

Unappreciated Cenozoic ecomorphological diversification of stem gars revealed by a new large species

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The evolutionary history of gars, an ancient group of ray-finned fishes, is excellently documented in the fossil record. These fishes are notable for how little the anatomy of extant species differs from that of their earliest known relatives from over 150 million years ago. As such, the low species richness of the gar crown group is thought to reflect the diversity of this clade over most of their history. Here, I describe the skeleton of a new gar species from the Eocene Willwood Formation of Wyoming, USA. Numerous features, including a shortened skull, ornamented external cranial bones, and microteeth ally the new species with Cuneatini, an obscure clade of gars restricted to the Eocene of southwestern North America. Yet, *Cuneatus maximus* sp. nov. is more than twice as large as its closest relatives. The holotype of the new species preserves a partial palate, providing new information about the anatomy of this poorly known cranial region in cuneatins. Phylogenetic analysis of gars with the new species *C. maximus* included implies a diversification of cuneatins in North America following the Cretaceous/Paleogene extinction. The presence of large-bodied stem-gars in the Eocene Willwood Formation also suggests that the fish fauna of this region was reminiscent of present-day ones from the American southeast. The discovery of *C. maximus* emphasizes the propensity of the fossil record to significantly increase the diversity and biogeographic range of even the most depauperate lineages.

Key words: Actinopterygii, Osteichthyes, *Cuneatus*, lepisosteid, Eocene, USA.

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Introduction

Holostei is one of four major branches along the evolutionary tree of ray-finned fishes (e.g., Grande 2010; Near et al. 2012; Wright et al. 2012; Clarke et al. 2016; Hughes et al. 2018). Yet, only a handful of species in two clades comprise the whole of surviving holostean diversity and disparity. The most diverse extant holosteans are gars, which originated in the middle Mesozoic and have since become restricted to North America (e.g., Grande 2010; Wright et al. 2012; Echelle and Grande 2014; Brito et al. 2017). The fossil record of gars has revealed that the gross anatomy of this lineage has been conserved over their long evolutionary history (e.g., Wiley and Schultze 1984; Grande 1985, 2010; Echelle and Grande 2014; Brito et al. 2017).

The past decade of research into early Cenozoic gar diversity has recognized the presence of at least two extinct clades in the gar family Lepisosteidae with cranial anatomies that differ substantially from extant species (e.g., Grande 2010; Echelle and Grande 2014). These coexisted with early members of the living gar *Atractosteus* and *Lepisosteus*

in the system of massive lakes that are preserved as the Green River Formation (Wiley and Schultze 1984; Grande 1985, 2010; Echelle and Grande 2014). Unfortunately, the restricted set of fossils known for the short-snouted gars in the clade Cuneatini means that the anatomy and biogeography of these fishes are poorly understood.

Here, I describe the nearly complete skeleton of a large gar from the Willwood Formation of Wyoming, USA. The specimen includes a complete skull that preserves nearly all of the key specializations of cuneatins. These include the presence of packed “microteeth” in place of the large fangs found in extant species, a shortened rostrum, and heavily ornamented dermal skull roof bones (Grande 2010). The specimen is assignable to a new cuneatin that grew to more than twice the size of previously known species, demonstrating that the body size disparity of this clade is undersampled. In addition to expanding the range of this clade by nearly 1000 km, *Cuneatus maximus* sp. nov. reveals a diversification of cuneatin gars that likely postdated the K/Pg boundary.

Institutional abbreviations.—FMNH, Field Museum of Natural History, Chicago, USA; YPM VPPU, Yale Peabody

Museum Vertebrate Paleontology, collections from Princeton University, New Haven, CT, USA.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:093495E9-4517-4713-83C6-BB-F7AB96F5D0

Material and methods

The specimen described in this contribution (YPM VPPU.018063) was recovered from Willwood Formation exposures during a 1962 expedition to Wyoming by Roger C. Wood and includes portions of the surrounding sandstone matrix. In the Yale Peabody Museum collections, the specimen was identified as an individual of *Lepisosteus* sp. indet.

The new specimen was included in the phylogenetic analysis of Grande (2010) as updated by Brito et al. (2017) to assess its position among ginglymodian fishes (Appendix 1). The phylogenetic matrix to which YPM VPPU.018063 was added included 31 taxa coded for 105 morphological characteristics. I entered the resulting matrix into the program TNT v.1.5 (Goloboff and Catalano 2016) for analysis. An initial Wagner search with space for 1000 trees and default settings for ratchet, tree fuse, tree drift, and sectorial search was employed and followed by traditional bisection-reconnection (TBR) branch-swapping over 100 000 trees to further explore tree islands. The resulting most parsimonious trees were resampled over 100 replicates to generate bootstrap supports for each estimated node (Appendix 2). Finally, a strict consensus tree was used to summarize the most parsimonious topologies. All tree files and morphological matrices used in this study are in the Supplementary Online Material available at http://app.pan.pl/SOM/app67-Brownstein_SOM.pdf.

