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Redescription of the holotypes of *Tylosaurus proriger* and *Tylosaurus nepaeolicus* (Squamata: Mosasauridae)

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ABSTRACT
Mosasaurs are a clade of extinct secondarily marine-adapted lizards whose fossils are relatively common in museum collections around the world. While mosasaurs have been studied for over 200 years, many important specimens, including holotypes, are insufficiently documented or completely absent from the scientific literature. This limits the accessibility of these specimens to the scientific community, particularly to researchers who, for many possible reasons, cannot travel to see the specimens firsthand. The mosasaur genus *Tylosaurus* has been the subject of many recent projects aiming to study intraspecific variation (i.e., ontogeny) in mosasaurs; however, hypotheses of intraspecific variation must be assessed in the context of confident species delimitation, which is a difficult problem in vertebrate paleontology, compounded by poor preservation or documentation of holotype specimens. This is the case for most tylosaurine species, which are poorly figured, and in the case of the type species, *T. proriger*, completely absent from the modern scientific literature. In this work, we redescribe and figure two important *Tylosaurus* holotype specimens, *T. proriger* and *T. nepaeolicus*, rediagnosing both species by comparison with over 100 tylosaurine specimens.

Keywords Mosasauridae, Tylosaurinae, taxonomy, morphology, historical paleontology

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INTRODUCTION

Mosasaurs are a clade of extinct marine lizards that occupied many niches, including apex predator, in the Late Cretaceous oceans and inland seas globally (Fig. 1). *Tylosaurus* was the third mosasaur genus to be described from North America, and is characterized in part by a long, edentulous premaxillary rostrum (Cope, 1870). As the second most common mosasaur in North American museum collections (Table 1), it is theoretically an ideal candidate for studying inter- and intraspecific morphological variation and macroevolutionary questions

Figure 1 Reconstruction of *Tylosaurus proriger* hunting polycotylid plesiosaurs. Illustration by Andrey Atuchin.

Genus	**This Work**	**Driscoll *et al.* 2018**	**TOTAL**
Clidastes	373	153	526
Mosasaurus	219	56	275
Platecarpus	910	71	981
Tylosaurus	484	151	635
Other	1137	872	2009
TOTAL	3123	1303	4426

Table 1 Counts of mosasaur specimens, identified to the genus level, in North American institutions. In this work, specimens were counted using the supplemental data 1 of Driscoll *et al.* (2018) as well as online databases and personal observation of specimens by A.R.Z. in the following institutions: AMNH (263 specimens), CMN (142 specimens), FHSM (212 specimens), FMNH (129 specimens), KUVP (392 specimens), MCZ (55 specimens), TMP (171 specimens), USNM (247 specimens), and YPM (1512 specimens). Note: all specimens from those institutions listed were excluded from the Driscoll *et al.* (2018) dataset counts, although many of them are listed therein, to avoid counting them twice.

that depend on accurate species identification. These lines of research are challenging due to brief and outdated descriptions and a general absence of clear, comprehensive figures, necessitating reassessment of many historical specimens.

The type species of *Tylosaurus, T. proriger* (Cope, 1869), is known from dozens of specimens, mostly found in the Niobrara Formation of Kansas and South Dakota. It has served as the basis for several recent studies of intraspecific variation in mosasaurs (e.g., Jiménez-Huidobro *et al.* 2016; Stewart and Mallon 2018; Zietlow 2020) without critical taxonomic assessment of the dozens of specimens referred to the species. These studies have also largely excluded the holotype specimen, MCZ VPRA 4374, which has not been figured nor otherwise addressed in detail in any publication since it was first described over 150 years ago. Holotype specimens are critically important as their morphology is the data upon which fossil taxa are erected, and thus diagnostic morphology directly comparable with the holotype should underly new species referrals.

The second described *Tylosaurus* species, *T. nepaeolicus* (Cope 1874), also remains poorly-documented. Its holotype

(AMNH FARB 1565) has recently been partially figured (Jiménez-Huidobro *et al.* 2016: 69), but it has not been redescribed. Underscoring the importance of well-documented holotypes are a recent series of studies that question whether *T. kansasensis* Everhart (2005) is a junior synonym of *T. nepaeolicus*, and possibly an ontogenetic stage of the latter taxon (Jiménez-Huidobro *et al.* 2016; Stewart and Mallon 2018; Zietlow 2020). Perhaps because the holotype of *T. nepaeolicus* is largely absent from the literature, this hypothesis of synonymy relies primarily on *referred* specimens, which introduces the possibility that the specimens being compared may not actually belong to the species of interest. While we will not address this hypothesis in detail here, additional work on that subject is forthcoming (Zietlow 2024, and other work in prep).

The objective of this work is to redescribe two historic *Tylosaurus* holotype specimens, *T. proriger* (MCZ VPRA 4374) and *T. nepaeolicus* (AMNH FARB 1565), rediagnose both species, and briefly discuss new diagnostic characters.

Provenance

Although neither of the holotypes have precise locality or stratigraphic data, we provide historical context and some contemporaneous accounts of the discovery and institutional acquisitions of *Tylosaurus proriger* (MCZ VPRA 4374) and *T. nepaeolicus* (AMNH FARB 1565).

Tylosaurus proriger: MCZ VPRA 4374

The first documented accounts of *Tylosaurus proriger* (MCZ VPRA 4374) were in regional newspapers (*Wyandotte Commercial Gazette*, November 21, 1868; the *White Cloud Kansas Chief,* December 3, 1868), in which the discovery was attributed to a Mr. William Webb. At the December 21, 1868 meeting of the Academy of Natural Sciences in Philadelphia (ANSP), Joseph Leidy exhibited photographs of a specimen he had received from Webb (Leidy 1868:316), noting the presence of "vertebrae, and fragments of the jaws with teeth". Thus, it appears that at that time, the specimen referred to in the newspaper articles was still in possession of Mr. Webb. Webb (1872:326) later wrote that the fossil "now rests in the museum at Cambridge, Massachusetts," and also noted that it had been "forwarded to Agassiz" (Webb 1875:832). Additionally, a receipt for the transfer of $500.00 from Dr. Agassiz to Mr. Webb, dated April 6th, 1869 (Fig. 2), survives with the holotype of *Tylosaurus proriger* (MCZ VPRA 4374) today, confirming the acquisition of the specimen around that time. Apparently, E.D. Cope borrowed the specimen soon after its acquisition, briefly describing and naming it orally at the June 1, 1869 meeting of the ANSP (Cope 1869:123), and the following year it was figured and more thoroughly described (Cope 1870:202-205, Plate XII:22-24). From the various accounts above, the chain of custody of MCZ VPRA 4374 from Webb, to Agassiz, to Cope is clear. However, a

Museum of Comparative Zoology,
Cambridge, April 6th 1869.

$ 500 $

Received of Prof. Agassiz – Five Hundred —— dollars,
for ~~services rendered in Museum Comp. Zoology during~~ a fossil Saurian &c.

W. E. Webb

U.S. INTER. REV. TWO CENTS 2 2 2 2 U.S. INTER. REV.
W.E.W. Apl 6th

Figure 2 A photocopy of the receipt of sale for the holotype specimen of *Tylosaurus proriger*, now accessioned as MCZ VPRA 4374. Photocopy courtesy of the Ernst Mayer Library.

subsequent account by Williston (1898), crediting Captain John Conyngham and a Mr. Minor with the collection of the specimen near Monument station, and its subsequent transfer to Agassiz, though apparently at odds with the documented contemporaneous record, may provide some clues to its probable locality.

Conyngham was stationed at Fort Monument, which served as a stagecoach station prior to completion of the railroad and was located some 20-25 miles south of the railroad. In June of 1868, Conyngham relocated his troops to Monument (originally Antelope) then being established along the railroad (Wetzel 1960). In August of 1868, a party of Federal government officials, including Louis Agassiz of Harvard University, traveled through Monument (*Leavenworth Conservative*, August 28, 1868). It is likely that Agassiz met Webb on that visit (Taft 1953; Everhart 2016), and possibly also Conyngham. The records for MCZ VPRA 4374 at Harvard University's Museum of Comparative Zoology indicate it came from near Monument Rocks (Smoky Hill Chalk) in western Gove County, the location of Conyngham's assigned post until June of 1868. We conjecture that Williston was at least in part correct in his crediting Conyngham and Minor with the discovery, as the matrix still preserved with the specimen is lithologically consistent with the Smoky Hill Chalk, and unlike the Pierre Shale present near Sheridan, the location reported in popular accounts of the discovery (e.g., *Wyandotte Commercial Gazette*, November 21, 1868; the *White Cloud Kansas Chief,* December 3, 1868), and in Webb's own fictional accounts (Webb 1872:326; 1875:832). In any event, future work will be required to analyze the matrix adhered to the specimen and to thoroughly explore institutional archives that may contain additional relevant data regarding the provenience of the holotype of *Tylosaurus proriger* (MCZ VPRA 4374).

Taxonomy and early work

E.D. Cope likely saw the photos of the specimen reported by Leidy (1868) at the December 21, 1868 ANSP meeting. He subsequently borrowed the remains from the MCZ, and briefly described and named the new species orally at the June 1, 1869 meeting of the ANSP. Cope (1869:123) "made some remarks on a fine fragment of the muzzle of a large Mosasauroid, which pertained to a cranium of near five feet in length. The pterygoid bones were separated from each other, and support nine teeth. A peculiarity of physiognomy was produced by the cylindric prolongation of the premaxillary bone beyond the teeth, and a similar flat prolongation of the extremity of the dentary. He referred the species to *Macrosaurus* Owen, under the name *M. proriger.* The specimen he stated belonged to Prof. Agassiz, who obtained it from Western Kansas, probably from the No. 3 of the Upper Cretaceous [Niobrara Fm.] of Hayden."

The following year, Cope describes the specimen more thoroughly, refers it to another genus (*Liodon* Owen 1841) without explanation, and figures the partial muzzle (premaxilla, anterior palate, right maxilla) (Cope 1870:202-205, Plate XII:22-24). Two years later, O.C. Marsh, apparently recognizing significant differences between the American and European mosasaurs, proposed a new genus (*Rhinosaurus*) from a more complete specimen (YPM VP 1268, referred to *Rhinosaurus micromus*) he had collected "on the south side of the Smoky Hill River" in 1871. However, that name was preoccupied and so Cope (1872) then proposed the genus name *Rhamphosaurus* instead. In a brief note, Marsh (1872:147) wrote that: "As this name [*Rhinosaurus*] proves to be preoccupied, it may be replaced with *Tylosaurus.* The name *Rhamphosaurus*, since suggested by Prof. Cope, cannot be retained, as it was given to a genus of lizards in 1843 by Fitzinger." Leidy (1873:274) was the first to place '*Macrosaurus*' *proriger* Cope into *Tylosaurus* Marsh.

Perhaps unsurprisingly, Cope did not give up on his own proposed genus name. In his *Review of the Vertebrata of the Cretaceous Period found West of the Mississippi River* (1874:36), he included the following disclaimer as part of his description of a new species of *Rhamphosaurus* (*Tylosaurus nepaeolicus*): "[*Rhamphosaurus*] was applied by Fitzinger to two species of lizards, which had already received several generic names, and hence became at once a synonym. Further, he did not characterize it; for these reasons the name was not preoccupied at the time I employed it as above; hence there is no necessity for Prof. Marsh's subsequent name *Tylosaurus*, given on the supposition of preoccupation." In the description itself, however, he refers the species to *Liodon.* Then, in 1875 (pp 160-167), Cope then describes MCZ VPRA 4374 once again (nearly identically to the 1870 description) without additional figures, but including reference to other specimens (e.g., Plates XXVIII, XXX). He refers both species (*T. proriger* and *T. nepaeolicus*) to *Liodon* Owen, reiterating his claim that "there is as yet no evidence" that the specimens are referable to a genus distinct from *Liodon,* but if they are found to be distinct, Cope adds in a footnote, they ought to be called *Rhamphosaurus* Cope, and not *Tylosaurus* Marsh (Cope 1875:161).

