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Two new plioplatecarpine mosasaurs (Mosasauridae; Plioplatecarpinae) of the genus *Ectenosaurus* from the Upper Cretaceous of North America

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Two new species of the rare mosasaur *Ectenosaurus* are reported from the Upper Cretaceous of North America. *Ectenosaurus tlemonectes* sp. nov. (YPM VP4673) consists of a largely complete skull and some associated post-cranial elements that were derived from an unknown level within the Smoky Hill Member of the Niobrara Chalk (upper Coniacian-lower Campanian), of Kansas, USA. *Ectenosaurus shannoni* sp. nov. (ALMNH:Paleo:5452) is described from a much more fragmentary specimen collected from the unnamed member of the Mooreville Chalk (upper Santonian-lower Campanian) of Alabama, USA. These new taxa can be distinguished from the other members of the genus, *E. clidastoides* (Merriam, 1894) and *E. everhartorum* Willman et al. (2021), by clear morphological differences in the skull and jaws. Two parsimony analyses of a data matrix consisting of 98 characters and 20 terminal taxa were carried out, the first without constraints and the second constrained by the assumption of monophyly in *Ectenosaurus.* Both analyses resulted in 30 equally parsimonious trees of 255 steps. Neither analysis yielded definitive information about the position of *Ectenosaurus* within Plio-platecarpinae, suggesting the need for an expanded data matrix. Although *Ectenosaurus* is an extremely rare component of the mosasaur assemblages from which it is found, it is also a diverse genus, with now at least four recognized species. This raises questions about the paleoecology and paleobiogeography of this genus and requires additional investigation.

Keywords: Alabama, Kansas, Russellosaurina, Mooreville Chalk, Niobrara Chalk, Squamata, Santonian, Campanian

INTRODUCTION

Following the end-Cenomanian anoxic event, semi-aquatic varanoid lizards rapidly evolved to fill ecomor-phological niches left vacant by the extinction of both pliosaurid plesiosaurs and the last ichthyosaurs. By the mid-Turonian, the most successful of these lineages, the mosasaurs, had become apex marine predators (Fischer et al. 2016, Stubbs and Benton 2016). Mosasaurs were extremely successful throughout the remainder of the Cretaceous, dominating marine reptile assemblages worldwide for more than 30 Ma (Skawiński 2022). Be-sides filling the role of generalist apex predator, some taxa specialized to exploit a diverse range of trophic roles, including durophagy *(Globidens* Gilmore, 1912; *Carinodens* Thurmond, 1969), piscivory (*Plotosaurus* Camp, 1951; *Gavialimimus* Strong et al., 2020), and possibly even scavenging (*Xenodens* Longrich et al., 2021). Mosasaurs flourished worldwide until the K-Pg boundary, when they perished during the catastrophic global extinction event that combined the effects of an asteroid impact with a variety of environmental changes (i.e., increased volcanism, sea-level regression, increased greenhouse effect) in a "perfect storm" that claimed ap-proximately 75% of all species on Earth (Archibald et al. 2010).

The mosasaur genus *Ectenosaurus* was erected by Russell (1967) as part of his larger revision of the Mosa-sauridae Gervais (1852). Russell (1967) included a single species within this new genus, *Ectenosaurus clidastoides* (Merriam, 1894), that combined two taxa, *Platecarpus clidastoides* and *P. oxyrhinus*, that were both named by Merriam (1894). Although neither of Merriam's specimens were figured, the holotype of *P. clidastoides*

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was reported to consist of the posterior portion of a skull and several vertebrae, whereas the holotype of *P. oxyrhinus* consisted of the anterior portion of a presumably different skull. Both specimens were reportedly derived from the "Niobraraschichten der oberen Kreide von Logan County, Kansas" (Merriam 1894; in current usage, the upper Coniacian-lower Campanian Smoky Hill Chalk Member of the Niobrara Formation) and both were reposited within the collections at the Bayerishe Staatssammlung für Paläontologie in Germany, where they were likely destroyed during Allied bombing of Munich in April 1944 (Russell 1967). Although Russell (1967:158) did not directly examine either specimen, he concluded that Merriam's taxa probably "belonged to the same species, if not the same individual." Russell based this assumption on his examination of a nearly complete plioplatecarpine skull and partial skeleton in the collections of the Sternberg Museum of Natural History (FHSM VP-401, formerly FHM 7937) that was collected from the Niobrara Chalk in Trego County, Kansas. Russell used specimen FHSM VP-401 as the basis for his new genus, *Ectenosaurus*, as well has his new combination, *E. clidastoides* Russell (1967).
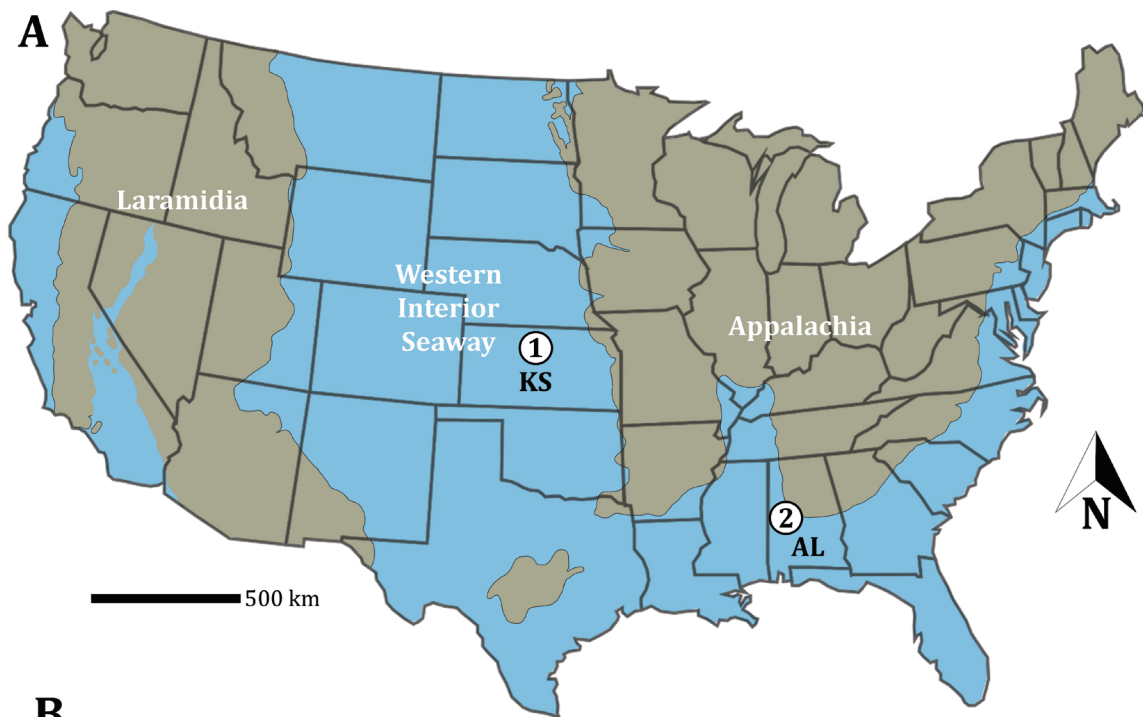
Russell (1967) referred four additional specimens from the Yale Peabody Collections in New Haven, CT, USA to *E. clidastoides* (YPM VP4671, YPM VP4672, YPM VP4673, and YPM VP4674), but did not provide any justification for doing so. These referrals went unquestioned until Bell (1997) included the four Yale specimens, along with a specimen from the collections at University of Kansas (KU 1024), into a group he listed as "*Ectenosaurus* composite," that he concluded was separate from *E. clidastoides* (i.e., FHSM VP-401). Kiernan (2002) also reported the occurrence of an undescribed member of the genus, based on a fragmentary specimen in the collections at the Alabama Museum of Natural History in Tuscaloosa, USA (ALMNH:Paleo:5452) that was collected from the Mooreville Chalk (upper Santonian-lower Campanian) of western Alabama. Bell et al. (2013) discussed a second, albeit more complete, undescribed *Ectenosaurus* specimen in the Southern Methodist University collection in Dallas, TX, USA (SMU 76350) that was collected from the Pen Formation (middle to upper Santonian) of the Big Bend region of Texas. Willman et al. (2021) later named a second species of *Ectenosaurus*, *E. everhartorum,* based on new material from the middle Santonian levels in the Smoky Hill Member of the Niobrara Chalk of Kansas (FHSM VP-5515). Importantly, in this study Willman et al. (2021) also formally designated FHSM VP-401 as the neotype of *E. clidastoides*, following Russell's (1967)

conclusion that Merriam's (1894) holotype was lost.

Although the skull of FHSM VP-401 is essentially complete and articulated*,* it has suffered significant taphonomic deformation (both plastic and brittle), as is typical of vertebrates recovered from the Niobrara Chalk in Kansas*.* Plastic deformation is most evident in the dorsoventral and mediolateral crushing of the skull and in the leftward deflection of the snout away from the sagittal plane. Brittle deformation is evident on the specimen in the form of many cracked bones. Additionally, a considerable portion of the skull has been restored with plaster and the plaster has been painted to match the specimen. Together, these factors have made examination of many important anatomical features difficult or impossible with the naked eye. For example, the position of the left mandible entirely obscures the palatine-vomers, much of the pterygoids, and most of the undersurface of the frontal. This not only hampers efforts to fully describe the morphology of *E. clidastoides,* but it complicates erection of any putative new species within the genus. This problem can only be resolved by the recovery of additional examples of the type species and/or reexamination of the neotype using high-resolution computed tomography (CT scanned), an undertaking that is beyond the scope of this study.

Although the phylogenetic position of *Ectenosaurus* remains unresolved, Russell (1967:202–203), in his non-cladistic mosasaur "diagrammatic family tree," envisioned *Ectenosaurus* as occupying a position near the base of the Plioplatecarpinae Dollo (1884). This proposal was supported by Bell's (1997, figs. 2–4) PAUP analysis and by most subsequent investigations of mosasaur phylogeny (i.e., Polcyn and Bell 2005, Konishi and Caldwell 2011, Palci et al. 2013, Fanti at al. 2014, Madzia and Caul 2017), in which *Ectenosaurus* usually occupies a basal position proximal to two other early diverging plioplatecarpines, *Angolasaurus* Antunes (1964) and *Selmasaurus* Wright and Shannon (1988). Konishi and Caldwell (2011:774–775) interpreted "its [*Ectenosaurus*] aberrant anatomy (i.e., elongate snout with high tooth count) as reflecting its high degree of specialization versus phylogenetically primitive characteristics within the Russellosaurina," a conclusion with which we concur.

Herein we describe two new species of *Ectenosaurus* from the Late Cretaceous of North America (Fig. 1). In addition, we also examine the implications of these new taxa for plioplatecarpine phylogeny and include discussions of the paleobiodiversity and paleobiogeography of the genus and issues regarding the relative scarcity of *Ectenosaurus* specimens.

Figure 1. Geography and Stratigraphy. **A**. Generalized map of the United States during the Santonian Stage of the Cretaceous (~85 mya) with localities for YPM VP4673 (1) and ALMNH:Paleo:4673 (2). **B**. Generalized correlation chart of Coniacian to Campanian surface stratigraphy for Kansas and Alabama, USA. Base map data modified from Blakey (2014). Stratigraphic chart modified from Szabo et al. (1988) and Everhart (2014).

INSTITUTIONAL ABBREVIATIONS

ALMNH, University of Alabama Museum of Natural History, Tuscaloosa, Alabama, USA; **FHM, FHSM VP,** Sternberg Museum of Natural History, Hays, Kansas, USA; **GSA V,** Geological Survey of Alabama, Tuscaloosa, Alabama, USA; **KU,** University of Kansas Museum of Natural History, Lawrence, Kansas, USA; **SMU,** Southern Methodist University, Dallas, Texas, USA; **YPM VP,** Yale Peabody Museum, New Haven, Connecticut, USA.

MATERIALS AND METHODS

All measurements are in mm, rounded to the nearest tenth, and were taken using Edmt digital calipers and Westward outside firm-joint calipers. Photographs were taken with a handheld Panasonic LUMIX DC-FZ80 digital camera. The phylogenetic analysis of YPM VP4673 used

PAUP 4.a169 (Swofford 2002), with the resulting trees imported into FigTree 1.4.4. All specimen photographs and phylogenetic trees were rendered in Photoshop 22.5.9 as part of production of the presented figures. Figure 13F was created with NextEngine HD laser scanner and scan studio and exported as a Wavefront object, imported and rendered in Lightwave 3d 2018; the cast was produced, and the image provided to us, by M.J. Polcyn (SMU). The cast, though imperfect and displaying flash lines, does faithfully capture the morphology present. The two specimens described in this study, YPM VP4673 and ALMNH:Paleo:5452, are permanently accessioned into the scientific collections at the YPM and ALMNH, respectively.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758
SQUAMATA Oppel, 1811
MOSASAURIDAE Gervais, 1852
RUSSELLOSAURINA Polcyn and Bell, 2005
PLIOPLATECARPINAE Dollo, 1884

Diagnosis (after Konishi and Caldwell 2011**)—**Russellosaurines generally of medium size, mandible length rarely reaching 100 cm; quadrate ala laterally expanded with uniformly curved border, thin in the center; distinct alar concavity present immediately dorsal to mandibular condyle; surprastapedial process elongate, at least reaching mid-height of quadrate; process often ending with blunt terminus; canal(s) for basilar artery through basisphenoid and basioccipital exiting as large opening(s) on medullary floor; jaws slender; a large foramina on lateroventral/ventral face of retroarticular process; marginal tooth crowns slender, distally tapering and posteromedially recurved from mid-height; middle and posterior tooth crowns typically bicarinate, two carinae aligned in anteroposterior orientation and dividing crown surface semi-equally; marginal tooth crown medially finely striated, laterally faceted or fluted to various extent; tooth crown with sub-circular basal cross-section; intermediate and terminal caudal centra horizontally short, centrum length not exceeding centrum height more than 1.5 times.