Geological setting

The Willwood Formation of the Bighorn Basin in north-western Wyoming represents an ecosystem of flood basins and channels that existed during the latest Paleocene to earliest Eocene epochs of the Paleogene period (e.g., Neasham and Vondra 1972; Bown and Kraus 1981; Smith et al. 2008; Chew 2009). This unit consists of mudstone and fine-grained sandstone rich in quartz, feldspar, and chert (Neasham and Vondra 1972). The red, purple, and brown mudstone of the unit are considered to be overbank paleosols (Kraus and Gwinn 1997).

The Willwood Formation is widely known for its extremely fossiliferous alluvial horizons, which have produced mammal fossils in particularly high quantities (e.g., Rose 1990, 2001; Bown et al. 1994; Chew 2009) and have allowed for several hypotheses regarding the impact of rather short-term climactic and other environmental shifts on faunal change in Paleocene–Eocene mammalian assemblages

(Bown et al. 1994; Bao et al. 1999; Wing et al. 2000; Clyde 2001; Gingerich and Clyde 2001; Clyde et al. 2007; Chew 2009). Studies of paleosols in the Willwood Formation suggest that the majority of these fossils likely experienced minimal transport and represent a local vertebrate assemblage (Bown 1979; Bown and Kraus 1981; Bown and Beard 1990; Chew 2009).

Systematic palaeontology

Actinopterygii Cope, 1887

Neopterygii Regan, 1923

Holostei Müller, 1844

Ginglymodi Cope, 1872

Lepisosteiformes Hay, 1929

Lepisosteidae Cuvier, 1825

Cuneatini Grande, 2010

Genus *Cuneatus* Grande, 2010

Type species: *Cuneatus cuneatus* Cope, 1878; upper Paleocene–lower Eocene units in Utah, USA.

Cuneatus maximus sp. nov.

Figs. 1–4.

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Etymology: From Latin *maximus*, superlative of large, referencing the size of the new species relative to other cuneatins.

Holotype: YPM VPPU.018063, the skeleton of a large-bodied lepisosteid gar consisting of the skull, thorax, and portions of the fins.

Type locality: ~27 km west of Powell, Park County, Wyoming, USA.

Type horizon: Willwood Formation, upper Paleocene to lower Eocene (Bown 1980).

Diagnosis.—Distinguished from other *Cuneatus* species by: large size (Figs. 1, 4; head length = 181.5 mm; 60–112 mm in *Cuneatus cuneatus* Cope, 1878 and *Cuneatus wileyi* Grande, 2010); skull subtriangular in dorsal view, with confluent lateral margins of the preorbital and postorbital portions (Fig. 2); palatal teeth cover the ectopterygoid, vomer, and dermopalatine, with especially large crowns on the lattermost element (Fig. 3); dermal skull roof ornamentation includes extensive pitting (Figs. 1, 4).

Description.—YPM VPPU 0.018063 is the partial skeleton of a large-bodied lepisosteid that has been three-dimensionally preserved in deposits of the Willwood Formation (Fig. 1). The skull of the specimen is still partially encapsulated within the matrix. The size of the skull of the specimen relative to its body length as indicated by the presence of the base of fins at the posterior end of the ventral margin of the specimen shows that the skull/body length ratio was high.

The skull roof of *Cuneatus maximus* sp. nov. is formed by the extrascapulars, frontals, nasals, premaxillae, parietals, and dermopterotics (Fig. 2A₁). The supraoccipital

