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Bonefish (Elopomorpha, Albuliformes) remains from Late Cretaceous outcrops of San Carlos Quarry, Coahuila, Northern Mexico: evidence of a new giant Teleost in the Western Interior Seaway

Restos de fósiles de Macabí (Elopomorpha, Albuliformes) del Cretácico Tardío en los depósitos marinos de la cantera San Carlos, Coahuila, en el norte de México: evidencia de un nuevo teleósteo gigante en el Mar Interior Occidental

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ABSTRACT

The discovery of suspensorium bones, comprising the hyomandibular and metapterygoid, indicates the presence of a giant species belonging to the order Albuliformes in the Late Cretaceous outcrops of Northern Coahuila. The taxonomic designation in the order Albuliformes is due to the presence of the metapterygoid cup, a postero-dorsal concavity on the metapterygoid bone which, together with its articulation with the hyomandibular, composes the hyomandibular-metapterygoid fenestra. Although the function of this structure has been debated, its presence represents a diagnostic feature for both fossil and extant Albuliformes species. Comparing the hyomandibular-metapterygoid fenestra with other bonefish is evidence that this structure is quite variable inside the order. The hyomandibular length indicates that this specimen measured approximately 3.9 meters in length, which represents three times the size of †*Farinichthys gigas*, the largest bonefish known to date, collected in Paleocene outcrops from Brazil. This taxon represents a new giant form inside the Western Interior Seaway, which differs from the other large teleostean fishes of this ancient sea for being a secondary consumer.

Keywords: Albuliformes, Late Cretaceous, Coahuila, Mexico, Western Interior Seaway.

RESUMEN

En este trabajo se describen los huesos del suspensorio de un ejemplar fósil del orden Albuliformes recuperado en los depósitos marinos del Cretácico Tardío de la región norte de Coahuila. Aunque el ejemplar sólo conserva los huesos hiomandibular y el metapterigoides, éste muestra un rasgo diagnóstico de los albuliformes: la presencia de la fenestra hyomandibular-metapterigoides formada entre las mellas presentes en los bordes posterodorsal del metapterygoides (=metapterygoid cup) y anteroventral del hiomandibular. Aunque la función de esa estructura es discutible, su presencia representa una característica exclusiva observada en especies fósiles y vivientes del orden Albuliformes.

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La comparación de dicha fenestra observada en este fósil con las de otros Albuliformes revela dos rasgos peculiares en el ejemplar estudiado. Por un lado, los huesos hiomandibular y metapterigoides son de tamaño inusualmente grandes. A partir de estos huesos, es posible estimar que la longitud del individuo al que pertenecieron pudo ser cercana a 3.9 m, triplicando el tamaño del mayor albuliforme antes conocido, †Farinichthys gigas del Paleoceno de Brasil. Por otro lado, la fenestra hiomandibular-metapterygoides del ejemplar estudiado muestra una combinación peculiar de rasgos no observada en otros albuliformes, ésta es notablemente oblonga, aguda en ambos extremos y ventroposteriormente inclinada. Las presentes observaciones confirman que el fósil estudiado potencialmente representa una nueva especie albuliforme del Cretácico Tardío que vivió en la región limítrofe entre el sur del Mar Interior de Occidental y el norte del proto-Golfo de México, lo cual difiere de los demás teleósteos gigantes por ser un consumidor secundario en la cadena trófica.

Palabras clave: *Albuliformes, Cretácico Tardío, Coahuila, México, Mar Interior Occidental.*

1. Introduction

During the Cretaceous, the Earth's geography and climate were different from today. The landmass had changed significantly during this period, and the average global temperature was higher than in the present day, precluding the formation of polar ice caps (Hay and Floegel, 2012). Therefore, the Cretaceous represents when the sea level was higher than in recent geological periods. As a result, the lands were flooded with marine waters from diverse epicontinental seas around the globe (Hay and Floegel, 2012; Scotese, 2014).

In North America, the Western Interior Seaway (WIS) was a large tectonically regulated epicontinental sea formed and extinguished by a series of transgressions and regressions of marine waters during the Cretaceous (Kauffman and Caldwell, 1993; Miall, 2009). The WIS was a relatively shallow sea that extended 4800 kilometers crossing from the current Arctic Ocean to the Gulf of Mexico, separating North America into two landmasses named Appalachia and Laramidia (Kaufmann, 1977, 1984; Cumbaa *et al.*, 2010).

