LATE DEVONIAN (FAMENNIAN) CHONDRICHTHYES FROM MEXICO

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The Paleozoic vertebrate fossil record from Mexico is very scarce and strongly biased by rock exposure, composed mainly of upper Paleozoic (Carboniferous and Permian) outcrops (e.g., Sánchez-Zavala et al., 1999; Poole et al., 2005; González-Rodríguez et al., 2013). In particular, the Mexican Paleozoic fish fossil record comprises a few isolated chondrichthyan scales and some semiaarticulated symphysial tooth whors belonging to the iconic shark Helicoprion, with ages ranging from the Late Carboniferous to the early Permian. The first reported Paleozoic fish from Mexico belongs to a semiaarticulated symphysial tooth whorl of Helicoprion mexicanus from the Permian of Coahuila, near Las Delicias County, originally described by Mülleried (1945) and subsequently republished by Applegate (1989). A second Helicoprion tooth whorl (not formally named) was discovered in Mina Plomosas (central-west Chihuahua) and dated as Wolfcampian (early Permian in age) (Bridges and De Ford, 1961). More recently, a third Helicoprion specimen, consisting of one broken symphysial tooth whorl, was reported by Sour-Tovar et al. (1991) in the Leonardian (Permian) of Patlanoaya Formation (Puebla, central Mexico) and described in detail by Sour-Tovar et al. (2000).

In addition to those remains, a few isolated chondrichthyan microichthyoliths have been described, first by Brunner (1987) and later by Derrycke-Khatir et al. (2005), from the Upper Pennsylvania and lower Permian Patlanoaya Formation. The few studied dermal denticles have been identified as belonging to Cooperella typicalis, Moreyella typicalis, ‘Sturgeomela’ quinqueloba, and probably a hybodontid shark. To date, these studies represent the complete record of vertebrate remains known from the Paleozoic rocks of Mexico, emphasizing its scarcity and hence the importance of expanding our knowledge of this vertebrate fossil record.

In this context, here we describe new Famennian (Late Devonian) fish remains, represented by isolated chondrichthyan teeth, from Cerro Las Pintas in the municipality of Fronteras, northeast Sonora, Mexico. This finding represents not only the oldest fish record but also the oldest vertebrate remains found in Mexico. The study of the chondrichthyan assemblage, although scarce, shows a relative diverse community comparable to the one described for similar ages in neighboring regions.

Institutional Abbreviation — ERNO NP, Estación Regional del Noroeste del Instituto de Geología, Universidad Nacional Autónoma de México, Hermosillo, Mexico.

GEOLOGICAL SETTING AND AGE

The study area lies in the eastern part of the Cerro Las Pintas, 2 km northeast of the Rancho La Mesa, in the municipality of Fronteras, northeast Sonora. The area can be reached through the Federal Mexican Road 17, between Fronteras and Agua Prieta, about 15 km north of the town of Fronteras (Fig. 1A, B). Geologically, the region is composed of rocks from the Proterozoic eon, represented by the Mesteñas Granite (1589 ± 3 Ma) and the Pinal Schist (1640 Ma), and Quaternary alluvium deposits (Gómez-Tagle, 1967; Peiffer-Rangin, 1988). Paleozoic outcrops include the Cambrian Bolsa Quartzite and Abrigo Limestone and, probably laying unconformably, the Devonian Martin Limestone, the Mississippian Escabrosa Limestone, and the Pennsylvanian Naco Limestone. The study section, in the northeast area of Cerro Las Pintas (Fig. 1C), is mainly composed of a carbonate sequence of limestone and sandstone, with medium to coarse strata at the base and coarse to massive strata at the top, reaching a thickness of 360 m (Fig. 1D). The fish remains come from the upper 50 m of the sequence (between coordinates 109°44′43″W, 30°58′31″ N and 109°44′36″W, 30°58′34″N), belonging to the Martin Limestone and dated as Famennian (Late Devonian), upper part of the Lower posteria Zone to the Upper expansa Zone (equivalent to the lower part of the Bispadolithus ultimus Zone) based on the occurrence of Polygnathus experplexus, Palamatoepis perlaborata posteria, Palamatoepis rugosa rugosa transitional to Palamatoepis rugosa ampla, and Icriodus darbyensis. From the 43 carbonate rock samples taken (ca. 2 kg per sample), only one (PI-36) yielded microichthyolith remains. From this sample, an extra sampling effort of total of 45 kg, was taken and dissolved using 5–10% formic acid. After disaggregation, the residues were screened with sieve meshes of 0.6 and 0.125 μm, respectively. Microichthyoliths were mainly represented by chondrichthyan remains, but also conodonts, and some fragments of scales and conical teeth of actinopterygians, not diagnostic at specific level were recovered. The studied teeth were photographed using a scanning electron microscope at the University of Valencia, Spain, and are stored in the paleontological collection of the Estación Regional del Noroeste del Instituto de Geología, Universidad Nacional Autónoma de México, Hermosillo, Mexico.

