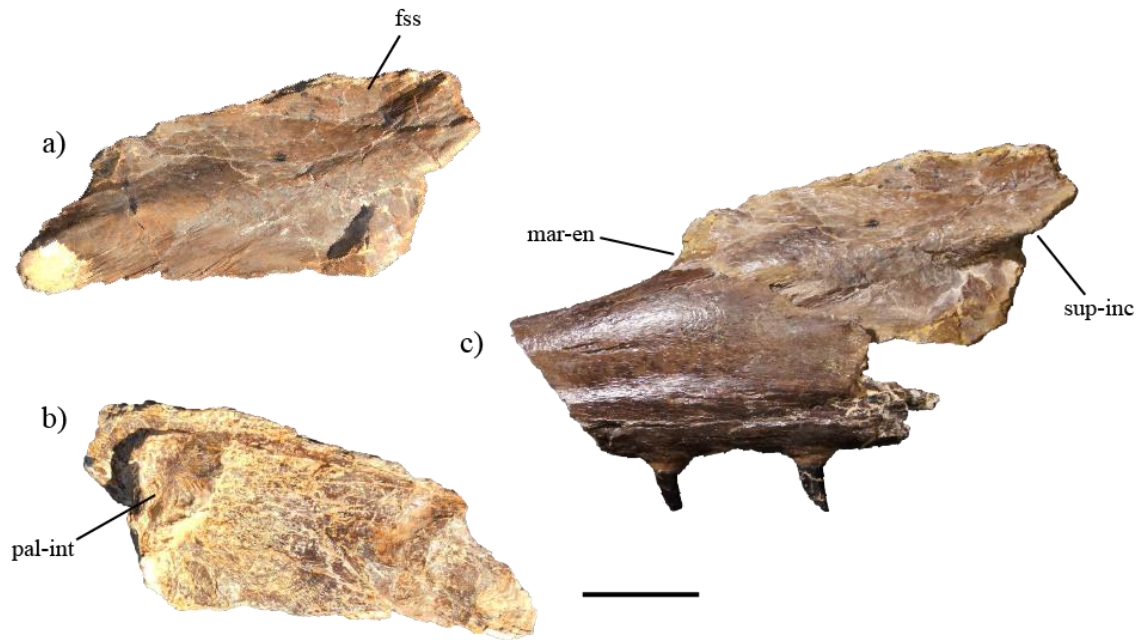
Figure 10. Left prefrontal of the new taxon in a) lateral and b) medial views; c) in articulation with a partial left maxilla. Anatomical abbreviations: fss: frontal sutural surface; mar-en: margin of external naris; pal-int: interlocking ridges with palatine; sup-inc: incipient supraorbital process. Scale bar = 3 cm.

Figure 11. Partial left jugal of the new taxon in a) lateral and b) medial views. Anatomical abbreviations: ect-a: ectopterygoid articulation; pv: posteroventral process. Scale bar = 3 cm.

Figure 12. Squamosals of the new taxon. Right squamosal a) dorsolateral and b) ventromedial views; left squamosal in c) dorsolateral and d) dorsomedial. Anatomical abbreviations: par-p: parietal process; qf: quadrate facet; st-f: supratemporal facet; st-s: supratemporal suture. Scale bar = 3 cm.

Figure 13. Partial right palatine of the new taxon in a) dorsal and b) ventral views. Anatomical abbreviations: mx-a: maxilla articulation; prf-a: prefrontal articulation. Scale bar = 1 cm.
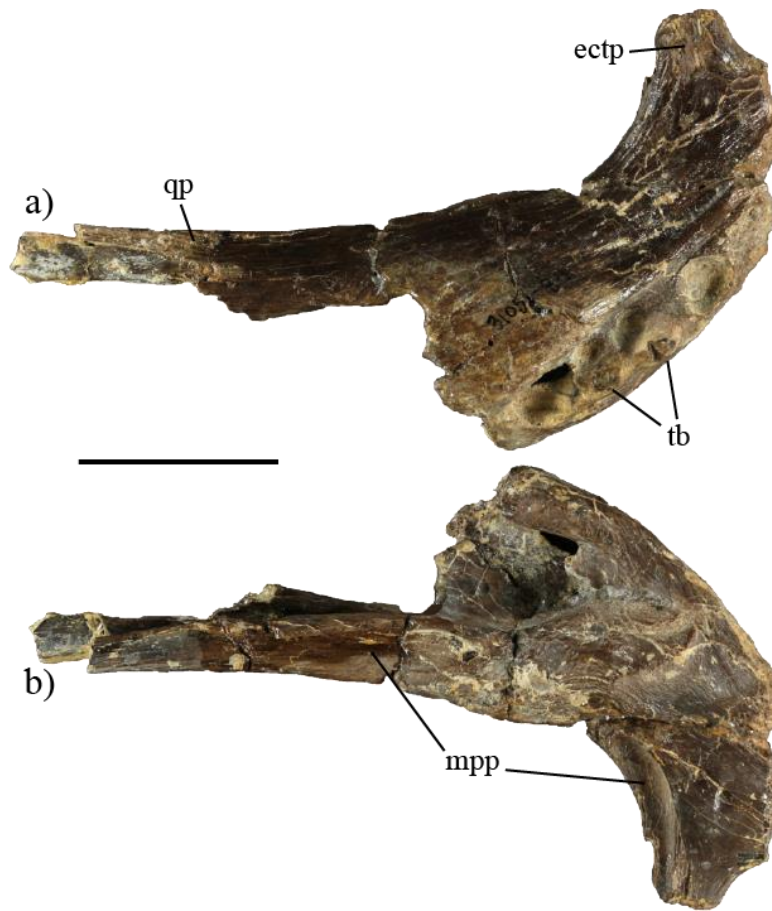
Figure 14. Partial right pterygoid of the new taxon in a) dorsal and b) ventral views. Anatomical abbreviations: ectp: ectopterygoid process; mpp: probable attachment of the *m. pterygoideus profundus*; qp: quadrate process; tb: tooth base. Scale bar = 3 cm.