There is remarkable biodiversity reported to the WIS and its corresponding landmasses. Invertebrate fauna, for example, comprises bivalves, gastropods, cephalopods, crustaceans, and echinoderms. Vertebrates include cartilaginous and bony fishes, marine turtles, ichthyosaurs, plesiosaurs, pterosaurs, dinosaurs, among others (*e.g.*, Russel, 1988; Cumbaa *et al.*, 2013; Murray and Cook, 2016). Earliest paleontological studies concentrate on fossil localities in the United States of America (USA) and Canada (*e.g.*, Cope, 1872; Hattin, 1975; Russel, 1988; Kirkland, 1989; Polcyn *et al.*, 2008; Cumbaa *et al.*, 2010; 2013; Underwood and Cumbaa, 2010; Bice *et al.*, 2013; Murray and Cook, 2016); however, current studies in several Late Cretaceous outcrops of northern Coahuila de Zaragoza state have been revealing the paleontological potential of Mexico to understand the biodiversity distributed in the austral region of the WIS, close to the opening in the proto-Gulf of Mexico (Blanco-Piñón and Alvarado-Ortega, 2005; Stinnesbeck *et al.*, 2005; Giersch *et al.*, 2008; Alvarado-Ortega and Porras-Múzquiz, 2009; Riquelme *et al.*, 2013; Stinnesbeck *et al.*, 2023).

The marine fossil assemblage in these Mexican fossil beds comprises planktonic foraminifera, bivalves, ammonoids, crustaceans, chondrichthyans, actinopterygians, turtles, and mosasaurs (Blanco-Piñón & Alvarado-Ortega, 2005; Stinnesbeck *et al.*, 2005; Giersch *et al.*, 2008; Alvarado-Ortega and Porras-Múzquiz, 2009; Riquelme *et al.*, 2013). The fossil diversity and geology of the Late Cretaceous marine localities from northern Coahuila de Zaragoza are poorly understood. The lithology is poorly known, and several taxa need identification. Here we describe a new teleost fish belonging to the order Albuliformes. Although incomplete, this specimen constitutes a new report of a bonefish and the largest albuliform fish documented until now; consequently, its discovery indicates the presence of giant teleost species inhabiting the WIS belonging to different trophic niches.

1.1. Area of study

The Múzquiz Lagerstätte is a series of outcrops belonging to both Eagle Ford and Austin groups ranging from the Turonian to Campanian (Stinnesbeck *et al.*, 2005; Alvarado-Ortega *et al.*, 2006; Ifrim *et al.*, 2007; Alvarado-Ortega and Porras-Múzquiz, 2009; 2022; Riquelme *et al.*, 2013; López-Conde *et al.*, 2019). They are named Múzquiz Lagerstätte because of its proximity to the Melchor Múzquiz municipality (about 150 km) and its great diversity of fossils found, with several specimens showing an exceptional degree of preservation. The geological settings of these quarries are poorly understood, so the stratigraphic group and age are based mainly on the fossil record.

The specimen studied was collected in the San Carlos quarry, one of the fossil beds of the Múzquiz Lagerstätte that belonged to the Austin group. The San Carlos quarry is in 29°04'11"N and 100°47'12"W coordinates, near Jimenez municipality, northern Coahuila de Zaragoza. According to previous studies (i.e., Carrasco, 1963; Piedad-Sánchez *et al.*, 2011; López-Conde *et al.*, 2019), the Austin Group in Jimenez is divided into two distinct members belonging to the Campanian and named La Dessau and Los Tecolotes. Here, the fossil record comes from the Los Tecolotes member, dated of the Campanian based on the presence of the ammonites †*Scaphites* *hippocrepis* DeKay, 1828 and †*Delawarella delawarensis* Collignon, 1948 (Carrasco, 1969; Silva-Martínez *et al.*, 2014; López-Conde *et al.*, 2019).

The San Carlos quarry consists of parallel laminate strata ranging between 20 to 100 cm thick and comprising siltstone and reddish-brown shale, interleaved with yellowish-gray marls. Thin anhydrite layers of about 3 cm are occasionally present. Only one turtle fossil, †*Desmatochelys* cf. *lowi* Williston, 1894, and teleost fragments belonging to the order Tsefaltiiformes have been reported from the San Carlos quarry (López-Conde *et al.*, 2019; Stinnesbeck *et al.*, 2023, fig.1); however, several other species need identification, such as mollusks, crustaceans, sharks, and bony fishes (Piedad-Sánchez *et al.*, 2011, personal observation). The environment of the San Carlos quarry is tentatively assigned to a regressive sedimentary deposit of marine origin on a shallow shelf near the coast (Piedad-Sánchez *et al.*, 2011).