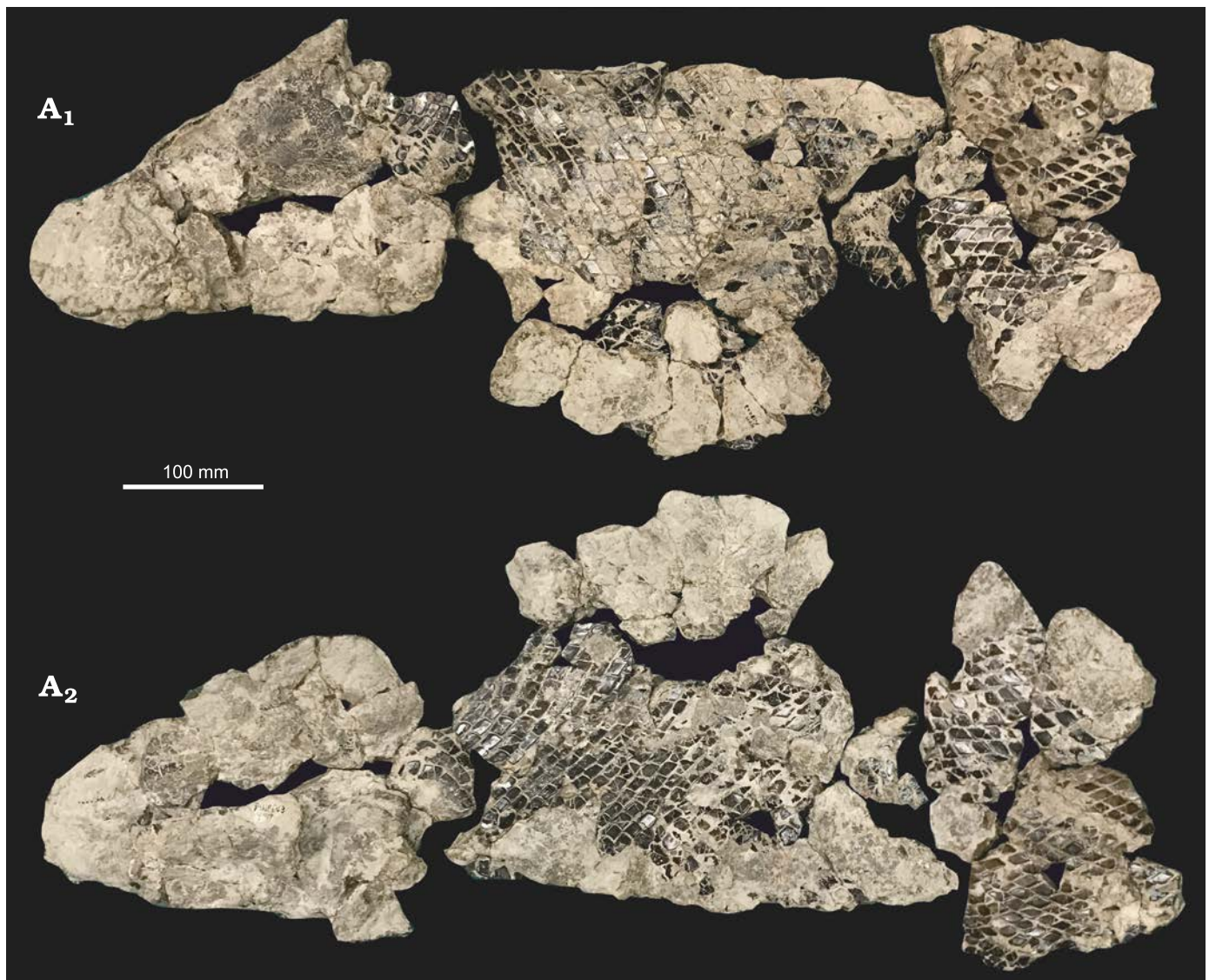


Fig. 1. Holotype of the cuneatin fish *Cuneatus maximus* sp. nov. (YPM VPPU.018063), from Upper Paleocene to lower Eocene Willwood Formation of Wyoming, USA; dorsal (A_1) and ventral (A_2) views. Note the ganoid scales characteristic of lepisosteiform fishes and relatives.

bone is absent as in other holosteans. The external surfaces of the posterior frontals, parietals, and extrascapulars show the developed ornamentation characteristic of cuneatin gars (Fig. 2A₁, A₂). This ornamentation includes extensive pitting, which differs from other species of cuneatins (Fig. 4), the stem-lepisosteid *Masillosteus* spp., *Atractosteus messelensis* Grande, 2010, and *Atractosteus tropicus* (Gill, 1863).

Anteriorly, the premaxillae bear the large marginal pores (Fig. 2A₂) characteristic of cuneatin gars (Grande 2010). The premaxillae themselves are shortened elements tightly sutured to the rest of the skull. The olfactory foramina are prominent and positioned anterodorsally. The nasals and frontals are both poorly preserved and obscured by tough matrix. The parietals are widened and subrectangular, contacting the frontals anteriorly and the dermopterotics laterally (Fig. 2A₁). These paired elements contact the posterior edge of the skull roof and sit atop the posterior portion of the braincase. The dermopterotics are only partially repre-

sented and are the lateral borders of the posterior skull roof. These bones flare outward laterally at their posterior ends and seem to have been similarly rugose in surface texture. The parietals and dermopterotics form a line of bone sitting between the frontals and the posteriormost elements of the skull roof. All these bones are extensively ornamented and form the tight sutural connections characteristic of lepisosteids (e.g., Wiley and Schultze 1984; Grande 1985, 2010; Brito et al. 2017). Posterior to the dermopterotics and parietals, three extrascapulars compose the posterior section of the skull roof (Fig. 2A₁). Three extrascapulars are also present in *C. wileyi*, *C. cuneatus*, and other lepisosteid species (Grande 2010). All skull roof bones contribute to a subtriangular skull shape in dorsal view with anteromedially tapering lateral margins. In other species of *Cuneatus*, *Atractosteus*, and *Lepisosteus*, the rostrum of the skull is medially offset from the postorbital region in dorsal view (Grande 1985, 2010; Scherrer et al. 2017: fig. 4A).