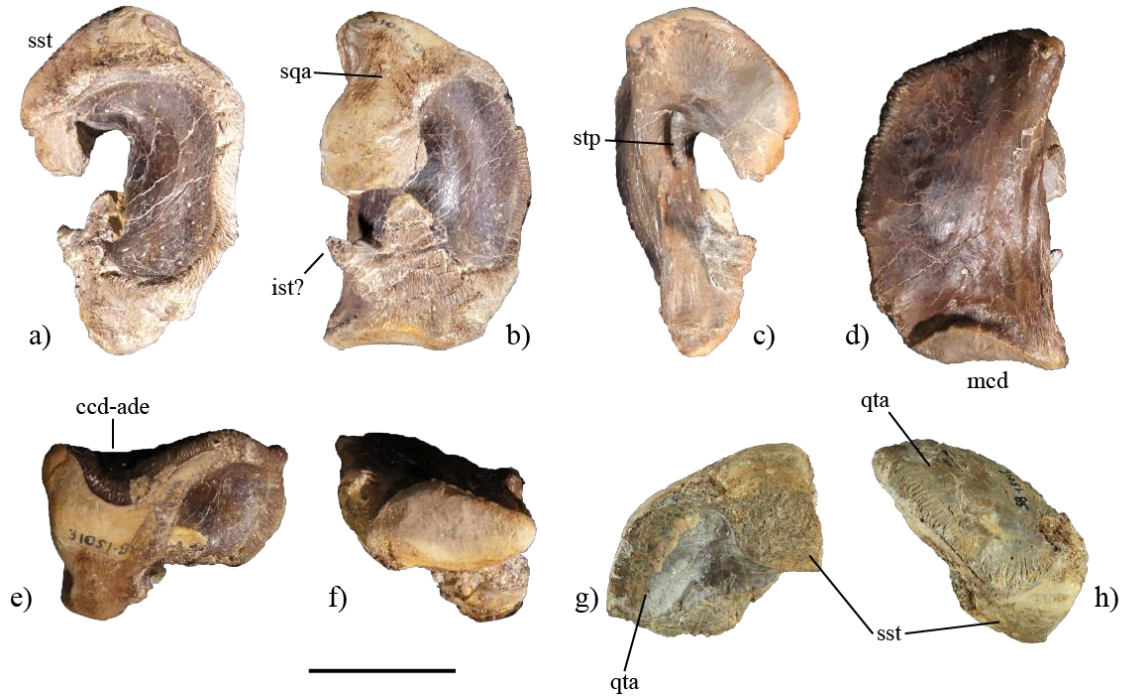
Figure 15. Quadrates of the new taxon. Right quadrate in a) lateral, b) posterior, c) medial, d) anterior, e) dorsal, and f) ventral views; partial left quadrate in g) posterior and h) anterodorsal views. Anatomical abbreviations: ccd-ade: cephalic condyle anterodorsal excavation; ist?: possibly pathologic infrastapedial process; mcd: mandibular condyle, qta: quadrate tympanic ala; sqa: squamosal articulation; stp: stapedial pit; sst: suprastapedial process. Scale bar = 3 cm.
