



The Sumidero Quarry, an Albian fossil fish site in San Cristóbal de las Casas, Chiapas, southeastern Mexico

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ABSTRACT

The Sumidero Quarry is a new Albian paleontological site of the Cantelhá Formation at the escarped southwestern edge of the San Cristóbal de las Casas town, State of Chiapas, southeastern Mexico. The fossil assemblage recovered at this site includes ray-finned fishes as the predominant element, along with mollusk shells, plants, microfossils, and ichnofossils. To date, no cartilaginous fish remains have been recovered at this site. The fishes identified here include *Teichthys brevipina*, *Notogogus novomundi*, indeterminate specimens of the family Pycnodontidae, and the genera *Belenostomus* and *Thorectichthys*. The Sumidero Quarry is the second fossil locality preserving shallow marine fishes of Albian age (113—100.5 Ma) found in Mexico and one of the few in the Americas. Comparisons of the Sumidero ichthyofauna to those of coeval and geographically nearby sites yield contrasting results. The Albian assemblage of the Sumidero shares some genera with that of the middle-late Albian from the Tlayúa Quarry, but it is entirely different from the Muhi Quarry assemblage of the Albian-Cenomanian boundary. Assessing the taxonomic diversity of the Sumidero fossils complements our current understanding of Albian marine fishes within North America and their affinities to other coeval deposits globally, allowing a more complete picture of marine fish diversity trends across the Albian–Cenomanian boundary.

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INTRODUCTION

In 2008, paleontologists of the Instituto de Geología of the Universidad Nacional Autónoma de México (Igl, UNAM) and archaeologists of the Instituto Nacional de Antropología e Historia (INAH) launched a joint research project to identify the geological source of the fossil fishes recovered within the Mayan archeological site of Palenque (Cuevas-García and Alvarado-Ortega, 2009). Since then, this team has explored different sedimentary sequences within Chiapas, southeastern Mexico. So far, the achievements have been extraordinary; we discovered numerous fossiliferous localities, including the geological origin of the fossils that the ancient Maya incorporated into their ritual acts, offerings, and architectural structures, as well as numerous new fossil fish species (e.g., Alvarado-Ortega et al., 2015, 2018, 2020; Cantalice and Alvarado-Ortega, 2016; Cantalice et al., 2018, 2020).

The Sumidero Quarry (Figures 1, 2) is one of the fossiliferous sites identified in the aforementioned project. This site is a small outcrop of laminated marly limestones on the outskirts of the San Cristóbal de las Casas town, Chiapas, discovered about 20 years ago and intermittently exploited by the local people. The fossil assemblage found in this site includes marine organisms, mainly bony fishes and invertebrates. Here, such fossils overlie the interstratification planes of the extractable limestones of the small ledges or steps present along the gorge at the southeastern limit of San Cristóbal de las Casas, on the northern edge of the rugged hills known as the El Gavilán. We report the dis-

covery of this new site, providing a general description of its geology and an overview of its ichthyofauna, which includes Ophidiformes, Macrosemiformes, Pycnodontiformes, Aspidorhynchiformes, and Ellimmichthyiformes.

The Sumidero Quarry is on the southwestern border of the town of San Cristóbal de las Casas, Chiapas, southeastern Mexico, at the coordinates 16°42'33.90" N and 92°39'9.60" W (Figure 1). The limestone sequence exposed in this small commercial quarry belongs to the Sierra Madre Group. Here, the locals often extract beige-to-brown slabs of thin, laminar, and parallel marly limestones used to make floors or wall coverings. Massive yellowish limestone strata bound these thin, marly layers. The Sierra Madre Group is a Cretaceous (Aptian-Santonian) marine carbonate succession of at least 2575 m thickness, present in the central and western parts of the State of Chiapas, as well as in the north of Guatemala and the east of Belize (Steele, 1986; Waite, 1986). According to Salas (1949), in 1929, Nuttall W.L.F. identified this sequence in an unpublished work about the stratigraphy of southeastern Mexico, which he named the Sierra Madre Limestones. Subsequently, these were recognized as a tripartite Group involving the Albian-Cenomanian Cantelhá Formation plus the Turonian-Santonian Jolpabuchil and Cintalapa Formations (see Quezada-Muñetón, 1987). Steele (1986) and Waite (1986) studied the Sierra Madre limestones through 21 and 11 levels (named by them as units), respectively, concluding that units 1–2 are of Albian age, while the upper units are Cenomanian-Santonian. Recently, Eguiluz de

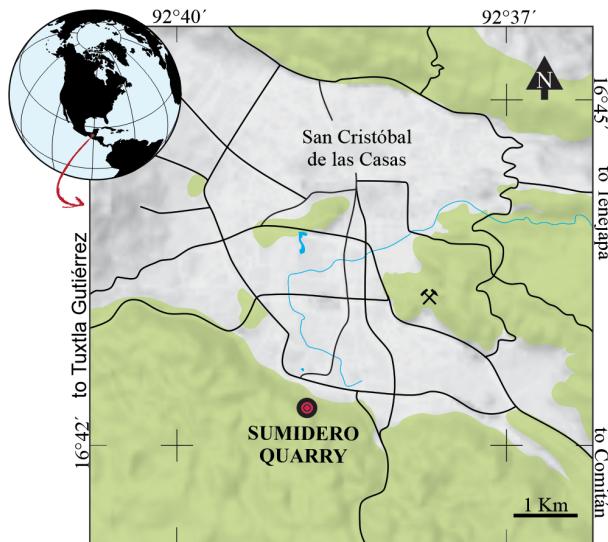


FIGURE 1. Map of the Sumidero Quarry showing the outcrops of the Sierra Madre Group outside Cristóbal de las Casas, Chiapas (based on Alvarado-Ortega and Than-Marchese 2012, fig. 1).

Antuñano et al. (2023) suggested the separation of this group into three sequences: the Albian Cantelhá Sucession, the Cenomanian El Chango Sucession, and the Turonian-Santonian Cintalapa Sucession.

The preliminary review of the petrology and microfossils of the Sumidero Quarry fossiliferous strata reveals that these are of the Albian age and represent part of the Cantelhá Succession of the Sierra Madre limestones. These packstone strata have abundant miliolids (Figure 3), though also contain ostracods, pellets, small gastropods, and a diverse benthonic foraminiferal assemblage that includes specimens attributable to the following taxa: Anomalidae; *Globorotalites* Brotzen, 1942; *Nezzazata* Omara, 1956; *Nummoloculina* Steinmann, 1881; *Quinqueloculina* d'Orbigny, 1826; *Spiroloculina* d'Orbigny, 1826; *Spiroplectammina* Cushman, 1926; *Textularia* Defrance, 1924; *Triloculina* d'Orbigny, 1826; *Valvulammina* Cushman, 1933; and *Valvulinaria* Cushman, 1926.

Similar lithology and microfossil content are present in Unit 2, documented by Steele (1986, p. 25) and Waite (1986, chert of biostratigraphic zones, p. 40–141), as well as in the Cantelhá Formation (e.g., Castro-Mora et al., 1975; Eguiluz de Antuñano et al., 2023). Such lithology and microfossil assemblage suggest that the fossiliferous strata of the Sumidero Quarry were deposited in a shallow marine environment, within a euphotic zone with moderate to high energy, in an open



FIGURE 2. A view of the Sumidero Quarry, San Cristóbal de las Casas, Chiapas.

marine platform or an open lagoon (Quezada-Muñetón, 1987; Eguiluz de Antuñano et al., 2023).

MATERIALS AND METHODS

Preparation methods. Fossils were prepared mechanically with needles and dental excavators under a stereoscopic microscope. When necessary, the fossils were glued with cyanoacrylate and hardened with a weak solution of plexigum and methacrylate acetate applied with a fine brush. The specimen IGM 14038 is an impression; therefore, we prepared the fossils using the resin-transference and cleaning procedures with acetic acid, as described by Toombs and Rixon (1959). We studied all the specimens under the naked eye, stereomicroscope, and high-resolution photographs obtained under white light and UV light, with the specimens non-coated and coated with magnesium.

Institutional abbreviations. All the fossils reported in this work are deposited and cataloged into Colección Nacional de Paleontología, housed in the Instituto de Geología of the Universidad Nacional Autónoma de México, cataloged under the acronym IGLM. Microfossils illustrated here form part of three sedimentological thin sections of the Sumidero Quarry catalogued with the acronym IGM-mi.

Anatomical nomenclature and abbreviations. The taxonomical descriptions of the fossils studied here follow the anatomical nomenclature and

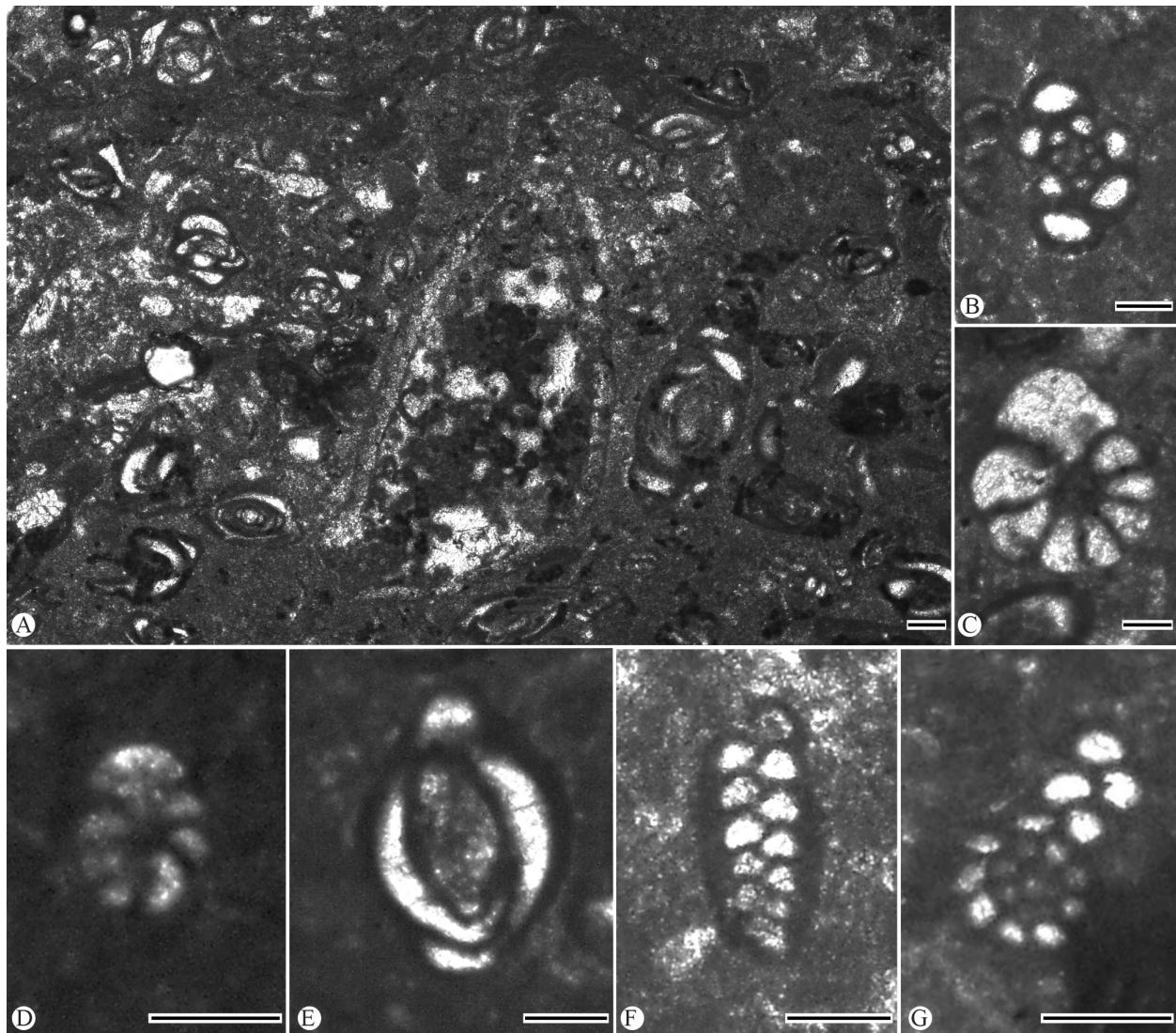


FIGURE 3. Thin-section and some microfossils of the fossiliferous miliolid mudstone from the Sumidero Quarry, San Cristóbal de las Casas, Chiapas. A) General view of IGML-525-Mi. B) *Quinqueloculina* sp., in IGML-526-Mi. C) *Nezazata* sp., IGML-526-Mi. D) *Globorotalites* sp., in IGML-526-Mi. E) *Triloculina* sp. in IGML-528-Mi. F) *Pseudobolivina* sp., in IGML-525-Mi. G) *Spiroplectammina* sp., in IGML-527-Mi. All scales bars equal to 100µm.

abbreviations used in the publications cited in the Systematic Paleontology section.