Current status of MCZ VPRA 4374

Today, MCZ VPRA 4374 comprises a premaxilla, maxillae, partial vomers, partial palatines, partial prefrontal, right dentary, seven small indeterminate skull fragments, and three vertebrae (one dorsal, one pygal, one caudal). Cope repeatedly (1869; 1870:201-202, 204; 1875:161) describes the specimen as including at least one pterygoid, and in 1875, he also mistakenly refers to mosasaur pterygoids as palatines in several places; e.g., see Plate XXXVI). However, given that we could not find any part of either pterygoid preserved with the specimen nor figured by Cope (1870, Plate XII:22-24), we believe that he may have misidentified the fragment of left maxilla which preserves nine tooth positions, which is adpressed to the right dentary. Arguing against this is the fact that the bone is correctly figured as the left maxilla in 1870 (Plate XII:22).

Other bones that are reported by Cope as being present with the holotype, but that we could not find with the specimen as it currently exists, are "one cervical vertebra (with hypapophysis)" and "ten caudals without diapophysis" (1870:202; 1875:161). Cope does not figure any vertebrae of the holotype in 1870 (Plate XII:22-24), and only figures eight (one cervical, seven caudals) of the 13 that he claims belong to the specimen in 1875 (Plate XXX:10-14); however, only one of those (Plate XXX:13a, 13b) looks anything like one of the three vertebrae currently associated with the specimen. Additionally, Russell (1967:175) reports that the entire holotype specimen is missing – anecdotally, this was said to be because Cope borrowed the fossil for study at some point and did not return it (M.J.E., pers. comm. with D.A. Russell). While Russell's claim that the entire type specimen is missing is not entirely true, it may be relevant to the missing vertebrae. At this time, it is unclear whether the other vertebrae that Cope describes and apparently measured (1870:202-203; 1875:162-163) are lost or were never associated with MCZ VPRA 4374 to begin with.

Tylosaurus nepaeolicus: AMNH FARB 1565

Cope describes *Tylosaurus nepaeolicus* (as *Liodon nepaeolicus*) in 1874 (pp. 37-38) but does not figure the specimen until the following year (1875, Plate XXXV:11-15). Compared to MCZ VPRA 4374, the circumstances surrounding the collection of the holotype specimen of *T. nepaeolicus*, AMNH FARB 1565, are more ambiguous. The collections records for AMNH FARB 1565 indicate it was collected by Benjamin E. Mudge, likely in 1872 or 1873 given that Cope does not mention it earlier despite having visited Mudge in 1871 (e.g., Cope 1872). Accompanying the description of the specimen, Cope reports that Mudge found it in "the gray shale of the Niobrara Cretaceous, a half mile south of the Solomon River," in north-central Kansas (Cope 1874:38). The native American name for the Solomon River is Nepaholla (which Cope does use in an earlier report of a fish, "from the yellow chalk of the upper cretaceous (sic) of Kansas near the Solomon or Nepaholla River"; Cope 1871:416), which is presumably the source for the species name.

Current status of AMNH FARB 1565

AMNH FARB 1565 currently comprises a fragment of the premaxilla, a fragment of the right maxilla, the right quadrate, a fragment of the posteromedial parietal, a fragment of the left pterygoid, the right posterior mandibular unit, a right splenial, fragments of the right dentary, the odontoid, and a dorsal vertebra. While the box containing the holotype specimen does include several other bones, one of those other bones is a second right splenial, which does not articulate with the posterior mandibular unit (as the other does), and is thus not part of the holotype. The rest of the bones are primarily fragmentary ribs, which are not known to be diagnostic in mosasaurs. We are thus conservative in our conception of the holotype specimen and are only including the bones (listed above) that are: (1) indisputably figured and described as *Liodon* (*Tylosaurus*) *nepaeolicus* by Cope (1874:37-38; 1875:177-178, Plate XXXV); (2) articulate with one another; (3) are consistent with a tylosaurine identity; (4) and or unambiguously match each other in preservation quality and color.

It is also worth noting that Cope's figure depicts the dentary and splenial as much more complete than we were able to reassemble from the fragments currently in the specimen's box. According to Cope (1875:177), "Professor Mudge, who discovered the specimen, states that the jaw, when together, measured twenty-six inches in length, which would leave thirteen inches for the dentary bone", and he posits that the dentary would have likely had 13 teeth. It is unclear from this statement whether the jaw was complete when Mudge found and measured it, then later broken, resulting in the loss of some pieces, or if the length of the "jaw, when together" that he reported to Cope was an estimate then used to 'fill out' the figure.

Anatomical abbreviations

amf, anterior mylohyoid foramen; ang, angular; ar, articular; ax, axis; bc, basicranium; bm, bite marks; bn, bony external narial opening; c, coronoid; ch, internal choana; d, dentary; dla, splenial dorsolateral ala; dma, splenial dorsomedial ala; dMdm, depression for the attachment of the depressor mandibulae; dorp, dorsal process of the dentary; dsym, dentary symphysis; dv, dorsal vertebra; f, frontal; gf, glenoid fossa; ha, haemal arch; haf, facet for haemal arch; hu, humerus; ip, incisive process of the premaxilla; iptv, interpterygoid vacuity; L, left; lsaf, lateral adductor fossa of the surangular; Mc, Meckelian canal; mr, quadrate median ridge; msaf, medial adductor fossa of the surangular; mx, maxilla; mxf, maxilla facet of the palatine; neu ca, neural canal; neu sp, neural spine; nu, premaxilla nubbin; nuf, nuchal fossa of the parietal; pa, parietal; pl, palatine; plf, palatine facet of the maxilla; plp, quadrate posterolateral process; pmxa, premaxilla-maxilla aperture; pmp, quadrate posteromedial process; pmx, premaxilla; pmxf, premaxilla foramen; posdor, posterodorsal; po, postzygapophysis; pra, prearticular process of the articular; pre, prezygapophysis; prf, prefrontal; pt, pterygoid; q, quadrate; qad, quadrate mandibular condyle anterior deflection; R, right; ra, radius; sa, surangular; smx, septomaxilla; sn, stapedial notch; sp, quadrate stapedial pit; spl, splenial; ssp, quadrate suprastapedial process; sy, synapophysis; trv proc, transverse process; vo, vomer; vof, vomeronasal fenestra; vofo, vomerine foramen; vomx, vomeromaxillary process of the premaxilla; vomxs, suture for the vomeromaxillary process of the premaxilla; vop, vomer process of the palatine.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, New York, USA; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; FHSM, Sternberg Museum of Natural History, Hays, Kansas, USA; FFHM, Fick Fossil and History Museum, Oakley, Kansas, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KUVP, Kansas University Museum of Natural History, Lawrence, Kansas, USA; MCZ, Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; PMNS, Perot Museum of Nature and Science (formerly DMNH, Dallas Museum of Natural History), Dallas, Texas, USA; TMP, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; USNM, Smithsonian Museum of Natural History, Washington D.C., USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

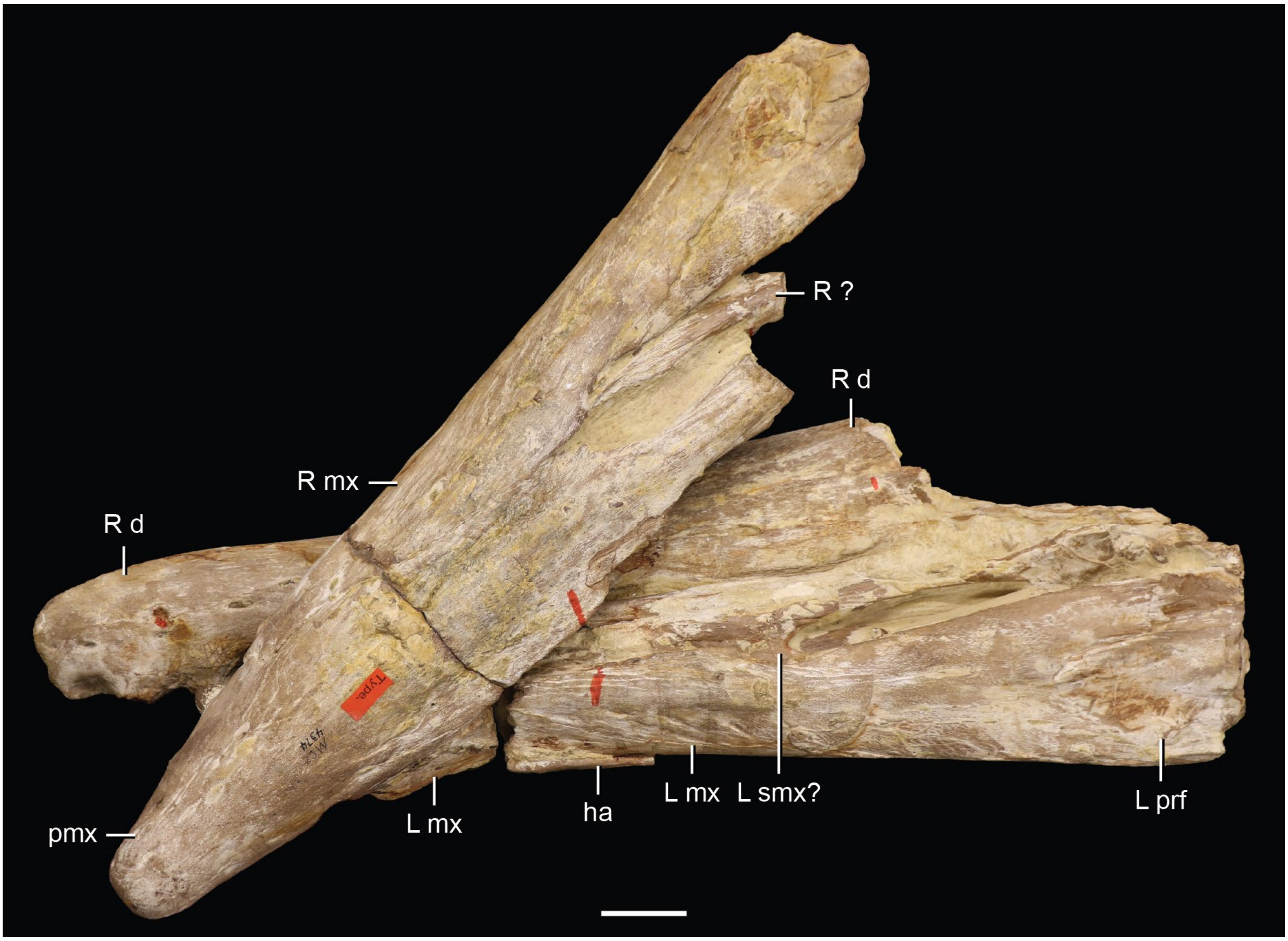

Figure 3 Skull and jaw of the holotype of *Tylosaurus proriger*, MCZ VPRA 4374, positioned as it was most likely was when discovered by articulating the broken left maxilla. Scale bar is 5 cm. Photograph by Amelia R. Zietlow.

SYSTEMATIC PALEONTOLOGY

Order Squamata Oppel 1811
Family Mosasauridae Gervais 1853
Subfamily Tylosaurinae Williston 1897
Genus *Tylosaurus* Marsh 1872

Type species: *Tylosaurus proriger* Cope 1869

Etymology

"Knob lizard" for the genus and "prow-bearing" for the species, both in reference to the elongate edentulous rostrum of the premaxilla (Everhart 2017).

Holotype

MCZ VPRA 4374 (Figs. 3, 4, 5, 6, 7, 8). We note that, medial to the sixth right maxillary tooth, another accession number, "MCZ 1596," is also written on the specimen in error (C.J. Byrd, pers. comm. 2024); the correct number is written on other parts of the same chunk.

Type locality

Smoky Hill Member of the Niobrara Formation. The holotype was initially reported as "from western Kansas, probably from the No. 3 of the Upper Cretaceous of Hayden" (Cope 1869:123). One year later (Cope 1870:202), the locality given is "the Cretaceous beds in the neighborhood of Fort Hays, Kansas, and near the line of the Southern Pacific Railroad," but this is corrected five years later (Cope 1875:161) to "the Cretaceous beds in the neighborhood of Monument, Kansas, and near the line of the Kansas Pacific Railroad," including a statement that the prior report of it being found near Fort Hays was "erroneous" (Cope 1875:167).

Referred specimens

The following specimens, which preserve bones that overlap without conflict with the holotype, were used to supplement our diagnosis of *T. proriger*: AMNH FARB 221, AMNH FARB 1555, FFHM 1997-10, FHSM VP-3, KUVP 28705, and MCZ VPRA 8790. We also use AMNH FARB 14799 and AMNH FARB 24426, which include several skull bones that are numbered separately, but likely belong to the same individual (they are identical in size and color/preservation, do not share overlapping elements, and originally shared the number 'AMNH FARB 14799;' A.R.Z., pers. obs.). Using the emended diagnosis, we also refer the following specimens to *T. proriger*: FMNH UR902, USNM 6086, YPM VP 1268, and YPM VP 4000.