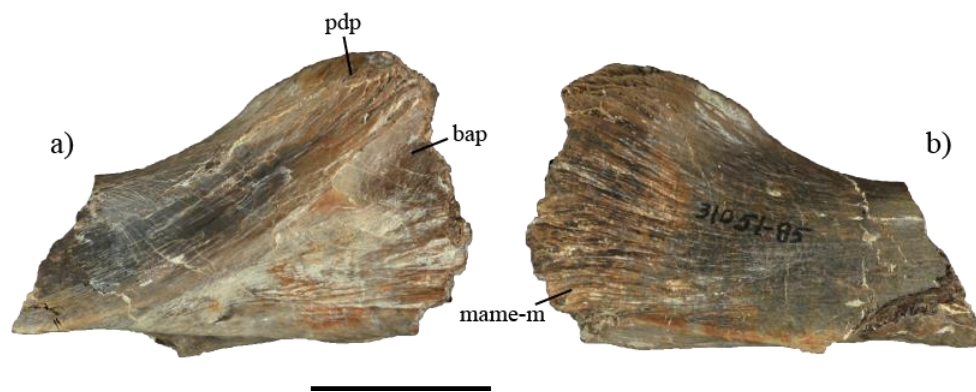
Figure 16. Partial left coronoid of the new taxon in a) lateral and b) medial views. Anatomical abbreviations: bap: probable attachment of the bodenaponeurosis; mame-m: probable attachment of the *m. adductor mandibulae externus superficialis* and *externus*, and the *medius*; pdp: posterodorsal process. Scale bar = 2 cm.
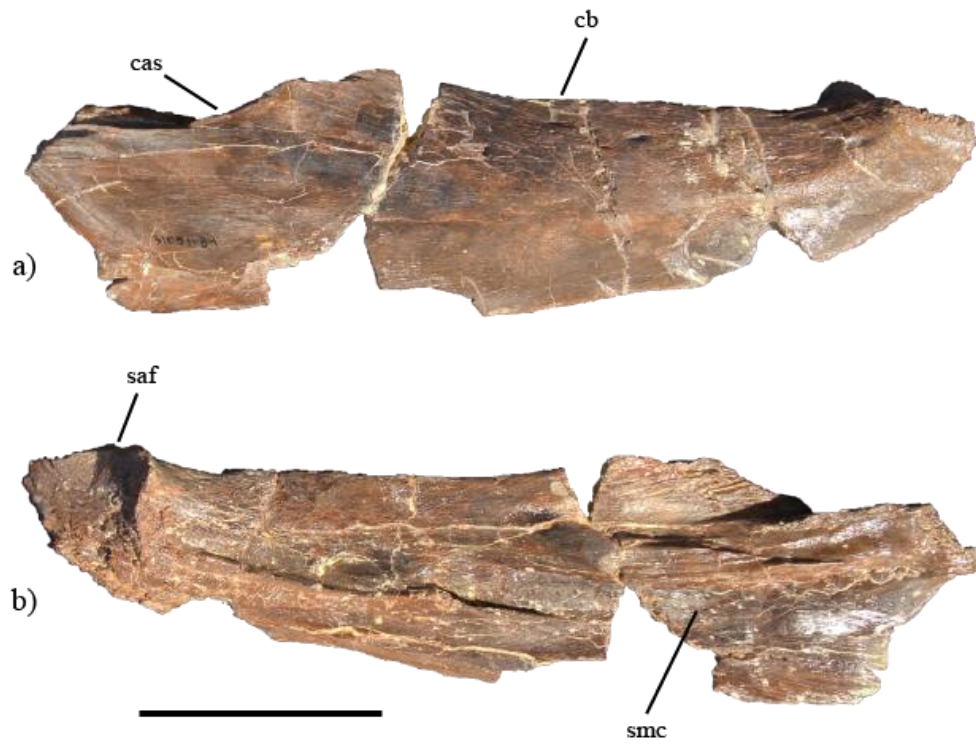
Figure 17. Left surangular of the new taxon in a) lateral and b) medial views. Anatomical abbreviations: cas: coronoid articulation surface on the surangular; cb: coronoid buttress; saf: surangular contribution to the articular ('glenoid') fossa; smc: surangular potion of Meckel's canal. Scale bar = 5 cm.
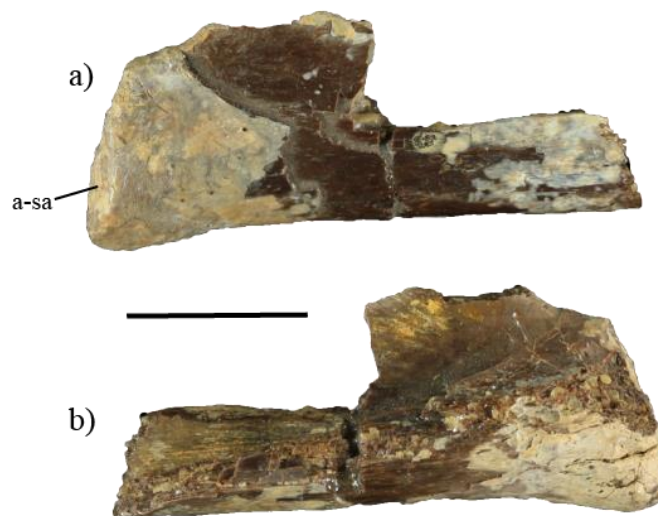
Figure 18. Partial left angular of the new taxon in a) lateral and medial views. Anatomical abbreviation: a-sa: angular-splenial articulation. Scale bar = 2 cm.