Included Genera—*Platecarpus* Cope (1869), *Plioplatecarpus* Dollo (1882), *Goronyosaurus* Azzaroli et al. (1972), *Angolasaurus* Antunes (1964), *Ectenosaurus* Russell (1967); *Selmasaurus* Wright and Shannon (1988), *Russellosaurus* Polcyn and Bell (2005), *Latoplatecarpus* Konishi and Caldwell (2011), *Plesioplatecarpus* Konishi and Caldwell (2011), *Gavialimimus* Strong et al. (2020),

and *Sarabosaurus dahli* Polcyn et al. (2023).

ECTENOSAURUS Russell, 1967

Generic Type—*Ectenosaurus clidastoides* (Merriam, 1894).

Generic Holotype—Formerly at Bayerishe Staatssammlung für Paläontologie (Munich, Germany), probably destroyed in Second World War, included "posterior portion of the skull and several vertebrae" collected from the Niobrara Chalk of Logan County, Kansas, USA (Russell 1967:158).

Generic Neotype—FHSM VP-401, designated the neotype by Willman et al. (2021), includes an essentially complete, articulated skull with both mandibles, articulated vertebral column to the 29th prepygal, ribs (with fragments of calcified costal cartilage), sternum, both scapulo-coracoids, and the majority of both forelimbs. It should be stressed that portions of the neotype have been heavily restored with plaster. Specimen was collected from the Smoky Hill Member of the Niobrara Chalk (upper Santonian-lower Campanian) at "Garret Ranch, seven or eight miles northwest of Wakeeney, Trego County, Kansas" (Russell 1967:158, Schumacher 1993).

Generic Diagnosis (modified from Willman at al. 2021)—Plioplatecarpine possessing the following apomorphies: premaxilla-maxilla suture extending posteriorly beyond posterior end of third maxillary tooth; maxillary and dentary tooth count each exceeding 12; prefrontal excluded from posterolateral margin of external nares by wing of maxilla; frontal emarginate above orbits; prefrontal and postorbitofrontal not in contact; parietal table wider than long; posteroventral process on jugal present; anterior border of jugal vertical ramus convex near jugal corner; 9–11 teeth in pterygoid; pterygoid tooth row anterior to ectopterygoid process straight; pterygoid teeth subequal in size; suprastapedial process medially excavated; posterolateral infrastapedial process of quadrate overlapping posteriorly onto distal terminus of surprastapedial process; stapedial pit narrowly rectangular; medial parapet of dentary higher than lateral wall; coronoid dorsal process extending posteriorly over free dorsal border of surangular, terminating acutely in profile; post-glenoid notch on dorsal rim of articular; at least 29 presacral, five pygal, and 28 intermediate caudal vertebrae; hypapophysis laterally compressed; anteroventral ridge extending from hypapophysis distinct, almost reaching cotyle; articular surface of pygal square in outline, not triangular; up to seven well ossified carpals. See Russell (1967:157–158) for additional diagnostic postcranial characters, based on the neotype specimen

(FHSM VP-401, *Ectenosaurus clidastoides*).

<div align="center">

Ectenosaurus tlemonectes SP. NOV.

FIGS. 2–10

</div>

ZooBank LSID—urn:lsid:zoobank.org:act:E2E61DA4-E21D-4643-A0B6A8C04418062

Ectenosaurus clidastoides (Merriam, 1894) in Russell
(1967: 158).
"*Ectenosaurus* composite" in Bell (1997).
Ectenosaurus sp. in Konishi (2008).
Ectenosaurus sp. in Willman et al. (2021).

Diagnosis—A medium-sized plioplatecarpine mosasaur referable to the genus *Ectenosaurus* and exhibits the following unique combination of characteristics: a) very prominent median dorsal ride on frontal, extending back at least to interorbital embayment, wider posteriorly than anteriorly; b) olfactory canal long and tightly bracketed by broad, hour-glass shaped descending processes; c) frontal subtriangular with weakly developed, incipient interorbital embayments; d) suprastapedial process broadly fused with infrastapedial process, the latter partially overlapping the former; e) mandibular condyle deeply concave, saddle-shaped; f) medial face of squamosal rugose and highly vascularized; g) angular surface for contact with surangular posteriorly recurved; h) premaxilla dorsally planar, except for prominent median keel; i) step-wise constriction present anteriorly on internarial bar; j) short edentulous rostrum on premaxilla; k) premaxillary-maxillary contact terminates between the third and fourth maxillary teeth, at the anteriorly deepest portion of the maxilla; l) teeth with smooth enamel at bases, overprint of striations and fluting higher on crown, carinate and fluted toward cusps. Characteristics a, c, e, g, h, i, j, k, and l distinguish the taxon from *Ectenosaurus clidastoides* and *E. everhartorum*, as well as from ALMNH:Paleo:5452, are considered apomorphic, and justify the erection of a new species. Feature b) distinguishes the taxon from ALMNH:Paleo:5452, but it is unclear whether this characteristic is present in other members of the genus.

Holotype—YPM VP4673, a mostly complete, disarticulated skull and mandibles, several cervical and dorsal vertebrae representing a medium-sized mosasaur (skull ~70 cm; total length ~4.0 m, based of dimensions of *Platecarpus "ictericus"* provided in Russell (1967) after Williston (1898). Cranial material includes premaxilla, both maxillae, both dentaries, the posterior ends of both splenials, the anterior ends of both angulars, almost complete left posterior mandibular unit (i.e., surangular,

articular, prearticular) and less complete left posterior mandibular unit (i.e., fragmentary surangular, articular, prearticular, plus coronoid), frontal, portions of both jugals, almost complete left quadrate, proximal fragment of right quadrate, the posterior end of the right squamosal, fragmentary right pterygoid, much of the neurocranium (including the basioccipital, supraoccipital, the left paroccipital process of the opisthotic, and portions of the prootic), several associated teeth or tooth fragments, along with numerous other miscellaneous bone fragments believed to belong to the skull. The only preserved postcranial material consists of several cervical and dorsal vertebrae or fragments of vertebrae, all badly distorted and weathered.

Occurrence—Collected June 1875 by S. W. Williston from erosional gullies in the Smoky Hill Chalk Member of the Niobrara Chalk Formation (upper Coniacian-lower Campanian; Fig. 1B), Gove County, Kansas (Fig. 1A). The precise locality and stratigraphic level within the Smoky Hill Chalk are unknown.

Etymology—Species name from τλήμων [tlḗmōn], Classical Greek for "patient" + νήκτης [nḗktēs], Classical Greek for "swimmer," referring to the 147 years that elapsed between the holotype's discovery in 1875 and its eventual recognition as a distinct taxon in 2022.

Description

*Frontal—*The frontal (Fig. 2A, B) is an elongate, triangular bone with very slight antoribital bulges and short, roughly triangular posterolateral alae. The posterior quarter of the frontal is weathered and broken into three fragments. As preserved, the midline length is ~200 mm, with a maximum width of 87.9 mm and an interorbital width of 68 mm. A very well-developed median dorsal ridge (Fig. 2A) extends at least three-quarters of the frontal's length (~132.8 mm), widening markedly posteriorly (from 3.9 mm to 8.6 mm). Ventrally (Fig. 2B, C), a pair of broad, rounded, and roughly violin-shaped descending processes (the crista cranii frontalis of some authors) bracket the olfactory tract, almost completely enclosing it for nearly half its length (59.3 mm) before opening anteromedially into a flat amygdaliform sulcus to accommodate the olfactory lobes. Though neither the prefrontals nor postorbitofrontals are preserved, articulation between these elements and the frontal is evident from well-defined, striated depressions on the ventral surface of the frontal. These articular surfaces are completely separated from one another by a wedge or ridge (the ventral separation ridge of Konishi and Caldwell 2007), oriented approximately 90° to the sagittal plane,
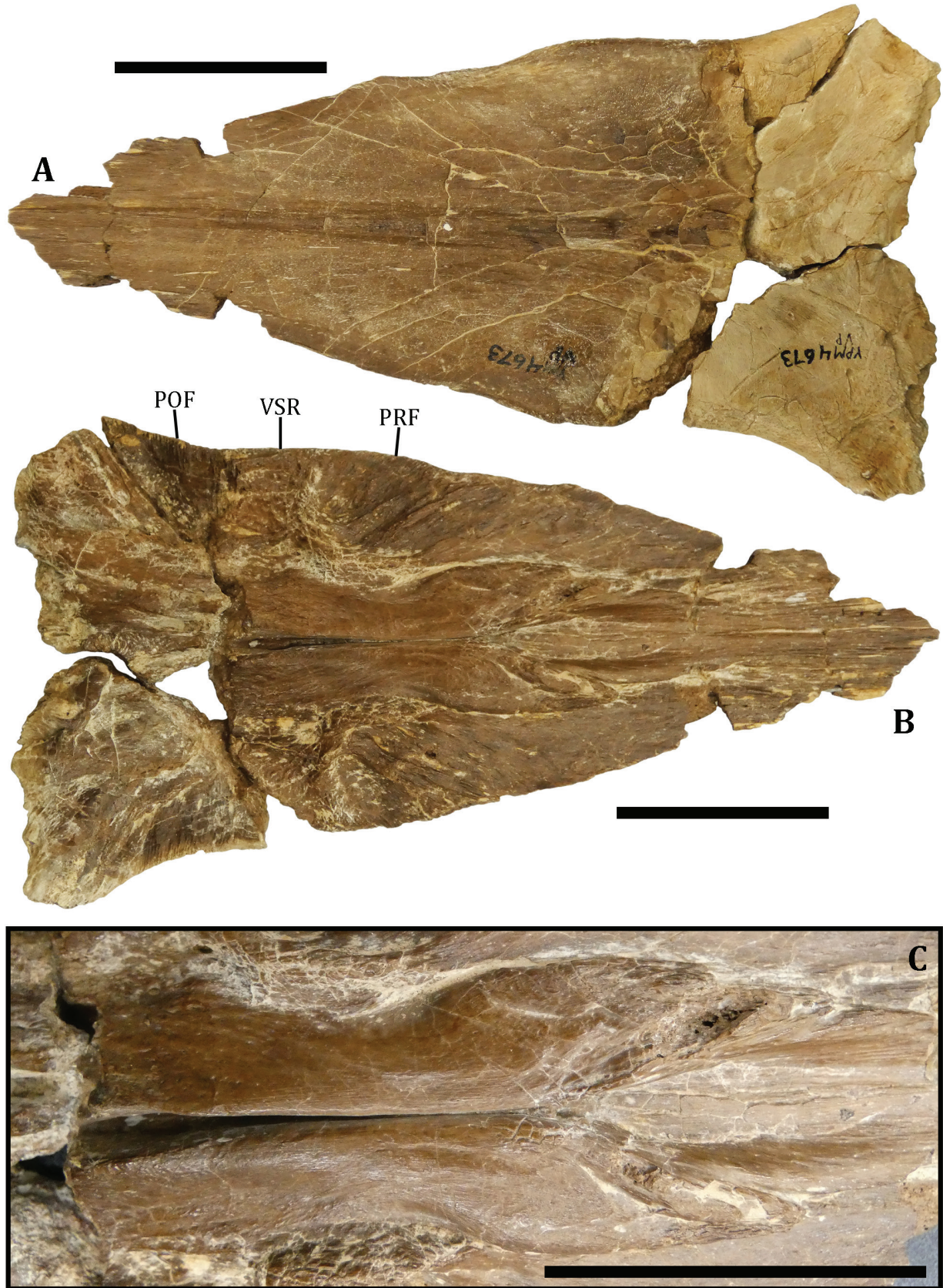
Figure 2. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. **A-C**. Frontal in dorsal (**A**) and ventral (**B**) views. **C**. Detail of olfactory canal. **Abbreviations: POF**, excavation for postorbitofrontal; **PRF**, excavation for prefrontal; **VSR**, ventral separation ridge. Scale bars=5 cm.

permitting the frontal to form a small portion of the supraorbital border. Among other plioplatecarpines, this trait has only been reported in *Russellosaurus* and *Plesioplatecarpus,* but it is also present in *Yaguarasaurus* Páramo (2000), the halisaurines, and in the mosasaurine *Clidastes* (*sensu C. propython* Cope, 1869); it is presumed to be plesiomorphic for the Mosasauridae (DeBraga and Carroll 1993). The contact with the parietal is roughly transverse and possesses no prominent posteromedial projections onto the parietal. The parietal is not preserved, and it is unclear whether, and to what degree, it may have invaded/overlapped the frontal anteromedially.

Quadrates and Squamosals—The left quadrate (Fig. 3A–C) is reasonably complete but lacks most of the tympanic ala and portions of the anterior quadratic shaft. The suprastapedial process is medially deflected and is large and elongate, as is typical of plioplatecarpines, measuring ~60% of the quadrate height. The borders of the suprastapedial process are straight medially, slightly concave laterally, and expand distally to form a bulbous, irregularly rounded extremity that is fused with the infrastapedial process. In the case of *Ectenosaurus*, the "infrastapedial" process is formed by a greatly developed posteroventral ascending quadratic rim (see Bell 1997 and Palci et al. 2020 for reviews of issues of homoplasy and inconsistent terminology related to this structure) and includes a flange-like process that overlaps the suprastapedial posterodistally. Though the two processes contact to varying degrees in multiple halisaurine, plioplatecarpine, and mosasaurine taxa, the particular mode of contact seen in *Ectenosaurus* is distinctive, in that the distal end of the suprastapedial is not only solidly fused with but partially embraced by a projection from the infrastapedial process. We revisit this character state in the description of ALMNH:Paleo:5452.