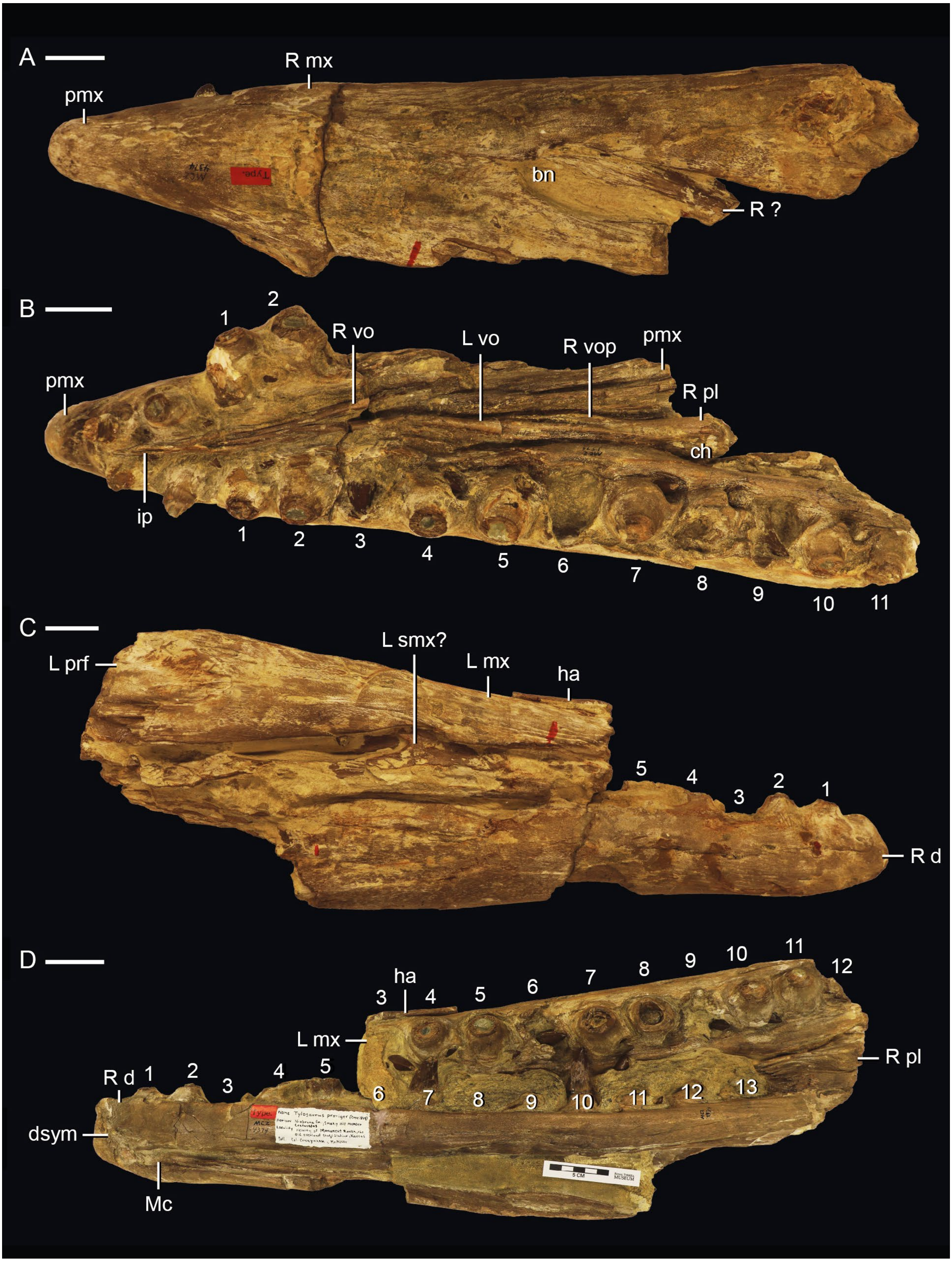

Figure 4 Snout (A, B) and right dentary plus left maxilla (C, D) of *Tylosaurus proriger* MCZ VPRA 4374; **A** the snout in dorsal view, **B** the snout in ventral view, **C** the right dentary in lateral view and the left maxilla in dorsolateral view, **D** the right dentary in medial view and the left maxilla in ventral view. Numbers indicate tooth positions, and question marks indicate uncertain identifications. All scale bars are 5 cm. Photographs by Amelia R. Zietlow.

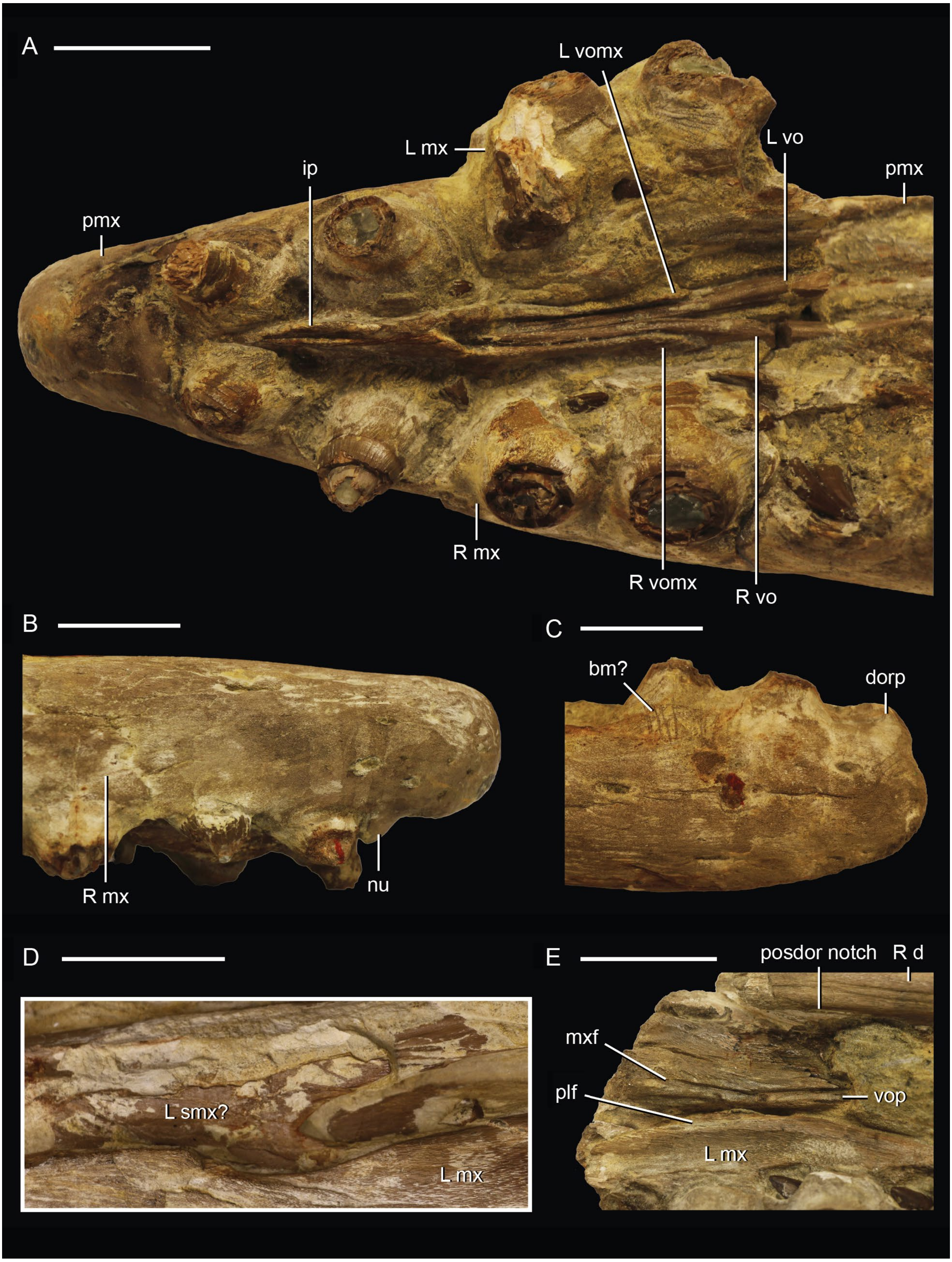

Figure 5 Various anatomical details of *Tylosaurus proriger* MCZ VPRA 4374; **A** the anterior palate in ventral view, **B** the anterior premaxilla in right lateral view, **C** the anterior right dentary in right lateral view, **D** a bone that we tentatively identify as the left septomaxilla, **E** the articulation between the left palatine and left maxilla. All scale bars are 5 cm. Photographs by Amelia R. Zietlow.

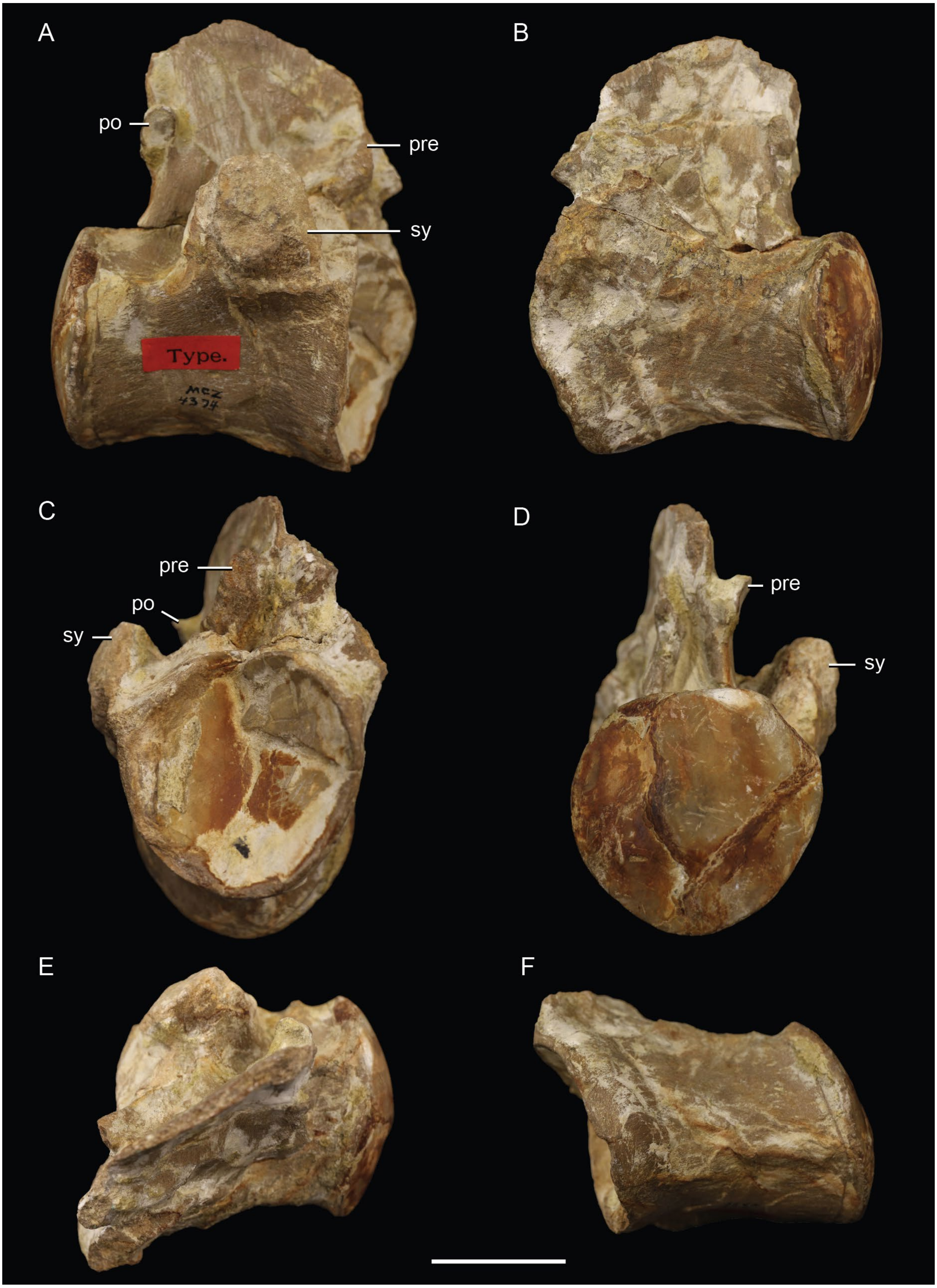

Figure 6 The dorsal vertebra of *Tylosaurus proriger* MCZ VPRA 4374; **A** right lateral view, **B** left lateral view, **C** anterior view, **D** posterior view, **E** dorsal view, **F** ventral view. Scale bar is 5 cm. Photographs by Amelia R. Zietlow.