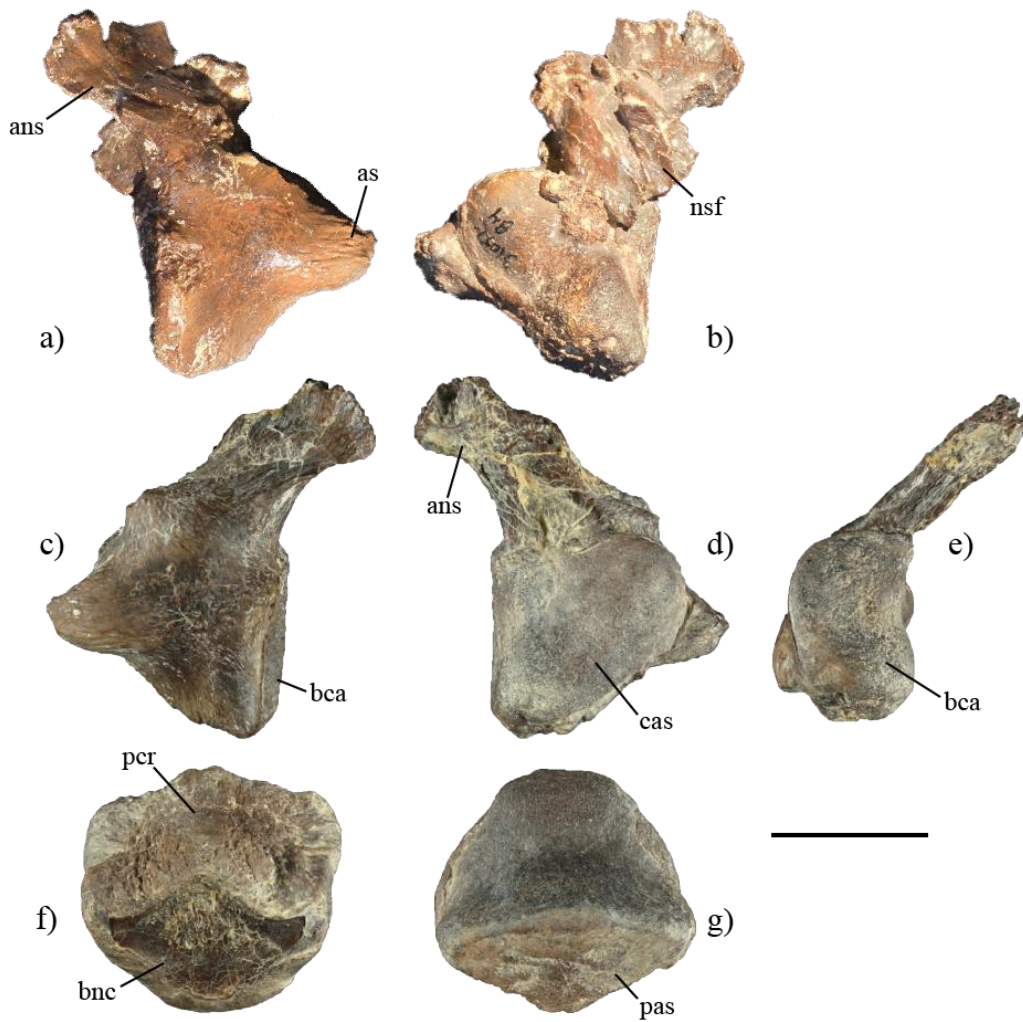
Figure 19. Elements of the atlas of the new taxon. Left atlantal neural arch in a) lateral and b) medial views; right atlantal neural arch in c) lateral, d) medial, and e) anterior views; atlantal centrum in f) posterodorsal and g) anteroventral views. Anatomical abbreviations: ans: atlantal neural spine; as: atlantal synapophysis; bca: brain case articulation surface; bnc: base of the neural canal; cas: centrum articulation surface; nsf: neural spine fragment (likely from another vertebra); pas: pleurocentrum articulation surface; pcr: posterior centrum ridge. Scale bar = 2 cm.