SYSTEMATIC PALEONTOLOGY

Subclass ACTINOPTERYGII Cope, 1887

Order OPHIOPSIFORMES Ebert, 2018

Family OPHIOPSIELLIDAE Ebert, 2018

Genus *TEOICHTHYS* Applegate, 1988

TEOICHTHYS BREVIPINA Machado, Alvarado-Ortega, Machado, and Brito, 2013.

Specimen referred. IGM 14037, an incomplete specimen showing the left side of the head well preserved and the anterior part of the trunk some-

what twisted, with a partial length of approximately 51 mm (Figure 4).

Occurrence. Albian marine deposits of the Cantelhá Formation exposed in the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico.

Description. The head is triangular and elongated; its length up to the posterior opercular edge is nearly 18 mm, and its maximum height at the nape is 11 mm. The skull represents three-quarters of the head length; the postorbital region is short and extends in the posterior third of the skull length, while the ethmoid and orbital areas are similar and occupy the remaining two-thirds. The mandibular

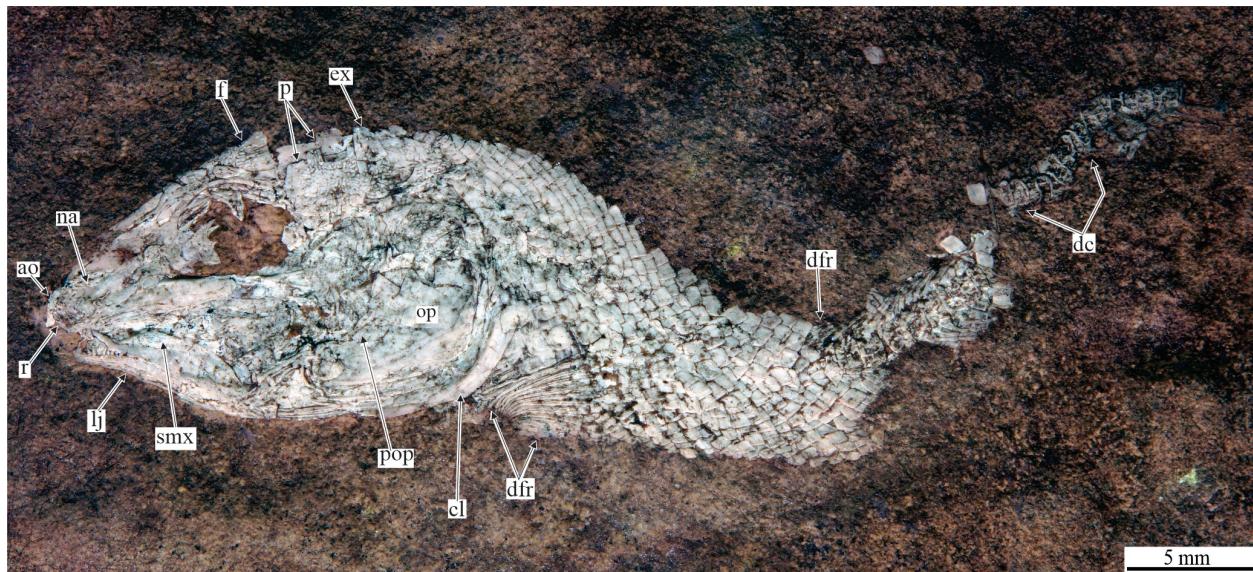


FIGURE 4. IGM 14037 under UV light, *Teoichthys brevipina* from the Albian deposits of the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, Mexico. Abbreviations: ao, antorbital; cl, cleithrum; dc, diplospondylus centrum; dfr, dorsal fin ray; ex, extrascapular; f, frontal; lj, lower jaw; na, nasal; op, opercle; pa, parietal; pfr, pectoral fin ray; pop, preopercle; r, rostral; smx, supramaxilla.

joint is below the anterior third of the orbit. The rostral bone is roughly V-shaped in the ethmoid region and carries the anterior sensory commissure. The oblong nasal bone is expanded and slightly longer than wide.

In the skull, the frontal, parietal, dermosphenotic, and dermopterotic bones are sutured firmly to each other. Above, below, and behind the orbit, these and other bones are ornamented intensely with irregular tubercles and ridges of ganoine that reach the dorsal opercle tip and pectoral girdle bones. Notably, the parietals are rectangular, elongated, narrow, have a deep sinuous interparietal suture, and cover practically the entire postorbital skull region. Below the parietal, the small dermosphenotic bone forms the posterior orbital border. Posteriorly, the narrow dermopterotic bone is as long as the respective parietal. A large triangular extrascapular bone covers the occiput.

The circumorbital series is composed of at least three supraorbital bones, the dermosphenotic sutured to the skull, a mass of numerous suborbital bones covering most of the cheek, at least one high and smooth infraorbital, and an acicular antorbital extending to the rostral. The upper jaw involves a small triangular premaxilla, an elongated triangular maxilla with a long and straight anterodorsal projection, a notched posterior edge, and a single long supramaxilla. The triangular lower jaw shows a shallow and long alveolar part. The jaw

teeth are conical, broad-based, shallow, and acute-ended.

The opercular series includes four laminar bones; the opercle is kidney-shaped and higher than long; the preopercle is very narrow and crescent-shaped; the subopercle is elongated and semicircular; and the infraopercle is a small triangular bone. IGM 14037 has at least eight elongated and thin branchiostegal rays.

The vertebral column is incomplete; however, it is notable that the exposed centra are well ossified and laterally perforated by a pair of elongated cavities, and possibly, those behind the dorsal fin are diplospondylous. The pectoral girdle has a narrow, crescent-shaped cleithrum, a high oblong supracleithrum, and a triangular posttemporal. At least two large postcleithra are present. The pectoral fin is triangular, arises in the ventral edge of the trunk, involves nearly 23 rays, and covers a little less than the anterior half of the predorsal length of the trunk.

IGM 14037 only preserves the anterior 11 rays of the dorsal fin, far from the head. The predorsal distance of the trunk is slightly less than the length of the head; there are 19 scale rows before this fin, and this distance is at least twice the length of the pectoral fin. Thick rhomboid ganoine scales cover the trunk. These scales are smooth and not serrated. The scales are higher than long behind the head; however, these are square-shaped in the rest of the body.

Remarks. *Teoichthys* is an Albian Mexican representative of the order Ophiopsiformes, a clade of marine halecomorph fishes erected by Ebert (2018), which includes the Sinemurian (Middle Triassic)-Cenomanian (Middle Cretaceous) relatives of *Ophiopsis* Agassiz, 1834a. These fish represent 14 or 15 genera from Europe, America, Africa, and the Middle East (Ebert, 2019, 2020, 2021; Taverne, 2014; Taverne and Capasso, 2017). Among the diagnostic features of the order, the most easily observable include the presence of massive ganoine scales covering the trunk, the dermosphenotic incorporated into the skull, the maxilla notched posteriorly, narrow crescent-shaped preopercle, and the roughly V-shaped rostral bone with lateral horns carrying the anterior sensory commissure. IGM 14037 is an undoubted member of this order because it presents all these features.

The family Ophiopsiellidae, established by Ebert (2018), is the most derived clade within the Ophiopsiformes. This family includes Middle Triassic-Late Jurassic species of *Ophiopsiella* Lane and Ebert, 2015, from Europe and Africa, initially classified under the genus *Ophiopsis*. It also encompasses Aptian-Cenomanian species related to *Ophiopsiella* from America, Africa, and the Middle East. The diagnostic features of this family present in IGM 14037 include the presence of one extrascapular on each side of the body and vertebral centra solid, perichordally ossified, and diplospondylous in the posterior part of the trunk.

Among ophiopsiellids, *Ophiopsiella* shows putative primitive features, such as the presence of

ganoine rhomboidal scales equally longer than wide and serrated caudally; dorsal fin single, relatively small, and rising in the anterior half of the standard length (SL); skull bones unornamented; and cheek covered with scarce suborbital bones. Other ophiopsiellids show alternative conditions of these features (Table 1).

While the scales on *Macrepistius* and *Agoultichthys* are generally higher than they are long (Schaeffer, 1960; Murray and Wilson, 2009), those on *Petalopterix*, *Teoichthys*, and *Placidichthys* are higher than long at least in the predorsal trunk region (Pictet, 1850; Applegate, 1988; Brito, 2000; Brito and Alvarado-Ortega, 2008; Machado et al. 2013). Ophiopsiellids have scales with serrated posterior edges, with the exception of *Teoichthys brevipina*, which has scales that are not serrated. *Teoichthys kallistos* is an ophiopsiellid with a long and undivided dorsal fin (Applegate, 1988); however, in its sister species, *T. brevipina*, this is short and rises far from the head, at the beginning of the posterior half of the SL. In other ophiopsiellids (*Petalopterix*, *Placidichthys*, and *Agoultichthys*), the long dorsal fin occupies a large part of the anterior half of the SL and consists of two lobes. In *Macrepistius*, the dorsal fin is incomplete, but it is probably like in *T. kallistos*. Additionally, *Teoichthys* show two outstanding diagnostic features, including numerous ganoine tubercles and irregular ridges ornamenting the posterodorsal part of the skull and numerous small suborbitals covering the cheek. Other ophiopsiellids have an unornamented skull and scarce larger suborbitals, like those of *Ophiop-*

TABLE 1. Comparison of generic features of Ophiopsiformes (based on data published by Pictet, 1850; Schaeffer, 1960; Applegate, 1988; Lane and Ebert, 2015; Murray and Wilson, 2009; Brito, 2000; and Brito and Alvarado-Ortega, 2008). Abbreviations: DFB, dorsal fin base as the percentage of the standard length; PDL, predorsal length as the percentage of standard length. Tb, *Teoichthys brevipina*; Tk, *Teoichthys kallistos*.

	<i>Teoichthys</i>	<i>Macrepistius</i>	<i>Ophiopsiella</i>	<i>Petalopterix</i>	<i>Agoultichthys</i>	<i>Placidichthys</i>
Skull ornaments	Weak-intensely ornamented	Intensely ornamented	Weak ornamented	Weak ornamented	Weak ornamented	?
Suborbitals	Small, numerous, and from a mosaic.	Scarce	Scarce	?	?	?
Dorsal fin	Short-long. Undivided. DFL = 53 (Tk), 22 (Tb). PDL= 33 (Tk), 50.4–52.7 (Tb).	Long. Divided?. ?. ?	Short, Undivided. DFL=33. PDL= 44-52.	Long. Divided. DFL≈ 49. PDL≈ 38.	Long. Divided. DFL= 49. PDL≈ 35.	Long. Divided. DFL=45-58. PDL= 33-36.7.
Scales	Anteriors are higher than long, and others are nearly as high as long. Serrated in Tk, unserrated in Tb.	Mostly higher than long and serrated.	All are nearly as high as long and serrated.	Anteriors are higher than long, and others are as high as long. Serrated.	All higher than long and not serrated.	All are higher than long and serrated. <i>P. tucanensis</i> ?

siella. Here, we identify IGM 14037 as *Teoichthys* because it shares this genus's aforementioned features.