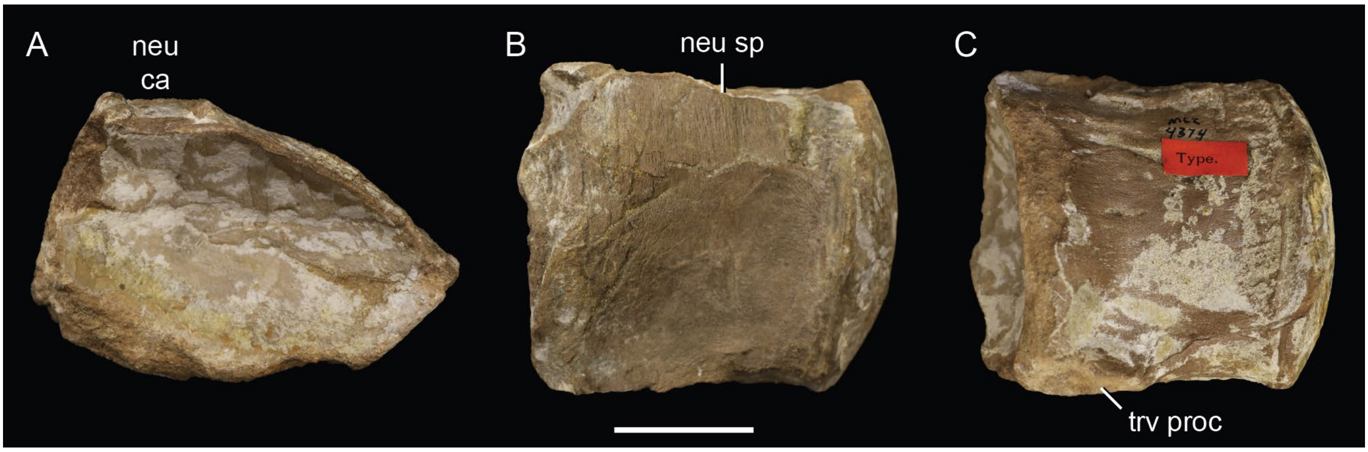

Figure 7 The pygal vertebra of *Tylosaurus proriger* MCZ VPRA 4374; **A** anterior view, **B** left dorsolateral view, **C** ventral view. Scale bar is 5 cm. Photographs by Amelia R. Zietlow.

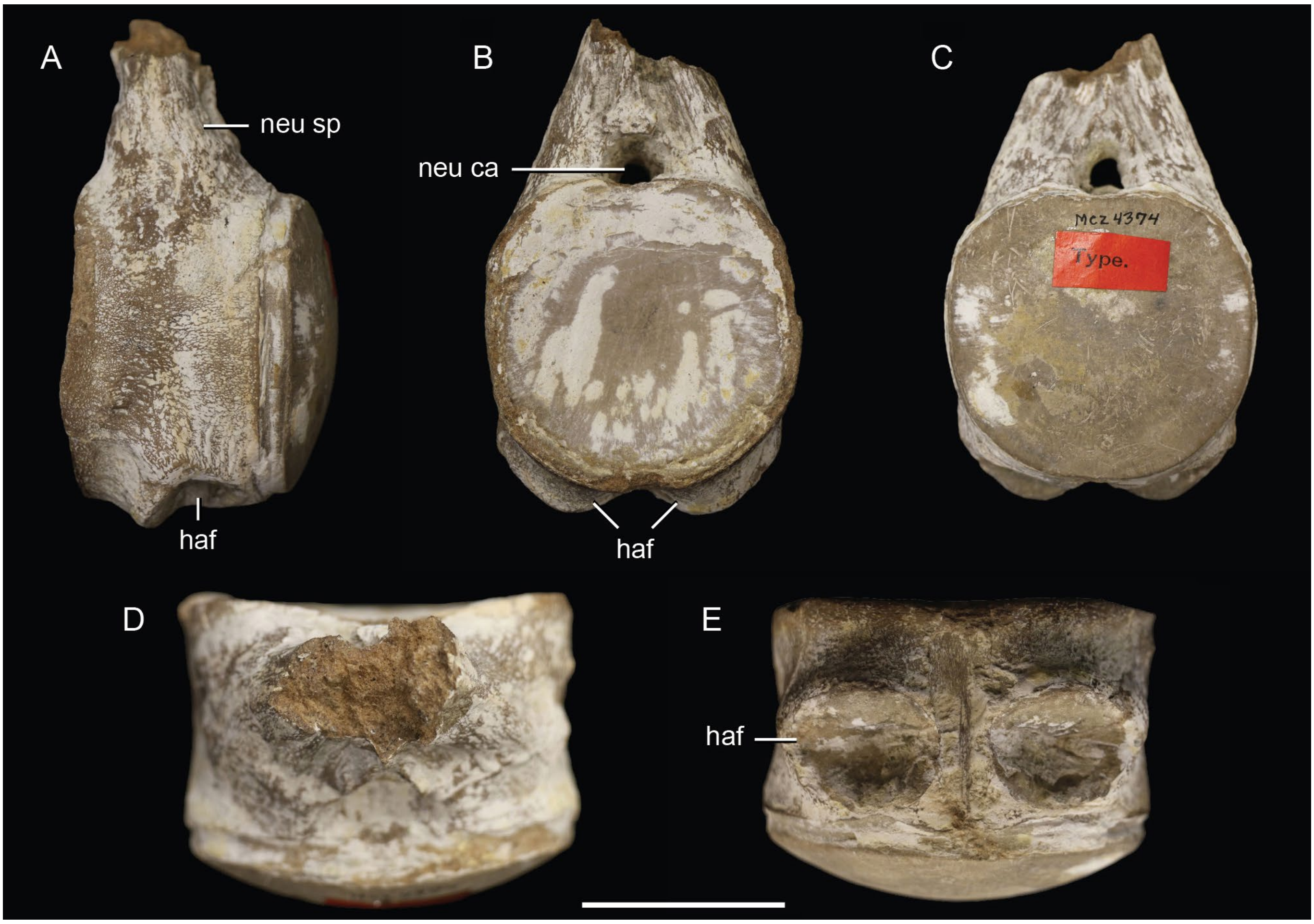

Figure 8 The caudal vertebra of *Tylosaurus proriger* MCZ VPRA 4374; **A** left lateral view, **B** anterior view, **C** posterior view, **D** dorsal view, **E** ventral view. Scale bar is 5 cm. Photographs by Amelia R. Zietlow.

Emended Diagnosis

Tylosaurine mosasaur distinguished by possessing the following suite of character states: knoblike, edentulous rostrum on the premaxilla that is typically 5% or more the length of the skull; presence of nubbin on ventral midline of the rostrum; the lateral premaxilla-maxilla suture terminates (and the bony naris begins) above the fourth or fifth maxillary tooth position; 13 maxilla tooth positions is typical, although AMNH FARB 221 has 12; both posterolateral and posteromedial processes of the quadrate are well-developed and crest-like; the mandibular condyle of the quadrate is saddle-shaped; the presence of a distinct dorsal ridge on the anterior edentulous extension

Measurement	***T. proriger*** **MCZ VPRA 4374**	***T. nepaeolicus*** **AMNH FARB 1565**
Body length	**8.24 m	**4.87 m
Skull length	*1.09 m	*0.63 m
Premaxilla rostrum length	5.5 cm	-
1st-6th maxilla teeth	25 cm	-
Quadrate height	**14.1 cm	8.2 cm
Jaw length	*1.14 m	*0.68 m
Dentary length	65.8 cm	-
1st-6th dentary teeth	24 cm	-
Mesoplodon grayi RGM 12340	0	1
Mesoplodon layardi RGM 13155, 14339	1-2	2

Table 2. Select measurements and estimates of the holotype specimens, *Tylosaurus proriger* MCZ VPRA 4374 and *Tylosaurus nepaeolicus* AMNH FARB 1565. When both left and right bones are preserved, an average of the two is given. Estimates, explained in the text, are indicated by asterisks, and estimates calculated from other estimates are indicated by two asterisks.

of the dentary, giving the anterior margin of the bone an "m" shape in lateral view; 13 ± 1 dentary tooth positions; absence of narial emargination into the frontal; distal margins of the quadrate suprastapedial process that are mostly parallel; quadrate ala that is thin and usually not preserved; marginal dentition with weak distal carinae that sometimes preserve crenulation.

Description of the holotype

The premaxilla is complete except for the posteriormost portion of the posterior process (Figs. 3, 4a-b, 5a). A long (55 mm), edentulous rostrum projects anteriorly from the snout (Table 2). It is, as the genus name describes, knob-like, and its anterior margin is blunt in lateral view. The elongate rostrum is unique to Tylosaurinae, with a single known exception (the mosasaurine *Plesiotylosaurus crassidens*; Lindgren 2009). Numerous neurovascular foramina are distributed irregularly across the rostrum, particularly on its anterior and lateral surfaces. Posteriorly, the internarial bar is broken; anteriorly, it is nearly as wide as the rostrum and subtriangular in cross section. The premaxilla-maxilla suture is M-shaped anteriorly, and its posterior terminus is dorsal to the midline of the fifth maxillary tooth, as is typical for *T. proriger*; in one referred specimen, AMNH FARB 221, the suture terminates dorsal to the fourth maxillary tooth.

A nubbin (sensu Russell 1967) is present on its ventral midline just anterior to the first tooth positions (Fig. 5b); it is absent in the other known Niobrara tylosaurines (*T. nepaeolicus*, e.g. AMNH FARB 1565; *T. kansasensis*, e.g., FHSM VP-2295), but present in later species (e.g., *Hainosaurus bernardi*, *Tylosaurus* sp. nov. from Texas; Zietlow *et al.*, in press). Like all mosasaurids (Russell 1967), the premaxilla bears four tooth positions. Proximally, the left and right pairs of alveoli are separated by a deeply grooved incisive process (typically referred to as the "grooved median ridge" in mosasaur literature, e.g., Russell 1967). Posteroventrally, the premaxilla bifurcates into the vomeromaxillary processes, forming a 'hood' that embraces the anterior vomer processes anteriorly; altogether, these structures give the anterior palate a yonic appearance. The vomeromaxillary processes are much longer in tylosaurines than they are in other mosasaurids (Fig. 17).

Both maxillae are preserved but incomplete, preserving only 11 tooth positions (13 tooth positions are typically observed in specimens confidently referable to *T. proriger*, e.g., FFHM 1997-10 and FHSM VP-3, but AMNH FARB 221 has only 12). Posterior to the premaxilla-maxilla suture terminus, the dorsal margin of the bone is embayed by the external narial opening and slightly concave. The maxilla forks posteriorly, and a long posterodorsal process overlaps the anterior process of the prefrontal; the bones articulate with one another via deep, sharply defined longitudinal ridges. A bone that is most likely the left septomaxilla is visible through the left narial opening (Fig. 5d); it is deeply notched posteriorly. Within the right narial opening is a shard of bone with longitudinal anterior ridges that overlies the right palatine; it is possible that this shard is the anterior process of the right prefrontal that has been broken off from the rest of the bone and displaced anteriorly.

The anterior palate, comprised of the ventral premaxilla and vomers, is exquisitely preserved in MCZ 4374 (Fig. 5a). The vomers are long and thin, and contact one another along the midline of the palate anteriorly until diverging at the level of the second maxillary tooth position. The vomeronasal fenestra is present medial to the fourth maxillary tooth; the vomer then contacts the maxilla again at the fifth maxillary tooth and appears to remain in contact with the maxilla until the seventh maxillary tooth. An embayment in the medial margin of the maxilla, beginning posterior to the seventh maxillary tooth, demarcates the margin of the internal choana. The anterior process of the right palatine articulates with the vomer along its medial face. Part of the left palatine is preserved in ventral view and turned slightly out of place, exposing the long, groove-like facet for articulation with the maxilla (Fig. 5e).