2. Materials and methods

The unique specimen (MUZ-3915) is conserved in part and counterpart in a yellowish stratum about 40 cm thick. This specimen is currently housed at the Museo de Paleontología de Múzquiz [Paleontological Museum of Múzquiz], at Melchor Múzquiz municipality, Coahuila de Zaragoza State, northern Mexico. Measures were performed using a digital dial caliper and photographs with a Nikon DSLR D5500. The free softwares GIMP v. 2.10.32 and Inkscape v.1.2 were used for the image edition and line drawings.

The anatomical interpretation follows that of Forey (1973). The comparative material comprises the unique specimen of †*Nunaneichthys mexicanus* Hernández-Guerrero, Cantalice, González-Rodríguez, and Bravo-Cuevas, 2021 (UAHMP-4232), housed at the Museo de Paleontología of the Universidad Autónoma del Estado de Hidalgo [Museum of Paleontology of the Autonomous University of Hidalgo State]; 12 specimens of †*Macabi tojolabalensis* L-Recinos, Cantalice, Caballero-Viñas, and Alvarado-Ortega, 2023 (IGM 13105 to IGM 13116) housed at Colección Nacional de Paleontología [National Collection of Paleontology] of the Universidad Nacional Autónoma de México [Autonomous National University of Mexico] (CNP-UNAM); and finally, one dry skeleton of the living species *Albula vulpes* (Linnaeus, 1758) (CRM-1246), from Paraíba State, Northeast Brazil, and housed at the extant specimen section of the CNP-UNAM. Data about other Albuliformes have been taken from the literature (*e.g.*, Woodward, 1893; Ridewood, 1904; Blake, 1940; Estes, 1969; Forey, 1973; Forey *et al.*, 1996, 2003; Filleul, 2001; Gallo and Figueiredo, 2002; Forey and Maisey, 2010; Mayrinck *et al.*, 2010; Figueiredo *et al.*, 2012; Bartholomai, 2013; Taverne and Capasso, 2018; Hernández-Guerrero *et al.*, 2021; L-Recinos *et al.*, 2023).

3. Results

3.1. Systematic Paleontology

Infraclass Teleostei Müller, 1845
Super cohort Teleocephala De Pinna, 1996
Cohort Elopomorpha Greenwood, Rosen, Weitzman, and Myers, 1966
Order Albuliformes Greenwood, Rosen, Weitzman, and Myers, 1966
Albuliformes *incertae sedis*

Referred specimen. MUZ-3915; part and counterpart (Figure 1).

Locality and horizon. San Carlos quarry, 29°04′11″N, and 100°47′12″W, at Jimenez municipality, Coahuila de Zaragoza, northern Mexico. This fossil bed belongs to the Campanian strata of the Austin Group.

3.2. Description

The metapterygoid (mpt) is inclined and presents a concavity on its anteroventral border. The ventral border is semi-circular and medially presents several grooves. Posteriorly, the ventral edge of the metapterygoid covers the anterior crest (an.c) of the hyomandibular (Figure 2). Above this region is the metapterygoid cup (mpt.cup), a concavity of this bone commonly found in Elopomorpha (Forey, 1973). Like in Albuliformes, this structure in MUZ-3915 forms a fenestra (Figure 2A, C); the hyomandibular-metapterygoid fenestra (hy-mpt.f), which according to Forey (1973), is for the passage of the levator arcus palatine muscle to insert upon the medial face of the metapterygoid (see discussion). The dorsal edge of the metapterygoid is prolonged and exceeds the articulation with the hyomandibular (Figure 2C). At least four grooves are discernible running along this region.

The hyomandibular is cross-shaped and is larger than the metapterygoid (Figure 1). The anterior edge is projected, forming the facet for articulation with the metapterygoid (mpt.fc), which composes the dorsal limit of the hyomandibular-metapterygoid fenestra (Figure 2). The dorsal border of the hyomandibular articulates the suspensorium with the neurocranium. In the specimen studied, the anterodorsal (ad.p) and posterodorsal (pd.p) projections are separated by a shallow groove. The opercular projection (op.p) is posterior, articulating the hyomandibular and the opercle. The ventral edge of the hyomandibular (v.p) is prolonged and presents a well-developed anterior groove, named