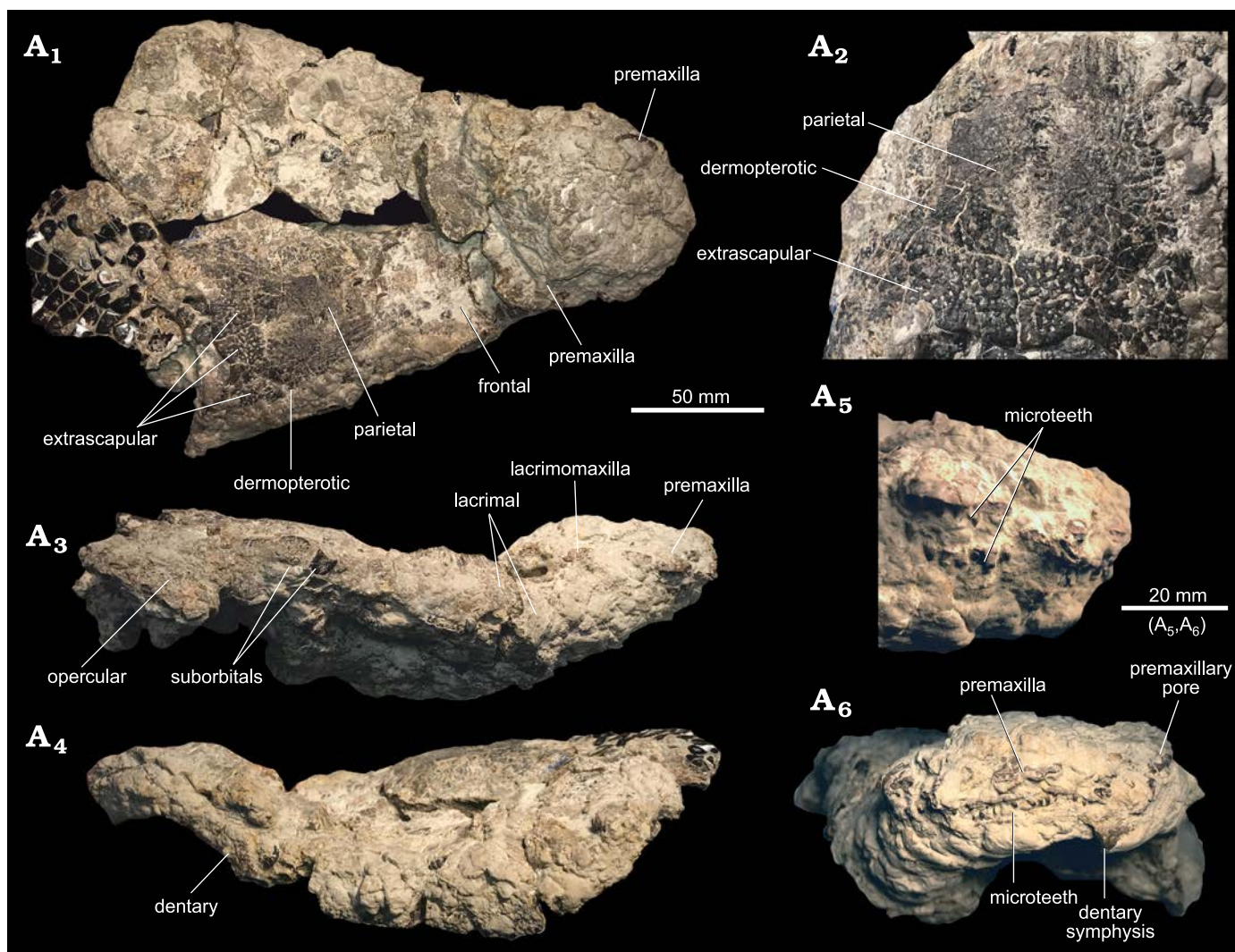


Fig. 2. Cranial anatomy of the skull of the cuneatin fish *Cuneatus maximus* sp. nov. (YPM VPPU.018063), from Upper Paleocene to lower Eocene Willwood Formation of Wyoming, USA; dorsal view (A₁), detail of the dermal skull roof ornamentation (A₂), left (A₃) and right (A₄) lateral views, detail of the anterior rostrum and dentition in left lateral view (A₅), anterior view (A₆).

The lateral surface of the skull preserves portions of the premaxillae, the lacrimomaxillae, supraorbitals, and post- and subinfraorbitals (Fig. 2A₃–A₅). The lacrimomaxillae are large and few in number, contrasting with the condition in crown lepisosteids (Grande 2010). The orbital region is poorly preserved, but several portions of bone below the orbit are identifiable as the strip-like subinfraorbitals. Two ornamented lacrimals are placed anterodorsal to the orbit. Posterior to the orbit, the suborbitals appear as distinct rectangular elements anterior to the opercle. The whole lateral profile of the skull lacks the wedge shape present in *C. cuneatus*, but whether the posterior mandible was expanded as in both *C. cuneatus* and *C. wileyi* is unclear (Grande 2010).

The palate of *C. maximus* sp. nov. is mostly complete and includes detailed surface texture for many of the anterior bones (Fig. 3). The palatal anatomy of cuneatin gars is somewhat obscure (Grande 2010) so the preservation of these region in YPM VPPU.018063 is particularly important. The anterior palate is formed by the slender vomers medially

and the dermopalatines laterally. The anterior half of the ectopterygoid invades the space between these two elements. The expansion of the ectopterygoid to form a large portion of the palate is a distinguishing feature of Lepisosteidae (Grande 2010). All these bones are lined with developed plates of palatal teeth. The palatal tooth crowns appear as clustered papules and are especially large on the vomers and dermopalatines (Fig. 3A₂, A₃). Similarly extensive palatal tooth plates are known for “*Lepisosteus*” *indicus* Woodward, 1890, among lepisosteids. Extant species of *Lepisosteus* show reduced palatal tooth rows that tend to disappear towards the posterior of the palate (Grande 2010). Given that the palates of obaichthyids, the oldest lepisosteid *Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega, and Meunier, 2017, and the Cretaceous form *Herreraichthys coahuilensis* Alvarado-Ortega, Brito, Porrás-Múzquiz, and Mújica-Monroy, 2016; are poorly known (Grande 2010; Alvarado-Ortega et al. 2016; Brito et al. 2016, 2017), the polarity of developed palatal tooth rows as a character is unclear. Because previously recognized