The genus *Teoichthys* includes two species—*T. kallistos* and *T. brevipina*—described with specimens from the Albian marine deposits of Tlayúa Quarry (Applegate, 1988; Machado et al., 2013). As noted above, the dorsal fin is long in the first, whereas this fin is noticeably shorter in the last. Additionally, *T. brevipina* has a condition that differs from the other ophiopsiellids; its dorsal fin is far from the head, rises slightly behind the 50% of the SL after 23 scale rows, and its predorsal distance in the trunk is somewhat longer than the head length and at least two times the pectoral fin length (Machado et al., 2013, figure 1A). In other ophiopsiellids, regardless of whether this fin is long or short, it originates more anteriorly between the head and the middle of the SL. Notably, in *T. kallistos*, this fin increases by about 37% of the S.L. at a distance 1.4 times greater than the head length. Although the dorsal fin of IGM 14037 is incomplete, this specimen is identified as *T. brevipinna* because its dorsal fin arises far from the head, at a point on the body that at least doubles the length of the head and the pectoral fin length, and behind 19 lines of scales. Finally, although the skull ornamentation of IGM 14037 resembles the holotype of *T. kallistos* (IGM 3460), we dismiss its possible diagnostic value because this seems to be a widely variable feature in the type series of *T. brevipinna* (IGM 6741-IGM 6747, and IGM 6604), in which the skull is practically smooth in some specimens and exhibits more conspicuous ornamentation in others.

Order MACROSEMIFORMES Grande, 2010

Family MACROSEMIIDAE Thiolière 1858

Genus *NOTAGOGUS* Agassiz, 1833

Notagogus novomundi González-Rodríguez and Reynoso, 2004

Specimen referred. IGM 14038, a complete specimen with an SL of about 78.5 mm and a somewhat twisted specimen transferred to resin, exposing the skull dorsal surface and the trunk left-dorsal surface (Figure 5).

Occurrence. Albian marine deposits of the Candelhá Formation exposed in the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico.

Description. Given the preservation of this specimen, it is impossible to describe its body shape; however, it seems to be somewhat elongated, with the trunk covered by rhomboid scales. Its elongated head occupies about 30% of SL. The pecto-

ral fin is broad, rounded, and probably restricted to the predorsal trunk region. A pair of possible rounded dorsal fins separated by a small hiatus occupy about 49% of the SL, between 38.5 and 84% of this length. The caudal peduncle is relatively high, and the caudal fin consists of 14 rays.

The rostral is a small acicular bone projected laterally in the skull ethmoid region. The nasal is a flat, smooth, drop-shaped bone covering most of this ethmoid region. The frontal bone is an elongated triangular bone that occupies nearly 80% of the skull length. This bone is smooth and has a straight interfrontal suture in its preorbital part. In contrast, the postorbital region shows sinuous sutures and tiny superficial ridges. Each frontal posteriorly joins a rectangular parietal with ornaments like the frontal. In the specimen, the skull bones are largely disarticulated and covered, making it difficult to describe.

The opercular series seems to be reduced to three bones because the interopercle is not discernible. The opercle is a broad and kidney-shaped bone superficially ornamented with tiny ridges. Below, the subopercle is an elongated ventrally-curving bone ornamented like the opercle. The preopercle is narrow and crescent-shaped, with large pores as openings of the preopercular-mandibular sensory canal. The circumorbital series is not well preserved; however, it is possible to recognize that the upper half of the orbit shows a mosaic of small supraorbital bones arranged in at least two rows. The dermosphenotic is crescent-shaped and sutured to the skull. The circumorbitals preserved below and behind the orbit are tiny scroll-like structures with no laminar component.

The jaw bones are not well-preserved. Nonetheless, the supramaxilla appears to be absent; the premaxilla is small and triangular; and the maxilla is elongated, posteriorly expanded, and bears a longitudinal maxillary sensory canal laterally exposed. The mandibular joint is below the middle of the orbit. The upper and lower jaws show robust and sharp conical teeth fragments.

Bones of the axial skeleton are mostly covered by the scales; however, some partially exposed vertebrae along the body show that probably all of them, including those of the caudal skeleton, are well ossified, at least perichordally. In the pectoral girdle, the cleithrum is narrow and inverted-C shaped in lateral view, and posteriorly, it has at least three large-scale-like postcleithra. At the dorsal end of the pectoral girdle, the posttemporal bone is triangular, expanded ventrally, with rounded edges, and ornamented with reticular

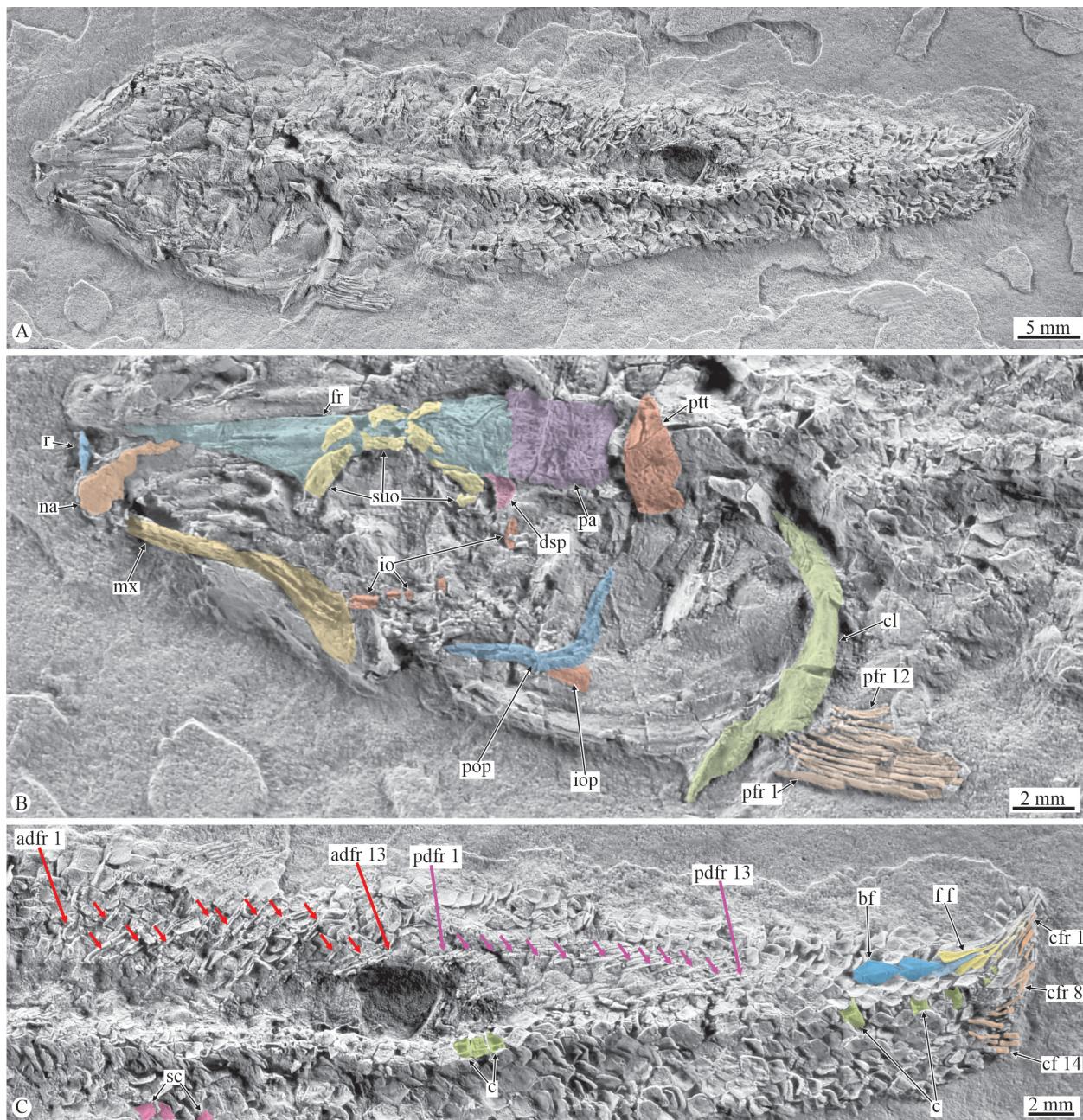


FIGURE 5. IGM 14038 transferred to resin and coated with magnesium, *Notagogus novomundi* from the Albian deposits of the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, Mexico. Abbreviations: adfr 1-13, anterior-dorsal fin rays; bf, basal fulcra; c, centrum (ossified); cfr 1-14, caudal fin rays; cl, cleithrum; dsp, demosphenoctic; ff, fringing fulcra; io, infraorbital; iop, infraopercle; mx, maxilla; na, nasal; pa, parietal; pdfr 1-13, posterior-dorsal fin rays; pfr 1-12, pectoral fin ray; pop, preopercle; ptt, posttemporal; r, rostral; sc, scutes; suo, supraorbital; red arrows show the rays of the anterior dorsal fin; violet arrows show the rays of the posterior dorsal fin.

ridges. The pectoral fin consists of 12 rays with no preceding fulcra. The anal and pelvic fins are not exposed. Two dorsal fins divided by a small hiatus occupy most of the trunk length; these are similarly sized and have 13 rays each. The caudal fin is bent and rests below the body; however, its base

reveals that it consists of 14 rays dorsally preceded by at least three large basal and six fringing fulcra.

Rhomboid scales cover the whole trunk. These scales are evenly sized, have peg-and-socket joints, and are finely serrated along the posterior edges (observed in well-preserved scales).

These lack or have a weak ganoine layer that exhibits the growth rings. The scales do not carry the lateral line.

Remarks. Macrosemiidae Thiolière, 1858 (=Macrosemiiformes, Grande (2010, p. 860), but see López-Arbarello (2019)) is an extinct clade of ginglymodian fishes that includes 8–10 marine genera of Norian (Late Triassic)–Cenomanian (Late Cretaceous) deposits of Europe, northwestern Africa, and southern North America (Mexico). According to different authors, the members of this group share some diagnostic features; these are long-dorsal fin fishes with small interopercle located far from the mandible, pectoral fin with no fulcra, and nine scroll-like infraorbitals bones with two placed behind the orbit (e.g., Bartram 1977; González-Rodríguez and Reynoso, 2004; Arratia and Schultze, 2012). IGM 14038 is identified as an unmistakable member of this group because it exhibits all these features. Although it does not preserve all the infraorbitals, those present are scroll-like behind and below the orbit (Figure 5).

Among macrosemiiforms, only *Notagogus* Agassiz, 1833, has the following distinctive diagnostic features: scales cover the whole of the trunk; a short hiatus separates two dorsal fins; and all centra are perichordally well ossified (Bartram, 1977; Saint-Seine, 1949, figure 86). Other macrosemiiforms have a scale-less area below the dorsal fin, one long dorsal fin or two dorsal fins separated by a comparative long inter-dorsal hiatus. In the vertebral column, only the most anterior centra show poor ossification. In addition, according to González-Rodríguez and Reynoso (2004), the monophyly of *Notagogus* is supported by three synapomorphies, including the medium depth of the body, infraorbitals without laminar component and a reduced ganoine layer in the scales. Here again, we identified IGM 14038 as part of *Notagogus* because it shows all the distinctive and synapomorphic features, except for that referred to the body shape, which is undefinable in this specimen.

Among macrosemiiform, *Notagogus* is the most diverse genus and includes eight nominal species, seven from European Late Jurassic sites and one from the Albian limestones of the Tlayúa Quarry, Mexico (e.g., Bartram, 1977; Bravi, 1994). Although it is a homoplastic feature, González-Rodríguez and Reynoso (2004) discovered that the presence of a mosaic of small supraorbital bones ordered in two rows is present in only three *Notagogus* species, including their *N. novomundi* from the Tlayúa Quarry, *N. heleneae* (Thiolière 1850) from Cerin, France, and *N. pentlandi* Agassiz,

1834b, from the Albian deposits of Torre d'Orlando, Italy. This character is also in *Macrosemiocotzus americanus* González-Rodríguez, Applegate, and Espinosa-Arrubarrena (2004) from Tlayúa Quarry. IGM 14038 is identified here as *N. novomundi* because its anterior and posterior dorsal fins have 13 rays each, and its maxilla shows an open sensory canal along the maxilla. In contrast, *N. heleneae* and *N. pentlandi* have no exposed sensory canal in the maxilla, and their anterior and posterior dorsal fins have 15+10-12 and 14+10 rays, respectively (Bartram, 1977).