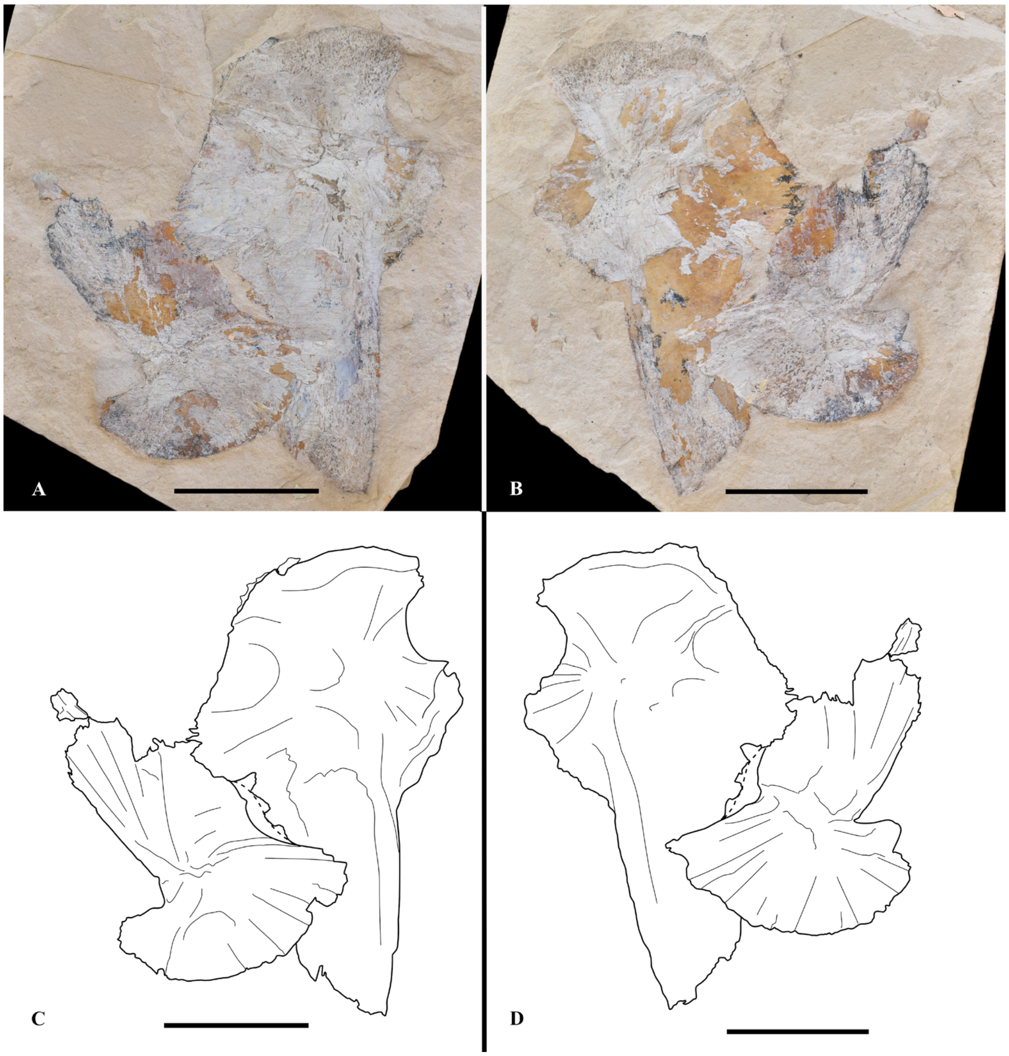

Figure 1. Photography (A, B) and line drawing (C, D) of MUZ-3915, in part (A, C) and counterpart (B, D). The scale indicates 50 mm.

preopercular groove (pop.g). The ventral border of the hyomandibular is covered by the posterior portion of the metapterygoid, forming the ventral border of the hyomandibular-metapterygoid fenestra.

3.3. Remarks

In addition to the specimen described herein, bonefishes distributed inside the WIS domains include members of the extinct subfamily †Phyllodontinae, composed of three genera, †*Casierus* Estes, 1969, †*Phyllodus* Agassiz, 1843 and †*Paralbula* Blake, 1940, which are recognized by fragmented tooth plates from the Late Cretaceous of USA and Canada (*e.g.*, Estes, 1969; Applegate, 1970; Cumbaa *et al.*, 2010, 2013; Murray and Cook, 2016). The best-preserved fossil Albuliformes in the WIS is the species †*Albula dunklei,* from Mooreville Shalk of the Selma Formation, Late Cretaceous (Santonian to Campanian) of Alabama (Applegate, 1970) and †*Deltaichthys albuloides,* from the Upper Cretaceous of Eagle Ford formation, Texas (Fielitz and Bardack, 1992).

