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Evidence of large sturgeons in the Paleocene of North America

Chase Doran Brownstein*

Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520, and Stamford Museum and Nature Center, Stamford, Connecticut 06903, USA <chase.brownstein@yale.edu>

Abstract.—Ray-finned fishes comprise nearly half of extant vertebrate species and include several ancient lineages with fossil records that stretch over 200 Myr in time. One of these old clades, the sturgeons and paddlefishes, is distributed across the Northern Hemisphere and includes some of the largest known freshwater fishes. Yet, the fossil record of this lineage (Acipenseriformes) is poor compared to similarly ancient ray-finned fish clades. Here, I describe sturgeon fossils from two geological units in North America < 10 Myr younger than the Cretaceous-Paleogene boundary. Both come from individuals of ∼1.5 m in length. These Paleogene forms establish the long history of large body size in Acipenseriforms and reveal sturgeons were some of the largest inhabitants of freshwater ecosystems that were still recovering from the Cretaceous-Paleogene extinction.

Introduction

North America is a hotspot of ancient aquatic vertebrate diversity. All but one of the classic ancient lineages of ray-finned fishes (Polypteridae; e.g., Near et al., 2014) are found on the continent, and at least three of these are presently entirely confined to North America (gars, Bowfin, *Hiodon* Lesueur, 1818; Grande and Bemis, 1998; Hilton, 2003; Hilton and Grande, 2008; Grande, 2010). Acipenseriformes, which currently comprises 27 species of sturgeons and the Paddlefish and includes some of the largest living freshwater fishes (*Huso* Linneaus, 1758; see Berg, 1948) is the most diverse and geographically widespread of the major ancient ray-finned fish clades. Despite the status of this clade, the evolutionary history of Acipenseriformes remains poorly understood. The anatomy, fossil record, and interrelationships of this clade have been the subject of numerous detailed morphological studies (Grande and Bemis, 1991; Bemis et al., 1997; Grande and Hilton, 2006; Hilton and Grande, 2006; Hilton et al., 2011; Sato et al., 2018; Murray et al., 2020; During et al., 2022).

Despite the large number of specialized features unique to Paddlefish and sturgeons, the available fossil record for these fishes indicates the phenotype in Acipenseriformes has remained remarkably unchanged over perhaps 100 Myr (Hilton et al., 2011; Sato et al., 2018; Murray et al., 2020). Unfortunately, gaps in the fossil record of Acipenseriformes for key intervals like the aftermath of the Cretaceous-Paleogene mass extinction 66 Ma have obscured whether this pattern of phenotypic conservatism is a biological reality or an artifact of sampling (Grande and Hilton, 2006; Hilton and Grande, 2006; Hilton et al., 2011; Sato et al., 2018; Hilton and Grande, 2022).

*Corresponding author.

Here, I describe two records of sturgeons from the 7 Myr following the Cretaceous-Paleogene mass extinction in western North America (Fig. 1). These lateral osteoderms demonstrate the presence of large (>1.5 m) sturgeons in early-middle Paleocene freshwater ecosystems. In turn, they extend the record of large (>1 m) body size in Acipenseriformes back by 60 Myr and imply that the high degree of body size disparity observed in this clade relative to other vertebrates (Rabosky et al., 2013) is a consistent pattern in their evolutionary history.

Materials

Repository and institutional abbreviation.—YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Systematic paleontology

Actinopterygii Cope, 1887
Acipenseriformes Berg, 1940
Acipenseridae Bonaparte, 1831
Acipenseridae morphotype A
Figures 2, 3

Occurrence.—Layer #3, Eagle Mine near Bear Creek, Carbon County, Montana (Bear Creek Local Fauna, Fort Union Formation, Tiffanian-Clarkfordian, 61.2–56.6 Ma; Barnosky et al., 2014, fig. 1). Precise coordinates are available to qualified researchers at YPM.