Order PYCNOTIFORMES Berg, 1937

Family PYCNOTIDAE Agassiz, 1833 sensu
Nursall 1996a

Indeterminate genus and species

Specimen referred. IGM 14039, an incomplete specimen with 55 mm partial length, exposing the left side of the body, lacking the snout, jaws, and unpaired fins (Figure 6).

Occurrence. Albian marine deposits of the Cantelhá Formation exposed in the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico.

Description. IGM 14039 preserves almost the entire trunk and perhaps only lacks the arcocentra of the caudal peduncle. The preserved trunk suggests the specimen is a nearly round-bodied fish, slightly longer than high (body depth ratio 55/50 mm). Here, the insertion point of the pelvic fin is in the middle of the trunk, opposing the end of the first third of the dorsal fin base. The cloacal notch is equidistant between the bases of the anal and pelvic fins. The positions of the dorsal and anal pterygiophores reveal that the long dorsal fin extends in the posterior trunk half, and the short anal fin opposes the posterior half of the dorsal fin.

On the skull roof, the dermosupraoccipital rotated in its position and now shows its ventral surface. The left preopercle and the right parietal and opercle are displaced upwards, so the supraoccipital exposes its laminar dorsal process. In this part of the skull, the sutures between the frontal, parietal, dermopterotic, and dermosphenotic bones are intensely zigzagging. The parietal is an X-shaped bone with wide arms; the anterior limb sutures the frontal; the dorsal and ventral ones reach the dermosupraoccipital and dermopterotic, respectively; and the posterior one represents the posterior parietal process that is distally branched. The parietal and dermosupraoccipital have confluent notches that form the posterior part of the temporal fenestra, which must have been closed by

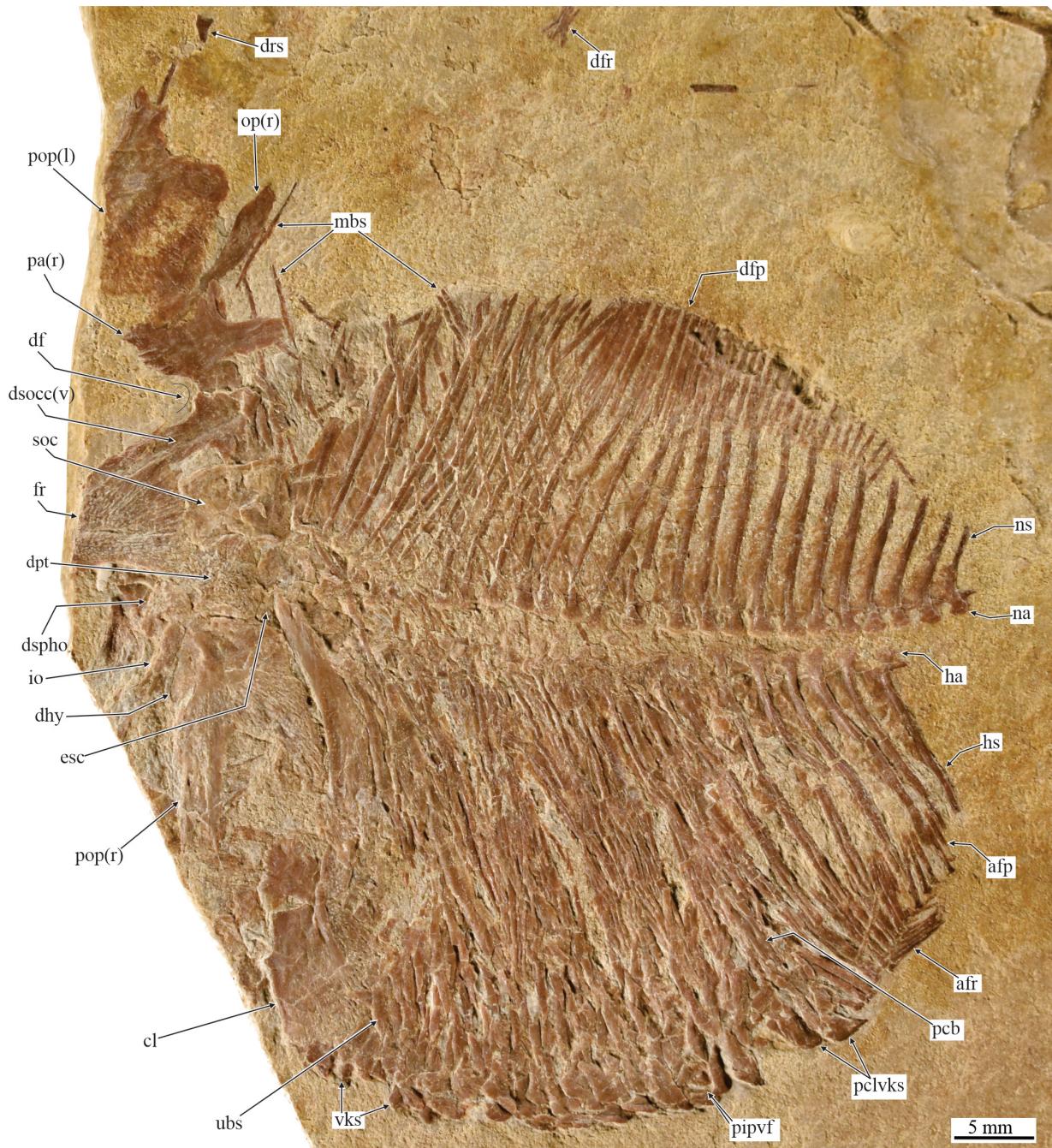


FIGURE 6. IGM 14039 under white light, indeterminate fish of the family Pycnodontidae, from the Albian deposits of the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, Mexico. Abbreviations: afp, anal fin pterygiophor; afr, anal fin ray; cl, cleithrum; df, dermocranial fenestra; dfp, dorsal fin pterygiophore; dfr, dorsal fin ray; dhy, dermalhyomandibula; dpt, dermopterotic; drs, dorsal ridge scute; dsoc, dermosupraoccipital; dsph, dermosphenotic; esc, extrascapular; fr, frontal; ha, hemal arcocentrum; hs, hemal spine; io, infraorbital; mbs, modified bar-like scale; na, neural arcocentrum; ns, neural spine; op, opercle; pa, parietal; pcb, postcoelomic bone; pcl, postcleithrum; pclvks, postcloacal ventral keel scute; pipvf, point of insertion of the pelvic fin; pop, preopercle; soc, supraoccipital; ubs, unmodified broad scale; vks, ventral keel scute; (l), paired element of the left side; (r), paired element of the right side; (v), ventral view.

the frontal. The dermopterotic is rectangular, occupies most of the postorbital skull region, and posteriorly sutures with a small extrascapular. All these bones are strongly ornamented with anastomosed reticulated ridges and numerous pores, which have a radial order from the central part of each bone. The dermosphenotic and the contiguous infraorbital are preserved and poorly ornamented.

Dermohyomandibular and preopercle occupy most of the cheek. The first is an elongated rectangular bone scarcely ornamented in the posterior part and ending on an elongated and curved dorsal articular head. The preopercle is rectangular, as long as the dermohyomandibular but at least three times higher, strongly ornamented like the skull bones, and bears a stout and long anterodorsal process. The opercle is a long bone, concave anteriorly, and expanded ventrally. The subopercle and infraopercle are not present.

The vertebral column consists of at least 26 pairs of arcocentra, including 14 abdominals and at least 12 caudals, which do not invade the notochordal canal that remains empty from the central arch 5. Anteriorly, the synarcual occupies this space. All neural and hemal arches are laterally triangular, small, autogenous, and show a broad notochordal border. The contact between adjacent arcocentra is simple through their pre- and postzygapophyses, which are short spine-like structures that are projected longitudinally and similar in shape and size throughout the trunk. All the neural and caudal-hemal arcocentra have long spines with anterior sagittal flanges or triangular laminar wings that rise from the prezygapophyses and border most of the anterior edge of each spine. An indeterminate number of ribs articulate with the abdominal-hemal arcocentra. These ribs are long, slightly curved, and possess wing-like structures from the head of the element.

All the fins are not preserved except for parts of their internal supports. In the pectoral girdle, the cleithrum is a short and high crescent bone, anteriorly concave and located between the ventral edge of the body and the vertebral column. Additionally, the cleithrum is dorsally acute, ventrally expanded, and with its ventral third surface strongly ornamented with ridges and pores. The point of insertion of the pelvic fin is present between scales just above the abdominal edge. The dorsal fin is wholly disarticulated and separated from the trunk; only a few scattered remains of dorsal rays are near the fossil. The fossil preserves eight rays of the anal fin. There are 34 dorsal pterygiophores extended in the posterior half of the dorsal body edge, while

only 20 anal pterygiophores are present in the posterior third of the ventral body edge. In both series, the pterygiophores are long, straight, and flat.

In this fish, the scale pattern is peltate. The trunk has no scales in the caudal region between the unpaired fins. In contrast, two types of scales cover only the most anterior part of the trunk. The predorsal trunk region shows 12 or 13 rows of modified bar-like scales, each row with three to six scales, anterodorsally tilted and overlay the neural spines. Broad and imbricate scales cover the abdominal trunk region and form 18 to 20 scale rows.

Although in life, this fish must have had a complete series of predorsal and preanal bordering scutes, only two dorsal ridge scutes are disarticulated and scattered near the trunk. The dorsal ridge scutes are stout, triangular, and non-serrated. Nineteen ventral keel scutes from a complete series between the isthmus and the anal fin; these scutes include 17 precloacals (the posterior one is behind the pelvic fin) and two postcloacals. The ventral keel scutes are triangular and ventrally thick, have blunt ends contacting the adjacent scutes, and show tiny, thin lateral wings. These scutes are unserrated, except for the postpelvic and both postcloacals, which have four or five medial spines, uniformly small and evenly spaced. Small, unmodified scales border the cloacal vestibule. The posterior postcloacal scute and last abdominal scales cover most of the postcoelomic; however, this is a high triangular bone, laterally flat, smooth, and extends up to the half of the abdominal cavity, far from the vertebral column.

Remarks. Pycnodontiformes is a globally distributed actinopterygian clade with controversial phylogenetic relationships. This Norian (Late Triassic)–Eocene (Paleogene) clade includes *Pycnodus* Agassiz, 1833, and relatives (Berg, 1937; Nursall, 1996b; Blot, 1987). These highly specialized, primarily marine fishes also had repetitive invasions in freshwater environments (Szabó et al., 2016; Cawley and Kriwet, 2024).

Early phylogenetic studies of Pycnodontiformes identified the features that support this order and its subordinal clades (Nursall, 1996a; Poyato-Ariza and Wenz, 2002). Among the multiple diagnostic features of this order listed by these authors, IGM 14039 shows a high and rounded body that is compressed laterally, the notochordal canal empty because the vertebrae are not ossified, and only ventral and hemal arcocentra occupy this part of the skeletal axis. The skull roof shows a single dermosupraoccipital. The subopercle and

interoperculum are missing. The opercle is crescent-shaped and small, and the preopercle is extremely large. The ribs are winged. Finally, the fish has a dorsal ridge and ventral keel scutes bordering its predorsal and preanal trunk regions.

Within Pycnodontiformes, the family Pycnodontidae is strongly supported by several diagnostic features (Payato-Ariza and Wenz, 2002). IGM 14039 is identified as part of this family because it shows the following diagnostic features: the posterior parietal process and dermohyomandibular are present; the scales of the predorsal trunk region are bar-like, and there are six or fewer postcloacal keel scutes.

Pycnodontidae is the most successful pycnodontiform clade. This family contains about 80 species representing 40 genera, and its classification still faces problems. In the latest phylogenetic analyses including this family, the existence of the contrasting traits of three subfamilies has been confirmed, including Pycnodontinae, Nursallinae, and Turboscinetinae (e.g., Nursall, 1996a; Ebert, 2016). It is worth noting three issues: 1) the monophyly of Pycnodontinae has recently been questioned because its members seem to represent different stem taxa located at the base of the nursallines (now reclassified as tribe Nursallini); 2) Turboscinetinae includes the members of Proscinetinae (now re-ranked as the tribe as Proscinetini); and 3) Ebert (2016) recognized his Group B as a monophyletic clade containing the members of the subfamily Pycnodontinae (see, Payato-Ariza and Wenz, 2002; Payato-Ariza, 2020; Ebert, 2016; Taverne and Capasso, 2018). In this scenario, considering only four features of GM 14039, including the presence of the dermocranial fenestra, the peltate scale pattern, the posterior part of the postorbital skull region well ossified, and the lack of free dorsal pterygiophores allow us to

identify it as a non-pycnodontine pycnodontid fish belonging to the Group B (Table 2).