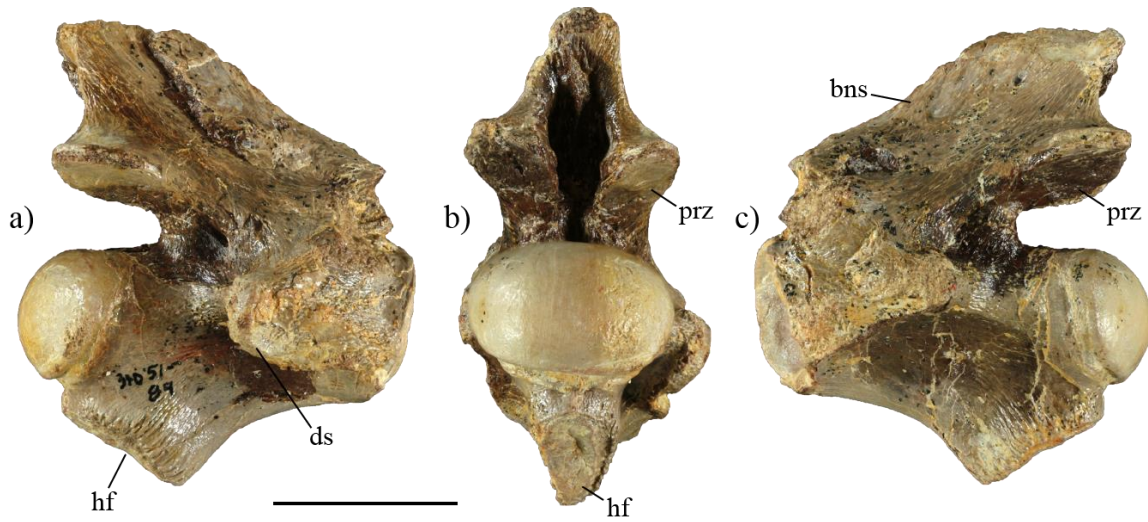
Figure 20. One of the more intact cervical vertebra of the new taxon in a) left lateral, b) anterior, and c) right lateral views. Anatomical abbreviations: bns: base of the neural spine; ds: distorted synapophysis; hf: hypapophyseal facet; prz: prezygapophysis. Scale bar = 3 cm.
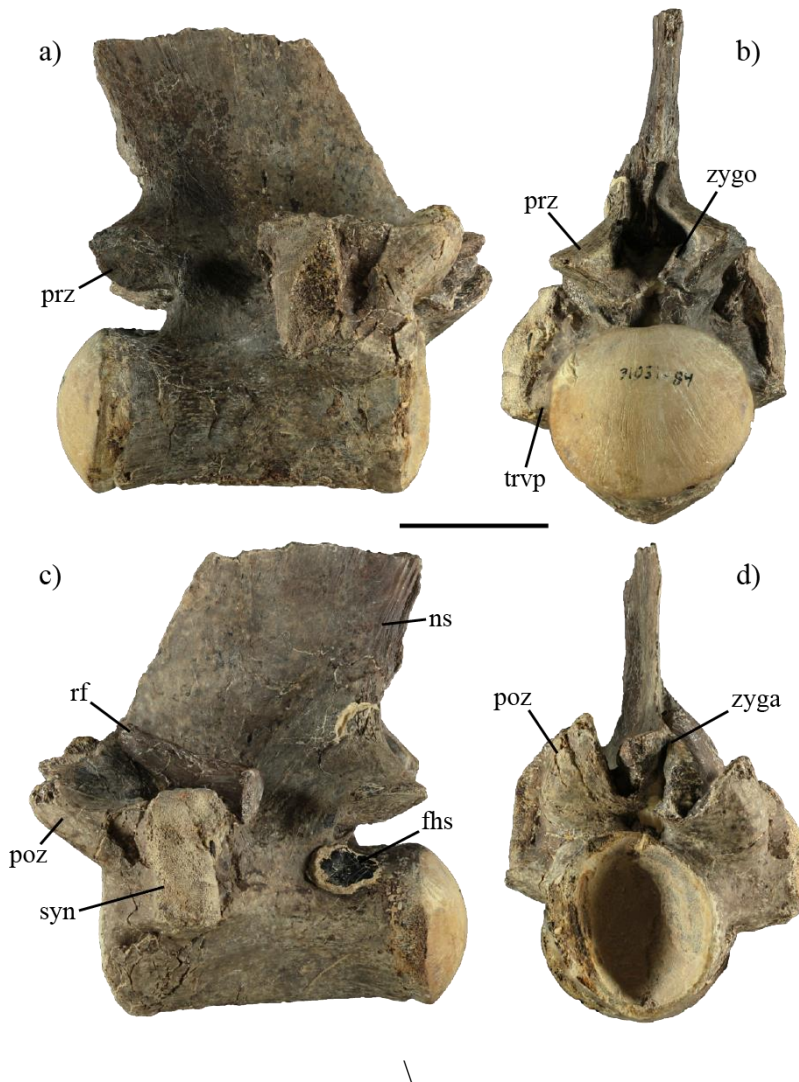
Figure 21. Anterior trunk vertebra of the new taxon in a) left lateral, b) anterior, c) right lateral, and d) posterior views. Anatomical abbreviations: fhs: fish scale; ns: neural spine; poz: postzygapophysis; prz: prezygapophysis; rf: rib fragment; syn: synapophysis; trvp: transverse process; zygo: zygosphenes; zyga: zygantra. Scale bar = 3 cm.

Figure 22. Mostly complete rib of the new taxon, shown on both sides a) and b). Anatomical abbreviation: syn-f: synapophyseal facet. Scale bar = 5 cm.