Description.—YPM VPPU 17066 consists of an exquisitely preserved, isolated dermal scute (Fig. 2.1–2.3) assignable to a large acipenserid sturgeon (Hilton and Grande, 2006; Hilton et al., 2011; Thieren et al., 2015; Sato et al., 2018; Murray

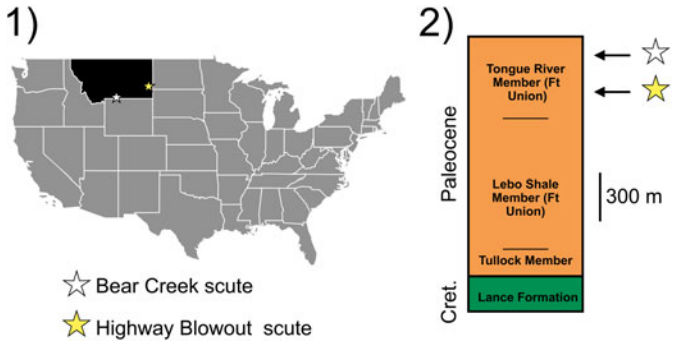

Figure 1. Locality and horizon of the new sturgeon material: (**1**) map of the United States showing localities where sturgeon records reported in this paper were recovered; (**2**) simplified stratigraphic column of the Cretaceous-Paleogene in Montana showing horizons from which sturgeon material reported in this paper was recovered.

et al., 2020). The size and shape of the scute allow assignment of YPM VPPU 17066 to the sturgeon crown group Acipenseridae because the closest fossil relatives of this lineage lack large lateral scutes (e.g., Hilton and Grande, 2006). The scute, which represents the best record of an acipenseriform from the Bear Creek Local Fauna, comes from the middle portion of the lateral row based on its dorsoventral asymmetry and median ridge size (Hilton et al., 2011), which produce a slight posterior slant for the scute in lateral and medial views (Fig. 2.1, 2.2).

The external surface is ornamented with unorganized deep pitting and several large ridges that radiate from the defined central ridge and produce a rugose outline. These ridges are much larger than those seen in extant sturgeons, e.g., *Acipenser* spp. (e.g., Hilton et al., 2011; Thieren et al., 2015). Pitting is not confined to the center of the external surface of the scute and variously reaches the borders of this bone (Fig. 2.1, 2.2). Size estimation using the lateral scute maximum equation of Thieren and Van Neer (2016) using the dorsoventral maximum height of YPM 17066 (70 mm) provides a total length of 1.650 m for YPM VPPU 17066 (Fig. 3).

Material.—YPM VPPU 17066, a complete lateral scute.

Remarks.—YPM VPPU 17066 is identifiable as the lateral dermal scute of an acipenserid.

Acipenseridae morphotype B
Figures 2, 3

Occurrence.—Highway Blowout Site, Fallon County, Montana (Tongue River Member, Fort Union Formation, Tiffanian-