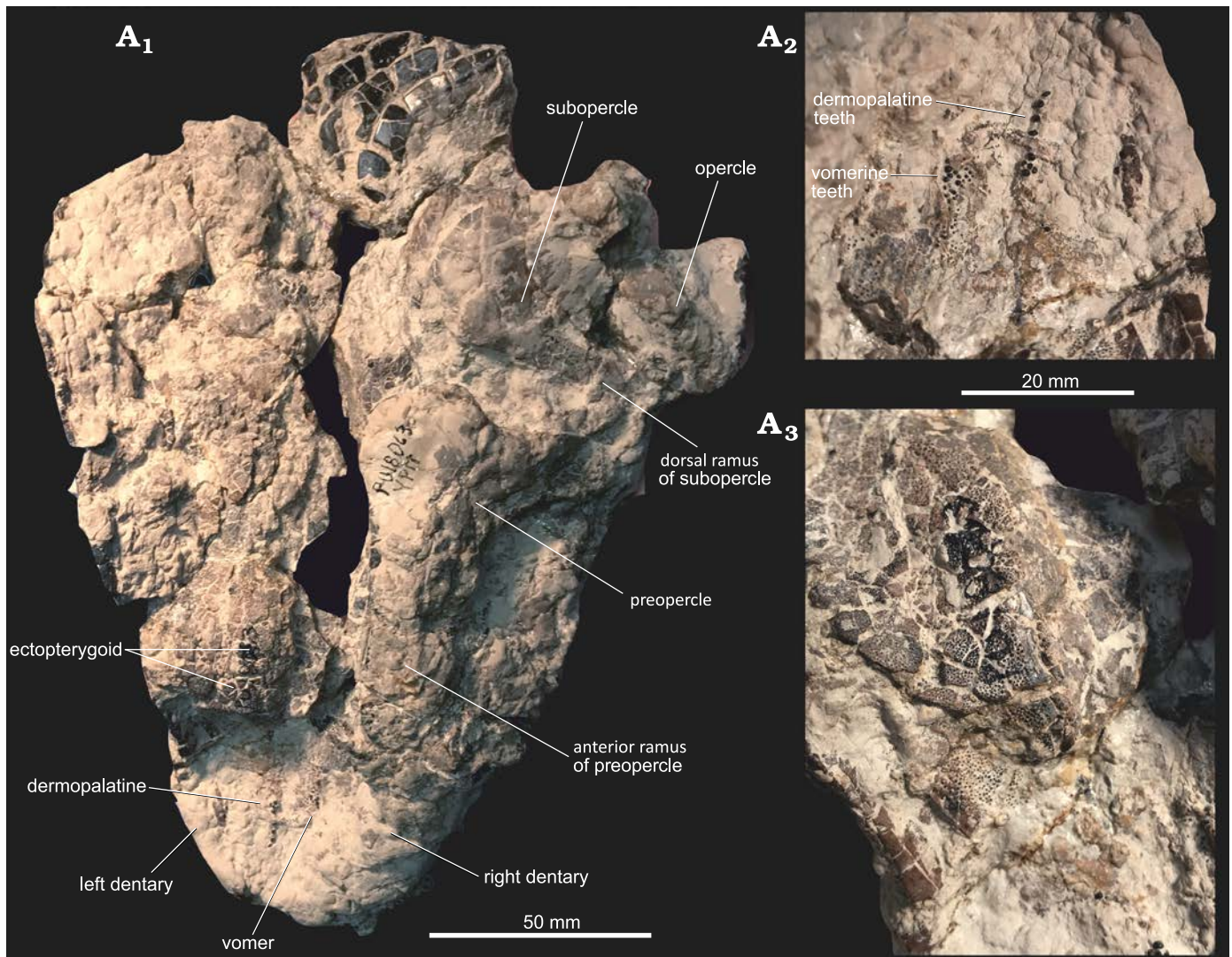


Fig. 3. Palatal and mandibular anatomy of the cuneatin fish *Cuneatus maximus* sp. nov. (YPM VPPU.018063), from Upper Paleocene to lower Eocene Willwood Formation of Wyoming, USA; ventral view (A₁), detail of the anterior palate (A₂), toothed ectopterygoid (A₃).

species of *Cuneatus* lack any clear palatal teeth (Grande 2010), we consider the condition in YPM VPPU.018063 an autapomorphy of *C. maximus*.

The lower jaw is very poorly preserved in the holotype of *C. maximus* sp. nov. Although it is clear both dentaries made up less than 36% of the total skull length (Fig. 3A₁) and had medially curved symphyses (Fig. 2A₅) as in other *Cuneatus* species (Grande 2010), not much more can be said about this region. The preserved opercular series consists of the preopercle, the subopercle, and the opercle. As in other lepisosteids with the exception of *Atractosteus falipoui* (Cavin, Boudad, Tong, Läng, Tabouelle, and Vullo, 2015), there is no interopercle (Grande 2010). The opercular series is eroded in *C. maximus*, and so the presence of extensive ornamentation could not be assessed. However, it is clear the long anterior ramus (horizontal arm of Grande 2010) characteristic of lepisosteids is present. Posteriorly, the plate-like preopercle articulates with the subopercle, which possesses the large anterodorsal ramus diagnostic for

species of *Cuneatus* (Grande 2010). The opercle appears as a subrectangular plate.