The genera †*Casierus*, †*Phyllodus*, and †*Paralbula* are represented by tooth plates (*e.g.*, Estes, 1969, Cumbaa *et al.*, 2013), a structure not observed in the specimen here analyzed. †*Albula dunklei* is also not compared with the presented fossil due to the lack of suspensorium bones. The preserved material includes the middle portion of the body (including the pectoral-fin girdle) and several scales, vertebrae, and isolated head bones (Applegate, 1970). On the contrary, †*D. albuloides* is a nearly complete and three-dimensional species that preserves both hyomandibular and metapterygoid bones (Fielitz and Bardack, 1992); however, the configuration is distinct from that found in the albuliform specimen of the San Carlos quarry (see discussion). All these features indicate that the albuliform from the San Carlos quarry should represent a new bonefish species; however, due to the absence of more detailed morphological evidence, this result should be

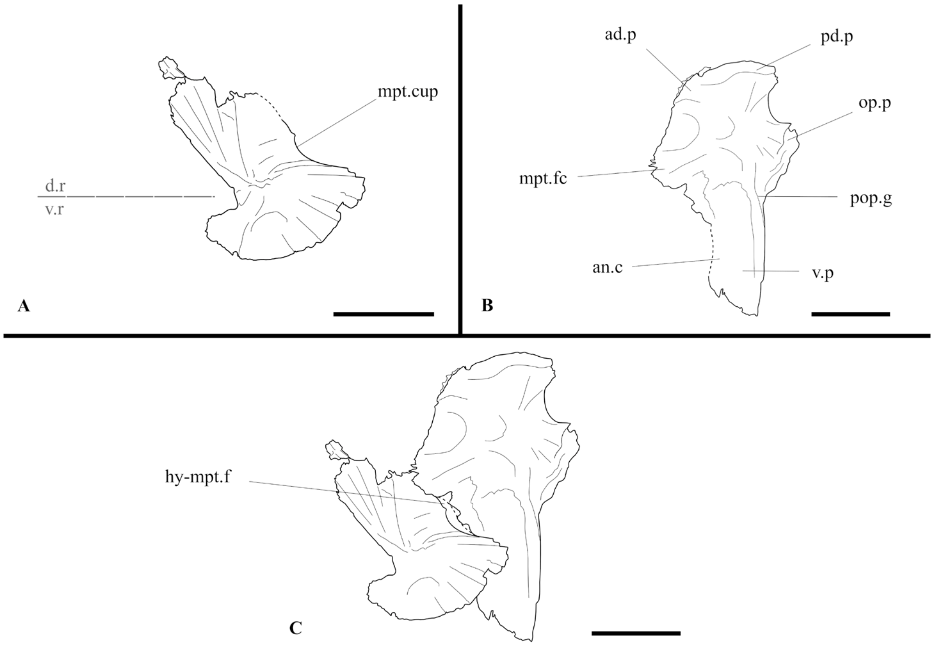

Figure 2. Schematic drawing of the metapterygoid (A, C) and hyomandibular (B, C) of MUZ-3915. The scales indicate 50 mm. Abbreviations: an.c., anterior crest; ad.p., antero-dorsal process; an.p., anterior portion; d.r., dorsal region; hy-mpt.f., hyomandibular-metapterygoid fenestra; mpt.cup: metapterygoid cup; mpt.fc., metapterygoid facet; op.p., opercular process; pd.p., postero-dorsal process; pop.g., preopercular groove; v.p. ventral portion; v.r. ventral region.

considered preliminary to the precise taxonomic assignation. At this moment, the present fossil described is an albuliform *incertae sedis.*

4. Discussion

4.1. The hyomandibular-metapterygoid fenestra in bonefishes

The presence of a hyomandibular-metapterygoid fenestra was first observed by Forey (1973) as a feature present in †*Osmeroides latifrons* Woodward, 1907, and the subfamilies Albulinae and Pterothrissinae. Currently, it is considered a diagnostic character to the order Albuliformes (Hernández-Guerrero *et al.*, 2021); however, there are several fossil species in which this structure is not observed due to the poor state of preservation, such as in all the subfamily Phyllodontidae (Estes, 1969) and †*Macabi tojolabalensis* (L-Recinos *et al.*, 2023).

The hyomandibular-metapterygoid fenestra is formed by the connection with the metapterygoid and the hyomandibular, together with the posterodorsal concavity of the metapterygoid (the mpt. cup), which, according to Forey (1973), passes a deep division of the *levator arcus palatine* muscle to insert upon the medial face of the metapterygoid (Forey, 1973, p. 132). Although this hypothesis is widely accepted, Figueiredo *et al.* (2012) stated that there is a membrane covering the hyomandibular-metapterygoid fenestra in extant Albuliformes, indicating that neither muscle nor nerves passed through this structure. These authors pointed out that this structure should be a transformation to reduce the pressure of the suspensorium when crushing their prey, an adaptation to the durophage feeding habit (Figueiredo *et al.*, 2012).