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FIGURE 1. A, map of Sonora, north of Mexico, showing Paleozoic outcrops and the location of the study section east of the Cerro Las Pintas. B, map of the study section showing its location in relation to the closest locality, Fronteras. C, geological map of the Cerro Las Pintas area, modified from Peiffer-Rangin (1988), star indicates the exact location of the study section. D, stratigraphic column of the study section with location of samples and distribution of fossils.
SYSTEMATIC PALEONTOLOGY

Class CHORDICHYTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order PHOEBODONTIFORMES Ginter, Hairapetian, and Klug, 2002
Family PHOEBODONTIDAE Williams in Zangerl, 1981
Genus PHOEBODUS St. John and Worthen, 1875

Type Species—Phoebodus sophiae St. John and Worthen, 1875.

PHOEBODUS LIMPIDUS Ginter, 1990
(Fig. 2A–D)

Referred Material—ERNO NP-PI-36-1, a specimen from sample PI-36, expansa Zone (late Famennian).

Description—Small cladodont tooth, 0.4 mm long and 0.6 mm wide, with three main cusps and two smaller intermediate intermediate cusps on the crown. The cusps are slightly inclined lingually, with the main lateral cusps diverging mesiodistally (Fig. 2A). A single intermediate cusp is partially preserved, and it is thinner than the main cusps. The tooth is heavily abraded, so no cristae on the labial or lingual side of the cusps are visible; however, a distinct blade separating the labial and lingual faces of the cusps is clearly visible (Fig. 2C). The base is thin, subelliptical or slightly triangular in shape, narrowing lingually, with just one visible nutritive foramina. The apical button is not well defined.

Remarks—The specimen generally conforms with the diagnosis of Ginter (1990) for Phoebodus limpidus, a five-cusped tooth, with intermediate cusps on the crown, slightly inclined lingually and diverging mesiodistally, with a subelliptical or slightly triangular base and a slight apical button. As stated by Ginter et al. (2002), Ph. limpidus has been associated with deep-water environments in several localities, indicating their open marine preferences.

Occurrence—Phoebodus limpidus is known from the Upper Devonian (upper Famennian) stratigraphic range, dated from the Early expansa Zone to the Early–Middle praesulcata Zone (Ginter, 2010), upper part of the expansa Zone in Mexico. In addition, according to Ginter et al. (2010), Ph. limpidus occurs in the U.S.A. (Nevada), Morocco (Anti-Atlas), France (Montagne Noire), Italy (Carnic Alps, Sardinia), Germany (Thuringia), Poland (Holy Cross Mountains), Russia (South Urals), and southern China.

Genus THRINACODUS St. John and Worthen, 1875

Type Species—Diplodus incurvus Newberry and Worthen, 1866.

THRINACODUS TRANQUILLUS (Ginter, 2000)
(Fig. 2E–M)

Referred Material—ERNO NP-PI-36-2 to ERNO NP-PI-36-4, three specimens from sample PI-36, expansa Zone (late Famennian).

Description—Teeth are large, more than 1 mm length labiolingually and 0.6 mm wide, and all are poorly preserved, with almost all their cusp and root bases broken or incomplete and their surfaces partially abraded. Despite this, their morphological features are clearly discernible, with teeth showing asymmetrical crowns with two or three almost straight (nonsigmoid) cusps slightly recurved lingually, and in some cases laterolingually. The cusps show size variation, and on one of them (ERNO NP-PI-36-3; Fig. 2I) a distinct crista ornamenting the internal surface of the cusps is preserved. In addition, a marked rib extends from the inside lateral edge of the outside cusp across and up the lateral edge of the middle cusp. Most of the cusps are broken, and it is difficult to know the exact relative size between them; however, one of the lateral cusps appears to be longer than the others. The base is moderately long and narrow, roughly rectangular, normally at least twice as long as wide and flattening dorsoventrally toward the distal margins. At least a single foramen opens in their middle part (Fig. 2F).

Remarks—Thrinacodus tranquillus, as other species of the genus, shows a clear asymmetry of the crowns with a wide range of tooth morphotypes, probably representing different positions in the jaw (monognathic heterodonty), varying from almost symmetrical specialized symphyseal teeth to asymmetrical teeth in the lateral and posterolateral parts of the jaw (Ginter et al., 2015). This asymmetry follows a process of gradual mesial cusp reduction, leading to a complete disappearance of cusps in the lateral areas of the jaws (bicuspitate teeth) and in the anterior teeth remaining tricuspid (Ginter and Turner, 2010). The specimen ERNO NP-PI-36-4 (Fig. 2K–M) could represent one of those mesial teeth, with just two cusps, whereas the rest of the specimens can be assigned to anterior teeth (Fig. 2E–J), showing a clear asymmetry and three well-developed cusps.

Occurrence—In Mexico, Th. tranquillus has been recorded from the expansa-praesulcata zones (late Famennian). However, globally, Th. tranquillus ranges from Late Devonian, late Famennian (Early expansa Zone), through Early Carboniferous, Serpukhovian (nodosus Zone) (Ginter et al., 2010). According to Ginter et al. (2002, 2010), teeth of Th. tranquillus have been reported from Morocco (Anti-Atlas), France (Montagne Noire), Germany (Thuringia), Poland (Holy Cross Mountains), Russia (South Urals), central Iran, and southern China.