Group B members and IGM 14039 have dermocranial fenestra, but this cavity does not occur in Turboscinetinae and Nursallinae. Considering the kind of scales (modified bar-like scales and unmodified broad scales) and their distributions in the predorsal, abdominal, and caudal trunk regions, Nursall (1996a, figure 19) recognized distinctive scale patterns in different pycnodontiform groups. The scale pattern of IGM 14039 and Turboscinetinae share a peltate pattern, with bar-like scales on the predorsal region, broad scales covering the abdomen, and the caudal region being nude. Nursallinae members show the imbricated pattern (broad scales cover the whole trunk) and a peculiar scale pattern that here is named peltate-expanded, in which the bar-like scales are on the predorsal and caudal regions of the trunk while broad scales cover the abdomen. Members of Group B show three patterns: non-Pycnodontinae are peltate as in Turboscinetinae, some Pycnodontinae are calthrate (the caudal region is nude, with broad scales covering a small part of the abdomen close to the ventral trunk edge and with bar-like scales covering the rest of the abdomen and all the predorsal trunk region, as in *Pycnodus*). Some Pycnodontinae also show clathrate-reduced morphology, in which the distributions of both kinds of scales are comparatively reduced, the broad scales covering a small area near the abdominal trunk edge, and the bar-like scales are only near the predorsal trunk edge, as in *Pseudopycnodus* Taverne, 1997. Within Group B, Pycnodontinae have reduced bones in the postorbital part of the skull and most of the supraoccipital bone in lateral view; in IGM 14039 and other pycnodontids, these bones are well ossified and cover the supraoccipital bone. Finally, in non-proscinetine members of Turboscinetinae, most anterior dorsal

TABLE 2. Comparison between the subfamilies recognized into the family Pycnodontidae. Character states highlighted in gray are present in IGM 14039. (based on Payato-Ariza and Wenz, 2002; Payato-Ariza, 2020; Ebert, 2016, 2016; Taverne and Capasso, 2018).

Taxa Feature	Turboscinetinae (including Proscinetiniae)	Group B (not ranked) (including Pycnodontinae)	Nursallinae
Dermocranial fenestra	No	Yes	No
Scale pattern	Peltate,	Peltate. Calthrate and clathrate-reduced in Pycnodontinae	Intricate, Peltate-expanded
Posterior skull ossification	Complete	Complete, reduced in Pycnodontinae	Complete
Free dorsal pterygiophores	Absent, present in Proscinetiniae	Absent	Absent

pterygiophores are free or do not meet with any dorsal ray; however, other pycnodontids have no free dorsal pterygiophores. IGM 14039 has no dorsal fin rays; therefore, it is impossible to recognize the presence or absence of the last condition.

Order ASPIDORHYNCHIFORMES Bleeker, 1859

Family ASPIDORHYNCHIDAE Nicholson and

Lydekker, 1889

Genus *BELONOSTOMUS* Agassiz, 1834b

Belenostomus sp.

Specimen referred. IGM 14040, an incomplete serpentiform and longirostrine fish exposed on the right side of the body, in which the head is impressed, and the tail and terminal part of the snout are missing (Figure 7). The length of the specimen is 175 mm.

Occurrence. Albian marine deposits of the Can telhá Formation exposed in the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico.

Description. The body of this fish is bent, with the tips of the snout and caudal region inclined ventrally. The specimen only preserves 175 mm of its total length. On the trunk length, the pelvic bone (= base of the pelvic fin) is at 97 mm, and the anal and dorsal fins (opposed to each other) are far in the back, at 152 mm. The height of the head is 22 mm, the most anterior part of the trunk shows the same size; however, this becomes shallower backward and reaches 12 mm at the base of the anal/dorsal fin (Figure 7).

Overall, the skull is incompletely impressed; however, the orbital and postorbital lengths are

similar. The lower and upper jaws are elongated, almost uniformly high through their length, and have straight alveolar borders. Below the ethmoid region, the part of the lower jaw corresponding to the dentary shows that the alveolar and ventral borders are parallel. The lower jaw articulation is below and near the posterior limit of the orbit.

The impression of the bones of the opercular series and pectoral girdle are imperfect. Here, small parts of the opercle, subopercle, and anterior limb of the cleithrum are present. A fragment of the posttemporal lays horizontally dorsal to the nape. Short, curved, and shallow ganoine ridges ornament these bones. The pectoral fin is trapezoidal, arises in the ventral edge of the body, and consists of 12 short rays, of which the first two are remarkably broad.

At least 53 vertical scale rows entirely cover the preserved part of the trunk, each composed of two dorsal, at least two ventral, and three flank scales. The dorsal flank scales are somewhat hexagonal with rounded edges. The ventral flank scales are rectangular and slightly longer than high. The three flank scales have different shapes; the lower and middle scales show a vertical alignment, and the upper scale is inclined anterodorsally. The lower flank scales are rectangular, slightly higher than long. The middle flank scales are rectangular, 3–4 times higher than long. In each flank scale, the lateral line runs at the base of the upper quarter, which is inflected anteriorly. The upper flank scales are rhomboidal, anteriorly tilted, and about 1.5 times higher than long. The dorsal edges of the scales of dorsal, ventral, and lower

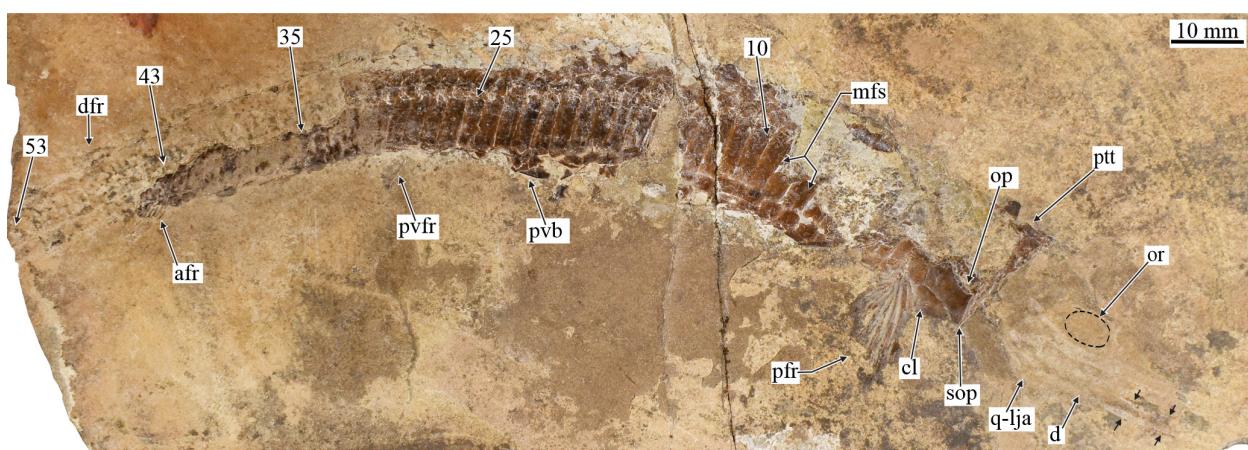


FIGURE 7. IGM 14040 under white light, *Belenostomus* sp. from the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico. Abbreviations: afr, anal fin ray; cl, cleithrum; d, dentary; dfr, dorsal fin ray; mfs, middle flank scale; pfr, pectoral fin ray; ptt, posttemporal, pvb, pelvic fin bone; pvfr, pelvic fin ray (displaced); q-lja, quadrate-lower jaw articulation; numbers show the vertical scale rows; op, opercle; or, orbit; sop, subopercle; black arrows on the head show the impression of the alveolar and ventral edges of the dentary bone.

flank rows have a triangular dorsal process, revealing their peg-and-socket joints. The middle and upper flank scales are poorly imbricated, and their joint is nearly straight. The joint between the upper flank and dorsal scales is unknown in the specimen referred. These scales do not have posterior denticles or serrae. Short, curved, and shallow ganoine ridges cover the surfaces of all these scales, though the ornamentation is more conspicuous in the dorsal members than those on the flanks and ventral portions of the body.

An unknown number of pelvic rays and bones of the pelvic girdle are disarticulated but lie within the posterior half of the abdomen, below the scale rows 21 and 29, respectively. Here, the pelvic bone is rectangular and anteriorly acute, and the impression of the pelvic rays shows that the first one is broad, like that of the pectoral fin. The anal and dorsal fins are placed far in the back of the body, and the anal and dorsal fin are below and above the scale rows 43 and 45, respectively. Given the specimen's poor preservation, the number of dorsal rays is unknown, but the anal fin is composed of at least seven rays.

Remarks. Aspidorhynchiformes (= Aspidorhynchidae) is an extinct single-family order of marine and highly specialized serpentiform fishes with elongated snouts (Van Vranken et al., 2019) that has a global distribution spanning the Middle Jurassic (Bathonian)–Late Paleocene (Thanetian) clade. IGM 14040 is assigned to this family because it shows some of its diagnostic features (Brito, 1997); the body is serpentiform, the anal and dorsal fins are placed far in the back of the body, and there are three longitudinal rows of flank scales.

Currently, Aspidorhynchidae comprises six genera that show noticeable differences in the bones of both jaws, opercular series, and proportions of the flank scales (Brito, 1997; Bartholomai, 2004; Gouiric-Cavalli, 2015, figures 6, 8; Arratia, 2015). In his comprehensive review of Aspidorhynchidae, Brito (1997) amended the diagnoses of *Belonostomus* and *Vinctifer* Jordan, 1919, pointing out that these share the presence of a longitudinal row of high rectangular flank scales (= middle flank scales in this work) that differ noticeably from the less high scales placed above and below. Later, *Jonoichthys* Gouiric-Cavalli, 2015, was revealed to have such flank-scale condition. However, in this Argentinian Late Jurassic fish, the articulation observed between the middle and upper flank scales is deeply curved, whereas, in the first two genera, this articulation is relatively straight.

Vinctifer, *Aspidorhynchus* Agassiz, 1833, and *Richmondichthys* Bartholomai, 2004, have short snout heads. These taxa and *Pseudovinctifer* Arratia, 2015, show a triangular lower mandible, including a small anterior pre dentary and a trapezoidal dentary that tapers anteriorly and is high posteriorly. Consequently, in these four fishes, the alveolar and ventral edges in the posterior part of the lower jaw (mainly formed by the dentary) are inclined to each other. In addition, at least in *Vinctifer* and *Richmondichthys*, the upper jaw consists of a triangular maxilla significantly expanded posteriorly plus a thick, saber-like premaxilla that is elongated, straight, and anteriorly projected far from the lower jaw tip (Brito, 1997, figures 6, 13). On the other hand, *Belonostomus* and *Jonoichthys* have noticeably elongated snouts, in which the alveolar and ventral edges of the lower jaw are parallel, plus an elongated triangular laminar premaxilla. These last two genera and *Aspidorhynchus* have a narrow and elongated maxilla (Brito, 1997, figures 42, 43).

Despite the lack of a preserved tail and anterior tip of the snout, IGM 14040 is identifiable as *Belonostomus*. In its head, the preorbital region has no space to accommodate an expanded bone like the maxilla in *Vinctifer* and *Richmondichthys*. Additionally, as *Belonostomus* and *Jonoichthys*, the proximal part of the lower jaw of this Mexican aspidorhynchid has parallel alveolar and ventral edges, and its middle flank scales are notably highest at their joint with the upper adjacent scales and are straight as in other aspidorhynchids except for *Jonoichthys* (in which these scales have peg-and-socket joints).

Among aspidorhynchids, the *Belonostomus* is the most diverse and widely distributed geographically and temporally. This genus contains at least 15 nominal species from Kimmeridgiano (Late Jurassic)–Thanetian (Late Paleocene) sites of Europe, Northern Africa, North and South America, and Asia (e.g., Taverne and Ross, 1973; Brito, 1997; Bogan et al., 2011; Ebert, 2014). These species differ in pterygial formula, body and scale proportions, ornamentation, and features of jaws, teeth, and skull bones. Given the incomplete preservation, we identify IGM 14040 as an indeterminate species of this genus.