The right dentary is the only bone to preserve a complete tooth row and has 13 tooth positions. The predental process is long, about equal to the mesiodistal width of the base of the first dentary tooth. The predental process possesses a dorsal ridge, giving the bone a notched anterior margin in lateral view (Fig. 5c), rather than the blunt to gently convex margin present in other *Tylosaurus* species (e.g., *T. nepaeolicus* YPM VP 3974). As is typical of tylosaurines, the height of the medial parapet is equal to the lateral wall of bone. A series of shallow, parallel scratches, possibly left by a scavenging shark (Schwimmer *et al.*, 1997), is present on the lateral surface of the bone just ventral to the second tooth position.

MCZ VPRA 4374 only preserves one complete tooth crown (the tenth tooth of the right dentary). It and the other partial tooth crowns that are present are conical, gently recurved, and striated medially, as is typical or *Tylosaurus*. The replacement tooth in the third position of the left maxilla preserves delicate crenulations on a weak anterior carina that are perceptible by touch but only visible with magnification. As is typical of mosasaurids, the premaxillary teeth are smaller than the rest of the marginal dentition, and the largest teeth are in the middle of the toothrow. The tooth bases are circular in cross section.

The dorsal vertebra is crushed mediolaterally, and the left synapophysis is broken off (Fig. 6). It does not possess zygosphenes and zygantra. Both pre- and postzygapophyses are small, and the synapophysis is only about half the height of the centrum; based on AMNH FARB 221 (Osborn 1899), which preserves a nearly complete vertebral series, it appears to be from the middle of the dorsal series. The neural spine appears to have a semicircular dorsal margin. Both the cotyle and condyle of the centrum are nearly circular, and the dorsal margin of the cotyle is notched.

The pygal vertebra is badly crushed dorsoventrally, and it is missing its neural spine, left transverse process, and most of its right transverse process due to breakage (Fig. 7). The caudal vertebra shows no evidence of transverse processes, and its neural spine is nearly straight vertically, suggesting, based on AMNH FARB 221 (Osborn 1899), that it was located near or just posterior to the apex of the tail fluke (Fig. 8). The height of the centrum is nearly identical to that of the dorsal vertebra, and ventrally, the facets for the haemal arch are circular and cup-like, their anterior margins protruding ventrally from the centrum. A shallow groove is present between the haemal arch facets (Fig. 8e). An isolated haemal arch is preserved adhered to the lateral surface of the left maxilla (Fig. 4c-d).

Tylosaurus nepaeolicus Cope 1874

Etymology

Most likely named for the Nepaholla (Solomon) River, near which the holotype was probably found (Cope 1871; Cope 1874; Everhart 2017).

Holotype

AMNH FARB 1565 (Fig. 9).

Type locality

Unknown unit of the Niobrara Formation, but likely from Rooks County, Kansas; the locality is only described as "from the gray shale of the Niobrara Cretaceous, a half mile south of the Solomon River, Kansas" (Cope 1874:38).

Referred specimens

It is worth noting that AMNH FARB 1565 is missing the bones that are typically used to refer specimens to *T. nepaeolicus* (most importantly, the frontal and parietal) based on the diagnosis for *T. nepaeolicus* given by Russell (1967), which relied on YPM VP 3980 (Fig. 10), instead of the holotype specimen. Because the bones that overlap between YPM VP 3980 and AMNH FARB 1565 are identical, we accept Russell's referral. Additionally, we include the following specimens to supplement our emended diagnosis of *T. nepaeolicus*: AMNH FARB 2167 and FHSM VP-3366. We furthermore use the emended diagnosis to refer the following specimens to *T. nepaeolicus*: PMNS 10409, YPM VP 3970, YPM VP 3974, and YPM VP 4026.

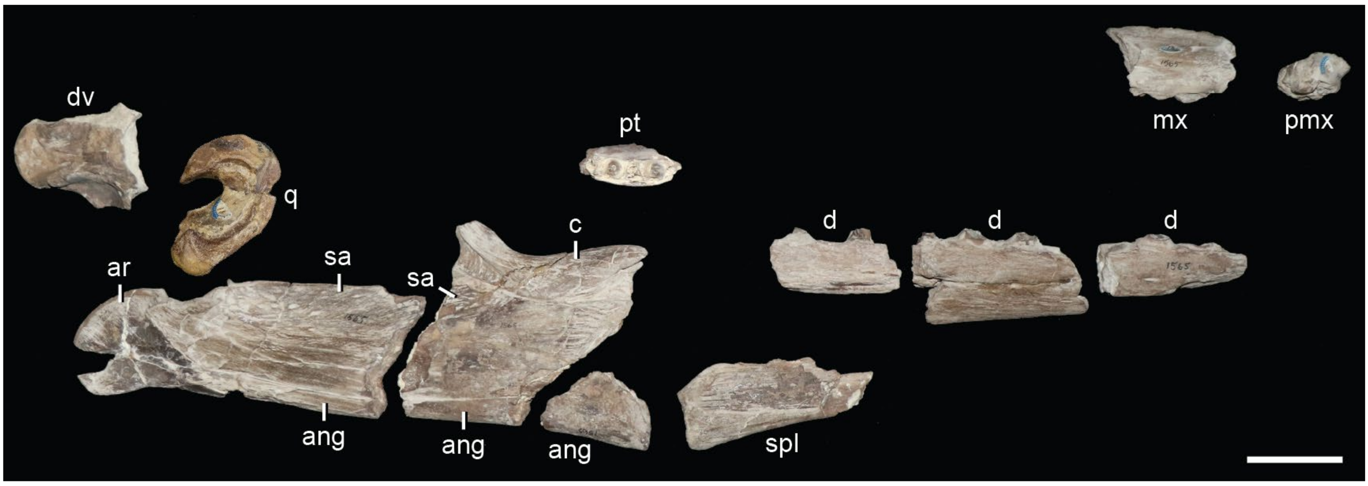

Figure 9 The holotype of *Tylosaurus nepaeolicus*, AMNH FARB 1565. Scale bar is 5 cm. Photographs by Amelia R. Zietlow.

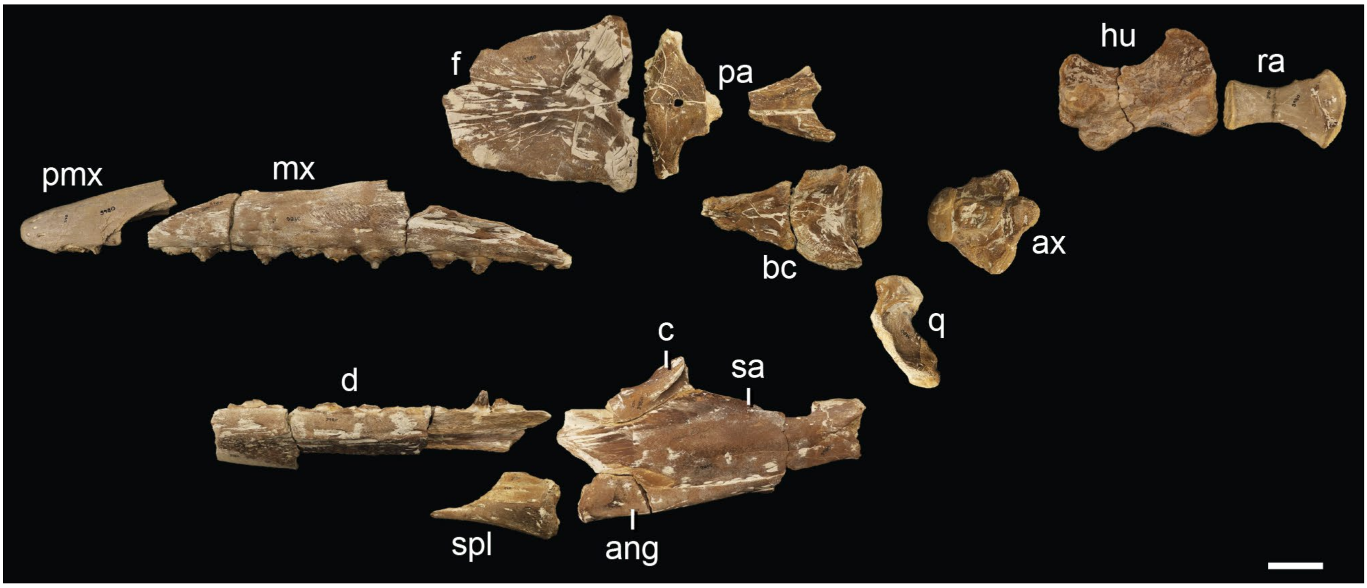

Figure 10 *Tylosaurus nepaeolicus* YPM VP 3980, which has served as the primary reference for the species following its use by Russell (1967) to describe *T. nepaeolicus*. Scale bar is 5 cm. Photographs by Amelia R. Zietlow.

Emended Diagnosis

Tylosaurine mosasaur possessing the following suite of character states: the lateral premaxilla-maxilla suture terminates (and the bony naris begins) above the third or fourth maxillary tooth position; the frontal lacks a well-developed dorsal median keel; the posterolateral margins of the frontal are slightly concave above the orbits; the parietal foramen is located far (more than one foramen length) from the frontal-parietal suture; the parietal table is rectangular and parallel-sided in dorsal view; the presence of a horizontal scar for the M. depressor mandibulae on the posterodistal tip of the quadrate suprastapedial process; medial curvature of the quadrate suprastapedial process is weak; the mandibular condyle of the quadrate is flat.

Description of the holotype

The premaxilla is incomplete and damaged (Fig. 11). It preserves the first two tooth positions, which are bounded anteriorly by a low rim. The nubbin that is present in *T. proriger* and other later branching tylosaurine species is absent. Although the rostrum itself is not preserved, the presence of a rostrum is indicated by an anterodorsal projection of bone anterior to the tooth positions. One identifiable fragment of the right maxilla is present (Fig. 12a-b). Its suture with the premaxilla appears m-shaped, as it typically is in *T. proriger*. The first two tooth positions and teeth are preserved; the better-preserved tooth lacks carinae, and the lingual surface is striated. The suture with the vomeromaxillary process of the premaxilla is present and extends at least to the second tooth position, but the incompleteness of the bone makes it impossible to determine whether it was longer. A small fragment of the posteromedial parietal preserves the nuchal fossa as a crescentic depression located posterodorsally (Fig. 12c).

The right quadrate is nearly complete but is taphonomically flattened mediolaterally (Fig. 13). It is roughly oval in lateral view, and less narrow than in *T. proriger* (Fig. 14). Unlike *T.*

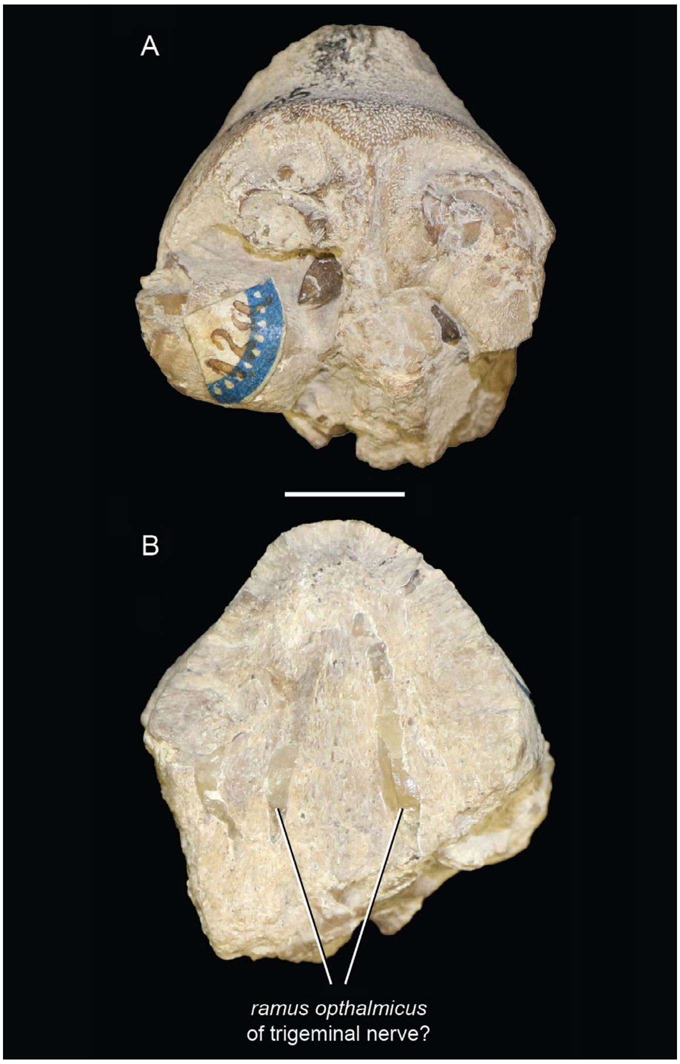

Figure 11 The premaxilla of *Tylosaurus nepaeolicus* AMNH FARB 1565; **A** ventral view, **B** dorsal view. Scale bar is 1 cm. Photographs by Amelia R. Zietlow.