The primary dentition consists of the distinctly striated teeth that characterize the family Lepisosteidae (Fig. 2A₅; Grande 2010; Echelle and Grande 2014). The folded dentine present in the teeth of gars is known as plicidentine (e.g., Wiley 1976; Grande 2010; Echelle and Grande 2014). The external dentition consists of the numerous small crowns (= microteeth of Grande 2010) characteristic of cuneatins. The three-dimensional preservation of the skull reveals that the rostrum of cuneatins appears mediolaterally widened relative to crown-group gars in anterior view (Fig. 2A₅). The anterior rostrum presents an arcade of microteeth, some of which appear very slightly recurved. The dentition of the primary tooth rows of *C. maximus* is larger than the palatal teeth.

The preserved portion of the body includes numerous ganoid scales (Fig. 1; e.g., Grande 1985, 2010; Echelle and Grande 2014). These are arranged in neat rows along the thorax of the specimen. Each scale is trapezoidal, with their

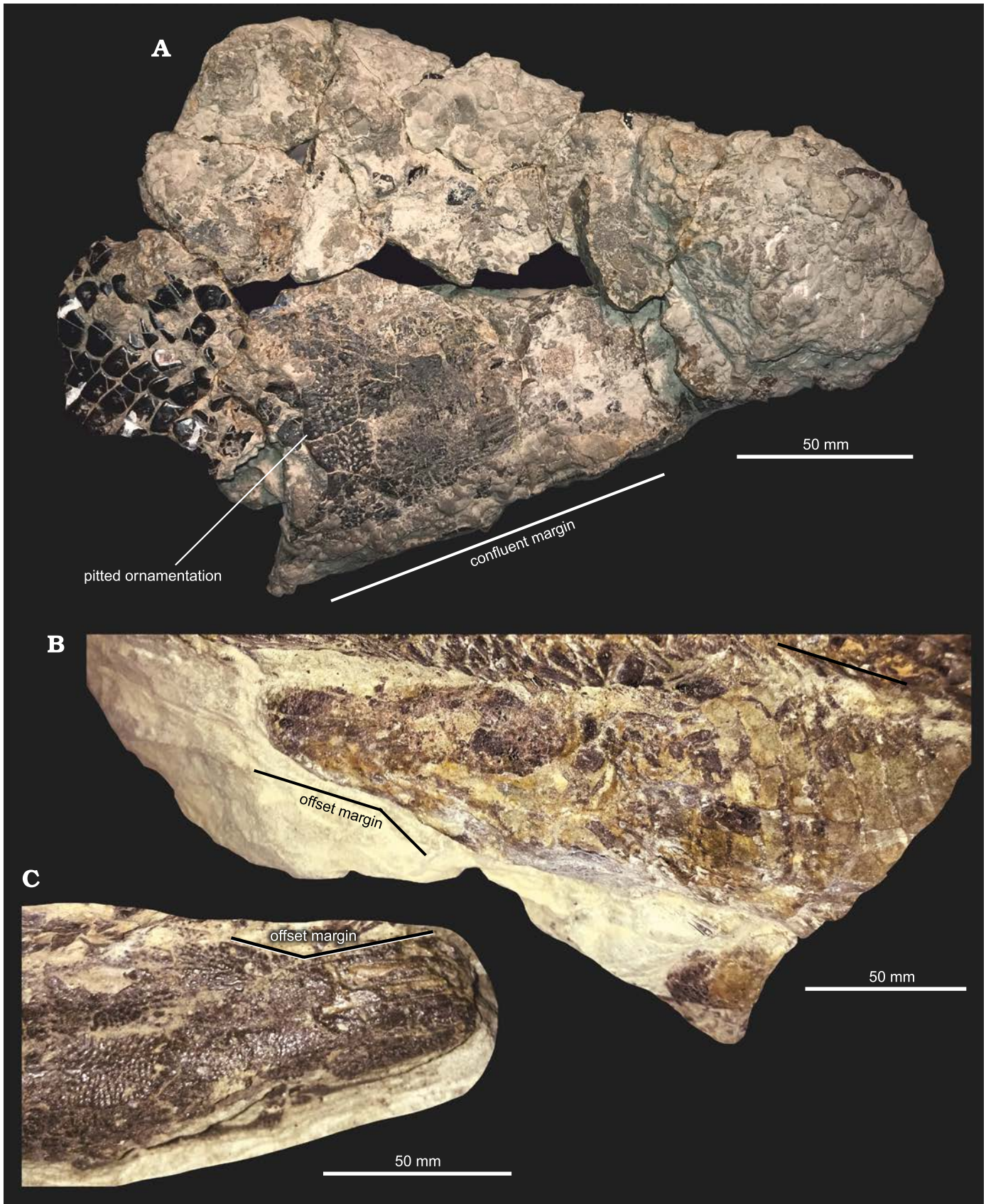


Fig. 4. Comparative anatomy of cuneatin skulls. **A.** *Cuneatus maximus* sp. nov., YPM VPPU.018063, from Upper Paleocene to lower Eocene Willwood Formation of Wyoming, USA; dorsal view. **B, C.** An uncatalogued portion of the *Cuneatus wileyi* Grande, 2010, mass death block (FMNH PF15202) discovered in the YPM collections where it is currently under transfer from FMNH.