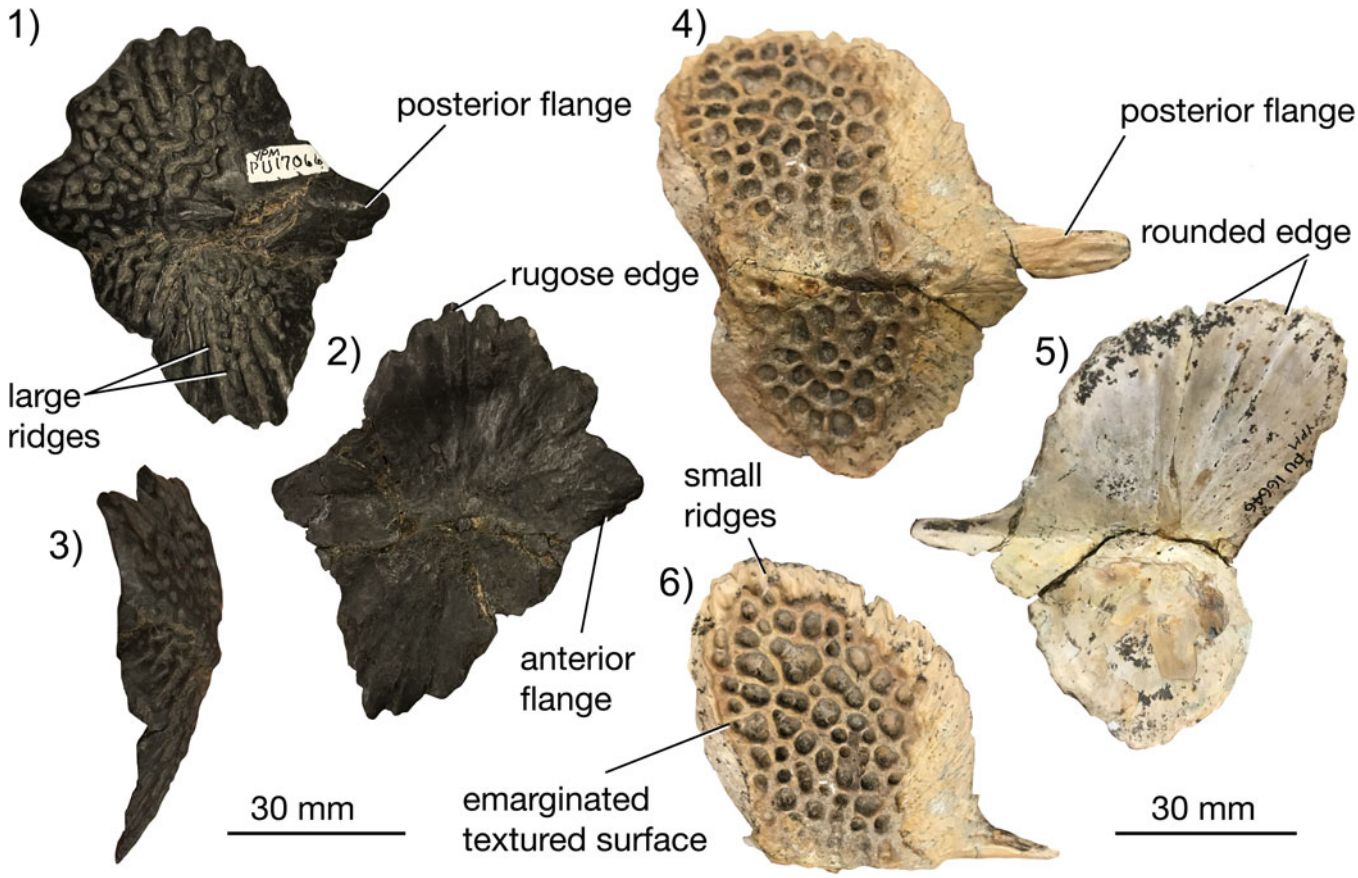

Figure 2. Anatomy of the new sturgeon specimens of Acipenseridae morphotype A: (**1–3**) YPM VPPU 17066, Bear Creek Site, Montana: (**1**) lateral view; (**2**) medial view; (**3**) anterior view; (**4–6**) YPM VPPU 16646, Highway Blowout Site, Montana; (**4**) lateral view; (**5**) medial view; (**6**) dorsal view.

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Clarkfordian, ~62–60 Ma; Peppe et al., 2011). Precise coordinates are available to qualified researchers at YPM.

Description.—YPM VPPU 16646 is another complete dermal scute from a large acipenserid fish (Fig. 2.4–2.6). This specimen is slightly larger than YPM VPPU 17066 and shows a very different set of features. Although the dorsoventral asymmetry of YPM VPPU 16646 demonstrates that it comes from the lateral scute row, the specimen is strongly angled along its dorsoventral midline (Fig. 2.4). This produces distinctive dorsal and ventral faces. The form of ornamentation on YPM VPPU 16646 is also markedly different from YPM VPPU 17066 and more closely resembles the ornamentation of extant sturgeons like *Acipenser* spp., *Huso* spp., *Scaphirhynchus* spp., and *Pseudoscaphirhynchus* spp. (Hilton et al., 2011; Thieren et al., 2015) and extinct crown-group acipenserids, e.g., †*Anchiacipenser acanthaspis* Sato et al., 2018. Although the size of individual pits on YPM VPPU 16646 is larger than most crown group sturgeons (Hilton et al., 2011; Thieren et al., 2015; Sato et al., 2018) and stem-group taxa from North America (Hilton et al., 2011; Sato et al., 2018), YPM VPPU 16646 shares with these forms reduced radiating ridges and pitting ornamentation that is widely separated from the scute border by a relatively smooth surface bearing small radiating ridges (Fig. 2.4–2.6).