Only a small portion of the thin tympanic ala is preserved. The mandibular condyle is deeply concave and saddle-shaped, possibly the most pronounced example of this condition in any mosasaur. Though the quadrate of FHSM VP 401 is crushed, *Ectenosaurus clidastoides* does not appear to share this feature. It is possibly incipient in *Selmasaurus johnsoni* Polcyn and Everhart (2008) but absent in *S. russelli*. Herein it is considered an apomorphy for *Ectenosaurus tlemonectes.* The suprastapedial pit is severely distorted anteroposteriorly, obscuring its original dimensions, but it appears to have been long and subrectangular.

The posterior end of the right squamosal (Fig. 3D–F) is preserved and in good condition. The medial face (Fig. 3E) is marked by an elaborate series of ridges and troughs that would have received corresponding surfaces on the supratemporal. Numerous large foramina are also present. The ventroposterior fossa for articulation with the quadrate (Fig. 3D) forms a rough isosceles triangle and is shallowly concave. Anterodorsally there is a small but distinct knob marking the posterior terminus of the groove for insertion of the postorbitofrontal processes.

Dentigerous elements—The premaxilla and the majority of both maxillae and dentaries are present in YPM VP4673. The premaxilla (Fig. 4A–C) is well preserved and complete except for the posteriormost portion of the internarial bar. There is a very short, spatulate edentulous rostrum (5.0 mm)*.* Dorsally, the premaxilla is planar and bears a small median keel or crest (19 mm) near the base of the internarial bar that is subtriangular in lateral profile (Fig. 4C). This structure has not been observed in any other specimen of *Ectenosaurus.* The posterior terminus of the premaxillary-maxillary suture occurs at the deepest anterior portion of the maxilla (Fig. 4D, E), at a position even with the fourth maxillary tooth. The internarial bar narrows abruptly behind the premaxillomaxillary suture (the "step-wise constriction" described by Willman et al. 2021), is triangular in cross section, and expands posteriorly to receive the anterior process from the frontal.

Neither maxilla is complete, so the tooth count can only be estimated. There are ten preserved tooth positions present in the right maxilla and 11 in the left, though there may have been as many as 12 teeth present in each, considering both are missing the posteriormost portion of the tooth row. As noted by Willman et al. (2021:744), the laterally expanded anterior portion of the external naris extends from the fourth to the midpoint of the seventh tooth in YPM VP4673, a distance of 3.5 tooth bases, which is slightly longer than that of *E. everhartorum* (2.5 tooth bases long), but shorter than *E. clidastoides* (four tooth bases long).

The dentaries (Fig. 5A–E) are gracile, delicately constructed bones, more so than in either *Ectenosaurus clidastoides* or *E. everhartorum*. Both the dorsal and ventral margins are straight. There are 13 teeth in each dentary. The anterior portions of the dentaries in FHSM VP-401 are restored with plaster, so a precise tooth count for the generic neotype is not possible. According to Willman et al. (2021), the restored dentaries are too short and do not match the maxillae, and the dentary tooth count of "15 and 14 teeth in the right and left dentaries, respectively" is too low. Based on the unrestored premaxilla and maxillae, they estimate the original dental formula for *E. clidastoides* to have been 2=17=17
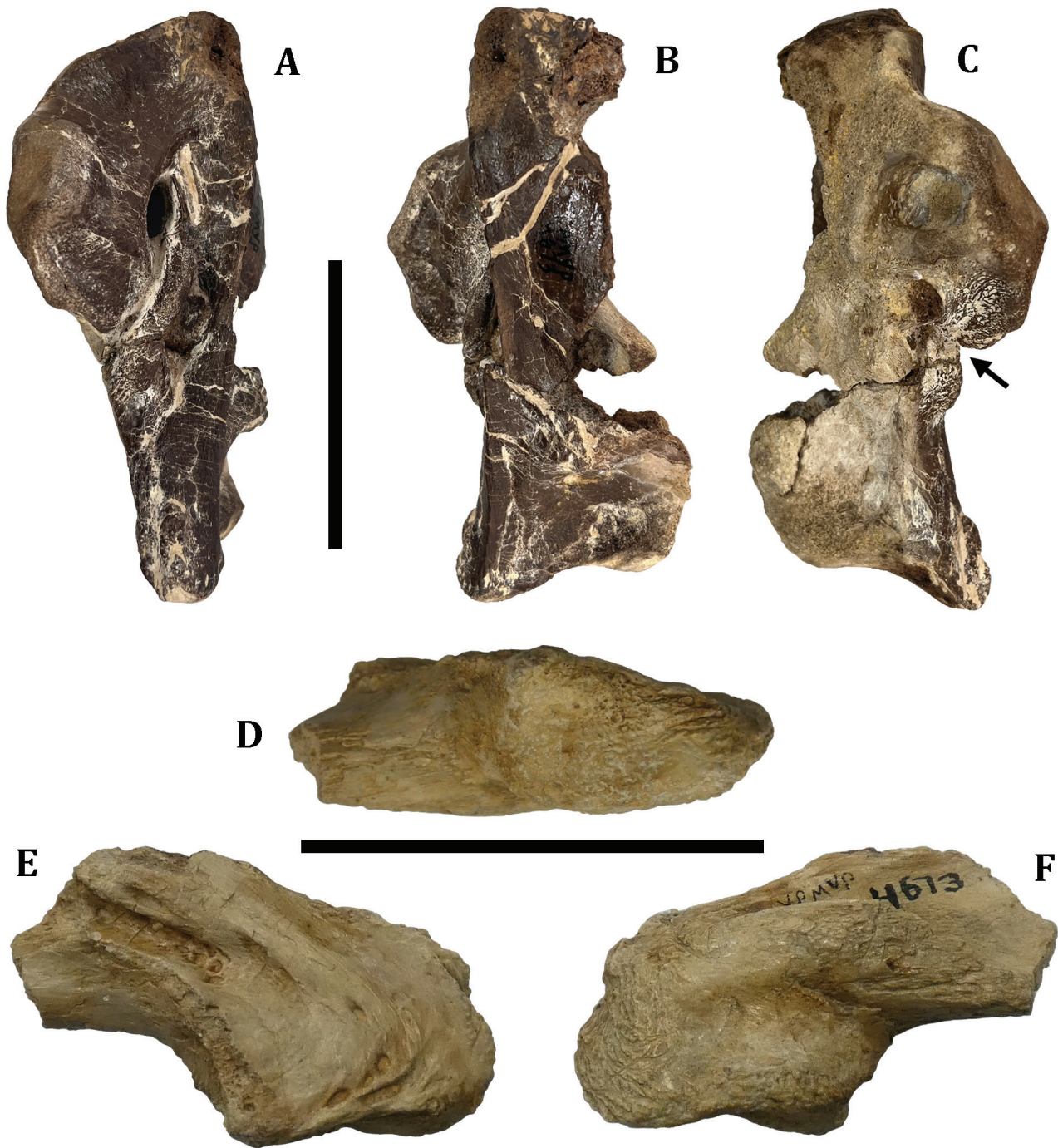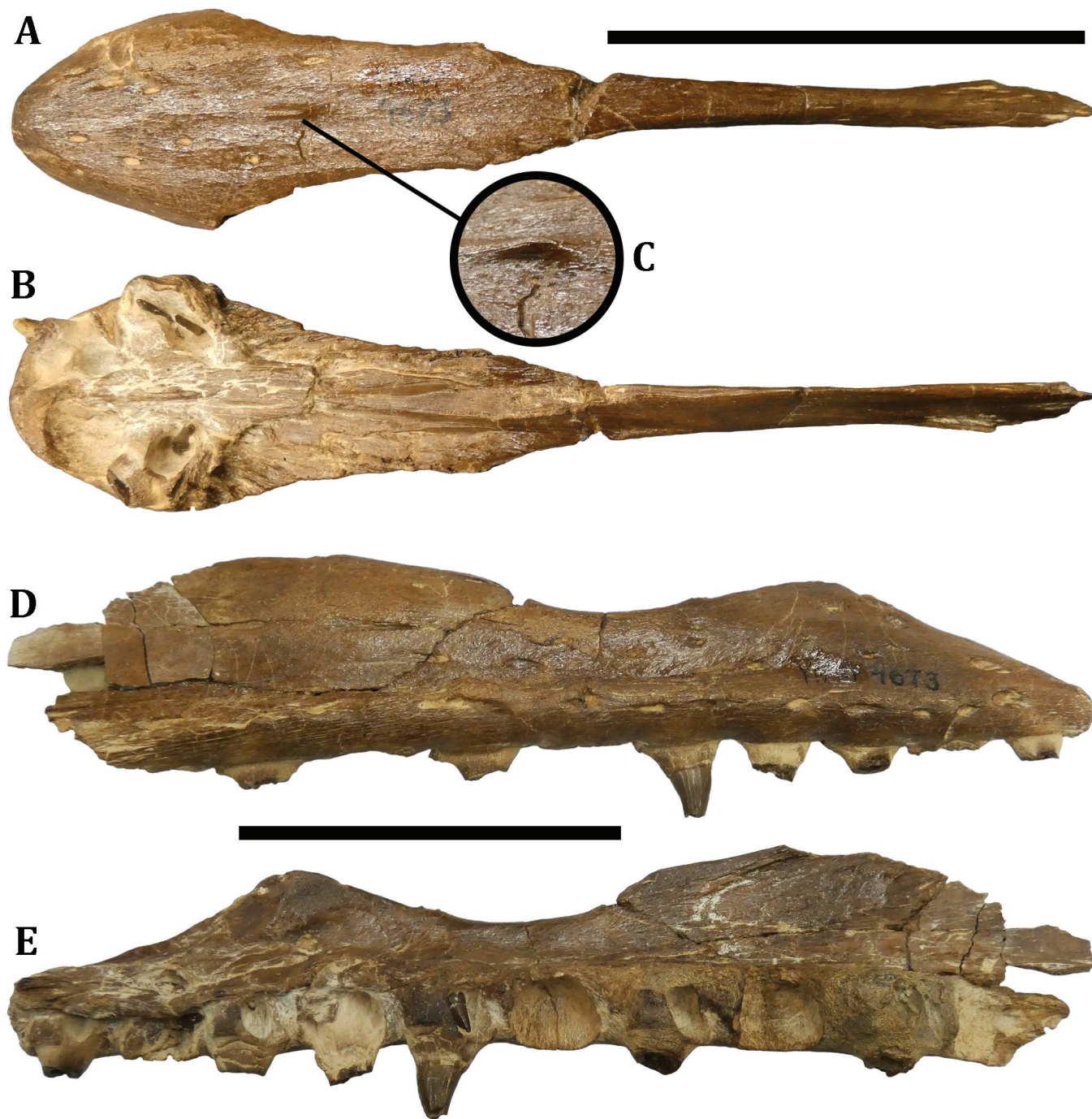
Figure 3. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. **A–C.** Left quadrate in medial (**A**), anterior (**B**), and posterior (**C**) views. **D–F.** Left squamosal in ventral (**D**), lateral (**E**), and medial (**F**) views. Arrow indicates suprastapedial/infrastapedial contact. Scale bars=5 cm.

(premaxilla=maxillae=dentary). This trend toward hyperdonty in *Ectenosaurus* is incipient in *E. tlemonectes,* where the dental formula is 2=~12=13, nearer to the formula seen in most plioplatecarpines (2=12=12).

As noted by Willman et al. (2021:746, 752; fig. 8f), in YPM VP4673 the strap-like medial parapet is raised above the level of the lateral wall in the dentaries, as in

E. clidastoides and *E. everhartorum,* as well as the highly derived *Plioplatecarpus marshi* Dollo (1882), a surprising similarity given the latter's phylogenetic distance from *Ectenosaurus.* Willman et al. (2021:752) explained this as a case convergent evolution, a conclusion with which we concur.

A small edentulous prow is present on the dentary,

Figure 4. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673, **A–C**. Premaxilla in dorsal (**A**) and ventral (**B**) views. **C**. Detail of dorsal ridge. D, E. Right maxilla in lateral (**D**) and medial (**E**) views. Scale bars=10 cm.

which on the right is severely deformed, probably from a healed injury (Fig. 6); the deformation involves the first dentary tooth. A very large and elongate, longitudinally oriented foramen is present below the tenth tooth position, a character also present in *E. everhartorum,* where the foramen occurs between the tenth and eleventh dentary teeth (Willman et al. 2021:746).

A fragment of the left pterygoid is present, preserving the bases of seven teeth and the base of the ectopterygoid process. The preserved portion of the tooth row is straight as in *E. everhartorum* (Willman et al. 2021), as opposed to the sigmoidal shape common to plioplatecarpines.