The presence or absence of muscle fibers through the hyomandibular-metapterygoid fenestra will be elucidated through a noninvasive morphological analysis of extant species, which is outside the scope of this work. Nevertheless, we corroborate the correlation between the hyomandibular and metapterygoid bones (and the hyomandibular-metapterygoid fenestra shape) with the feeding habitat (Figueiredo *et al.*, 2012) since it is notable the inter-specific variation of this structure (Figure 3).

In general, the hyomandibular-metapterygoid fenestra is larger in living species. Furthermore, in extant species of *Albula* and *Pterothrissus*, the dorsal border of the metapterygoid is directed to the posterior region of the body, and the anterior edge of the metapterygoid is expanded. Within the fossil record, the species †*Nunaneichthys mexicanus* presents the smallest fenestra (Hernández-Guerrero *et al.*, 2021). The hyomandibular and the fenestra shape of the species described herein resemble those of †*Farinichthys gigas* and †*Deltaichthys albuloides*, except for the hyomandibular in †*F. gigas, which* seems less developed (Gallo and Figueiredo, 2002). On the contrary, in †*D. albuloides*, the metapterygoid bone presents a reduced anterodorsal border, and the hyomandibular-metapterygoid fenestra is more developed (Figure 3D).

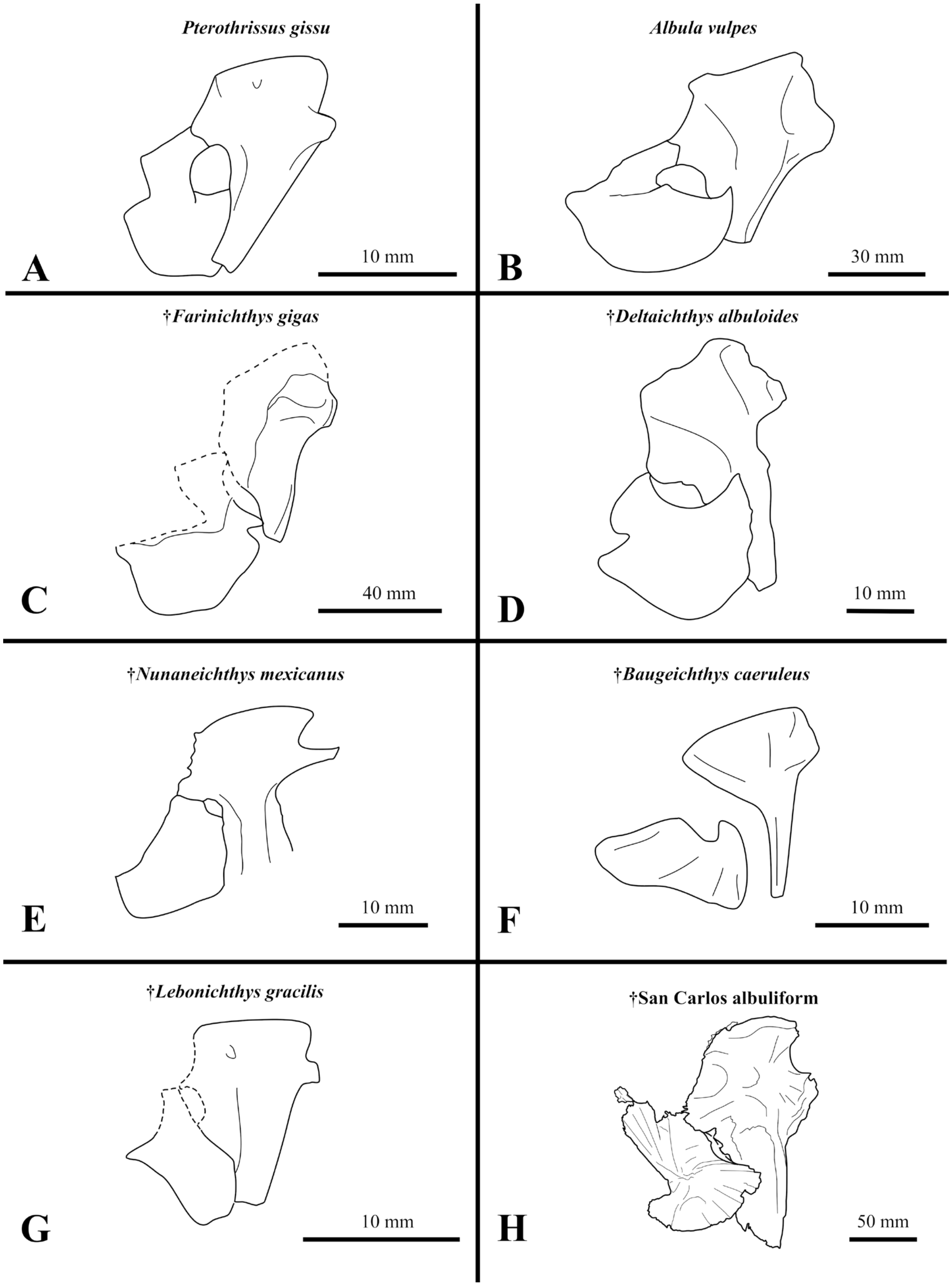

Figure 3. Line drawing of the type of articulation of the metapterygoid and the hyomandibular in different albuliform species. A and G are in internal view. References: A and G) Forey (1973); B) CRM-1246; C) Gallo and Figueiredo (2002); D) Fielitz and Bardack (1992); E) Hernández-Guerrero *et al.* (2021); F) Filleul (2001); H) MUZ-3915.

The species †*Baugeichyhys caeruleus* shows a different configuration of the hyomandibular and metapterygoid bones compared with other albuliform taxa (Figure 3). The ventral branch of the hyomandibular is straight, and the metapterygoid cup is dorsally positioned and not on the posterodorsal edge. The metapterygoid cup in the dorsal position is also noted in extant members of the order Elopiformes, such as *Megalops cyprinoides* (Forey, 1973). The albuliform from the San Carlos quarry, like other Mesozoic bonefishes, presents a small hyomandibular-metapterygoid fenestra, which indicates a modification of this structure in bonefishes during the Cenozoic.

4.2. The Giant Bonefish

Extant members of the order Albuliformes are not large species compared to other Elopomorphs, such as