YPM VPPU 16646 is unusual in that it bears a large flange directed toward the posterior end of the body. Although some extant sturgeon lateral scutes show small posterior spines (Thieren et al., 2015), the posterior flange on YPM VPPU 16646 is two-thirds of the anteroposterior length of the main body of the osteoderm. Another odd feature of YPM VPPU 16646 is the rounded outline of the main body of the scute. In most crown sturgeons, the lateral scutes have main bodies that terminate dorsally and ventrally at distinct apices, forming a rhomboid shape in lateral and medial views. Size estimation using the lateral scute maximum equation of Thieren and Van Neer (2016) using the dorsoventral maximum height of YPM VPPU 16646 (= 75 mm) gives a total length of 1.653 m for the Highway Blowout acipenserid (Fig. 3).

Material.—YPM VPPU 16646, a complete lateral scute.

Remarks.—YPM VPPU 16646 is identifiable as the lateral dermal scute of an acipenserid.

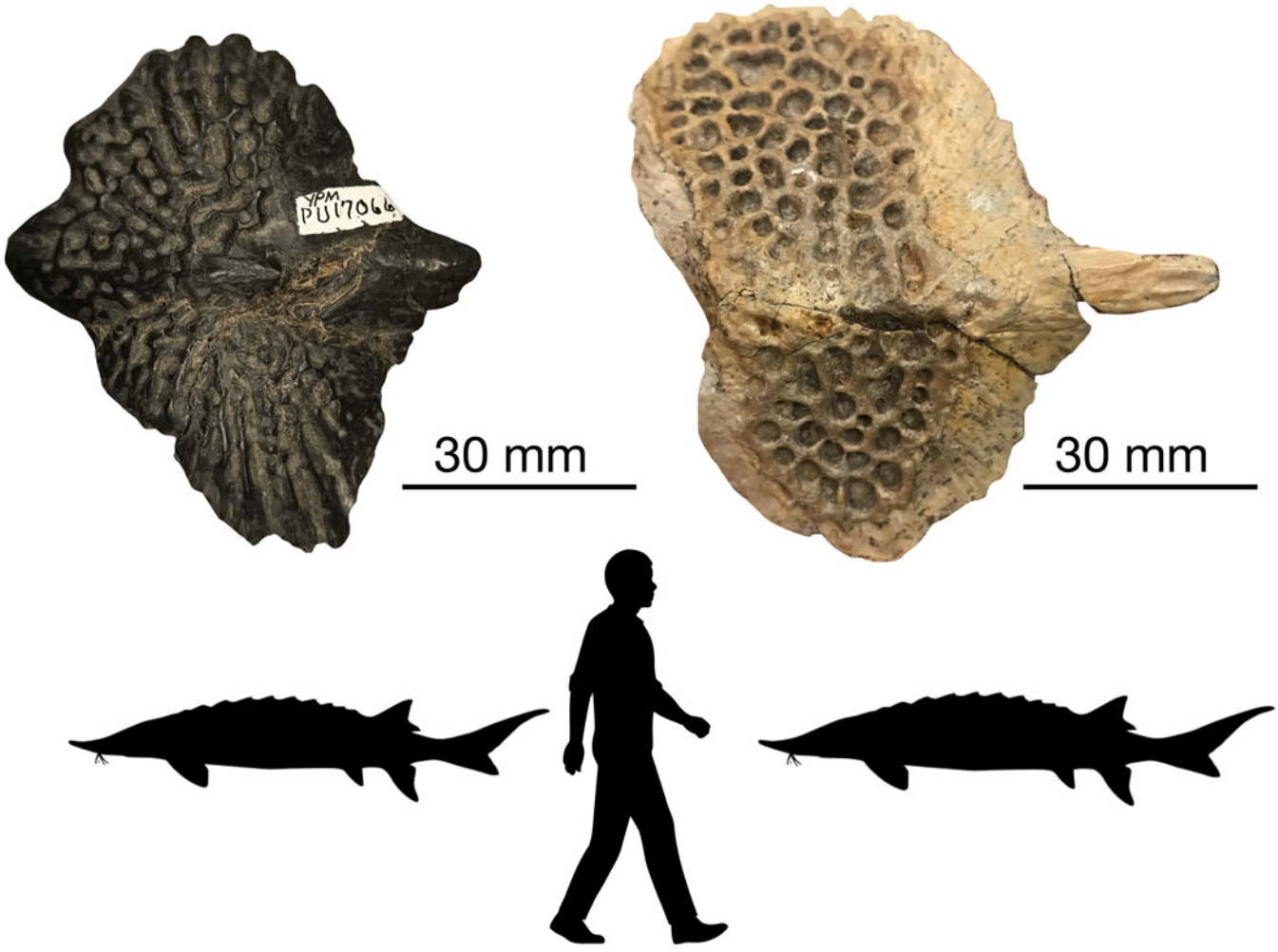

Figure 3. Size comparison of the two new sturgeon records of Acipenseridae morphotype A: Bear Creek sturgeon (left); Highway Blowout sturgeon (right). Silhouette is a 1.85 m tall man.

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Discussion

Eight extant sturgeon species are currently found in North America, but the fossil record of the crown group on the continent stretches back to the Cretaceous (Hilton and Grande, 2006; Hilton et al., 2011; Sato et al., 2018; Murray et al., 2020). Although living sturgeons in the genera *Acipenser* Linneaus, 1758 and *Huso* are the largest known freshwater fishes (e.g., Berg, 1948; Hilton et al., 2011), most of the published fossil record of the crown clade is comprised by relatively small (~1.0 m or less) species (Hilton and Grande, 2006; Sato et al., 2018; Murray et al., 2020). The ancient ages of the two lineages in the crown group are known to include giant species. For example, various time-calibrated molecular phylogenies suggest that giant species, e.g., *Acipenser transmontanus* Richardson, 1836 and *Huso* spp., last share common ancestry with other sturgeons varying between 8 and >50 Ma (Peng et al., 2007; Luo et al., 2019; Shen et al., 2020). These estimated ages imply long ghost lineages leading to extant giant sturgeons.