Jugals—Portions of both jugals are preserved (Fig.
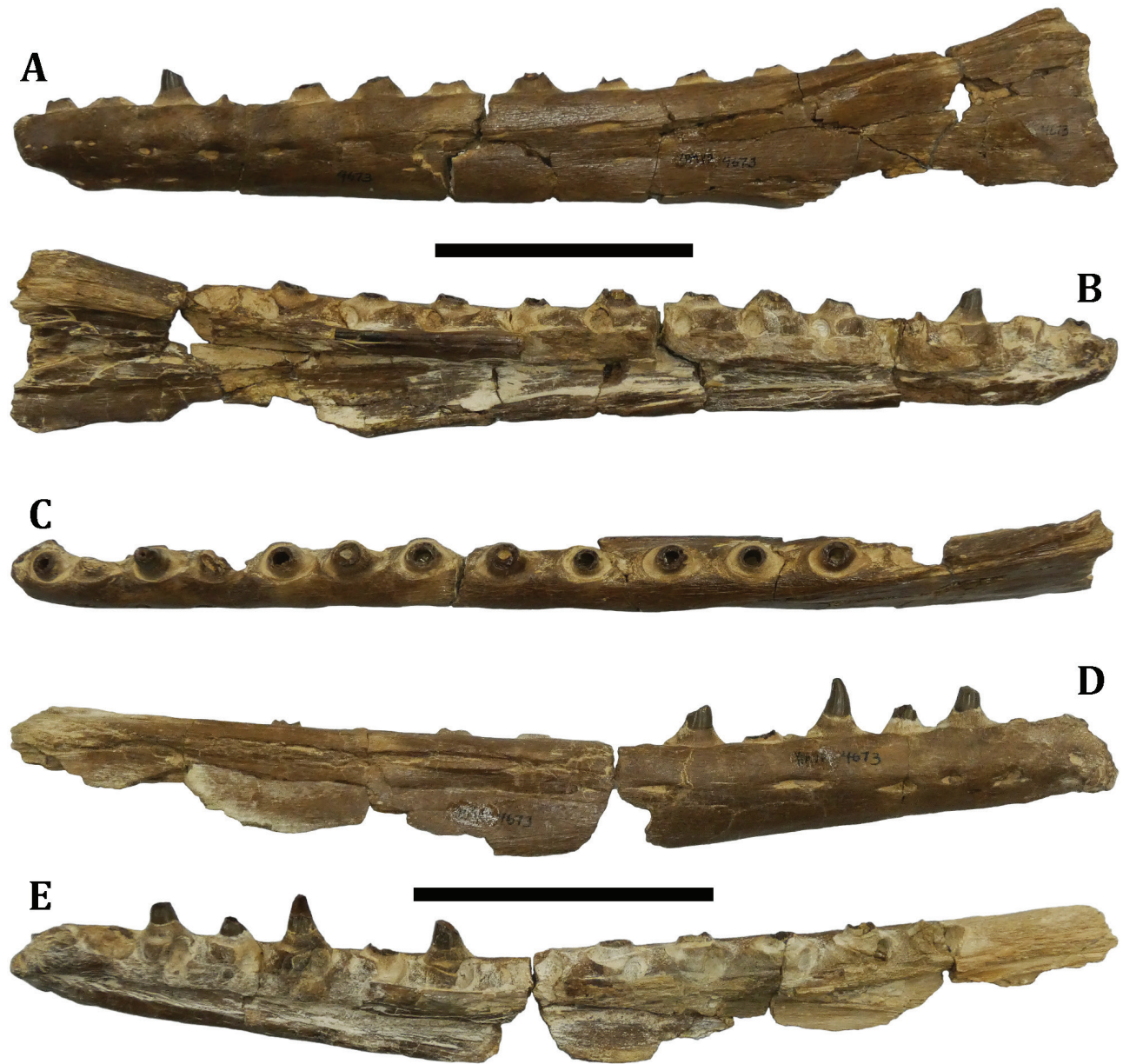
Figure 5. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. **A–E**. Dentaries in left lateral (**A**), left medial (**B**), left dorsal (**C**), right lateral (**D**), and right medial (**E**) views. Scale bars=10 cm.

7C–F). Posteroventral processes are present on both, though a considerable degree of asymmetry exists between the two elements. The process is small on the right jugal (Fig. 7C, D), but far more developed on the left (Fig. 7E, F), where it forms a scalloped posterior border for the vertical ramus. While we suspect this asymmetry is the result of pathology, additional examples of the species will be needed to determine which jugal exhibits the abnormality. A deep triangular depression on the lateral surface of the vertical ramus marks the point of articulation with the postorbitofrontal. The vertical ramus is short, less than 50% of the length of the horizontal ramus.

Coronoids—In most russellosaurines, the coronoid is a short, saddle-shaped wedge of bone straddling the anterodorsal margin of the surangular, which it encloses to varying degrees between simple medial and lateral descending processes or wings that reach the prearticular. In the plioplatecarpines, these wings are usually short, compared with those of mosasaurines. In YPM VP4673, only the right coronoid (Fig. 7A, B) is preserved and is slightly crushed lateromedially. As with most russellosaurines, the coronoid is a slender, short, selliform element

Figure 6. *Ectenosaurus tlemonectes* sp. nov., YPM VP 4673, **A–D**. Detail of pathologic and non-pathologic anterior terminus of left dentary in left lateral (nonpathologic) (**A**), right lateral (pathologic) (**B**), right medial (pathologic) (**C**), and right dorsal (pathologic) (**D**) views. Scale bars for A–C=5 cm. Scale bar for D=3 cm.

divided into lateral and medial wings which straddle the anterodorsal surface of the surangular. The coronoid dorsal margin is concave, and the ascending posterior process was well-developed, though the apex of the crest is missing. The stout medial wing would have overlapped the dorsomedial margin of the surangular, and the interior surface of this wing is highly vascularized, marked by numerous foramina. In contrast, the anterolateral wing is very short, and hardly more than a low, diagonal ridge. The shallow anteromedial bifurcation ("cleft" of Russell 1967:53) is long and well-defined, extending more than a third of the bone's length. We will discuss the coronoid of *Ectenosaurus* further in our description of ALMNH:Paleo:5452.

Articular and Surangular—The majority of both the left and right surangular-articular units are preserved (Fig. 8), though the left is the most complete. The dorsal margin of the surangular is slightly concave and broadens anteriorly as it approaches the contact with the coronoid, expanding from a height of about 3–~9 cm. The surangular-articular suture is obvious on the lateral side of the left mandible (Fig. 8A, B, D), curving beneath the glenoid fossa before running more or less straight beneath the coronoid to the intramadibular joint. The right and left articulars are both missing their posteroventral corners, but the ventral margins appear to have been generally straight. Most of the glenoid fossa is located on the articular. The posterodorsal tongue of
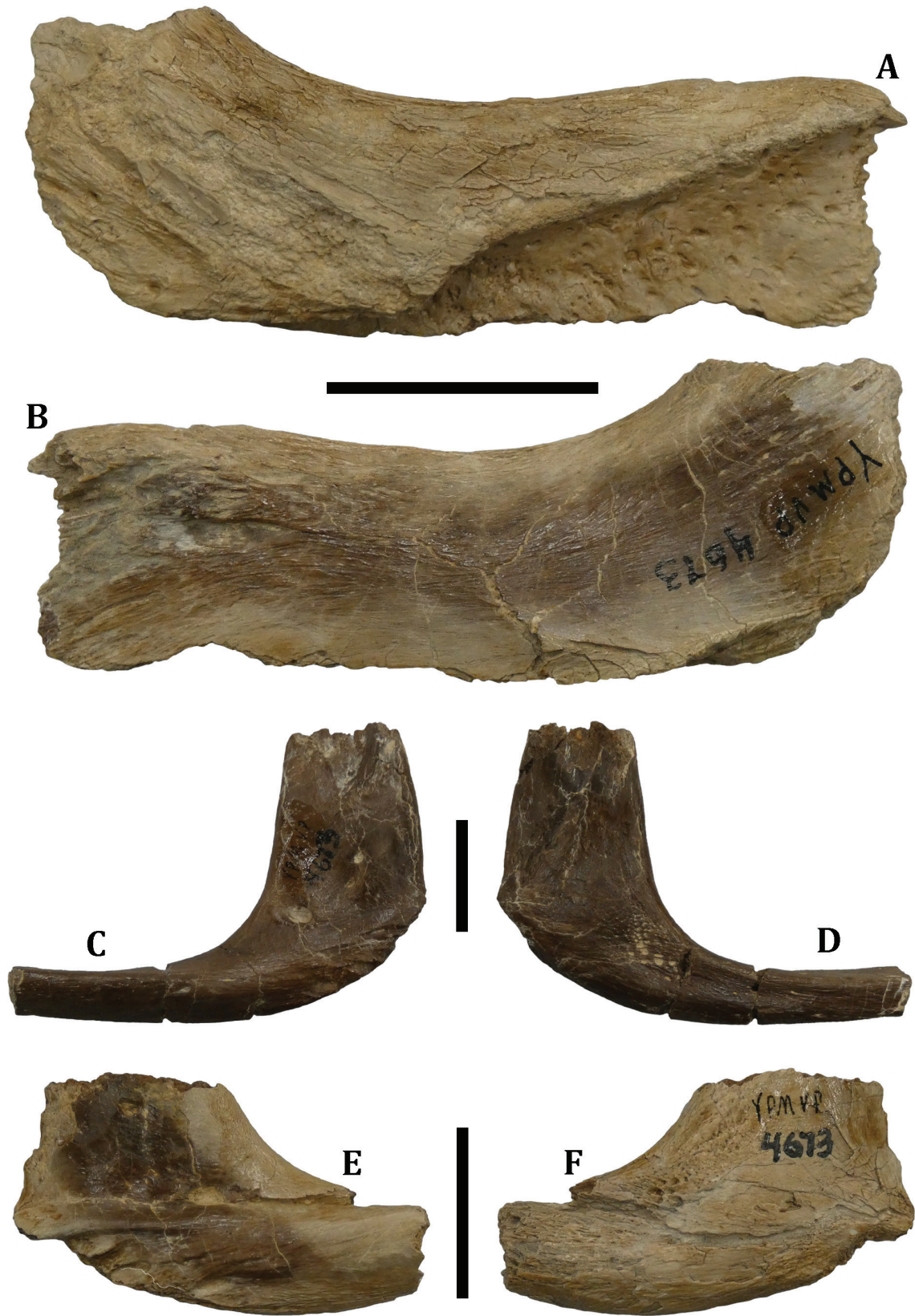
Figure 7. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. **A, B**. Right coronoid in lateral (**A**) and medial (**B**) views. **C, D**. Left jugal in lateral (**C**) and medial (**D**) views. **E, F**. Right jugal in lateral (**E**) and medial (**F**) views. Scale bars for A, B=5 cm. Scale bar for C–F=2 cm.
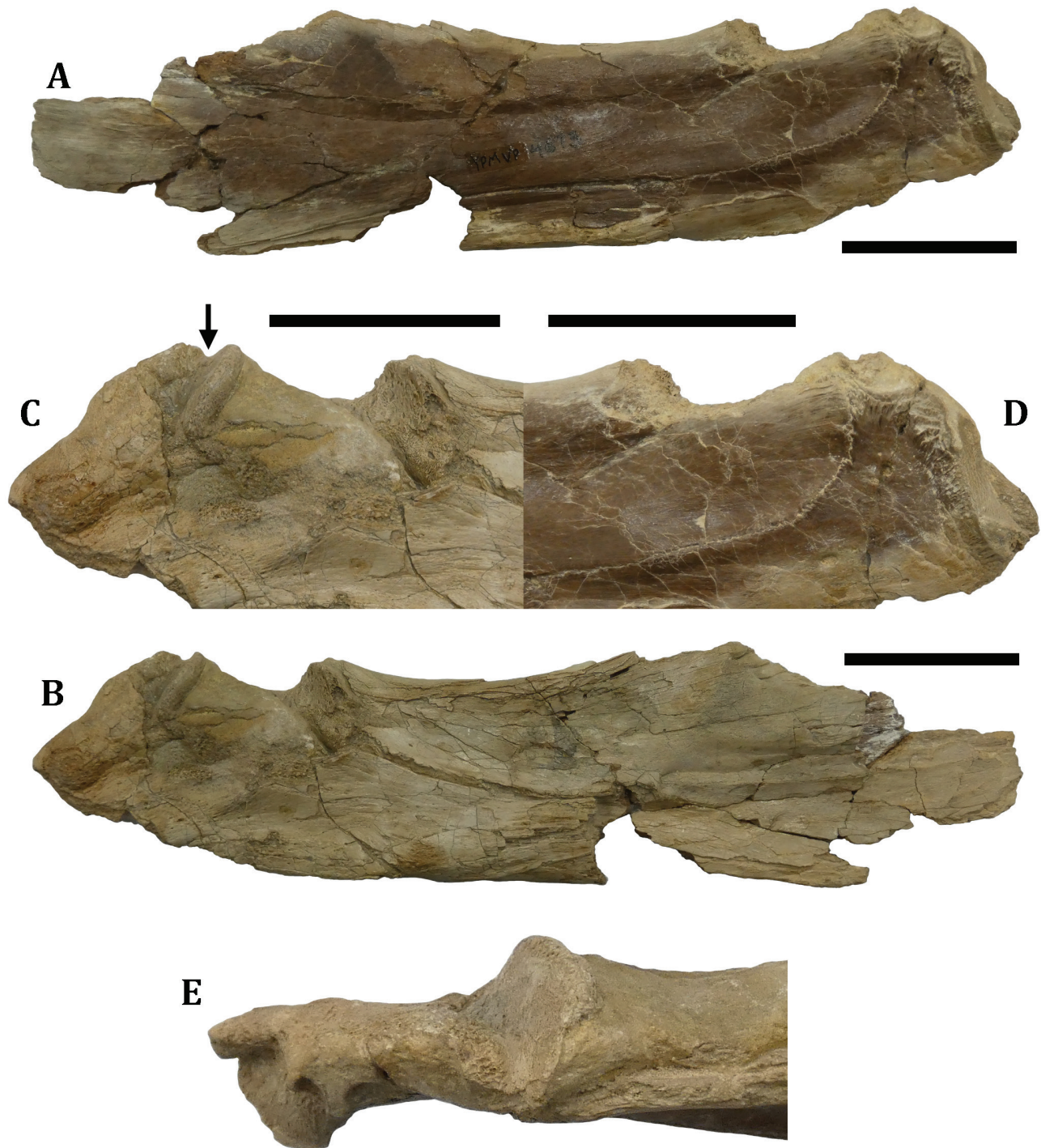
Figure 8. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. **A, B**. Left surangular-articular in lateral (**A**) and medial (**B**) views. **C**. Close-up of glenoid fossa in lateral view. **D**. Close-up of glenoid fossa in medial view. **E**. Close-up of glenoid fossa in dorsal view. Arrow indicates post-glenoid notch. Scale bars=5 cm.

the surangular terminates abruptly in a rugose, highly vascularized vertical face that forms the anterior wall of the glenoid fossa (Fig. 8C). Willman et al. (2021:747; fig. 12) stressed the presence of a "distinct notch on the dorsal surface...just prior to the glenoid fossae" in *E.*

clidastoides, E. everhartorum, and YPM VP4673 (Fig. 8C) as a character "absent in all other mosasauroids" and therefore considered diagnostic of the genus by those authors. In YPM VP4673, portions of the glenoid fossa are bordered dorsally and medially on both the angular

and surangular by a thick, raised rim with rounded edges (Fig. 8B, C).