Superorder CLUPEOMORPHA Greenwood et al.,
1966

Order ELLIMMICHTHYIFORMES Grande, 1982

Family UNNAMED

Genus THORECTICHTHYS Murray and Wilson,

2013
Thorectichthys sp.

Specimen referred. IGM 14041, a nearly complete fish, exposed on the left side, with an estimated SL of 58.91 mm, and without the bones in front of the orbit (Figure 8).

Occurrence. Albian marine deposits of the Cantelhá Formation exposed in the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico.

Description. The specimen lacks the anterior part of the head, while its rostral and caudal ends are somewhat curved dorsally; thus, all the following measurements are estimated. It is 79 and 62 mm in total and SL, respectively. Expressed as the percentage of the SL, the head length is 30% (18.6 mm), the predorsal length is 46% (28.8), the prepelvic length is 57% (35.7 mm), and the preanal length is 68.2% (42.3 mm). The height of the head is 33% (20.5 mm), the maximum height of the body is 37.5% (23.3 mm), with the height of the caudal peduncle being 9.6% (6 mm). The dorsal fin is shorter than the anal fin. Their respective lengths are 12.5% (7.8 mm) and 22.9% (15 mm).

Although the head is not well-preserved, it exposes some valuable features. The large parietals are rectangular, and probably both meet at the midline. The orbit is entirely circular; its diameter equals the postocular length of the skull, and two thin, semi-circular sclerotic bones occupy it. The jaw-quadratojugal joint is below the posterior half of

the orbit. The preopercle and subopercle are not well preserved in the opercular series. The interopercle is an oblong and sharp-ended bone. The operculum is a kidney-shaped bone with straight vertical striations ornamenting its ventral part.

The vertebral column involves 35 total centra, including 18 abdominals, 15 caudals, and two urals. There are 16 pairs of long curved ribs enclosing almost the entire abdomen. The eight posterior ribs articulate long parapophyses, and the anterior ones do this directly with the lateroventral cavities of the centra. There are seven predorsal bones. The most anterior neural spines are distally bifid; long epineurals are present along the trunk up to the end of the anal fin; those in the abdominal trunk are long and thread-like, and those behind become shorted and triradiated. On the caudal region, the epipleurals are similar and symmetrically opposed to the epineurals.

The cleithrum is S-shaped in lateral view, with a small descending anterior limb. Sixteen rays form a triangular pectoral fin rising slightly above the ventral trunk edge. The pelvic fin is small, opposed to the posterior half of the dorsal fin, and involves at least six rays. The dorsal fin is relatively short and consists of two procurent and 14 long rays that extend between 46% and 58.5% of the SL. The anal fin is long, opposed to the postdorsal part of the trunk, and consists of two procurent and 25 long anal rays extended between 68.2% and

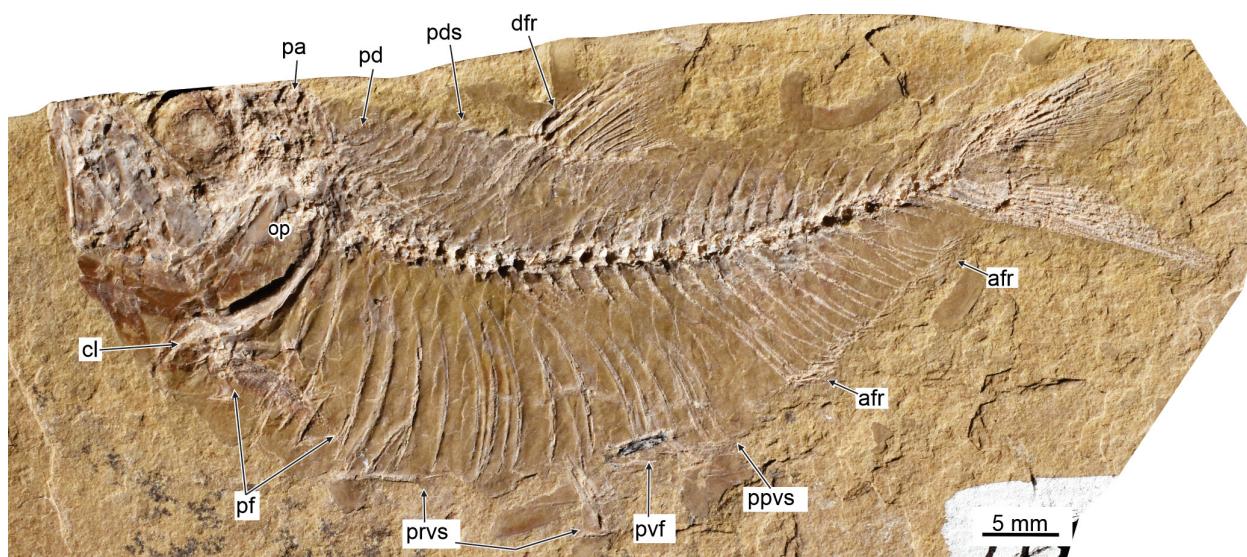


FIGURE 8. IGM 14041 under white light, *Thorectichthys* sp. from the Sumidero Quarry, San Cristóbal de las Casas, Chiapas, southeastern Mexico. Abbreviations: afr, anal fin ray; cl, cleithrum; dfr, dorsal fin ray; op, opercle; pa, parietal; pd, predorsal bones, pds, predorsal scutes; pf, pectoral fin ray; ppvs, postpelvic ventral scutes; prvs, prepelvic ventral scutes; pvf, pelvic fin ray.

91.1% of the SL. The caudal fin is deeply forked and consists of two long triangular lobes symmetrically opposed. Its caudal formula is viii+1+9—8+1+vi.

Oval-shaped cycloid oval scales cover the entire trunk. Numerous concentric sinuous circuli ornament the scales superficially. Thick scutes border the predorsal and preanal trunk edges. Nearly 11 predorsal scutes form a complete series between the occiput and the dorsal fin; these are oval, slightly expanded anterolaterally, and superficially ornamented with straight and parallel shallow ridges. A small middle posterior spine protrudes in the posterior edge of the most posterior predorsal scutes. The abdominal keel of this fish involves a complete series of at least 22 ventral scutes, including about 15 prepelvic and seven postpelvic. These scutes have a thick ventral edge and lateral triangular wings covering the ventral third of the abdomen. In the postpelvic ventral scutes, the medial thick bar is projected posteriorly as a stout spine.

Remarks. Grande (1982, 1985) erected Ellimmichthyiformes to include the putative primitive and extinct clupeomorph fishes resembling *Ellimmichthys* Jordan and Gilbert, 1919. Today, this clade includes nearly 50 nominal species, gathered in 22 genera, recovered in Valanginian (Early Cretaceous)-Eocene (Paleocene) marine and freshwater deposits worldwide. The different phylogenetic hypotheses of Ellimmichthyiformes recently proposed show contradictory details (Alvarado-Ortega et al., 2020). Nevertheless, as with all clupeomorph fish, the trunk of IGM 14041 shows a ventral keel. Additionally, this fossil is identified as part of Ellimmichthyiformes because it shows large parietals that contact one another medially, along with ornamented predorsal scutes expanded anterolaterally and bearing a posterior spine.

Murray and Wilson (2013) erected *Thorectichthys* for *T. marocensis* and *T. rhadinus*, two Moroccan species recovered in the marine Cenomanian-Turonian deposits of the Akrabou Formation. Recently, a North American species of this genus was named *T. fideli* Than-Marchese, Alvarado-Ortega, Murray, Velázquez-Velázquez, and Domínguez Domínguez, 2024, based on nicely preserved specimens from the early Cenomanian deposits of the El Chango Quarry, Chiapas, Mexico. IGM 14041 is identified as *Thorectichthys* because it shows the most conspicuous diagnostic features of the genus: straight longitudinal parallel ridges ornamenting the predorsal scutes.

A brief comparison of *Thorectichthys* species and IGM 14041 reveals some differences in the proportions of the body (see Than-Marchese et al., 2024, tbl. 2). This fossil is the slenderest of *Thorectichthys*, with its maximum body height (= 37.5% of the SL) surpassed by those observed in the three nominal species (= 40–65% of the SL). It is also the only *Thorectichthys* species with a dorsal fin so far on the body (46% of the SL versus 36–44% of the SL in nominal *Thorectichthys* species). Nonetheless, IGM 14041 does not refer to any of these species or a new one simply because its body proportions are estimated.

DISCUSSION

According to Guinot and Cavin (2016), ray-finned fishes experienced the second-largest diversification event in gnathostome evolutionary history during the Cenomanian. At this time, a dramatic taxonomic turnover occurred and led to the establishment of the Late Cretaceous ichthyofauna, which later led to the emergence of the dominant modern groups during the end-Cretaceous and early Cenozoic (Friedman et al., 2023). Among other factors, Guinot and Cavin (2016) also noted that the rise in sea levels and the fragmentation of the continents allowed the development of large epicontinental seas that favored the diversification processes of coastal fishes. Given the importance of such a biological event, considering some new questions to understand this holistically is valid. In this scenario, the review of the diversity of Albian–Cenomanian bony fishes of both marine contours and continental waters is essential to recognizing the possible regional or local components of the Cenomanian Diversification Event of Bony Fishes (CDEBF), as well as the potential effect of the different biological-environmental factors that triggered it.

In recent years, the diversity and paleontological sites of Cretaceous fossil fishes in North America have been reviewed on continental, regional, or local scopes by different authors (e.g., Applegate 1996; Wilson and Bruner, 2004; Alvarado-Ortega et al., 2006; Everhart, 2009; González-Rodríguez et al., 2013a, 2016; Murray and Cook, 2016). Without being copious yet, the accumulated data is beginning to reveal some traits of the CDEBF on the North American subcontinent. With this in mind, and to assess the importance of the Albian ichthyofauna from the Sumidero Quarry, we compiled data on the North American marine bony fishes from the Albian-early Cenomanian, only including nominal species and reliable generic

identifications. This work does not include materials of a more extended temporal range because the fossil fish record from Mexico is deficient between the Kimmeridgian and Early Albian, and the material recovered in two middle Cenomanian sites, El Tanque and La Mula, in the north of Coahuila, near the Mexico-U.S.A. border, lack a strict stratigraphic control within sequences that extend up to the Santonian (Giersch et al., 2008; Giersch, 2014).