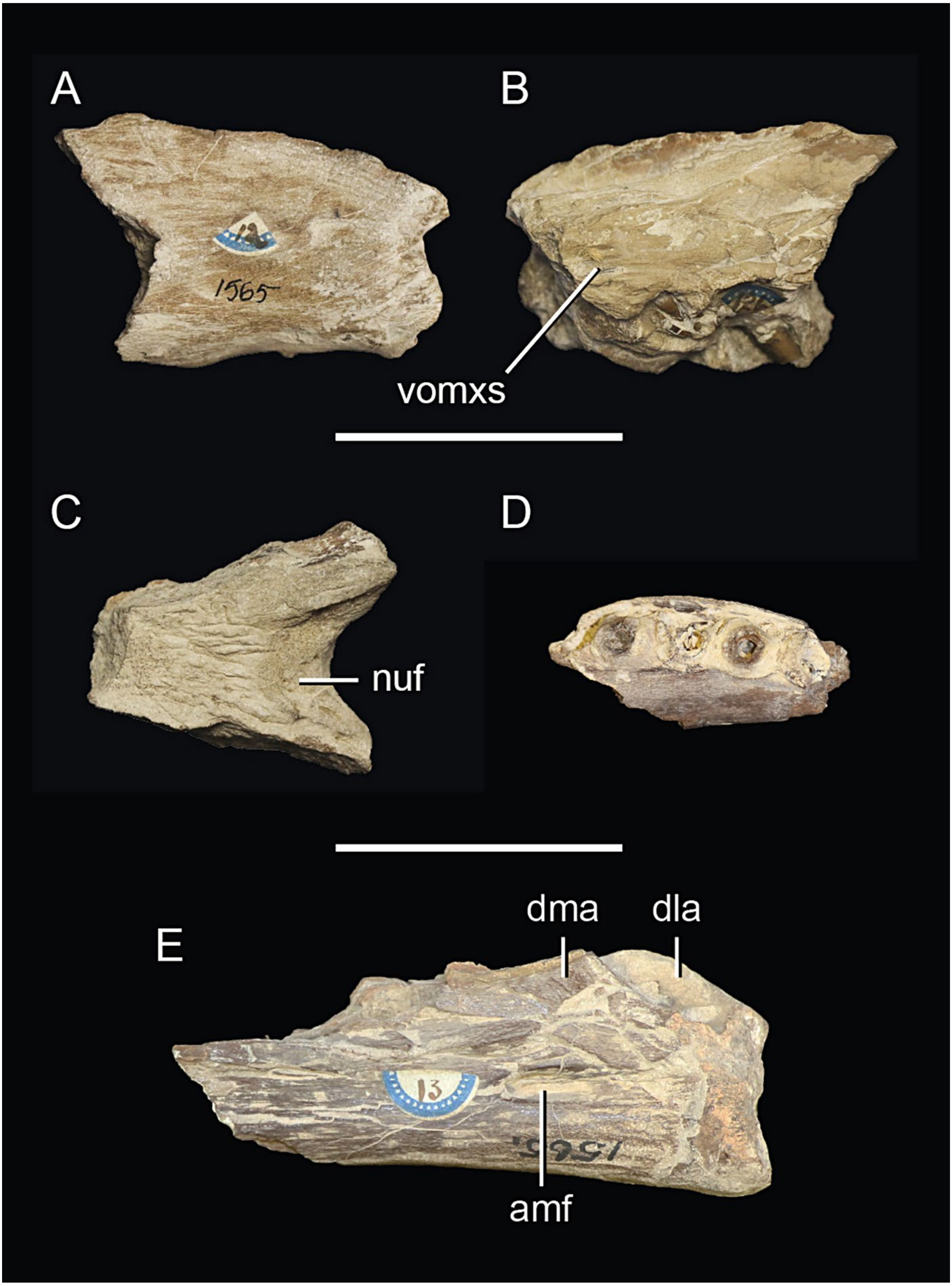

Figure 12 Skull and mandible fragments of *Tylosaurus nepaeolicus* AMNH FARB 1565; **A** right maxilla in lateral view, **B** fragment of right maxilla in medial view, **C** fragment of parietal in dorsal view, **D** fragment of left pterygoid in ventral view, **E** fragment of right splenial in medial view. Scale bars are 5 cm. Photographs by Amelia R. Zietlow.

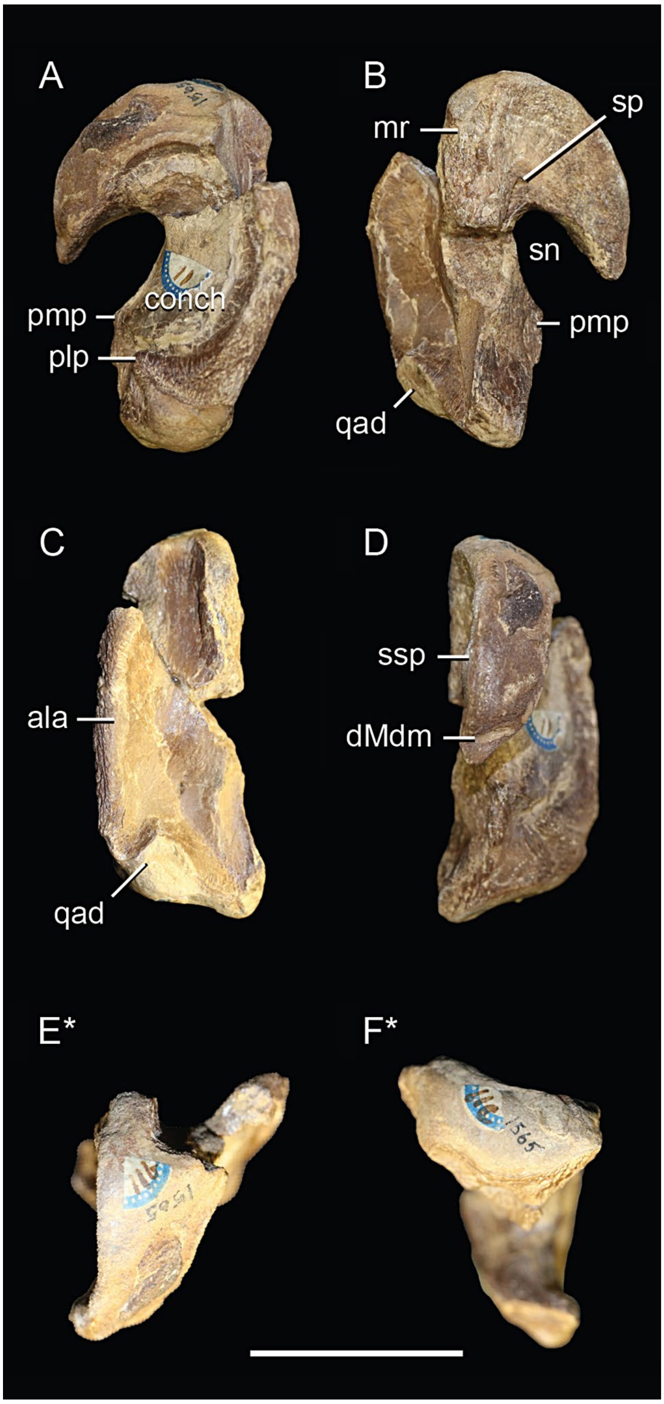

Figure 13 The right quadrate of *Tylosaurus nepaeolicus* AMNH FARB 1565; **A** lateral view, **B** medial view, **C** anterior view, **D** posterior view, **E** dorsal view, **F** ventral view. Scale bar is 5 cm; however, asterisks indicate images for which the scale is approximate. Photographs by Amelia R. Zietlow.

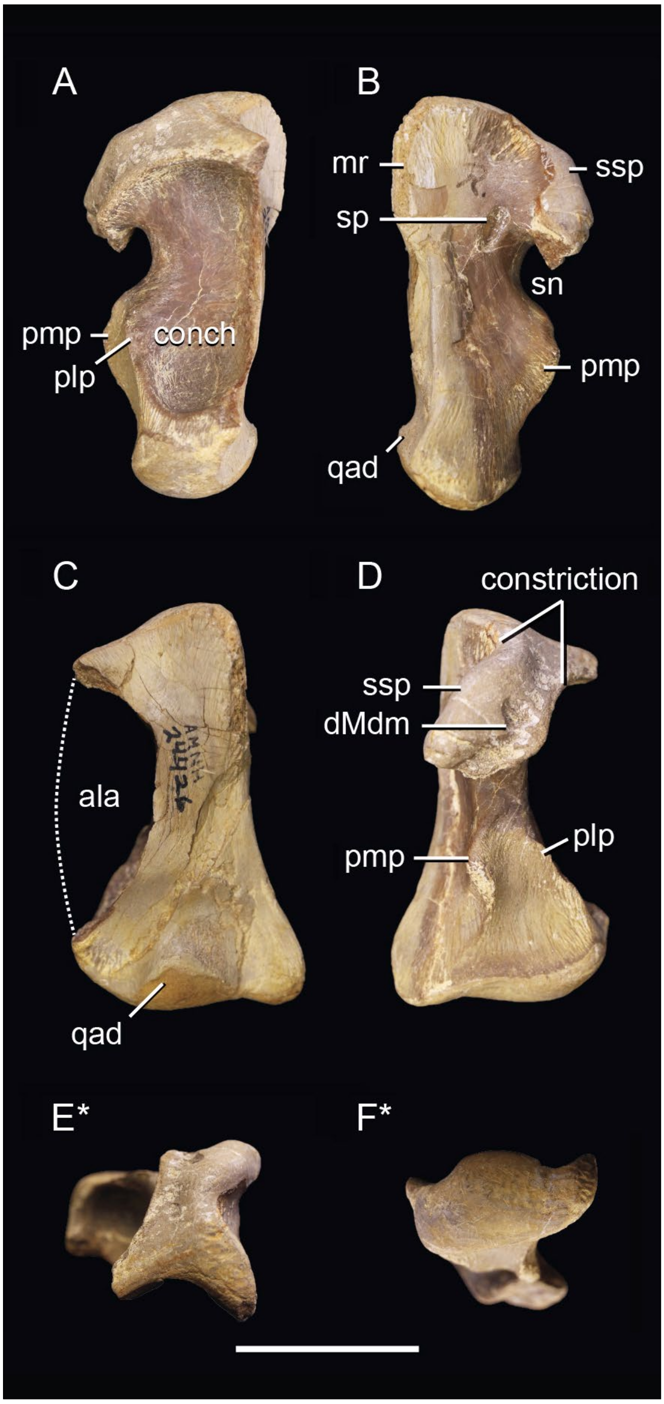

Figure 14 The right quadrate of *Tylosaurus proriger* AMNH FARB 14799; **A** lateral view, **B** medial view, **C** anterior view, **D** posterior view, **E** dorsal view, **F** ventral view. Scale bar is 5 cm; however, asterisks indicate images for which the scale is approximate. Photographs by Amelia R. Zietlow.

proriger, the lateral face of the bone is nearly circular, and the tympanic ala is thick and usually preserved. The alar rim encloses the ala ventrally and is extremely wrinkled along its ventral and anterior surfaces. Both posterolateral and posteromedial processes are poorly developed, and only present as small bumps, rather than the large crests present in *T. proriger*. The suprastapedial process is of intermediate length, about half as long as the entire bone, and is not strongly medially inflected as it is in *T. proriger* (some curvature is present in referred specimens, e.g., FHSM VP-3366, but it is still not as extreme as in referred specimens of *T. proriger*, e.g., AMNH FARB 1555). Its sides taper and terminate in an acute point, in contrast to the blunt terminus seen in *T. proriger*. An oblong, narrow depression is present distally on its dorsal surface, presumably for the origin of the M. depressor mandibulae (Russell 1967); it is worth noting that this feature is never present in