Splenial-Angular—Portions of both splenials and angulars are present (Fig. 9A–L), including the articulating faces for all four elements. Willman et al. ([2021:747]) described the posterior surface of the splenials in *E. everhartorum* and *E. clidastoides* as possessing a "robust, dorsomedially expanding flange" giving an "overall square shape, in which they are almost equidimensional in height and width." Neither splenial of YPM VP4673 has a complete articulating surface, and the left is slightly crushed lateromedially, but both have curving margins and appear to have been more rounded than square (Fig. 9J). Therefore, we do not consider a splenial with a squared articulating surface as diagnostic of the genus *Ectenosaurus.* Only the anterior termini of the angulars are preserved (Fig. 9A–H). While the left is less crushed, the right includes enough of the lateral wing that the surface for its contact with the surangular is preserved (Fig. 9C). This surface is marked by pronounced horizontal striations and, unlike the condition present in *E. clidastoides*, its ascending margin is distinctly recurved posteriorly, a trait here considered diagnostic of *E. tlemonectes.*

The splenio-articular joint in mosasaurs is usually described as a simple ball-and-socket joint ([Camp 1942], [Russell 1967], [Bell 1997], [Rieppel and Zaher 2000]), a cotyle (splenial)-condyle (angular) articulation that often fails to reflect the wide range of variation between taxa; Rieppel and Zaher ([2000:8]), for example, described it simply as "the splenial is the receiving part, the angular the received part." In YPM VP4673, the splenio-angular joint is more complex (Fig. 9L), with each element contributing to the cotyle/condyle arrangement in a contact consisting of a series of more or less vertically oriented ridges and sulci. A deep median sulcus is present on the angular, for example, receiving a matching ridge on the splenial, while strong medial and lateral ridges have matching splenial sulci. While it is possible to deduce the general nature of the splenio-angular joint in YPM VP4673, deformation has altered the details of the articular faces of the angulars (Fig. 9B, G). The elements do not match, and it is unclear which most closely approximates the original morphology.

An anteroventral rugosity on the right angular appears to be pathologic (Fig. 9E), as it is absent on the left angular. Considering the severe damage to the anterior end of the right dentary, it is possible this pathology resulted from the same trauma, produced by torsion inflicted on the intramandibular joint.

Neurocranium—As with much of the posterior portion of the skull of YPM VP4673, the occipital unit has suffered considerable weathering prior to collection. However, much of the neurocranium is preserved. Elements identified include the basioccipital,, supraoccipital, the left parocciptal process of the opisthotic, and portions of the prootic. It is likely that much of the basicranial circulatory pattern can be reconstructed, as the periotic labyrinth is often well preserved. This aspect of the morphology of YPM VP4673 will be the focus of a future collaborative study between the senior author and M.J. Polcyn (SMU).

Teeth—Almost all the marginal teeth of YP VP4673 have broken free of the bone and been lost during post-exposure weathering and/or during collection of the specimen. The few teeth that remain *in situ* are incomplete and missing their apices, though the apices can be observed for several replacement teeth. Possible pterygoid teeth are also present, but none are attached to the preserved fragments of the pterygoids. Preserved marginal teeth include the third tooth in the left dentary (Fig. 5A, B), the third, fourth, fifth, and seventh teeth in the right dentary (Fig. 5D, E), the fifth right maxillary tooth (with replacement tooth) (Fig. 4D, E), and the second left maxillary tooth (not figured). None of the four premaxillary teeth are preserved, but the bases indicate they may have been slightly prognathous (Fig. 4A, B). The bony tooth base is significantly taller in YPM VP4673 than in *E. clidastoides,* more closely resembling the condition present in *E. everhartorum, Selmasaurus johnsoni,* and *Platecarpus tympaniticus* Cope ([1869])*.* For example, the bony base of the fifth right dentary tooth (the most complete, preserving all but the cusp) is 5.8 mm tall labially, while the preserved portion of the crown measures 14.9 mm.

Russell ([1967:156]) did not describe the dentition of FHSM VP-401 in any detail, beyond noting the dental formula and that the teeth are "bicarinate, vertically striated, and medially recurved." However, additional observations are made here based on photographs provided to us by M.J. Polcyn (SMU). Willman et al. ([2021]) say nothing about the tooth morphology of *E. everhartorum.* Other than the second left maxillary tooth and the apices of replacement teeth, only broken bases are preserved in FHSM VP-5515. Fortunately, while most of the teeth in YPM VP4673 are missing, the ten fragmentary teeth, plus the replacement teeth, do allow for a description of the general dental morphology of YPM VP4673, including the apicobasal ornamentation of the enamel. All the teeth appear to be weakly faceted, though faceting has previously been considered absent in russellosaurines ([Street et al. 2021]). While the marginal dentition of *E. clidastoides*
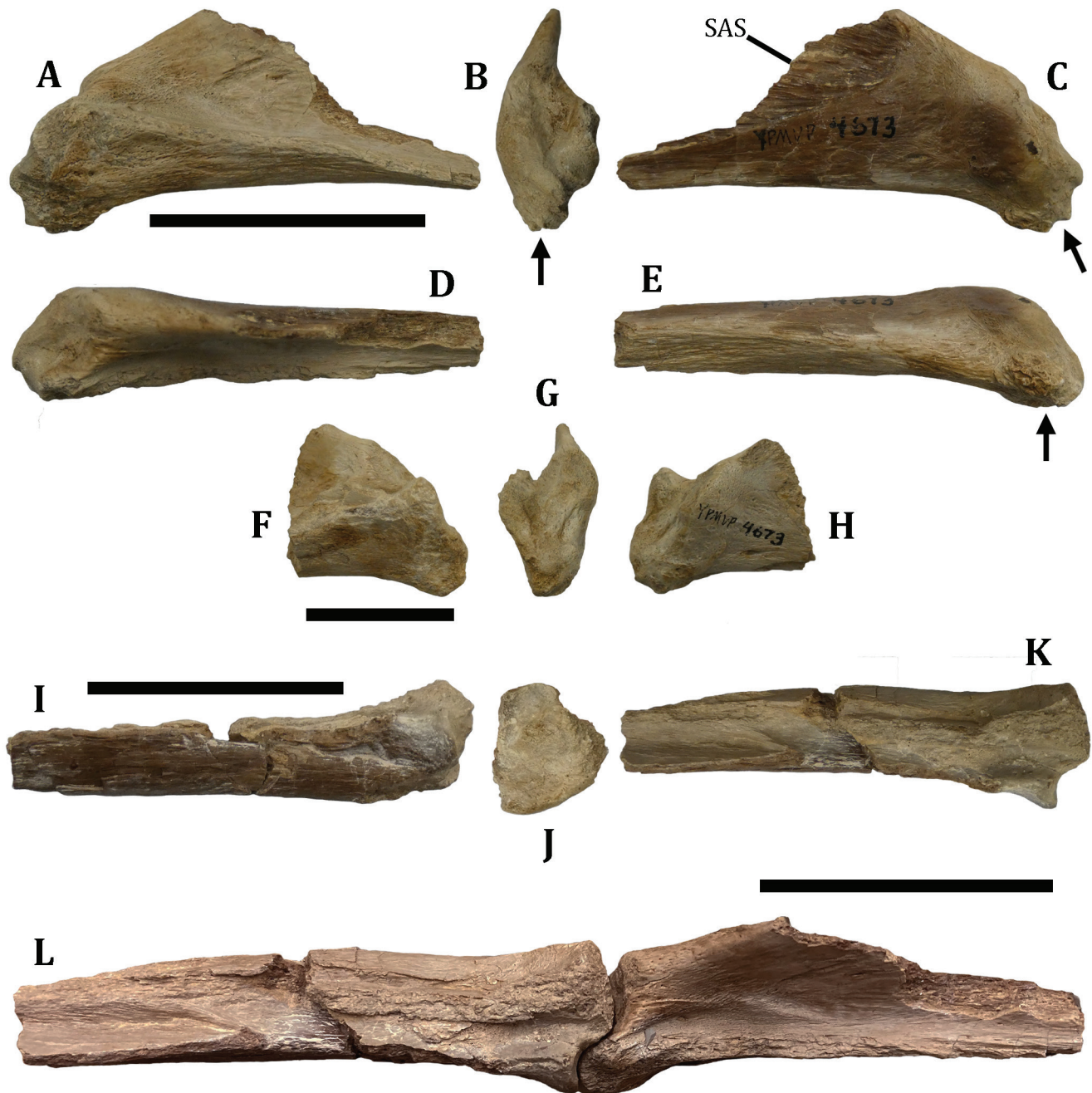
Figure 9. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. **A–E**. Left angular in lateral (**A**), medial (**B**), anterior (**C**), dorsal (**D**), and ventral (**E**) views. **F–H**. Right angular in lateral (**F**), anterior (**G**), and medial (**H**) views. **I–K**. Right splenial in lateral (**I**), anterior (**J**), and dorsal (**K**) view. **L**. Articulated right splenial and angular. Arrows point to pathologic ventral rugosity on left angular. **Abbreviations: SAS**, surangular articulation surface. Scale bars for A–E, I–K, L=5 cm. Scale bars for F–H=3 cm.

appears to be uniformly strongly bicarinate throughout, in YPM VP4673 carinae are only well developed near the cusp (most evident in replacement teeth) and never extend the full length of a tooth. Mesial carinae are generally better developed, and some teeth lack distal carinae. The carinae lack serrations (termed false denticulation by Prasad and de Lapparent de Broin (2002) and Street et al. 2021). Except for faceting, ornamentation is all

but absent on the basal region of the crowns. Apically, the enamel bears an overprint of striations and fluting that is usually more developed on the lingual surfaces. In general, ornamentation is less prominent than in *E. clidastoides,* where striations extend the full height of the teeth. Anteriorly, teeth in YPM VP4673 are subcircular in cross section, becoming slightly elliptical posteriorly. Teeth in YPM VP4673 are posteromedially recurved, as

in *E. clidastoides.* A number of loose teeth believed to have broken off the pterygoids are more elliptical in cross section, lack almost all ornamentation, but have strongly developed carinae.

Vertebrae—Vertebrae are the sole preserved elements of the postcranial skeleton, though only a few cervical (including the axis) and dorsal vertebrae were collected and so the vertebral formula is unknown. The vertebrae that are present have all suffered varying degrees of plastic deformation. Where the cotylar and condylar surfaces are preserved, the interarcticular surfaces appear to have been broadly elliptical. The two cervicals have strongly developed, posteriorly-inclined hypapophyses. The hypapophyses are joined to the ventral rim of the condyle by a narrow, gently concave ridge (Fig. 10). Willman et al. (2021) stated that this ridge is unknown in all other plioplatecarpines except *Selmasaurus johnsoni* and *Ectenosaurus everhartorum.* The hypapophyseal peduncles are slightly crushed but appear to have been elliptical in life.

Taxonomic note

Future work may show YPM VP4673 to be distinct from *Ectenosaurus* at the generic level as it does differ markedly in some respects (form of the frontal, concave mandibular condyle on quadrate, etc.), while possessing other characters considered diagnostic of the genus (post-glenoid notch, mode of contact between supra- and infrastapedial processes, etc.). In choosing here to include it in *Ectenosaurus* we have elected the more conservative approach. Curiously, YPM VP4673 was described on three separate occasions (Konishi 2008, Willman and Konishi 2019, and Willman et al. 2021), whole or in part, and never recognized as a unique species. Konishi (2008) described it as *Ectenosaurus* sp., Willman and Konishi (2019) suggested it was conspecific with the then-undescribed *E. everhartorum* (FHSM VP-5515), and Willman et al. (2021), in the description of *E. everhartorum,* returned to calling it *Ectenosaurus* sp. Notably, these authors consistently failed to locate both the frontal and splenials, key elements separating *E. tlemonectes* from *E. everhartorum* and *E. clidastoides.*
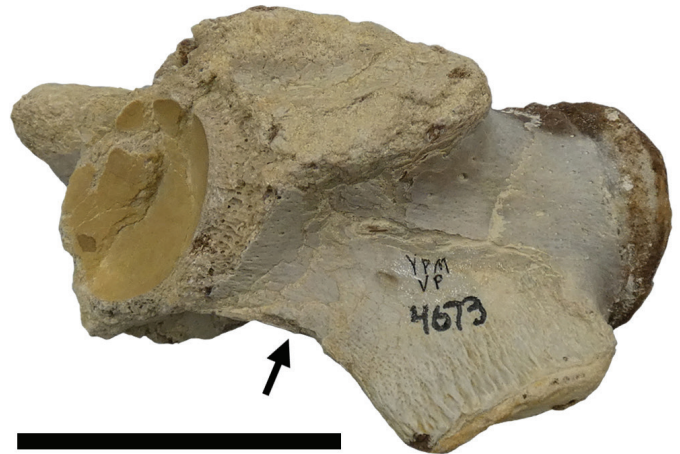
<center>

ECTENOSAURUS SHANNONI SP. NOV.
FIGS. 11–13

</center>

Zoobank LSID—urn:lsid:zoobank.org:act:4D791F56-9245-41CF-9290-A0AA0F7C6DA.