Table 3 and Figure 9 summarize the results of our analysis of the North American Albian–early Cenomanian fishes. Our study reveals that North America has only 11 Albian–early Cenomanian localities carrying well-preserved osteichthyans, where the quality of the fossils allows their accurate alpha taxonomic identifications. These well-preserved localities are essential for studying taxonomic diversification processes, as in the case of CDEBF. These localities have a remarkable unbalanced geographic distribution; three of them are in the west and north of Canada; other three are in the central, southeastern, and western regions of the USA, and with the addition of the Sumidero Quarry, the remaining five are in the central and southern portions of Mexico (Figure 9A and B). These sites include:

- 1) **Dragon Mountain**—Middle Albian marine sequence belonging to the Macdougall Point Member of the Christopher Formation, exposed on Dragon Mountain at the western part of Axel Heiberg Island, Nunavut, Canada (see Hermus et al., 2004; Murray and Cook, 2016).
- 2) **Hay River**—Middle-late? Albian marine deposits of the Loon River Formation exposed alongside the Hay River, Northwest Territories, Canada. (Forey, 1975; Wilson and Brunner, 2004; Murray and Cook, 2016; Maxwell and Caldwell, 2006; Vernygora et al., 2016).
- 3) **Kiowa Formation**—Outcrops of the late Albian Champion Shell Bed at the base of the Kiowa Formation, exposed in the vicinity of Belvidere in Kiowa County, as well as in the Kanopolis Reservoir in Ellsworth County, the area around the Clark County State lake in Clark County, and an unreported point in McPherson County, in Kansas, USA (Williston, 1894; Cragin, 1894; Scott, 1970; Schultze and Stewart, 1982; Russell, 1988; Beamon, 1999; Everhart, 2004, 2009, 2011).
- 4) **Glen Rose Formation**—The single valid nominal species as far known in this formation is *Macrepistius arenatus* Cope, 1894, described based on a fragmented specimen recovered in the marine deposits of the middle Albian along the Peluxi River that belong to the lower part of the Glen Rose Formation, near Glen Rose town, Somervell County, Texas. The deposit of this formation occurred in shallow marine conditions on the northern edge of the Paleo-Gulf of Mexico (Martha et al., 2019). Additional unidentified fish remains (a possible clupeiform and a holotean) of this formation are from the area near Granbury town, Hood County, Texas (Schaeffer, 1960).
- 5) **Sumidero Quarry**—Described in this work.
- 6) **Tlayúa Quarry**—Middle-late Albian limestone strata belonging to the Middle Member of the Tlayúa Formation (Pantoja-Alor, 1992), exposed in the Tlayúa Ravine, outside of Tepexi de Rodríguez, Puebla, central Mexico (e.g., Applegate and Espinosa-Arrubarrena, 1982; Applegate et al., 2006; Alvarado-Ortega et al., 2007, 2009; Espinosa-Arrubarrena and Alvarado-Ortega, 2010).
- 7) **Muhi Quarry**—Laminated calcareous sequence of the Albian-Cenomanian boundary belonging to the La Negra Facies of the El Doctor Formation, quarry in the eastern side of the Zimapán, Hidalgo, central Mexico (Bravo-Cuevas et al., 2012; López-Palomino et al., 2021)
- 8) **Smoky River**—According to Wilson and Murray (1996), this site is immediately west of the town of Judah Station, on the east bank of the Smoky River, Alberta, Canada. The site is an outcrop of the Fish Scale Zone of the Albian/Cenomanian boundary, which forms part of the Shaftesbury Formation.
- 9) **El Espinal Quarry**—The locality represents a small group of small artisanal quarries located west of the El Espinal de Morelos, Municipality of Ocozocoautla de Espinosa, Chiapas, southeastern Mexico (e.g., Alvarado-Ortega and Ovalles-Damián, 2008). Initially, the age of these fossiliferous outcrops was thought Albian; however, recent works have confirmed that this belongs to the early Cenomanian sequence of the Cintalapa Formation (Alvarado-Ortega et al., 2009; Alvarado-Ortega and Than-Marchese, 2012, 2013; Moreno-Bedmar et al., 2014; Eguiluz de Antuñano et al., 2023).
- 10) **El Chango Quarry**—Early Cenomanian laminar limestones of the Cintalapa Formation, exposed near the town Pluma de Oro, south

TABLE 3. Paleontological sites and generic/species diversity of North American Albian–early Cenomanian osteichthyan fishes. The abbreviations below the paleontological sites correspond to those in Figure 9.

	Dragon Mtn.	Hay River	Kiowa Fm.	Glen Rose Fm.	Sumidero Q.	Tlayúa Q.	Muhi Q.	Smoky River	EI Espinal Q.	EI Chango Q.	Mowry Fm.	
Abbreviations:	DM	HR	KF	GRF	SQ	TQ	MQ	SR	EQ	CQ	MF	
Albian						Alb-Cen. boundary		Early Cenomanian				
Acanthomorpha												
<i>Choichix alvaradoi</i> Cantalice, Than-Marchese, Villalobos?Segura, 2021.									x			
<i>Dalgoichthys tropicalis</i> González-Rodríguez, Schultze, Arratia, 2013b.							x					
<i>Muñichthys cordobai</i> González-Rodríguez, Fielitz, 2008.							x					
<i>Pepemkay maya</i> Alvarado-Ortega, Than-Marchese, 2013.									x			
<i>Pseudomonocentris microspinosa</i> González-Rodríguez, Schultze, Arratia, 2013b.							x					
<i>Handuichthys interopercularis</i> González-Rodríguez, Schultze, Arratia, 2013b.							x					
<i>Zoqueichthys carolinae</i> Alvarado-Ortega, Than-Marchese, 2012.									x			
<i>Xenyllion stewartia</i> Newbrey, Murray, Wilson, Brinkman, Neuman, 2013.									x			
<i>Xenyllion zenensis</i> Wilson and Murray, 1996.							x					
Amiiformes												
<i>Amblysemius</i> Agassiz, 1832 (see Alvarado-Ortega, 2005),							x					
<i>Pachyamia mexicana</i> Grande, Bemis, 1998.							x					
<i>Quetzalichthys perrilliatae</i> Alvarado-Ortega, Espinosa-Arrubarrena, 2008.							x					
Aspidorhynchiformes												
<i>Belonostomus</i> Agassiz, 1834b (see Applegate, 1996; Brito, 1997; Everhart, 2009).	x x x x											
<i>Vinctifer</i> Jordan, 1919 (see Applegate, 1996; Brito, 1997).							x					
Aulopiformes												
<i>Enchodus zimapanensis</i> Fielitz, González-Rodríguez, 2010.							x					
<i>Ichthyotringa mexicana</i> Fielitz, González-Rodríguez, 2008.							x		x x			
<i>Saurorhamphus</i> Heckel, 1850 (see Alvarado-Ortega et al., 2009).												
<i>Unicachichthys multidentata</i> Díaz-Cruz, Alvarado-Ortega, Carbot-Chanona, 2016.									x			
<i>Vgrandichthys coitecus</i> Díaz-Cruz, Alvarado-Ortega, Giles, 2020.									x			
<i>Veridagon avendanoi</i> Díaz-Cruz, Alvarado-Ortega, Carbot-Chanona, 2019a, b.									x			
Clupeomorpha												
<i>Armigatus</i> Grande, 1982									x			
<i>Armigatus carrenoae</i> Alvarado-Ortega, Than-Marchese, Melgarejo-Damián, 2020.							x					
<i>Armigatus felixi</i> Than-Marchese, Alvarado-Ortega, 2022.							x					

TABLE 3 (continued).

	Dragon Mtn.	Hay River	Kiowa Fm.	Glen Rose Fm.	Sumidero Q.	Tlayúa Q.	Muhi Q.	Smoky River	El Espinal Q.	El Chango Q.	Mowry Fm.
Abbreviations:	DM	HR	KF	GRF	SQ	TQ	MQ	SR	EQ	CQ	MF
	Albian						Alb-Cen. boundary		Early Cenomanian		
<i>Ellimmichthys</i> Jordan and Gilbert, 1919.						x					
<i>Foreyclupea loonensis</i> Vernygora, Murray, Wilson, 2016.		x							x		
<i>Paraclupea</i> Sun, 1956 (see Alvarado-Ortega, Ovalles-Damián, Arratia, 2008).									x		
<i>Paraclupea seilacheri</i> Alvarado-Ortega, Melgarejo-Damián, 2017.						x					
<i>Ranulfoichthys dorsonudum</i> Alvarado-Ortega, 2014.						x					
<i>Scombroclupea javieri</i> Than-Marchese, Alvarado-Ortega, Matamoros, Velázquez-Velázquez, 2020.									x		
<i>Thorectichthys</i> Murray and Wilson, 2013 (this work).					x						
<i>Triplomystus applegatei</i> Alvarado-Ortega, Ovalles-Damián, 2008.									x		
<i>Thorectichthys fidelis</i> Than-Marchese, Alvarado-Ortega, Murray, Velázquez-Velázquez, Domínguez-Domínguez, 2024.									x		
Coelacanthiformes											
<i>Axelrodichthys</i> Maisey, 1986 (see Espinosa-Arrubarrena et al., 1996).						x					
Crossognathiformes											
<i>Michin scernai</i> Alvarado-Ortega, Mayrinck, Brito, 2008.					x						
<i>Motlayoichthys sergioi</i> Arratia, González-Rodríguez, Hernández-Guerrero, 2018.						x					
<i>Nusaviichthys nerivelai</i> Alvarado-Ortega, Alves, 2022.					x						
<i>Pachyrhynchodus</i> Dixon, 1850 (see Hernández Guerrero, 2015).						x					
Elopocephala incertae sedis											
<i>Arripichthys weberi</i> Alvarado-Ortega, Brito, 2011.					x						
Elopomorpha											
<i>Brannerion</i> Jordan, 1919 (see Applegate, 1996),					x						
<i>Epaelops martinezi</i> Alves, Alvarado-Ortega, Brito, 2020.					x						
<i>Nunaneichthys mexicanus</i> Hernández-Guerrero, Cantalice, González-Rodríguez, Bravo-Cuevas, 2021.						x					
<i>Megalops</i> Lacépède, 1803 (Applegate, 1996)					x						
<i>Paraelops</i> Silva Santos, 1971 (see Maisey, 2000).					x						
Euteleosteii incertae sedis											
<i>Erichalcis arcata</i> Forey, 1975.	x										
<i>Erichalcis conspicua</i> Hermus, Wilson, Macrae, 2004.	x										
<i>Xeneichthys yanési</i> Arratia, González-Rodríguez, 2024.						x					
Halecomorphi incertae sedis											
<i>Cipactlichthys scutatus</i> Brito, Alvarado-Ortega, 2013.					x						

TABLE 3 (continued).

	Dragon Mtn.	Hay River	Kiowa Fm.	Glen Rose Fm.	Sumidero Q.	Tlayúa Q.	Muhi Q.	Smoky River	El Espinal Q.	El Chango Q.	Mowry Fm.	
Abbreviations:	DM	HR	KF	GRF	SQ	TQ	MQ	SR	EQ	CQ	MF	
Albian						Alb-Cen. boundary		Early Cenomanian				
Ichthodectiformes												
<i>Heckelichthys</i> Taverne, 2008 (Alvarado-Ortega, 2024, pers. obs.)									x			
<i>Heckelichthys preopercularis</i> Baños-Rodríguez, González-Rodríguez, Wilson, González-Martínez, 2020.							x					
<i>Unamichthys</i> Alvarado-Ortega, 2004 (see Alvarado-Ortega, 2005).							x					
<i>Unamichthys espinosai</i> Alvarado-Ortega, 2004.							x					
Macrosemiformes												
<i>Macrosemiocotzus americanus</i> González-Rodríguez, Applegate, Espinosa-Arrubarrena, 2004.							x		x			
<i>Notagogus novomundi</i> González-Rodríguez, Reynoso, 2004 (this work).							x		x			
Ophiopsiformes												
<i>Macrepistius arenatus</i> Cope, 1894.							x					
<i>Teiichthys brevipina</i> Machado, Alvarado-Ortega, Machado, Brito, 2013, and this work.							x		x			
<i>Teiichthys kallistos</i> Applegate, 1988.							x					
Ostariophysi												
<i>Caeus</i> Costa, 1857 (see Applegate, 1996, fig. 5; Alvarado-Ortega, 2024, pers. obs.).							x					
<i>Clupavus</i> Arambourg, 1950 (see Dunkle, 1971)							x				x	
<i>Sapperichthys chiapanensis</i> Amaral, Alvarado-Ortega, Brito, 2013.							x				x	
Pycnodontiformes												
<i>Neoproscinetes</i> Figueiredo, Silva Santos, 1987 (see Applegate, 2001).							x					
<i>Tahnaichthys magnuserrata</i> Pacheco-Ordaz, Mejía, Alvarado-Ortega, 2025.							x					
<i>Tepexichthys aranguthyorum</i> Applegate, 1992.							x					
Semionotiformes												
<i>Lepidotes</i> (Eastman, 1917, p. 262)							x					
<i>Tlayuamichin itzli</i> Lopez-Arbarello, Alvarado-Ortega, 2011.							x					

of the Municipality of Ocozocoautla de Espinosa, Chiapas, southeastern Mexico (Alvarado-Ortega et al., 2009; Alvarado-Ortega and Than-Marchese, 2012, 2013; Moreno-Bedmar et al., 2014; Eguiluz de Antuñano et al., 2023).

11) **Mowry Formation**—Earliest Cenomanian deposits of the Mowry Formation, exposed in

Vernal County, Utah, U.S.A. (Dunkle, D., 1971; Newbrey et al., 2013; Stewart and Hakel, 2006).