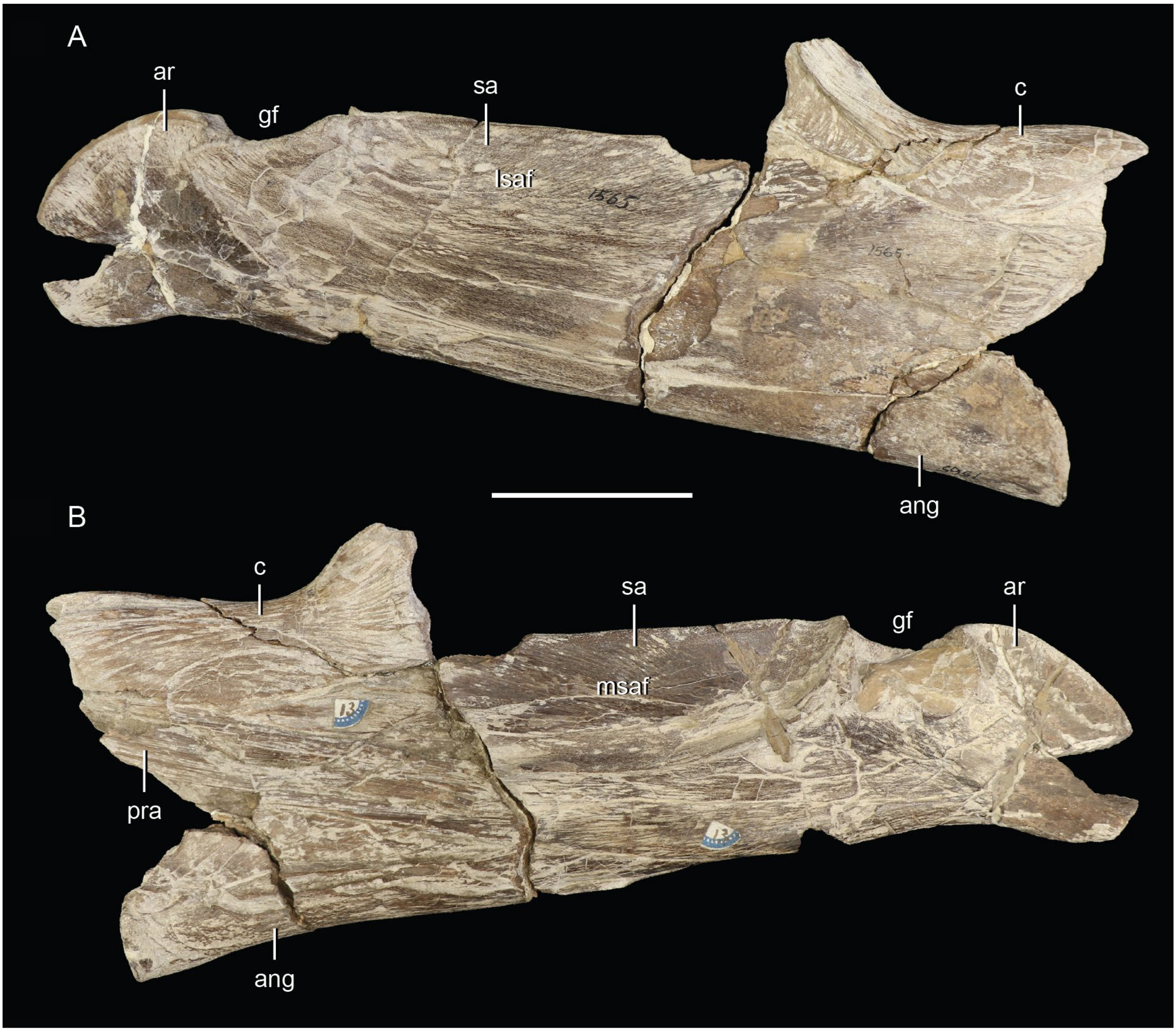

Figure 15 The right posterior mandibular unit of *Tylosaurus nepaeolicus* AMNH FARB 1565; **A** lateral view, **B** medial view. Scale bar is 5 cm. Photographs by Amelia R. Zietlow.

specimens referred to *T. kansasensis* (e.g., the holotype FHSM VP-2295). A larger subrectangular depression is also present further proximally.

The small fragment of pterygoid, likely the left bone, preserves four tooth positions (Fig. 12d). No pterygoid tooth crowns are preserved, but the bases are nearly circular in cross-section and indicate that they were notably smaller than the marginal dentition. Three identifiable fragments of the right dentary are preserved; the teeth do not appear to differ from those in the maxilla. The medial parapet of the dentary reaches a level parallel to the lateral wall of bone, as is typical of tylosaurines. The right splenial is preserved but incomplete (Fig. 12e); it is not notably different from the splenials of other tylosaurines, with a small, oblong anterior mylohyoid foramen and mediolaterally compressed, concave articular surface for the angular.

The posterior mandibular unit is the best-preserved portion of the specimen, in both its completeness and its lack of significant damage or other distortion (Fig. 15). The coronoid is saddle-shaped, as is typical of tylosaurines, with a dorsal curvature of about 140 degrees. Its ventral margins are without notches or other interruptions, as present in some mosasaurines (e.g., the anterolateral notch present in *Mosasaurus hoffmanni* Mantell 1829 holotype MNHN 9648), except for a groove present in its anterodorsal margin. Its posterolateral surface is depressed, continuous with the lateral adductor fossa of the surangular. Anteromedially, it contacts the prearticular process of the articular. Its posteromedial wing is small and does not contact the angular.

In lateral view, the surangular is roughly rhomboidal in shape. The lateral adductor fossa is shallow and not sharply demarcated ventrally, as it is in most mosasaurines (e.g., *Prognathodon solvayi* Dollo 1889 holotype IRSNB R 33). The anterior surangular foramen, presumably for the inferior alveolar

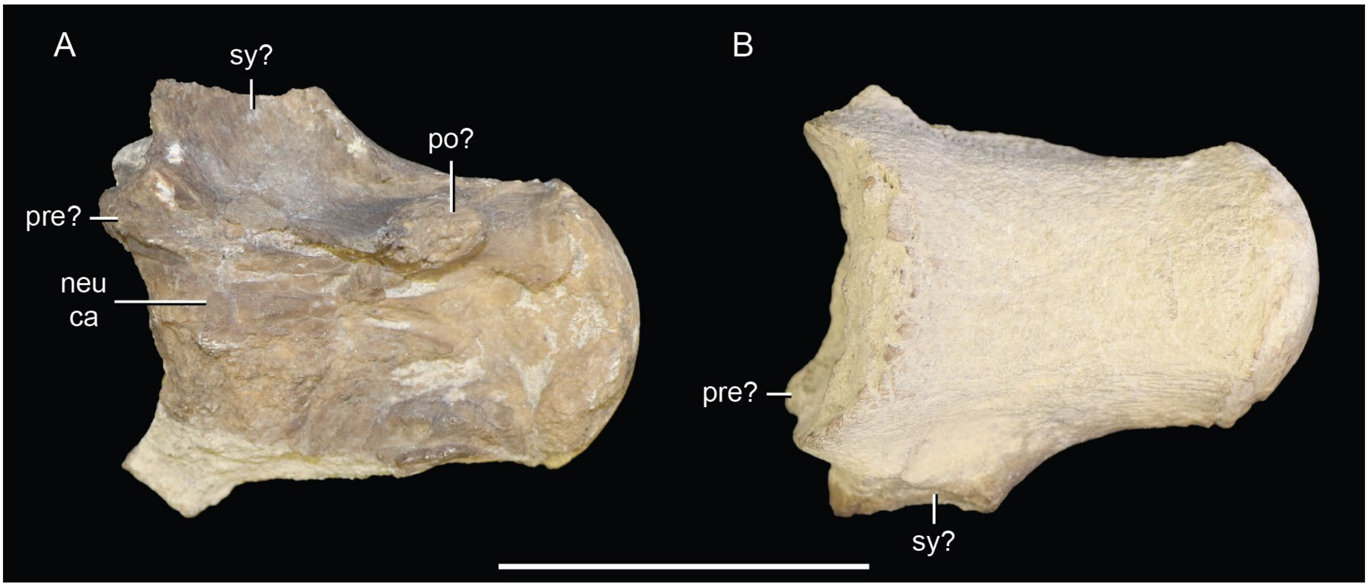

Figure 16 Dorsal vertebra of *Tylosaurus nepaeolicus* AMNH FARB 1565; **A** dorsal view, **B** ventral view. Photographs by Amelia R. Zietlow.

nerve, is present as a long groove and located just anterior to the midpoint of the coronoid, which is farther anterior than in extant lizards (Bahl 1937; Oelrich 1956). The dorsal margin of the surangular is low and nearly parallel to its ventral margin, as is typical of tylosaurines. The lateral suture between the surangular and articular extends just posterior to the glenoid fossa, then curves sharply anteroventrally. The medial adductor fossa is bounded ventrally by a sharp ridge, which terminates posterodorsally as the anterior rim of the glenoid fossa. Most of the medial face of the surangular is obscured by the articular and its prearticular process.

The angular is complete and nearly as long as the surangular. Its articular surface with the splenial is mediolaterally compressed, with a dorsal notch for a corresponding flange of the splenial. The posterior mylohyoid foramen is roughly the same size and shape as its anterior counterpart in the splenial. The prearticular process of the articular is exquisitely preserved as a thin wing of bone that gently broadens dorsally, ultimately contacting the coronoid anterodorsally. The retroarticular process of the articular is not strongly medially inflected, as is typical of tylosaurines, and lacks the lateral foramina present in plioplatecarpines (e.g., *Plesioplatecarpus planifrons* Cope 1874 FHSM VP-2296). Unfortunately, damage to the retroarticular process obscures the exact position and size of the chorda tympani foramen.

The odontoid is subrectangular and dorsally depressed. One dorsal vertebra is preserved, but it is badly damaged and weathered (Fig. 16). The centrum is longer than it is tall, and its articular surfaces are slightly dorsoventrally compressed, which is typical of tylosaurine anterior dorsal vertebrae. A horizontal process is preserved on the right side, but its distal surface is missing.

Body and skull length estimates

Key measurements and estimates for each holotype specimen are provided in Table 2. Both specimens are fragmentary, so skull and body length estimates were calculated using proportions found to be consistent within a comprehensive measurement dataset of 103 tylosaurines from museums in North America and Europe (Zietlow *et al.*, in press: supplemental data S1). We recognize that ontogenetic allometry may affect the accuracy of these measurements, and so these estimates are intended to provide a general sense of scale, rather than *exact* dimensions; forthcoming work, however, will include the full dataset and a reassessment of prior ontogenetic allometry hypotheses in *Tylosaurus* (e.g., Stewart & Mallon 2018) following a full taxonomic reassessment of all specimens therein (Zietlow 2024, and other work in prep).

Complete *Tylosaurus* specimens (AMNH FARB 221, FHSM VP-3, and USNM 8898) all have a jaw length (measured from the anterior margin of the dentary to the posterior margin of the articular) that is 14% of total body length (Everhart 2002), and tylosaurine dentaries tend to be about 57% jaw length. Therefore, the dentary length of MCZ VPRA 4374 was used to calculate its jaw length, which was then used to estimate the animal's body length. To calculate the skull length of MCZ VPRA 4374, we used the distance between the first and sixth maxillary teeth, which tends to be about 23% of total skull length (measured from the premaxilla to the posterior midpoint of the parietal, between the suspensorial rami). From this estimated skull length, the quadrate height, which is 13% of skull length on average in all specimens referred to *Tylosaurus*, was estimated.

The only measurement available for the holotype of *T. nepaeolicus*, AMNH FARB 1565, is the quadrate height. Quadrate height is, on average, 13% of skull length and 12% of jaw length in all specimens referred to *Tylosaurus*, so it could be used to estimate those lengths. The resultant estimate for jaw length was then used to estimate body length.