*Ectenosauru*s sp. in Kiernan (2002)

Diagnosis—A medium-sized plioplatecarpine mosasaur

Figure 10. *Ectenosaurus tlemonectes* sp. nov., YPM VP4673. Cervical vertebra in left lateral view. Arrow indicates ventral ridge connecting the hypapophyseal peduncle and cotyle. Scale bar=5 cm.

referable to a new species of *Ectenosaurus* based on the structure of the frontal, which possesses the following characteristics: a) a dorsal surface entirely lacking a median ridge, but with transverse doming anteriorly; b) a parietal dorsal table with rounded lateral margins and lacking parasagittal crest; c) a splenial with an elliptical posterior articulating surface. The species can be further distinguished from *Ectenosaurus clidastoides* and SMU 7650 by the simpler contact between the frontal and parietal and by a relatively shorter frontal. It can be distinguished from *E. everhartorum* and *E. clidastoides* by the form of the posterior terminus of the splenial, which is neither square nor rounded, but elliptical. Characteristics separating *Ectenosaurus shannoni* sp. nov. from *E. tlemonectes* include the absence of a median ridge on the frontal in *E shannoni,* the general ventral morphology of the frontal, a more elaborate sutural mode of contact between the coronoid and surangular in *E shannoni,* the differences in the splenio-angular joint between the two taxa, and a greater degree of fusion between the supra- and infrastapedial processes of the quadrate in *E. tlemonectes.*

Holotype—ALMNH:Paleo:5452 consists of several bones from a disarticulated skull and axial skeleton, including the frontal, parietal, right splenial, right coronoid, a fragment of the left quadrate, numerous indeterminate skull fragments, an incomplete scapula, and several badly weathered vertebrae, including five cervicals, thirteen dorsals, five pygals, and four caudals. Much of the specimen is weathered, especially the scapula and vertebrae, probably as a result of prolonged exposure to the elements before collection. Other than subaerial weathering,

the specimen is well preserved, lacking crushing and plastic deformation. The specimen was originally deposited in the collections of the Geological Survey of Alabama under the catalog number GSA V1048, but in 2005 was transferred to the ALMNH (Ebersole and Dean 2013) and subsequently assigned a new catalog number, ALMNH:Paleo:5452.

Occurrence—The specimen was collected in November 1976 by S.W. Shannon and J. Kidd from erosional gullies within the lower 21 meters of the unnamed member of the Mooreville Chalk (Selma Group, lower Campanian, Upper Cretaceous, Fig. 2B), located in the NE 1/4, SE 1/4 of Sec. 30, T22N, R1E., Greene County, Alabama, USA (Fig. 1A). The locality has since been reclaimed for farmland and is no longer available for study. Until recently, the Mooreville Chalk was subdivided into a thick lower unnamed member and the thin upper Arcola Limestone Member. Gentry et al. (2022) recognized a basal member of the Mooreville Chalk, informally designated the Erie Bend member. In this paper "unnamed member" refers specifically to the portion of the Mooreville Chalk that overlies the contact with the Erie Bend member and underlies the Arcola Limestone Member.

Etymology—The species epithet *shannoni* honors the late Samuel Wayne Shannon (1951–2020) for his contributions to Alabama Cretaceous vertebrate paleontology throughout the 1970s (see Shannon 1974, 1975, 1977); also for his co-discovery of the holotype specimen during graduate work at the University of Alabama, Tuscaloosa, USA, and for his early encouragement of the senior author's interest in the Mosasauridae.

Description

*Frontal—*The frontal of ALMNH:Paleo:5452 (Fig. 11A, B) is essentially complete, but suffered some minor subaerial weathering prior to collection, particularly on its dorsal side. In overall appearance, the frontal is strikingly similar to that of *Ectenosaurus clidastoides,* though it is relatively shorter and stouter. Anteriorly, the frontal forms a narrow bifurcate process to enclose the rear of the internarial bar within a V-shaped notch. This process is essentially complete and would have been intermediate in length between that of *E. clidastoides* and *E. tlemonectes* (unknown for *E. everhartorum*). A median dorsal ridge is completely absent in ALMNH:Paleo:5452, in contrast with *E. clidastoides, E. tlemonectes,* and SMU 76350. Instead, the anteriormost portion of the dorsal surface (Fig. 11A) of the frontal is transversely arched or domed anteriorly, a trait absent in other specimens referred to the genus. This arching gives way to a generally planar

dorsal surface, which thickens parasagittaly, then thins abruptly at the antorbital margins, and forms a broad, shallow sulcus posteriorly. Tiny foramina are present across the entire dorsal surface. The posterior sulcus deepens and expands to form a shallow depression that would have met the dorsal parietal table, forming the mesokinetic axis of the skull, movement along which may have been inhibited by a series of short vertical keels and overlapping flanges arising from the posterior margin of the frontal and the anterior margin of the parietal. This mode of contact appears to have been similar to, but simpler and less restrictive than, that seen in *E. clidastoides,* where each side of the dorsal table the parietal is overlapped by a posterior projection from the frontal. These projections are absent in *E. shannoni*.

The frontal alae are more prominent than in either *E. clidastoides* or *E. everhartorum,* linguiform in outline, and diverge posterolaterally at an angle of about 50° from the sagittal plane. There are well-developed supraorbital embayments, as with *E. clidastoides* and *E. everhartorum,* and within this embayment the frontal is emgarinate on the orbit. Some asymmetry is present in the frontal of ALMNH:Paleo:5452, and this is especially evident in the relative positions of the antorbital bulges. It is unclear whether this asymmetry is pathological or an artifact of preservation, but given the otherwise well-preserved, undistorted nature of the element, the former seems most likely.

The preserved portion of the frontal measures ~20 cm in length and is widest at its posterior margins (13.4 cm) and between the antorbital bulges (~11.1 cm; a precise measurement is not possible due to the aforementioned asymmetry). The frontal narrows substantially within the supraorbital embayments (8.8 cm), producing a waisted or hour-glass shaped dorsoventral profile.

As mentioned previously, any discussion of the frontal of *Ectenosaurus* is severely hampered by the ventral surface of the neotype frontal being almost completely obscured beneath the left mandible. In ALMNH:Paleo:5452 (Fig. 11B), the frontal is bisected ventrally by the olfactory canal, which is bordered on either side by prominent descending processes that run roughly parallel before converging abruptly, then immediately diverging where the canal opens to accommodate the olfactory bulb. This forms a roughly X-shaped configuration, with the descending processes thickest where they almost meet at the crux of the X. Posteroventrally, a pair of deep grooves bracket an elongated stilliform boss that contacts the frontoparietal suture.

As in *E. tlemonectes,* a narrow transverse ventral
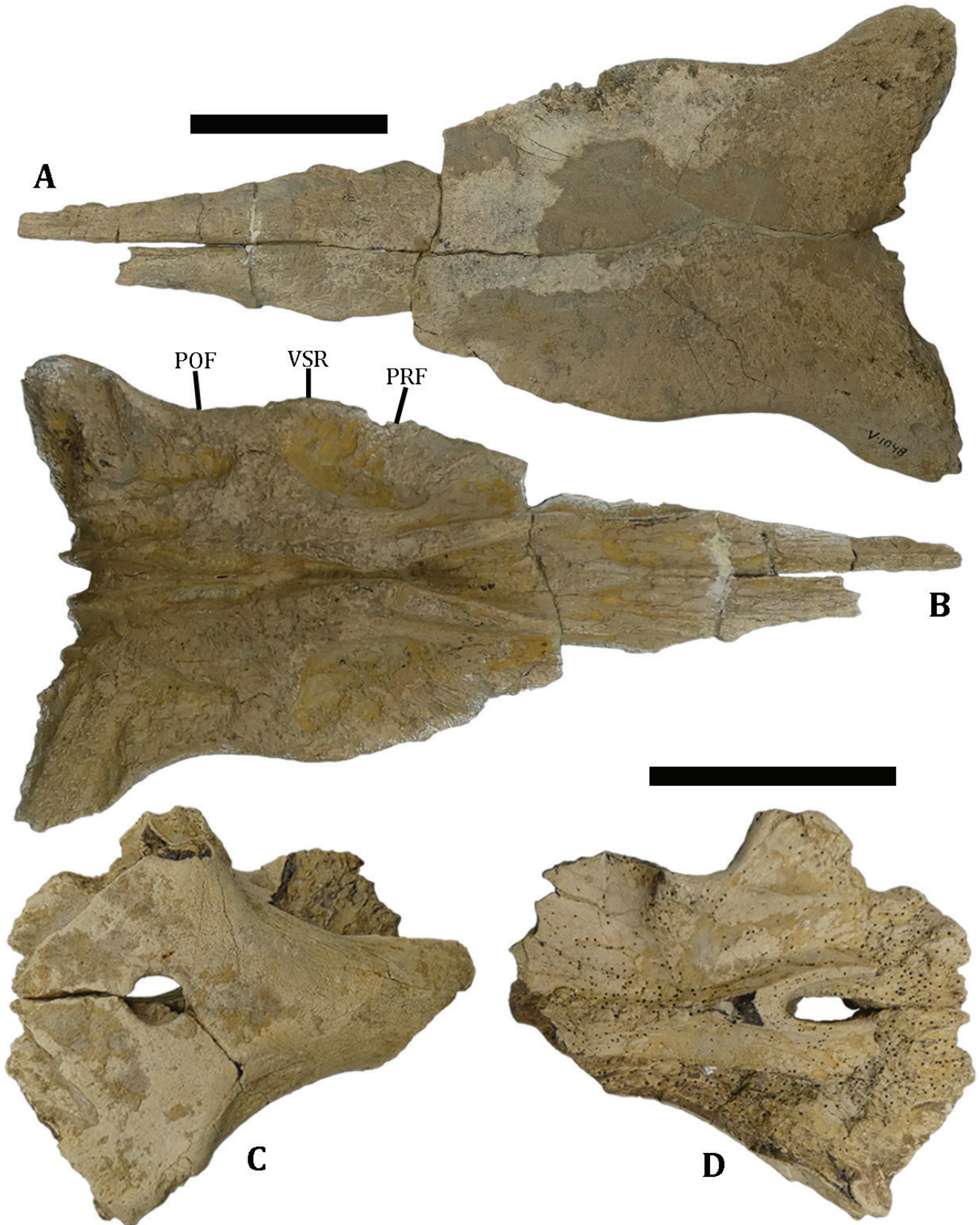
Figure 11. *Ectenosaurus shannoni* sp. nov., ALMNH:Paleo:5452. **A, B.** Frontal in dorsal (**A**) and ventral (**B**) views. **C, D**. Parietal in dorsal (**C**) and ventral (**D**) views. **Abbreviations: POF**, excavation for postorbitofrontal; **PRF**, excavation for prefrontal; **VSR**, ventral separation ridge. Scale bars=5 cm.

separating ridge situated within the supraorbital embayment would have prevented the prefrontal from contacting the postorbitofrontal. While the margins of this ridge are fairly straight in *E. tlemonectes* and reach the supraorbital rim, in *E. shannoni* they are concave and laterally recurved, allowing the frontal much broader access to the orbit, so that the entire embayment, as well as the antorbital bulge, are emarginate. In ALMNH:Paleo:5452, the wedge is notched anteriorly, providing a shallow fold into which the tongue-shaped supraorbital process of the prefrontal articulates. Unlike the prefrontal, the postorbitofrontal would have been largely excluded from the supraorbital border, its anterior process is enclosed dorsally on three sides within a shallow, boomerang-shaped sulcus, with the separating ridge forming the anterior rim of this sulcus. This approaches the condition present in *E. clidastoides* more closely than in *E. everhartorum,* where the frontal appears to comprise most of the supraorbital border. However, in *E. everhartorum* the prefrontal and postorbitofrontal are much more widely separated than in either *E. shannoni* or *E. tlemonectes* and the ventral separating ridge appears to be absent.

*Parietal—*Only the incomplete anterior half of the parietal is preserved on ALMNH:Paleo:5452 (Fig. 11C, D). Prior to collection, the parietal split horizontally into dorsal and ventral halves that were subsequently glued together during preparation. The dorsal parietal table (Fig. 11C) can be divided into two regions: a broad anterior subrhomboidal shelf that merges smoothly into an elongate posterior shaft with rounded, parallel sides, which would have branched into the missing suspensorial rami. There is no evidence of a parasagittal ridge. A large subcircular parietal foramen, very slightly longer than wide, is centered on the dorsal table, and set back from the frontoparietal suture by a distance roughly equal to twice its diameter. Dorsally, the position and shape of the foramen compares well with that of both FHSM VP-401 and SMU 76350. The surface of the table is planar. Where it would have contacted the frontal, the margin of the dorsal table forms a distinct W-shaped anterior margin, the central peak bounded by short flanges that must have been overlapped dorsally by posteriorly directed projections from the frontal. This is similar but not identical to the condition present in SMU 76350, where the frontoparietal contact appears to have been more complex (Bell et al. 2013; fig. m).

Most of the lateral descending process (descensus processus parietalis of Konishi and Caldwell 2011) is not preserved and what is present has been severely crushed. Postorbital processes at the anterolateral corners of the dorsal table appear to have been extremely short, so that the parietal would have contributed little to the anterior supratemporal fenestrae.