Megalops cyprinoides (Forey, 1973). The maximum length reported is 105 cm for an *Albula vulpes* species (Nelson *et al.*, 2016). The best-preserved albuliform fossil taxa also are not large, except by †*Farinichthys gigas* from the marine Paleocene outcrops of Maria Farinha Formation, Northeastern Brazil (Gallo and Figueredo, 2002). This species was described based on incomplete and semi-articulated fossils and considered the largest bonefish (Gallo and Figueiredo, 2002), reaching more than 1.30 meters (*cf.* †*F. gigas* is probably 23% larger than the extant species) (Figure 4).

Correlating the hyomandibular length of *Albula vulpes*, †*Farinichthys gigas*, and the species herein described, it indicates that the bonefish from the San Carlos quarry reaches about 3.9 meters in length (Figure 4). This feature implies that Mesozoic Bonefishes were bigger than Cenozoic species and, in the WIS, this group was three times longer in the maximum length compared to †*F. gigas*. Representing, thus, the largest albuliform fish reported to date.

4.3. A new giant species inside the Western Interior Seaway

Giant Albuliformes fishes are rare; however, large organisms are common inside the Western Interior Seaway. Giant bivalves inoceramids, such as †*Volviceramus grandis* Stoliczka, 1871, †*Cladoceramus undulatoplicatus* (Roemer, 1852), †*Platyceramus platinus* (Logan, 1898) were abundant inside the WIS domains. Another common giant invertebrate that lived in the WIS was the cephalopod †*Tusoteuthis longa* Logan, 1898, a squid that may have measured eight to 20 meters long. These invertebrates probably composed the main food source of the specimen herein described since extant Albuliformes are secondary predators, which usually prey on shelled invertebrates (Cumbaa *et al.*, 2013).

Giant cartilaginous fishes include the top predator †*Cretoxyrhina mantelli* (Agassiz, 1835), which could reach about 7 meters in length; and †*Ptychodus polygyrus* Agassiz, 1835, a durophage hybodontiform shark with about 10 meters (Shimada, 1997; Hamm, 2010). A giant sarcopterygian fish, †*Megalocoelacanthus dobiei* Schwimmer, Stewart, and Williams, 1994, the largest coelacanth known to date with about 3 meters, also inhabits the WIS (Schwimmer *et al.*, 1994). Giant teleost fishes are more diverse in this ancient sea and include †*Xiphactinus audax* Leidy, 1870, †*Gillicus arcuatus* Hay, 1898, †*Saurodon leanus* Hays, 1830, †*Ichthyodectes ctenodon* Cope, 1870, †*Bonnerichthys gladius* (Cope, 1873), and †*Pachyrhizodus caninus* (Russel, 1988; Alvarado-Ortega and Porras-Múzquiz, 2009; Friedman *et al.*, 2010; Shimada, 2015). Except for †*B. gladius*, which is a plankton-feeder fish reaching about 16 meters, the other giant teleostean fishes are piscivore top predators (Friedman *et al.*, 2010; Shimada, 2015; Table 1).