long axes oriented anteroposteriorly as in other lepisosteid gars (Grande 2010; Echelle and Grande 2014). The portions of the fins in *C. maximus* that are preserved are small, but they clearly show that as preserved the specimen includes the nearly complete thorax.

Remarks.—YPM VPPU.018063 can be confidently referred to the genus *Cuneatus* based on the following features: densely ornamented skull bones; numerous small microteeth in the place of fangs; robust anterodorsal process of subopercle; large series of marginal pores on premaxillae; mandibular length is 35–41% of head length (~36%); short, deep lacrimomaxillae.

Stratigraphic and geographic range.—Upper Paleocene to lower Eocene Willwood Formation of Wyoming, USA.

Phylogenetic results

Phylogenetic analysis resolved the new species alongside other lepisosteid gars as expected based on general morphological comparisons. The strict consensus topology of 15 most parsimonious trees (Fig. 5; length 184, consistency index 0.674, retention index 0.901) resolved *Cuneatus maximus* sp. nov. within a polytomy consisting of all *Cuneatus* species. The high consistency and retention indices imply that this result is unlikely to derive from morphological homoplasy. Bootstrap values indicate moderate support (53) for a monophyletic Cuneatini including *C. maximus* and weak support (3) for an ingroup containing only *C. wileyi* and *C. cuneatus*. All other major lepisosteid relationships remained consistent

with previous studies of this clade (e.g., Grande 2010; Brito et al. 2017). Cuneatini was united by characters 43 (1, microteeth in marginal upper jaw rows) and 66 (2, dermopalatine teeth lost). No autapomorphies were found for *C. wileyi*, whereas *C. maximus* was found to have the autapomorphic condition of 66:1 (dermopalatine teeth present but reduced) and *C. cuneatus* was found to have 88:2 (number of principal caudal fin rays in adults less than 12) as an autapomorphy.

Discussion

Cuneatus maximus sp. nov. is the largest species of cuneatin currently known. Despite clearly belonging to this obscure clade of short-snouted gars, *C. maximus* possesses features unique among cuneatins that have been used to separate whole genera (i.e., *Amia* and *Cyclurus*) and families (Obaichthyidae and Lepisosteidae) in Holostei (Grande 1985; Grande and Bemis 1998; Grande 2010; Echelle and Grande 2014; Brito et al. 2016, 2017). These include the texture of the dermal bones and scales and the presence of numerous rows of palatine teeth (Grande and Bemis 1998; Brito et al. 2000, 2016; Grande 2010). The anatomy of *C. maximus* therefore implies a relatively high level of unsampled morphological variability in cuneatin gars. Although further large-scale morphological phylogenetic analyses will be needed to validate this hypothesis, the palatal anatomy of *C. maximus* implies this species is the most basal cuneatin. This interpretation is weakly supported by our majority-rule tree, wherein the southern species *C. wileyi* and *C. cuneatus* form a clade.