The known taxonomic diversity of the North American marine osteichthyans during the Albian–early Cenomanian is low, partly due to the low number of paleontological localities (11) discovered in this continental region with well-preserved fossils

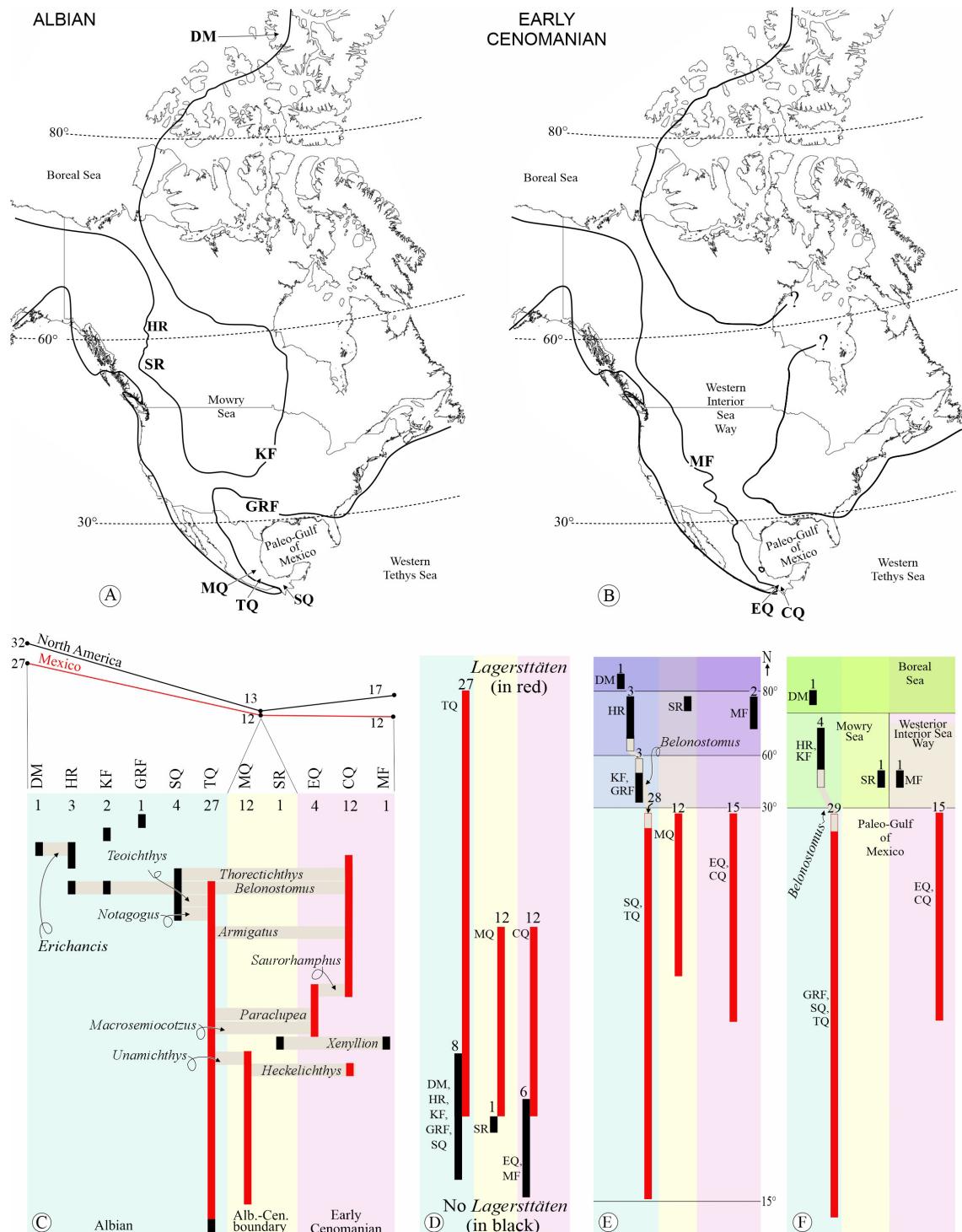


FIGURE 9. Diversity and geographic distribution of the North America Albian–early Cenomanian osteichthyan fishes. A) Map of the Late Albian showing the sites of the Albian and the Albian–Cenomanian boundary. B) Map of the early Cenomanian showing the fossil fish sites. C) Generic diversity in the range Albian–early Cenomanian showing the contribution of the Mexican sites (in red bars and line). D) The *Lagerstätten* effect on fish diversity in the localities considered. E) The latitudinal effect on fish diversity in the localities considered. G) The interconnectivity effect of the North American seas over fish diversity in the localities considered. Abbreviations: CQ, El Chango Quarry; DM, Dragon Mountain; EQ, El Espinal Quarry; GRF, Glen Rose Formation; HR, Hay River; KF, Kiowa Formation; MF, Mowry Formation; MQ, Muhi Quarry; SQ, Sumidero Quarry; SR, Smoky River; TQ, Tlayúa Quarry; numbers above the bars indicate the number of fish genera in each respective case.

(Figure 9A and B, Table 3). Nevertheless, the known taxonomic diversity includes 45 nominal species that could reach a maximum of 67 if we consider that all indeterminate generic reports represent at least one species (Table 3). The same record shows 55 genera, of which 32 are in the Albian (including 27 exclusively Albian, *Unamichthys* that reach the Albian–early Cenomanian boundary and *Armigatus*, *Thorectichthys*, *Paraclupea*, and *Macrosemiocotzus* also present in the early Cenomanian), 13 represent the Albian–Cenomanian boundary (including 10 exclusively present in this boundary, *Unamichthys* also present in the Albian, plus *Xenyllion* and *Heckelichthys* that reach the early Cenomanian (Figure 9C); this count does not include *Armigatus*, *Thorectichthys*, *Paraclupea*, and *Macrosemiocotzus* that could potentially be present in this boundary because their distributions range between the Albian to the early Cenomanian), 17 are early Cenomanian (including 11 exclusively of this age, *Xenyllion* and *Heckelichthys* present in the Albian–early Cenomanian boundary, plus *Armigatus*, *Thorectichthys*, *Paraclupea*, and *Macrosemiocotzus* also present from the Albian to early Cenomanian). At this point, it is essential to highlight the relevant contribution of Mexico to fossil record because together, its *Lagerstätten* (the Tlayúa, Muhi, and El Chango quarries) and its non-*Lagerstätten* sites (the Sumidero and El Espinal quarries) contribute most of the generic diversity of North American Albian–early Cenomanian bony fishes. In comparing the fossil contributions within the same geological periods, the Mexican sites include 27 of 32 known genera for the Albian, 12 of 13 genera for the Albian–Cenomanian boundary, and 15 of 17 genera for the early Cenomanian. However, such generic diversity barely changes if only the Mexican *Lagerstätten* are considered; this diversity is 27 of 32 for the Albian, 12 of 13 for the Albian–Cenomanian boundary, and 12 of 17 for the early Cenomanian (Figure 9C).

Recently, Arratia and González-Rodríguez (2024) noted that the early-middle Cretaceous fish localities in Mexico show high apparent endemism. This work confirms such observation, which also applies to the Albian–early Cenomanian localities in North America's northern, central, and southern regions. That is, except for the record of *Belenostomus* (in the Albian deposits of Hay River, Kiowa Formation, and the Sumidero Tlayúa quarries), there is no other genus common between the Albian sites of Canada, Albian–early Cenomanian of Mexico, and Albian Cenomanian boundary, and

early Cenomanian of Kansas and Utah. In this scenario, the other three taxa reported here from the Sumidero Quarry are important because of their geographical and temporal distribution to other localities (*Notagogus* and *Teoichthys* are also present in the middle-late Albian of Tlayúa, and *Thorectichthys* in the early Cenomanian of El Chango), complementing the biogeographic patterns in these fishes into the Paleo-Gulf of Mexico region. The other genera present in more than one locality in this southern North American region include *Unamichthys* (in Tlayúa and Muhi), *Armigatus* (in Tlayúa and El Chango), *Saurorhamphus* (in the El Espinal and El Chango quarries), *Heckelichthys* (in Muhi and El Chango), and *Paraclupea* and *Macrosemiocotzus* (in Tlayúa and El Espinal). The other genera already described in the Paleo-Gulf region of Mexico are endemic because these are unknown in more than one locality.

Three crucial factors help to explain the geographical-temporal pattern of the Albian–early Cenomanian bony fishes from North America described above and the remarkably high generic diversity observed in Mexico. There is a strong *Lagerstätten* effect in favor of Mexico because the three North American *Lagerstätten*-type localities (Tlayúa, Muhi, and El Chango quarries) known for Albian–early Cenomanian range are concentrated in this country (Figure 9D). Since the Cretaceous, the latitudinal position of North America has not changed significantly, so there is also a robust latitudinal effect directly linked to the climate that is also in favor of Mexico; all the Albian–early Cenomanian localities of Mexico are below 30° N and within the tropical region, where high biodiversity is common (Figure 9E).

The relatively high diversity of bony fishes of the Albian–early Cenomanian of Mexico may have been triggered by the interconnectivity effect of the North American sea bodies (Figure 9F). During the Albian period, the north-central region of North America, between Canada and the USA, was occupied by the Mowry Sea, which connected only to the Boreal Sea. In the Cenomanian, this intercontinental sea opened to the south, becoming the Western Interior Seaway of North America. The history of Mexico-adjacent seas is contrastingly more active. The Gulf of Mexico originated at the end of the Jurassic, while the Tethys Sea made its way between North and South America through the Hispanic Corridor; thus, Mexico housed marine taxa in the epicontinent regions of the Paleo-Gulf of Mexico, whose descendants survived in Mexican sites of the Cretaceous. The west opening of

the Hispanic Corridor also made it possible for taxa from the Paleo-Pacific Ocean to access Mexico. During the early Cretaceous, while North America, North Africa, and South America were still nearby, Mexico also received fish from the Paleo-Atlantic regions of Africa and South America (Maisey, 2000). Finally, the opening of the North American Inland Sea toward the Paleo-Gulf of Mexico, at least since the late Albian (Blakey, 2014; Slattery et al., 2015; Eldrett et al., 2017), allowed the exchange of marine fauna between these marine regions.

In the scenario described above, all the localities of Canada and the USA considered here naturally include exclusive taxa of the Boreal and Mowry seas, except for the presence of *Belonostomus* and probably *Lepidotes*, which is a genus of wide distribution that appeared in the Jurassic (Figure 9G). On the contrary, the Albian–early Cenomanian localities of the Paleo-Gulf of Mexico region share a significative number of genera present in the other areas; this has taxa with cosmopolitan distribution (*Belonostomus*, *Megalops*, *Enchodus*, and *Pachyrhizodus*), share genera with the eastern Tethys Sea (e.g., *Heckelichthys*, *Armigatus*, *Saurorhamphus*; *Scombroclupea*; *Thorectichthys*, and *Notagogus*), the epicontinental seas of the Early Cretaceous South America (e.g., *Neoproscopterus*, *Arripichthys*, *Axelrodichthys*, and *Branerion*). Finally, all the taxa described in the localities of Mexico, without a wider distribution, form the center of a typical association of the Paleo-Gulf of Mexico (e.g., *Unamichthys*, *Michin*, and *Macrosemiocotzus*).

The Colección Nacional de Paleontología (Igl-UNAM) houses nearly 30 additional fossil fish specimens from the Sumidero Quarry. Given their preservation mode, the entire account for the diversity of fishes from this site requires considerably more preparation time. Thus, the contributions of this locality to understanding the diversity of North

American bony fishes will surely increase in the coming future.

CONCLUSION

This paper provides a general report on the fossil fish found at the Sumidero Quarry. This site is the second Albian fish site in Mexico. The lithostratigraphic position within the Sierra Madre Group and the affinities of its microfossils and fishes, which include specimens of *Notagogus novomundi* and *Teoichthys brevipina* previously described from specimens of the Tlayúa Quarry, it is determined that the Sumidero Quarry is of Albian age. This finding provides valuable information that complements the knowledge of the Albian/Cenomanian ichthyofauna of North America and its contribution to the Cenomanian Diversification Event of Bony Fishes. Like other Albian–early Cenomanian fossil fish sites of Mexico, the fish assemblage of this site is eclectic because it contains taxa with cosmopolitan distribution (*Belonostomus*), genera with Tethys Sea affinities (*Thorectichthys*), and taxa exclusive of the Paleo-Gulf of Mexico region (*Notagogus* and *Teoichthys*).

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