The ventral surface of the parietal (Fig. 11D) is dominated by a large elliptical foramen, at least twice as long as wide, in contrast with its circular dorsal opening. It is unclear whether this dorsoventral variance is an artifact of plastic deformation or accurately reflects the anatomy of *E. shannoni.* In ALMNH:Paleo:5452 the foramen is surrounded by a steep-sided, narrow-walled parapet of bone whose borders converge just behind the foramen. The lateral walls of this parapet rise to meet its dorsal rim at a 90° angle, and the narrow dorsal rim is planar. This structure corresponds to what was referred to by Konishi et al. (2015) as the ventral triangular eminence, present in halisaurines and many russellosaurines (though it displays a wide range of variation within both groups), and its existence contradicts Holmes and Sues' (2000: 310) statement that in mosasaurs "the ventral margin of the foramen is not conspicuously raised."

*Quadrate—*Only a small portion of the left quadrate was collected (Fig. 12A–D), but it preserves the contact and fusion of the suprastapedial process with the infrastapedial and the presence of a dorsomedially directed flange from the infrastapedial that overlaps the expanded dorsodistal end of the suprastapedial, a trait already mentioned in the description of YPM VP4673 as unknown in any mosasaur other than *Ectenosaurus.* Indeed, in ALMNH:Paleo:5452 the contact is better preserved than in any other specimen of the genus previously described and can be viewed in its entirety, allowing for a better understanding of the precise nature of this unique contact, while also suggesting the trait may have been less developed in *E. shannoni* than in either *E. clidastoides* or *E. tlemonectes.* In ALMNH:Paleo:5452, the infrastapedial process forms a delicate cheliform structure that not only overlaps the suprastapedial posterodorsally, but ventrally as well, embracing it in a sort of pincer grip while also creating a cradle that abuts the suprastapedial terminus. Complete fusion between the two processes can only be observed ventromedially (Fig. 12B). While the full extent of fusion is unclear,, the processes are less extensively fused than in *E. clidastoides.* The infrastapedial process of YPM VP4673 (Fig. 3B) may have enfolded the suprastapedial in much the same way, but preservation makes this difficult to determine with any certainty; fusion appears to have been more extensive in the Niobrara Chalk specimen. In neither ALMNH:Paleo:5452 nor YPM VP4673 does the dorsodistal flange enter the deep, polygonal fossa for
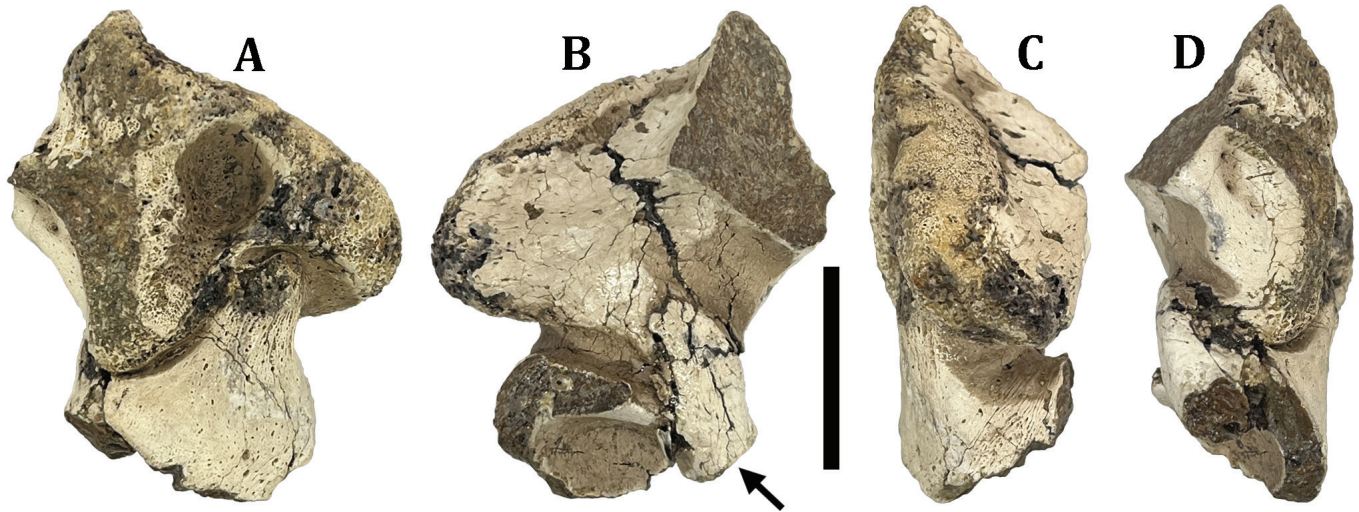
Figure 12: *Ectenosaurus shannoni* sp. nov., ALMNH:Paleo:5452. **A–D**. Left quadrate fragment with suprastapedial-infrastapedial contact in posterior (**A**), anterior/interior (**B**), lateral (**C**), and medial (**D**) views. Arrow indicates interior flange of infrastapedial process. Scale bar=2 cm.

insertion of M. depressor mandibulae, but contacts and parallels the fossa's distal rim. In ALMNH:Paleo:5452, the posterior (external) flange is highly vascularized, though the anterior (ventral) flange is not, and there is a distinct bulge along the ventrolateral rim of the suprastapedial process that does not appear in either *E. clidastoides* or *E. tlemonectes.*

*Splenial—*Much of the right splenial is preserved (Fig. 13A–C), including the base of the lateral ala. As the medial ala has been lost, it is only possible to approximate the true shape of the articular face at the intramandibular joint, which appears to have formed an elongated rhombus. The "robust, dorsomedially expanding flange" reported by Willman et al. (2021) for both *Ectenosaurus everhartorum* and *E. clidastoides,* giving a squarish shape to the articulating surface in those species, is absent in ALMNH:Paleo:5452. While the splenio-angular joint in ALMNH:Paleo:5452 is simpler than that of YPM VP4673, it would still have been more complex than the ball-and-socket condyle/cotyle arrangement often used as a blanket characterization of this joint in mosasaurs (see discussion above). Instead, the articular face is divided into a broad vertical keel positioned just medial to its center and a sulcus located between the lower terminus of the keel and the medioventral rim of the splenial; these would have received matching structures from the angular. A well-defined longitudinal ridge marks the base of the lateral wing.

*Coronoid—*The majority of the right coronoid (Fig. 13D–F) is preserved, though it should be noted that some portions have been heavily restored with plaster

by G.L. Bell, Jr. (M.J. Polcyn *personal communication* 2022). Fortunately, the restored portions are unpainted and easily discernible from the fossil itself. As in most russellosaurines, the coronoid is a short, saddle-shaped wedge of bone straddling the anterior rim of the surangular and forming a posteromedial sutural contact with a buttress on the surangular (Fig. 13E, F). This sutural contact is more complex in ALMNH:Paleo:5452 than in YPM VP4673 and even more so than in FHSM VP-401, with the interdigitating grooves and ridges being more numerous and more closely spaced. Based on the right coronoid figured in Willman et al. (2021: fig. 11b), it also appears more complex than in FHSM VP-5515. However, until more careful examinations of the latter two specimens can be conducted, as well as comparison with the Big Bend specimen (SMU 76350), we consider this feature in ALMNH:Paleo:5452 a provisional apomorphy for *E. shannoni.*

In ALMNH:Paleo:5452, the posterior crest of the coronoid is taller than in *E. tlemonectes,* but less developed than in *E. clidastoides;* and incomplete preservation makes it difficult to compare with FHSM VP-5515. The anterior bifurcation is less developed than in *E. tlemonectes.* and is more dorsally located. In ALMNH:Paleo:5452, the lateral descending wing (largely restored) is a thin, relatively delicate, ventrally-directed process, while the medial descending wing is much shorter and ventromedially directed, forming a stout, triangular wedge in anteroposterior cross-section. Though it is clear the lateral wing was shorter than the medial, the precise difference cannot be determined due to the incompleteness of the
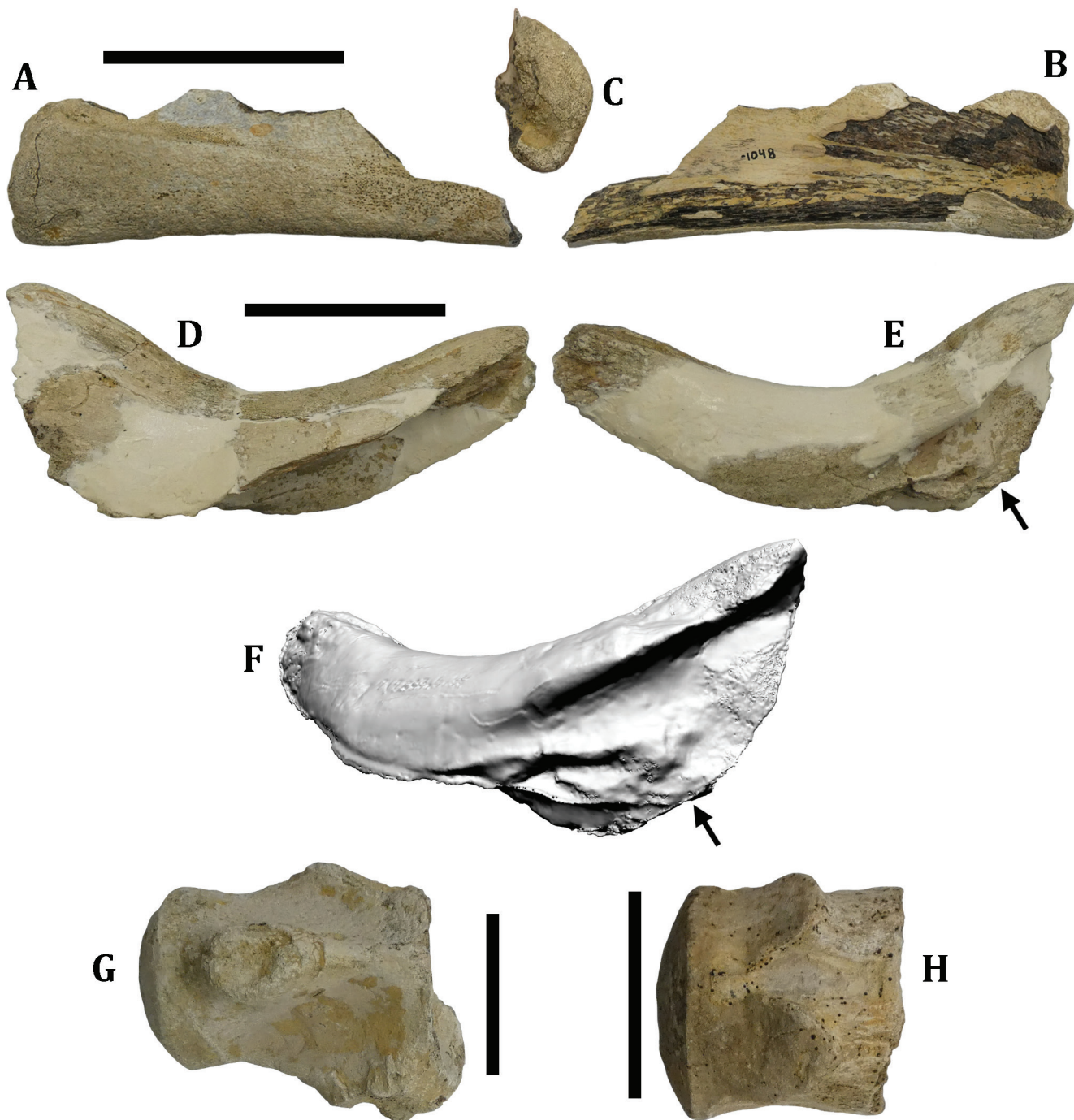
Figure 13: *Ectenosaurus shannoni* sp. nov., ALMNH:Paleo:5452. **A–C**. Right splenial in lateral (**A**), medial (**B**), and posterior (**C**) views. **D, E**. Right coronoid in lateral (**D**) and medial (**E**) views. **F**. Laser scan of cast of right coronoid of ALMNH:Paleo:5452 in posteromedial view. **G**. Cervical vertebra in ventral view. **H**. Caudal vertebra in ventral view. Scale bars for A–F=5 cm. Scale bar for G=4 cm.

latter. Numerous foramina are present within the ventral fold and, as in YPM VP4673, are especially prominent on the interior surface of the medial descending wing.

Vertebrae—A total of twenty-seven vertebrae are preserved with ALMNH:Paleo:5452, including five cervicals, thirteen dorsals, five pygals, and four caudals. Most of the vertebrae consist of badly weathered centra lacking most of the cortical surface, neural arches, synapophyses. zygopophyses, and transverse processes. The best cervical vertebra (Fig. 13F) preserves a distinct anteroventral ridge extending from the anterior rim of an elliptical hypapophyseal peduncle to the ventral rim of the cotyle.

In lateral profile, this ridge forms a shallowly concave arc, as seen in YPM VP4673 and other species of *Ectenosaurus.* The articular surfaces of the pygals are sub-square in anteroposterior view. Only one of the caudles is well preserved (Fig. 13G); it is subcircular in anteroposterior profile and preserves two rounded, posteroventrally oriented peduncles for articulation with the haemal arch.