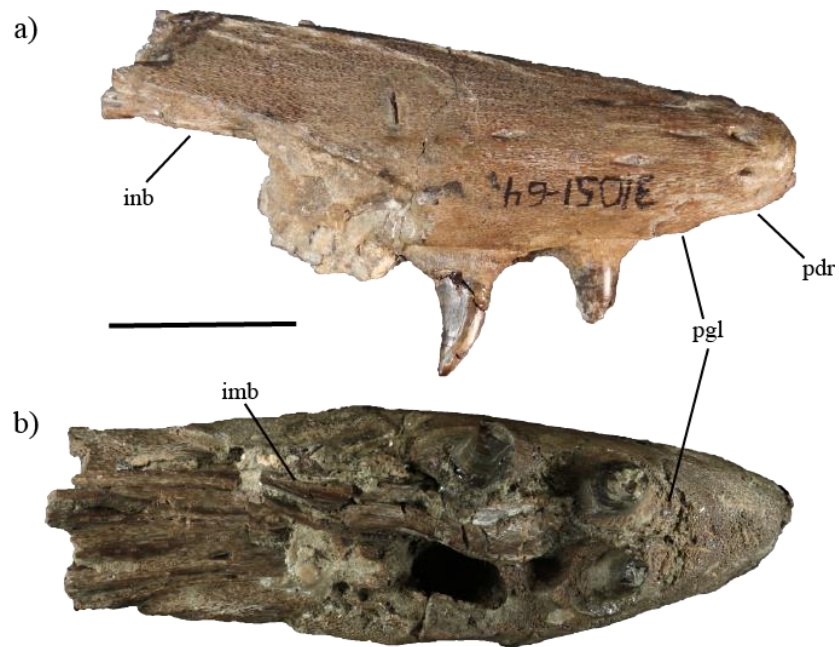Figure 23. Partial premaxilla of specimen TMM 31051-64, *Tylosaurus nepaeolicus*, in a) right lateral and b) ventral views. Anatomical abbreviations: imb: intermaxillary bar; inb: internarial bar; pdr: pre-dental rostrum on the premaxilla; pgl: premaxilla gum line (potential). Scale bar = 3 cm.

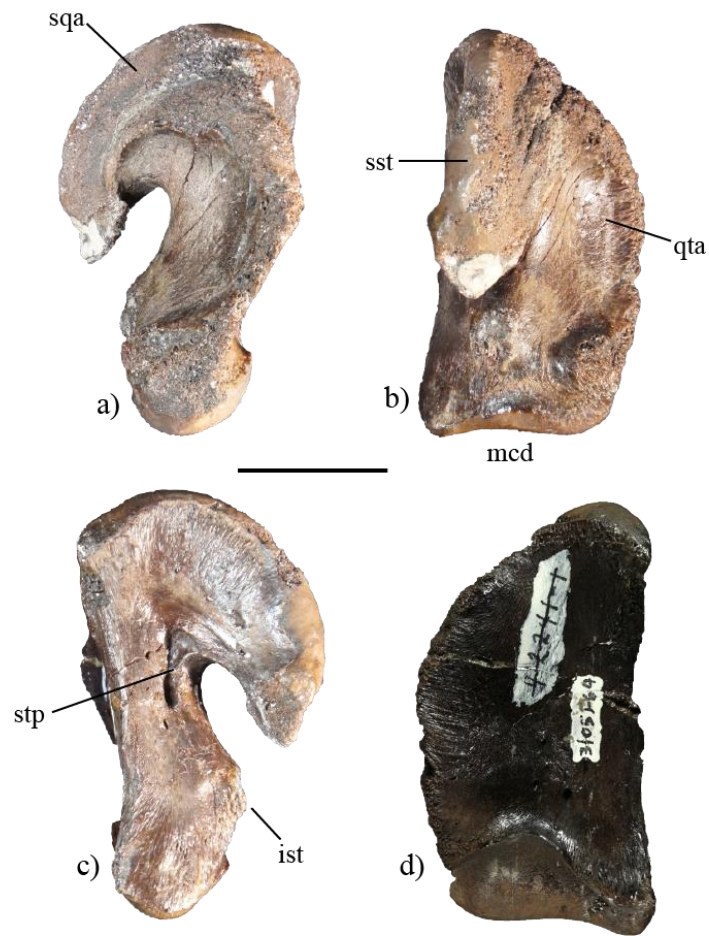Figure 24. Right quadrate of specimen TMM 31051-64, *Tylosaurus nepaeolicus*, in a) lateral, b) posterior, c) medial, and d) anterior views. Anatomical abbreviations: ccd: cephalic condyle; ccd-ade: cephalic condyle anterodorsal excavation; ist: infrastapedial process; mcd: mandibular condyle; qta: quadrate tympanic ala; sqa: squamosal articulation; stp: stapedial pit; sst: suprastapedial process. Scale bar = 3 cm.