The two new sturgeon specimens, although not complete enough to justify naming new species, represent giant acipenserids from two different geological units in the Paleocene of the American West. Both specimens are within the upper size bracket for Acipenseridae (Thieren et al., 2015; Thieren and Van Neer, 2016), stretching the record of large size in this clade back by at least 60 Myr to the recovery period following the Cretaceous-Paleogene mass extinction. Although their assignment to subclades in Acipenseridae is limited by the wide variability of osteoderm shape in sturgeons (Hilton and Grande, 2006; Hilton et al., 2011; Sato et al., 2018; Murray et al., 2020), both the Bear Creek and Highway Blowout scutes belong to pan-acipenserids, which are characterized by the presence of distinctive dermal osteoderms (Hilton and Grande, 2006; Hilton et al., 2011; Sato et al., 2018; Murray et al., 2020).

The high degree of body size disparity in extant sturgeons (Rabosky et al., 2013) contrasts with their status as a living fossil lineage, i.e., a long-lived, species-poor clade that shows little phenotypic change from ancient fossil relatives (Gardiner, 1984; Grande and Bemis, 1991; Bemis et al., 1997; Hilton et al., 2011). A similar pattern of proportionally high variation in body size relative to species diversity has also been documented in latimeroid coelacanths, which include the freshwater-brackish clade †Mawsoniidae (Cavin et al., 2021).

Finally, the new large-bodied sturgeon records add to the growing body of evidence that ancient freshwater fish assemblages from the Paleocene and Eocene of North America contained numerous large-bodied clades with different body plans (e.g., Grande and Bemis, 1991, 1998; Grande, 2010; Hilton et al., 2011; Brownstein, 2022). The suction-feeding style of sturgeons (e.g., Carroll and Wainwright, 2003) represents a unique component to these assemblages, which are already known to include durophagous and macropredatory gars with shortened to longirostrine skulls (Grande and Bemis, 1998; Grande, 2010; Brownstein, 2022), filter-feeding paddlefishes (Grande and Bemis, 1998), and large, predatory osteoglossiform fishes with the characteristic rasping device that gives the clade its name (Forey and Hilton, 2010; Hilton and Lavoué, 2018). In turn, the specimens described in this contribution indicate a legacy of giant acipenserids in Paleocene North American ecosystems in need of further discoveries to be fully revealed.

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