DISCUSSION

Phylogenetic analysis

Both new species described herein can confidently be referred to the genus *Ectenosaurus* (*sensu* Willman et al. 2021). Both exhibit fusion of the suprastapedial and the infrastapedial process of the quadrate, with a dorsomedially directed flange from the infrastapedial process overlapping the dorsodistal terminus of the suprastapedial. While contact and/or fusion of the supra- and infrastapedial process occurs in halisaurines, mosasaurines, and some plioplatecarpines, only in *Ectenosaurus* does this flange occur as part of the contact/fusion. Additionally, as first noted by Willman et al. (2021), a distinctive notch or groove is present on the dorsal border of the articular immediately posterior to the glenoid fossa in YPM VP4673. Though the articular is not preserved in ALMNH:Paleo:5452, the combination of the frontal and quadrate morphology justify the generic referral to *Ectenosaurus.*

In order to better understand the phylogenetic relationship of the new species, *Ectenosaurus tlemonectes,* a parsimony analysis was conducted. YPM VP4673 was scored following the character-taxon matrix of Willman et al. (2021), using their ingroup and outgroup selection. No new characters or character states were added. Given its fragmentary condition, ALMNH:Paleo:5452 was not included. Two parsimony analyses were run using PAUP version 4.0a (build 169) for Windows, using branch-and-bound search, all characters unordered and unweighted, and ACCTRAN selected for character-state optimizations.

The first analysis (Fig. 14A) was run without constraints and recovered 30 equally parsimonious trees (MPTs) of 255 steps (CI=0.6680; HI=0.3137; RI=0.7377; RC=0.5063), finding *Ectenosaurus* to be monophyletic in seven of the 30 trees; however, a strict consensus collapsed all of the *Ectenosaurus* species in a polytomy with *Yaguarasaurus, Angolasaurus, Plesioplatecarpus,* and *Platecarpus,* but retained a *Latoplatecarpus-Plioplatecarpus* clade, a *Tylosaurus* clade, a *Selmasaurus* clade, and a *Russellosaurus + Tethysaurus* Bardet et al. (2003) clade. This result is similar to the strict consensus of Willman

et al. (2021; fig. 16a).

Given the novel characteristics noted above that unite YPM VP4673 and ALMNH:Paleo:5452 with *E. clidastoides + E. everhartorum,* a second analysis (Fig. 14B) was performed holding the included *Ectenosaurus* species as monophyletic using the CONSTRAINT option, and the remaining settings as noted above. The second analysis recovered 8 MPTs of 255 steps (CI=0.6680; HI=0.3320; RI=0.7877; RC=0.5063), with no difference in tree length, CI or HI, versus the unconstrained run. The constrained analysis recovered the *Ectenosaurus* clade in a large polytomy nearly identical to the unconstrained run; however, a *Plesioplatecarpus-Platecarpus-Latoplatecarpus-Plioplatecarpus* clade was recovered which is topologically similar to that of Konishi and Caldwell (2011). *Tylosaurus* was recovered as the sister taxon to a large clade composed of tethysaurines, yaguarasaurines, and plioplatecarpines. Given the lack of structure and nearly complete collapse of the tree in both analyses, nothing definitive can be said regarding the position of *Ectenosaurus* within Plioplatecarpinae. This result, though unsatisfying, underscores the need for additional exploration for phylogenetically useful characters to better understand the branching patterns within russellosaurian mosasaurs.

Relative scarcity of specimens and diversity within *Ectenosaurus*

The mosasaur genus *Ectenosaurus* is rare, with only nine specimens—including the two described in this paper—reported worldwide (all from North America). The number rises to ten if we assume that Russell (1967) was correct in his belief that Merriam's lost types of *Platecarpus clidastoides* and *P. oxyrhinus* constituted two halves of a single skull conspecific with FHSM VP-401. This number is remarkably low considering that all but the Big Bend specimen (SMU 76350) were recovered from either the Niobrara Chalk or Mooreville Chalk, which between them have produced thousands of mosasaur fossils over a period of almost two hundred years (Ebersole and Dean 2013, Everhart 2005). Within both units, only the closely related basal plioplatecarpine *Selmasaurus* is scarcer, represented by only four specimens (three of *S. russelli* and one of *S. johnsoni*). More remarkable still is the diversity of *Ectenosaurus*, which now includes at least four distinct species—*E. clidastoides, E. everhartorum, E. tlemonectes, E. shannoni,* and perhaps a fifth undescribed species with SMU 76350 (Bell et al. 2013). By comparison, other mosasaur genera common to the Mooreville Chalk and Niobrara Chalk (i.e., *Tylosaurus, Platecarpus,*
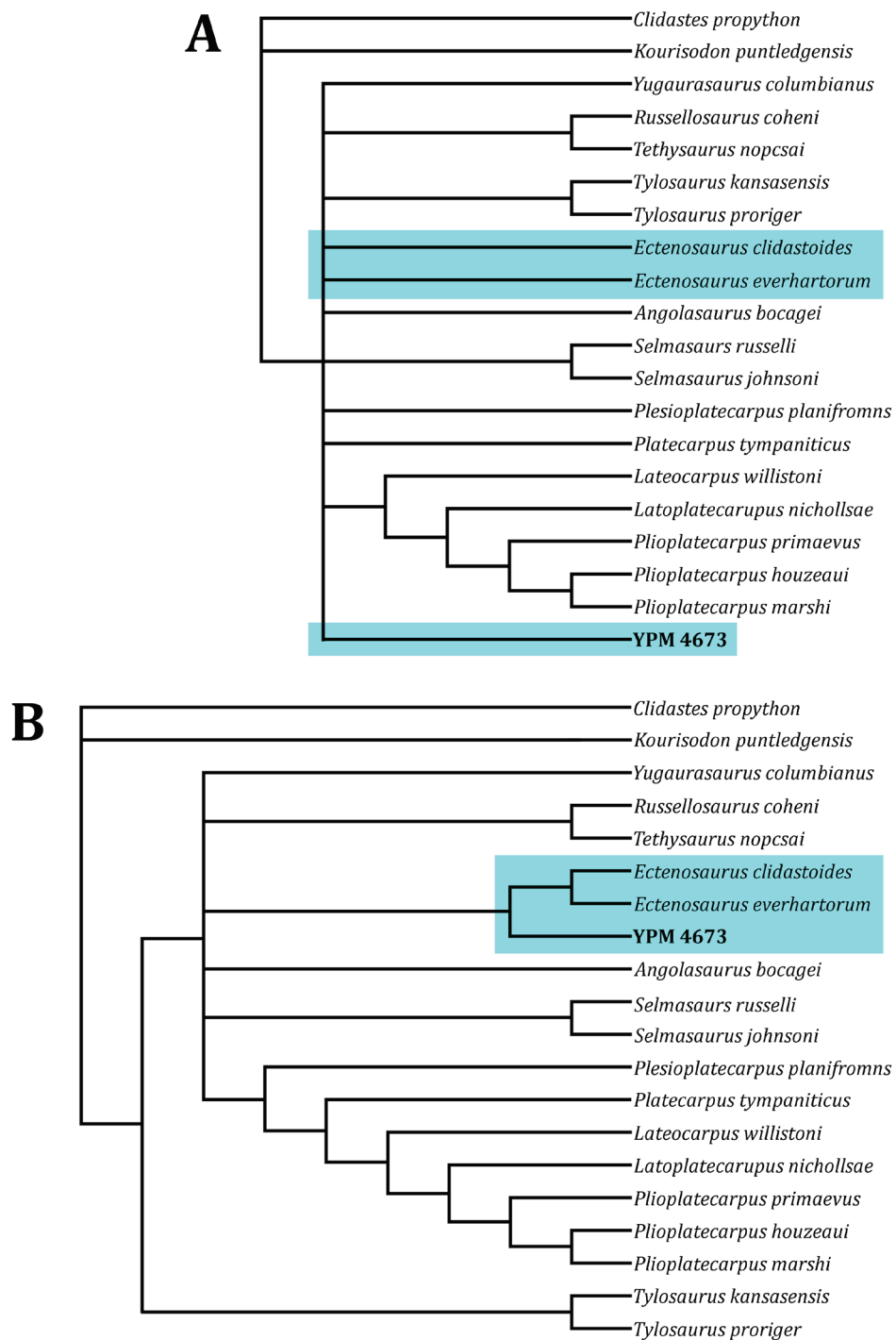
Figure 14: Phylogenetic trees. **A**. Strict consensus tree of 30 most parsimonious trees (MPTs; tree length=255, CI=0.6680; HI=0.3137; RI=0.7377; RC=0.5063). **B**. Tree produced using constraint option and assuming monophyly of *Ectenosaurus*, 30 MPTs (tree length=255, CI=06680; HI=0.3320; RI=0.7877; RC=0.5063).

Clidastes) are represented by hundreds of specimens and apparently low (or unrecognized) intrageneric diversity.

Three possible explanations present themselves to explain the pattern for the scarcity and diversity of *Ectenosaurus* within the Mississippi Embayment and Western Interior Seaway during the middle Santonian and early Campanian: 1) collecting bias has skewed the sample; 2) the taxon has been oversplit, artificially inflating diversity within the genus; and/or 3) *Ectenosaurus* specimens are scarce because the genus represents an allochthonous

element of the Mooreville Chalk and Niobrara Chalk faunas. It is easy to dispense with the second possibility, as there is no conceivable reason collectors should overlook *Ectenosaurus.* If we assume that the taxon has not been oversplit, we are left with two possibilities to explain the scarcity of this taxon: 1) *Ectenosaurus* is native to adjacent paleobiogeographic provinces and/or paleoenvironments, with "strays" very rarely preserved in the Mooreville Chalk and Niobrara Chalk, or 2) *Ectenosaurus* is truly a diverse but exceedingly rare genus, with multiple species sharing the same range.

Regarding the first option, the genus may have preferred brackish and even freshwater habitats, in which case the recovery of additional *Ectenosaurus* specimens could depend on prospecting strata produced by non-marine depositional environments. If this proves to be the case, the scarcity of *Ectenosaurus* specimens (and possibly the rarer *Selmasaurus*) in marine beds is comparable to infrequent discoveries of terrestrial, volant, and freshwater taxa recovered from the marine Mooreville Chalk and Niobrara Chalk (see Russell 1988 and Ikejiri et al. 2013 for reviews of non-marine vertebrates from the Niobrara Chalk and Mooreville Chalk, respectively). However, to date no *Ectenosaurus* specimens have been found in non-marine sediments, though non-marine strata coeval with the Mooreville Chalk and Niobrara Chalk have been heavily prospected for aquatic vertebrate fossils (e.g., the latest Santonian Deadhorse Coulee Member, Milk River Formation; Brinkman et al. 2016).

On the other hand, it may be that multiple species of *Ectenosaurus* inhabited the same or overlapping biogeographic ranges at roughly the same point in geologic history, but it is difficult to envision a means of testing this hypothesis. An examination of the biostratigraphy of the nine known specimens would be useful in determining the likelihood of this explanation being true, but more than half of the known specimens of *Ectenosaurus* have poor locality data, making it difficult to determine their precise stratigraphic provenance. However, a variety of approaches could yield better stratigraphic resolution for at least some of these specimens. Examination of nannoplankton and palynomorphs present in very small sediment samples taken from specimens with poor locality data can often yield better stratigraphic resolution. For example, the holotype of *Selmasaurus russelli* was determined to have come from the unnamed member of the Mooreville Chalk based on foraminifera extracted from the basilar canal of the specimen (Wright and Shannon 1988). In addition to microfossil analysis, examination of rare earth elements (REE) in fossil bone has proven

successful in determining the original stratigraphic position of certain mosasaur fossils (see Patrick et al. 2007, Makádi et al. 2012). Another approach would be the use of environmental and ecological inferences made by employing stable oxygen and carbon isotope analyses. Stable isotope ratios have been used for inferring foraging areas of mosasaurs (Robbins et al. 2008, Strganac et al 2015, Schulp et al. 2016, Giltaij et al. 2021). Based on the methods of Clements and Koch (2001) this approach appears to provide at least course resolution of preferred foraging habits and may be used to examine whether *Ectenosaurus* foraged in the same areas as more common contemporaneous taxa. Additionally, another study (Taylor et al. 2021) involving two specimens of *Clidastes* and one of *Platecarpus* employed stable oxygen isotope analysis of discrete samples taken along the length of the tooth suggests these taxa may have regularly visited freshwater sources. These methods offer future potential for understanding the difference observed in the relative abundance of taxa and in explaining the paradoxical diversity and scarcity of *Ectenosaurus.*

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Appendix. Nexus file adapted from Willman et al. (2021) with addition of YPM VP 4673.

Clidastes_propython	1011101111??????100000?000000??10?000?1???0?01010
Kourisodon_puntledgensis	1?110011110?0??010000?0?????010?01000-1-1?010?01?
Yaguarasaurus_columbianus	001?10111???10???001110????????????????????100?0??
Russellosaurus_coheni	00101011000000010011?00100???????????????10?10?0
Tethysaurus_nopcsai	0?10101100?010?01001110??0??0???10???????000100?
Tylosaurus_kansasensis	10000010110?????1000??001000????????1?????10000?0
Tylosaurus_proriger	10000010110000101000110010010001110110000010000010
Ectenosaurus_clidastoides	100010111???000?00001?001?0?0????1?0?2010?1001011
Ectenosaurus_everhartorum	10???011?????????????????101???0?1?????????1?????1
Angolasaurus_bocagei	????00111??0????0000?1??100?????1?????????10?10??
Selmasaurus_russelli	????0010110000??00001?0????1???????????????????1??
Selmasaurus_johnsoni	00100010110000?00000110011110????????????10011?0
Plesioplatecarpus_planifrons	001000111?00000000001?00100?0????0?0??0?0?1001010
Platecarpus_tympaniticus	00100010100000001101100100100001110100011011010
Latoplatecarpus_willistoni	01100010000?00000110?10011110???11????????10?1010
Latoplatecarpus_nichollsae	011000?01001001001101?001111001?11101???011011010
Plioplatecarpus_primaevus	01?001101011????01101110111100 1?11111010011??1010
Plioplatecarpus_houzeaui	01??0110101?01?10110?10??11?1???11?????????11010
Plioplatecarpus_marshi	0???0?00101??1?1011?11?1???1101?11111?????01??10
YPM VP4673	00??10010????00?0100??00101?????????????10010??