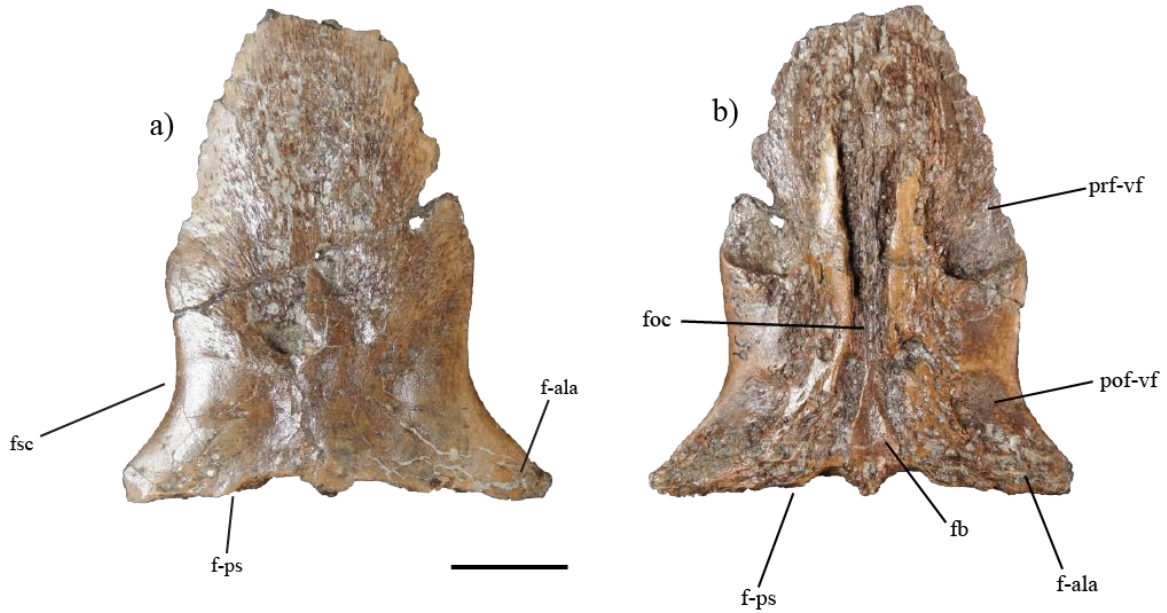
Figure 25. Isolated frontal of specimen TMM 31051-59 referred to Yaguarasaurinae cf. *Russellosaurus coheni* in a) dorsal and b) ventral views. Anatomical abbreviations: f-ala: frontal ala; fb: frontal boss (ventroposterior); foc: frontal olfactory canal; f-ps: fronto-parietal suture; fsc: frontal supraorbital constriction; pof-vf: postorbitofrontal ventral fossa on frontal; prf-vf = prefrontal ventral fossa on frontal. Scale bar = 2 cm.
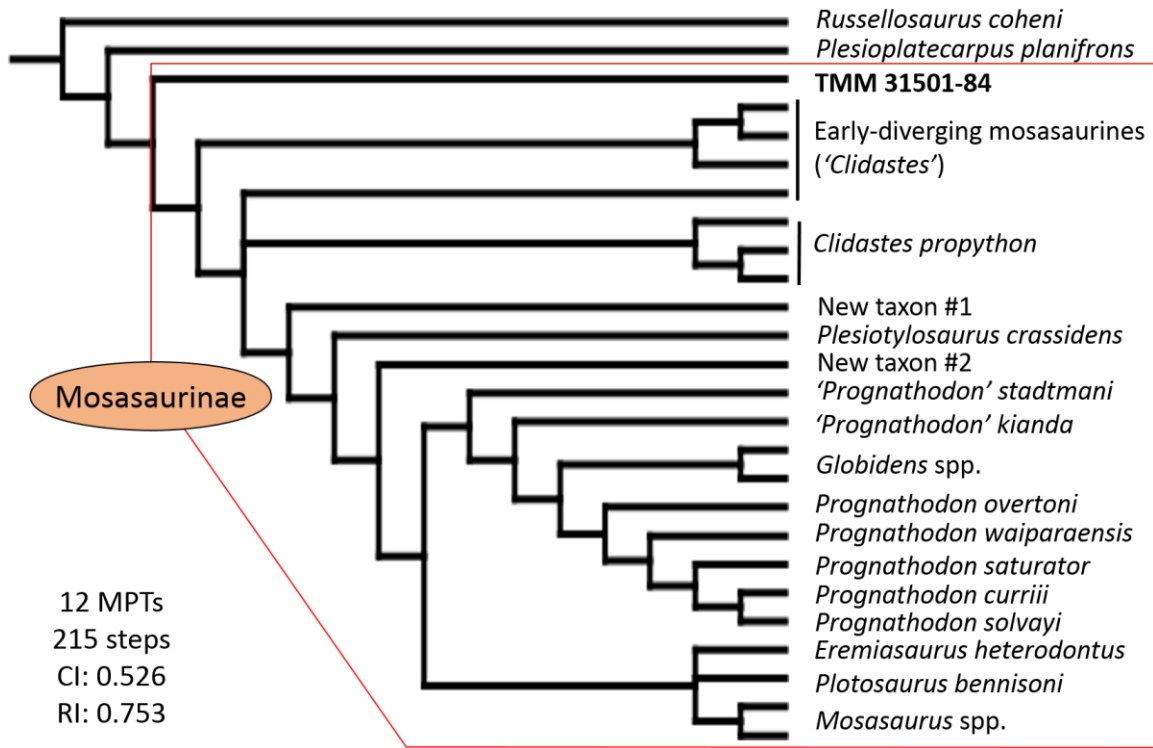
Figure 26. Phylogenetic hypothesis for Mosasaurinae based on pruned dataset and created as a strict consensus of maximum parsimony analysis. We scored TMM 31051-84 (highlighted in orange) and other mosasaurines using both novel discrete characters and those previously published by Russell (1967), Bell (1993, 1997), Bell and Polcyn (2005), and Konishi and Caldwell (2011). Outgroup taxa are the