Although the teeth are not observed in the present described species, the presence of molariform teeth in the parasphenoid and the branchial apparatus is a common feature present in members of the order

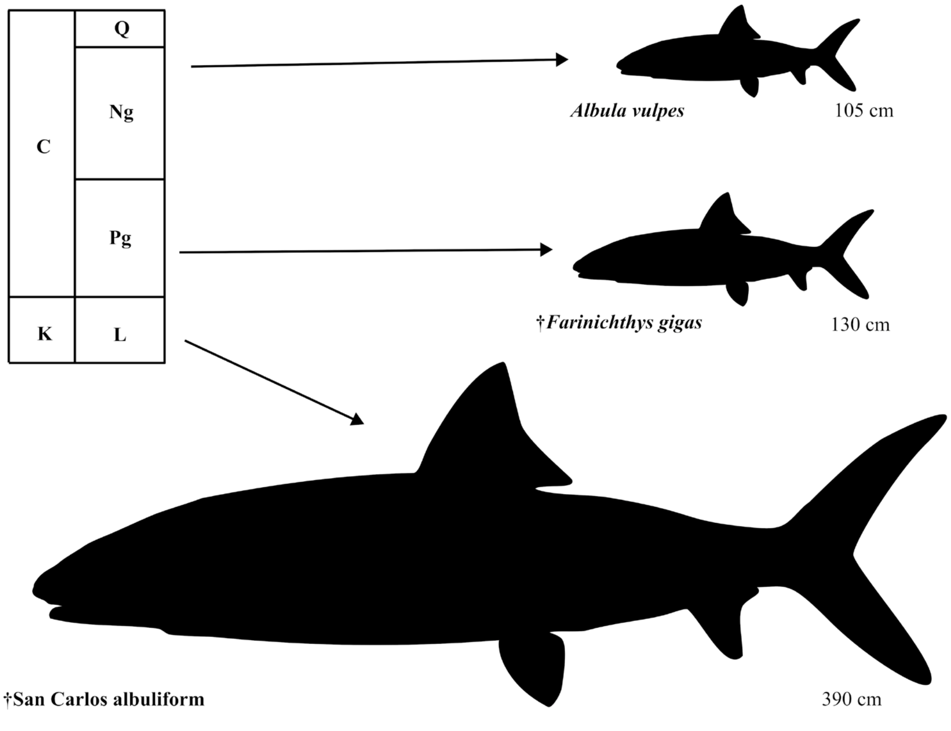

Figure 4. The Geological Age and the maximum length of Albuliformes fishes reported to date. References: Nelson *et al.* (2016) for *Albula vulpes*; Gallo and Figueredo (2002) for †*Farinichthys gigas*. Abbreviations: C, Cenozoic; K, Cretaceous, L, late; Ng, Neogene; Pg, Paleogene; Q, Quaternary.

Table 1. Some Giant teleostomorph fishes from the Western Interior Seaway and their respective trophic niches.

Taxon	Trophic niche	References
Pachyrhizodus caninus	Top predator (piscivore)	Shimada (2015)
Xiphactinus audax	Top predator (piscivore)	Walker (2006)
Ichthyodectes ctenodont	Top predator (piscivore)	Everhart *et al.* (2010)
Gillicus arcuatus	Top predator (piscivore)	Walker (2006)
Prorosphyraena perniciosa	Top predator (piscivore)	Liston *et al.* (2019)
Saurodon leanus	Top predator (piscivore)	Everhart *et al.* (2010)
Stratodus apicalis	Top predator (piscivore)	Cope (1871)
San Carlos albuliform	Secondary consumer (invertebrate-feeder)	Present study
Bonnerichthys gladius	Primary consumer (planktonic)	Friedman *et al.* (2010)

Albuliformes, which allows these groups to consume hard-shelled organisms. This species, therefore, represents an important complement to understanding the different trophic niches occupied by teleost fishes inside the WIS domains.

5. Conclusion

A new Mesozoic albuliform from the San Carlos quarry, Coahuila state, northern Mexico is described. Although incomplete, the presence of the hyomandibular-metapterygoid fenestra allows us to recognize this species as a bonefish. The correlation between the size of the bones preserved in this new taxon and other albuliform taxa indicates that the new species herein reported reaches about 3.9 meters in length, which represents the largest bonefish known to date. Giant teleost fishes are common inside the WIS domains, however, are represented mainly by piscivore taxa and one planktivorous. Since albuliforms are adapted to the durophage feeding habit, it is suggested that the taxon reported herein represents a complement of the trophic niche occupied by the teleost inside this remarkable extinct sea.

Acknowledgments

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