DISCUSSION

Mosasaur anterior palatal anatomy

The exceptional preservation of the anterior palate of MCZ VPRA 4374 and two other *T. proriger* specimens, MCZ VPRA

8790 and KUVP 28705, provides an opportunity to compare this region of anatomy with extant lizards (Lakjer 1927; McDowell & Bogert 1954; Oelrich 1956; Conrad 2004; Evans 2008; Rieppel *et al.* 2008; Paparella & Caldwell 2022) and other mosasaurs (Fig. 17; note, however, that halisaurines are excluded from this comparison, as this region of their anatomy is still unknown; see also Polcyn *et al.*, 2022).

Relative to *Varanus komodoensis* and other lizards, the anterior snouts of many derived mosasaurids are robust and extremely elongated. We could not see the premaxillary foramina present on either side of the incisive process present in *Varanus* and other extant lizards in any of our exemplar specimens; they are very small in mosasaurs and often obscured taphonomically (M.J.P., pers. obs.). A single pair of vomerine foramina are located at the level of the second maxillary tooth mosasaurs, in contrast to two to four pairs present along the anterior process in *Varanus* (Fig. 17). The maxillo-premaxillary aperture present in some *Varanus* (sensu Kubota *et al.* 2024) is obliterated in mosasaurids by anterior narial retraction and accompanying reorganization of the premaxillary-maxillary contact (Polcyn *et al.*, 2022).

While other lizards have short vomeromaxillary process of the premaxilla or lack them altogether, they tend to be well-developed and long in *Varanus* (Evans 2008). Their length varies by species, being longer in species with longer, narrower snouts, e.g., *V. bengalensis* and *V. beccarii* (Bahl 1937; A.R.Z., pers. obs.); a similar trend appears to exist within Mosasauridae. In *Mosasaurus* and *Latoplatecarpus*, the vomeromaxillary processes of the premaxilla do not extend beyond the first tooth position, and the vomeronasal fenestra is located medial to the third maxillary tooth position. In *T. proriger*, extreme elongation of the premaxilla vomeromaxillary processes to at least the second maxillary tooth position pushes the vomeronasal fenestra even further posterior, to at least the fourth maxillary tooth position.

The palates of *M. hoffmanni* and *T. proriger* converge upon the neochoanate condition of *V. komodoensis* (sensu Lakjer 1927 and Rieppel *et al.* 2008), in that the vomeronasal fenestra is separated from the choana by a lateral process of the vomer. However, unlike the "true" neochoanate condition in which the vomer *overlaps* the lingual shelf of the maxilla, in both mosasaurs, the vomer articulates with the maxilla via a vertically oriented suture. The vomer and maxilla share a much longer contact in *M. hoffmanni* and *T. proriger* (three tooth positions) than in *V. komodoensis* (one tooth position). In *Latoplatecarpus willistoni* (Konishi and Caldwell, 2011), the vomer does not contact the maxilla posterior to the vomeronasal fenestra at all, resembling the paleochoanate condition in that the vomeronasal fenestra and the choana occupy a single bony opening (the fenestra exochanalis sensu Lakjer 1927 and Rieppel *et al.* 2008). This condition is also seen in *Tethysaurus nopcsai*, a basal russellosaurina (potentially a basal plioplatecarpine; Polcyn *et al.*, 2022, Polcyn *et al.*, 2023).

The vomer is shorter (relative to the number of maxilla tooth positions crossed) in all three mosasaurs than it is in *V. komodoensis* (Fig. 17), and it is shorter in *L. willistoni* (crossing six maxilla tooth positions) than the other two mosasaurs (nine in *M. hoffmanni*, seven in *T. proriger*). The midline contact

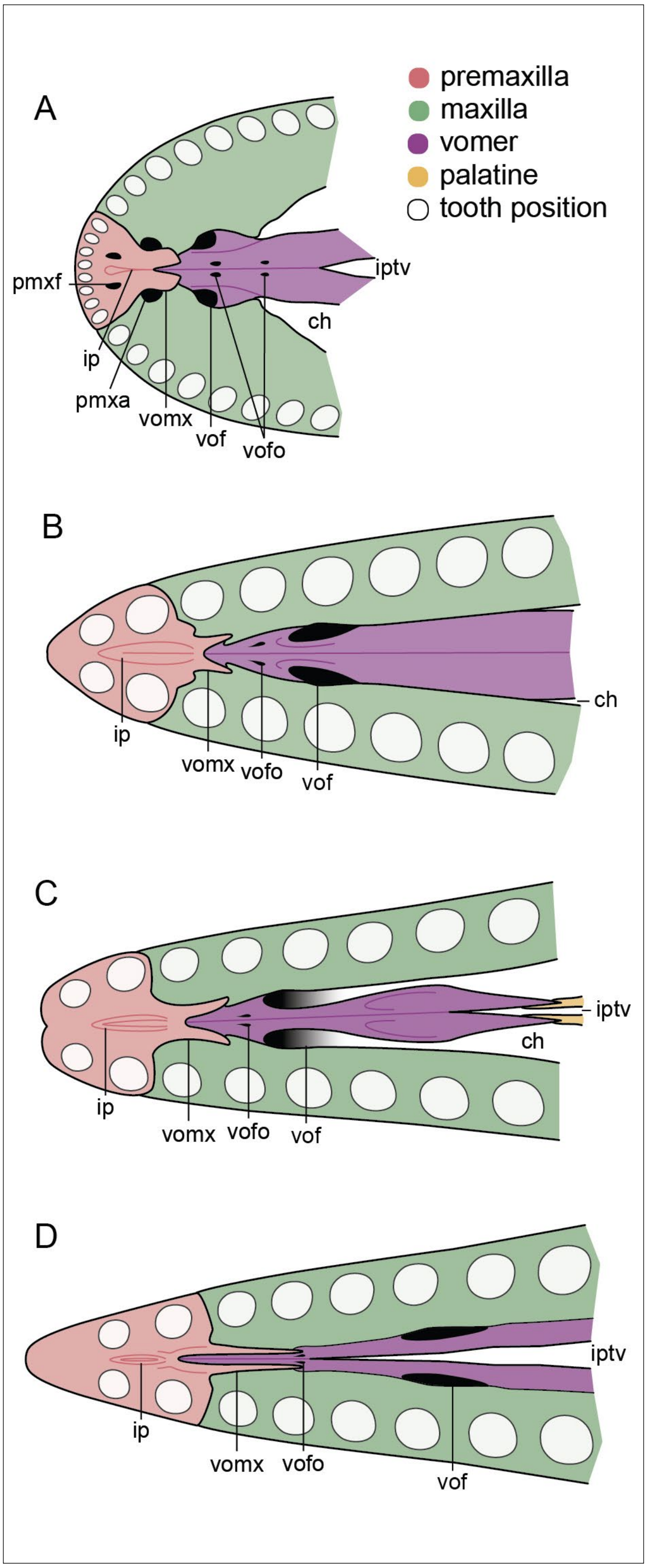

Figure 17 Simplified line drawings of the anterior palates of **A** *Varanus komodoensis*, based on AMNH R-37913, **B** *Mosasaurus hoffmanni*, based on IRSNB R 303, **C** *Latoplatecarpus willistoni*, based on the holotype TMP 84.162.01, and **D** *Tylosaurus proriger*, based on the holotype MCZ VPRA 4374 and MCZ VPRA 8790. Note: drawings are not to scale. Drawings by Amelia R. Zietlow.

between the vomers is short in *T. proriger* (two tooth positions), moderate in *L. willistoni* (five tooth positions), and long in *M. hoffmanni* (eight tooth positions, apparently persisting until contact with the palatines). In ventral view, the vomers are mostly straight and parallel-sided posterior to the vomeronasal fenestra in *V. komodoensis*, *M. hoffmanni*, and *T. proriger*, but become distally expanded and spade-like posteriorly in *L. willistoni*.

Mosasaur palatal anatomy is severely underrepresented in the standard mosasauroid phylogenetic character list; in the most recent analysis of mosasaur systematics (Zietlow *et al.* 2023), only three of 124 characters described the palate, two of them describing the pterygoid (tooth row elevation and tooth size) and the third describing the state of ectopterygoid contact with the maxilla. Here, we find significant variation in anterior palate anatomy between mosasaur clades, suggesting that the region is character-rich and ought to be included in future analyses of mosasaur systematics through increased representation in phylogenetic character lists. This may be facilitated by more thorough description and figuring of the region in future mosasaur osteological studies.

Significance of modern reassessments of historical holotype specimens

Mosasaur taxonomy, especially concerning species found in the Western Interior Seaway, is nothing short of vexing: many species resulted from overzealous "Bone Wars" naming practices, supported by insufficient description and the absence of detailed locality information. Paleontologists have spent decades unraveling the taxonomic havoc wrought by Cope, Marsh, and all the others who, to their credit, amassed an incredible collection of mosasaur fossils in North American museums that we are very fortunate to have. In contrast to other charismatic Mesozoic reptiles, which may have several dozen specimens at best, there are over *four thousand* mosasaurs in North American museums alone (Table 1). However, perhaps we have over-corrected in favor of 'lumping,' in modern attempts to study and explain North American mosasaur diversity. Although a conservative and careful approach to the introduction of new species is always good practice, defaulting to 'lumping' tends to obfuscate true diversity, and in some cases, artificially combine multiple taxa in a single 'species' (e.g., Jiménez-Huidobro *et al.* 2016, Zietlow 2020).

T. proriger has served as the 'control' species in several recent studies of intraspecific variation under the assumption that, because hundreds of specimens are referred to the species, it is "unquestionably valid" (Zietlow 2020, p. 4) and "the best known" (Jiménez-Huidobro *et al.* 2016, p. 69) mosasaur. However, these studies failed to reassess specimen referral to the species using the single most important specimen: the holotype, MCZ VPRA 4374. Furthermore, previous attempts to determine relative ontogenetic stages ultimately assume that character differences between small and large individuals are inherently more likely to be ontogenetic than interspecific, without any basis in neontological studies or developmental biology. Even cladistic analysis of ontogeny, which is intended to recover a growth series using size-independent characters, falls victim to this error, as the characters used in the analysis must still be polarized, and they are inevitably polarized using relative specimen size anyway (Zietlow 2020; Napoli 2024). The accurate identification of cryptic paleo-species in the fossil record is critical for studies of systematics and macroevolutionary trends. As we reassessed nearly 80 specimens in North American museums that are currently referred to *T. proriger* to determine our list of referred specimens, we found evidence of at least one, but *possibly two or three*, cryptic paleo-species of *Tylosaurus*; the variation observed in many of these specimens had been dismissed as ontogenetic in previous work (e.g., Zietlow 2020) because it was observed in both the smallest and largest specimens. Several factors were not accounted for in previous work that contributed to this oversight: (1) taphonomic size bias; (2) the presence of variation in specimens of near identical size; (3) geographic signal; (4) stratigraphic signal; and (5) the absence of intermediate character states. These problems are not unique to *T. proriger*; prior work investigating tylosaurine intraspecific variation has been centered on whether two other species, *T. nepaeolicus* and *T. kansasensis*, are synonymous. This hypothesis will be reassessed in detail in upcoming work (Zietlow 2024, and other works in prep), but it is worth noting here that, as in *T. proriger*, inconsistent and inaccurate specimen referrals, often without comparison to the relevant holotypes, have obfuscated not only the answer to this single question, but broader patterns in tylosaurine evolution.

We urge other mosasaur paleontologists to be cautious with specimen referral, especially with historic specimens that often lack precise locality data which, although it cannot by itself diagnose a species, may provide critical context that can inform taxonomic decisions. It is our opinion that clearly and explicitly stating uncertainty is better than referrals that artificially inflate sample size and risk creating patterns that are, simply put, not real. Altogether, this and future reassessments of mosasaur holotypes and species referrals will inform more accurate analyses of mosasaur systematics and provide additional insight into their biology, diversity, and ecology. Lastly, because holotype specimens are critical to studies of paleobiology, it is important that they are well documented (thoroughly described and figured) in the scientific literature so that they are accessible to all.

CONCLUSIONS

Our redescription of the holotypes of *T. proriger* and *T. nepaeolicus*, as well as our revised diagnoses and lists of specific referred specimens, will help to facilitate future studies investigating tylosaurine taxonomy and systematics, as well as broader studies of mosasaur macroevolution that are dependent on them. We recommend that specimen referrals be critically evaluated using the relevant holotype *before* proceeding with studies of intraspecific variation, rather than assuming that the existing referrals are accurate.

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