russellosaurines *Russellosaurus coheni* and *Plesioplatecarpus planifrons* (these form a monophyletic group though TNT will not allow a monophyletic outgroup). New Taxon #1 and New Taxon #2 correspond to unpublished specimens within the collections of the TMM, MSC, and FMNH. *Globidens spp. = Globidens alabamaensis* and *Globidens dakotaensis. Mosasaurus spp. = Mosasaurus hoffmannii* and *Mosasaurus missouriensis*. Abbreviations: MPTs = most parsimonious trees; CI = consistency index; RI = retention index.

Figure 27. Temporal distribution of select Late Cretaceous mosasaurs within the Western Interior Seaway. Distributions of described mosasaur species based on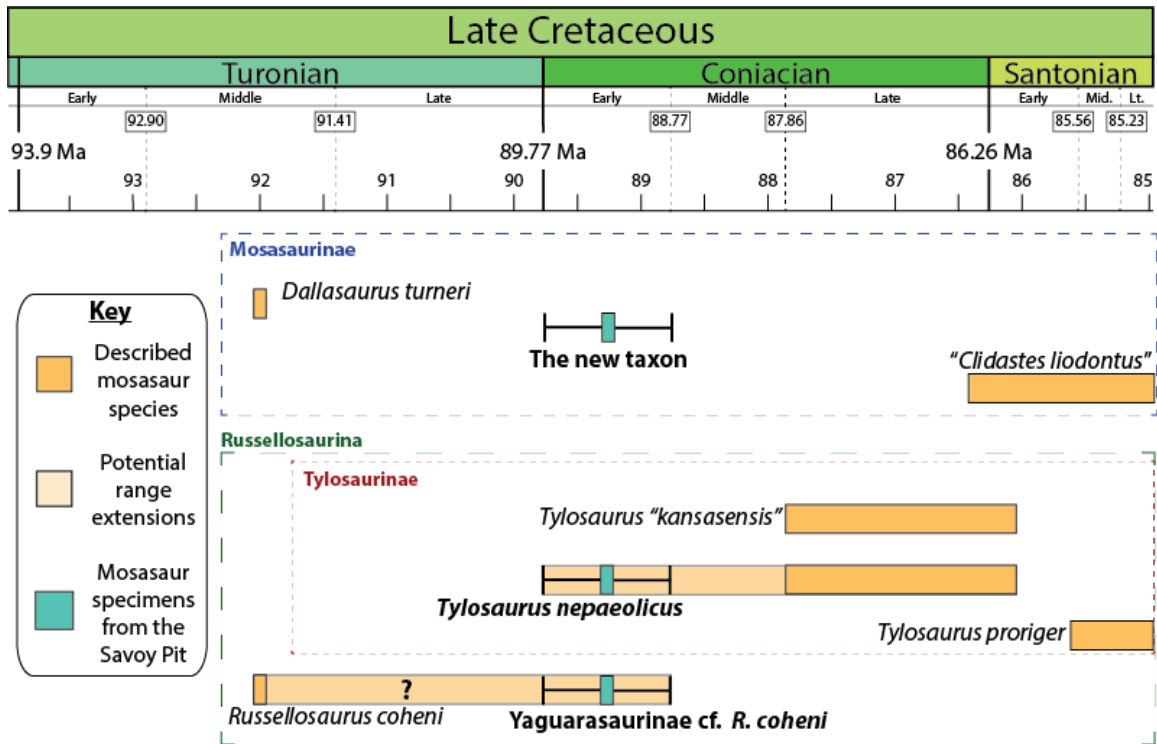 information in Everhart (2001), Bell and Polcyn (2005), and Polcyn, Bell, Shimada, & Everhart (2008). Chronologic age and subage boundaries are based on Ogg et al., 2012.

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