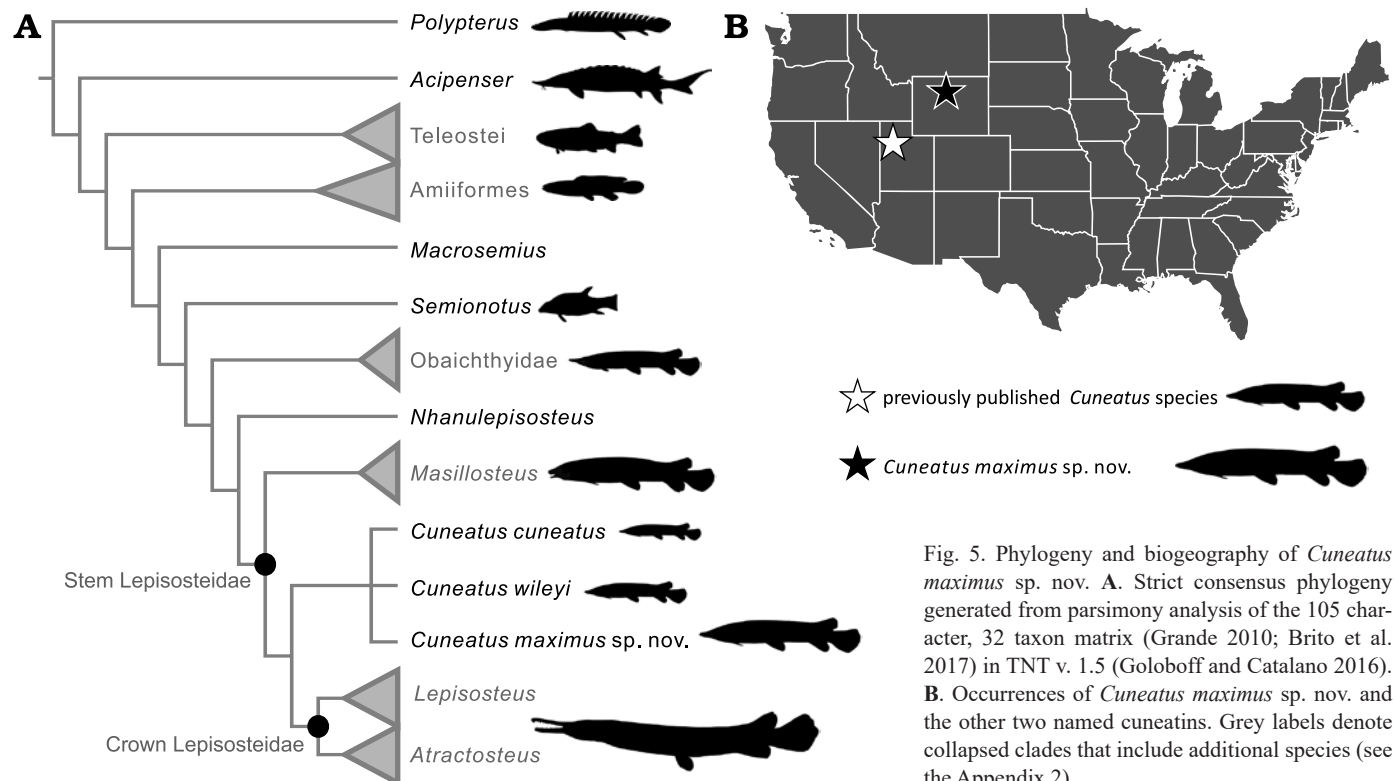


Fig. 5. Phylogeny and biogeography of *Cuneatus maximus* sp. nov. **A.** Strict consensus phylogeny generated from parsimony analysis of the 105 character, 32 taxon matrix (Grande 2010; Brito et al. 2017) in TNT v. 1.5 (Goloboff and Catalano 2016). **B.** Occurrences of *Cuneatus maximus* sp. nov. and the other two named cuneatins. Grey labels denote collapsed clades that include additional species (see the Appendix 2)

The discovery of *C. maximus* sp. nov. is also important for illuminating cuneatin biogeography. Cuneatini is one of three major branches in Lepisosteidae along with the Masillosteinae and crown Lepisosteidae (= Lepisosteini of Grande 2010) yet is restricted to a small region in the western United States (Grande 2010, this paper). This makes cuneatin gars the most regionalized major branch in the gar tree of life. Although the limited distribution of cuneatins might be a result of incomplete sampling, the excellent Cretaceous–Paleogene fossil record of lepisosteids in the northern hemisphere does not include any species identifiable as a cuneatin before the middle Eocene (e.g., Grande 1985, 2010; Echelle and Grande 2014; Cavin et al. 2015; Alvarado-Ortega et al. 2016; Brito et al. 2016; Szabó et al. 2016; Cooper et al. 2021). Thus, it is reasonable to infer that cuneatins were North American endemics.

The fauna of the Willwood Formation features heavily in discussions of vertebrate biogeography during the Eocene Thermal Maximum (ETM; e.g., Smith 2009, 2011; Bourque et al. 2015; Mayr 2016; Scarpetta 2020). Particularly, the Eocene herpetological faunas of this formation have been used to support the hypothesis that the ETM induced large-scale shifts in the distributions of major vertebrate clades (Smith 2009, 2011; Bourque et al. 2015). The presence of cuneatin gars in Wyoming adds to the evidence that the fauna of this region was “megathermal-adapted”, as lepisosteids and members of the sister lineage Obaichthyidae are almost exclusively known from warm environments (e.g., Grande 1985, 2010; Echelle and Grande 2014; Brito et al. 2017). To my knowledge, *C. maximus* sp. nov. is the only species of fish known only from the Willwood Formation and one of the only articulated fish fossils collected from this unit. Along with the holotype of this new species of gar, I have also examined several specimens referable to medium-sized members of the clade Amiidae (bowfins) from the Willwood Formation. The recognition of this new cuneatin suggests that the poorly known ichthyofauna of the Willwood Formation could provide further support for proposed patterns of migration and endemism in ETM terrestrial vertebrate faunas.

Cuneatus maximus sp. nov. evidences that lepisosteid disparity in the northern hemisphere remains considerably undersampled. This species was penecontemporaneous with the Green River gar fauna, which includes members of at least five species represented by numerous complete skeletons and a smattering of isolated material (Grande 1985, 2010; Echelle and Grande 2014). This specimen, initially labeled as *Lepisosteus* sp., illustrates how critical reassessment of previously identified material can drastically change our knowledge of the diversity of depauperate clades.

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Appendix 1

Codings for *Cuneatus maximus* sp. nov. in the morphological matrix of Grande (2010) with *Nhanulepisosteus* included after Brito et al. (2017).

Cuneatus maximus sp. nov. 00?0???1?0?111?1?111?????0??????1?00?11111????0??0??????11?
11????111????????????????????????????????

Appendix 2

Resampled tree with bootstrap supports.