Order CTENACANTHIFORMES Glikman 1964
Family CTENACANTHIDAE Dean 1909
Genus CLADODOIDES Maisey 2001

Type Species—Cladodoides wildungensis (Jaekel 1921).

CLADODOIDES sp.
(Fig. 2N–P)

Referred Material—ERNO NP-PI-36-5, one specimen from sample PI-36, expansa Zone (late Famennian).

Description—ERNO NP-PI-36-5 is ca. 1 mm wide with a typical cladodont-type crown comprising five cusps (Fig. 2N–P). The median cusp, although hardly eroded, is the biggest, with the lateral cusps being smaller and pointing outward, whereas the intermediate cusps are very poorly developed. The main cusps are slightly arched lingually and are subcircular (slightly compressed linguolabially) in cross-section. A marked longitudinal crrista is visible on the central and lateral cusps, extending from the base to the apex, being just visible in the labial side of the cusps. The base is quadrate or trapezoidal in shape, extending lingually with numerous small foramina. A lingual double button is not very well preserved. A very narrow, single, undivided, and rectangular labiobasal projection, approximately of the same size as the root of the median cusp, is present.

Remarks—Our unique specimen shows the three main cusps partially eroded, which, together with its general cladodont morphology, makes it difficult to identify. As stated by Ginter (2010), there are numerous small, isolated Devonian cladodont teeth that have been identified usually as Stethacanthus sp. or Symorium sp., if not included in Stethacanthiidae indet. Most of these teeth, as our specimen, show the cusps connected by the enameloid layer and have flattened median cusps and wide labiobasal shelves, which, according to Ginter (2010), are features of ctenacanths. Specimens similar to ERNO NP-PI-36-5 (Fig. 2N–P) have been assigned in the literature to Stethacanthus, e.g., S. thomasi.
(Turner, 1982:fig. 8j) or S. resistens (Ginter, 2002:fig. 2c–f), but as argued by Ginter (2010) and Ginter et al. (2010), they should be attributed to Cladodoides wildungensis. In any case, the existence of just one specimen, hardly eroded, does not allow for a confident assignment, so we prefer to leave it as Cladodoides sp.

**Occurrence**—Cladodoides, a monospecific genus that includes only C. wildungensis, has been only reported from late Frasnian–middle Famennian strata. Occurrences of the species are reported from Germany, Poland, Czech Republic (Moravia), Morocco (Anti-Atlas), and Russia (South Urals and Kuznetsk Basin), according to Ginter et al. (2010).

**Cohort EUSELACHII** Hay, 1902

**Superfamily PROTACRODONTIOIDEA** Zangerl, 1981

**Family PROTACRODONTIDAE** Cappetta, Duffin, and Zidek, 1993

**Genus** PROTACRODUS Jaekel, 1925

**Type Species**—Protacrodus vetustus Jaekel, 1925.

**PROTACRODUS SERRA** Ginter, Hairapetian, and Klug, 2002

(Fig. 3A–Q)
Referred Material—ERNO NP-PI-36-6 to ERNO NP-PI-36-11, one complete and five incomplete teeth from sample PI-36, *expansa* Zone (late Famennian).

Description—The protacrodont material shows a wide morphological range. The specimens are relatively well preserved, although incomplete, ranging in size from around 0.3 mm wide in the smallest tooth (Fig. 3A, B) to 0.6 mm wide in the biggest tooth (Fig. 3F–I). Despite their morphological differences, all teeth show the typical protacrodont tooth morphology, with teeth mesiodistally elongated, crowns formed by pyramidal to bulbous, labiolingually compressed cusps (ornamented by distinct wavy cristae on both lingual and labial sides), and a distinct occlusal blade that connects all the cusps (Fig. 3F, L). The central cusp seems to be the biggest, with one (Fig. 3A, N) to three (Fig. 3C, G) lateral cusps on each side that, normally, decrease in size laterally. In one specimen (Fig. 3F–I), small cusplets are developed between the main lateral cusps (Fig. 3I). In all cases, the lower parts of the cusps are fused, and in one specimen, the cista on the labial face thickens around the crown-base interface, resembling small cusplets (Fig. 3I). The bases are laterally elongated and perforated, with numerous horizontal canals that cross the base labiolingually.

Remarks—Almost all the specimens are broken and slightly abraded, but it is possible to determine the pyramidal to bulbous cusp shape and the mesiodistal tooth elongation typical of protacrodontids. Our specimens are characterized by crowns composed of three to seven cusps connected by an occlusal blade. All these features are typical of *P. serra*, with our teeth representing examples of the morphotypes M1 (Fig. 3A–B, M–O), M2 (Fig. 3J–L), and M4 (Fig. 3D, I) described by Ginter et al. (2002) from Iran and Morocco. However, morphologies such as that of the holotype of *P. serra* (morphotype M3) are absent in our sample. This morphotype possesses large, triangular, blade-like median cusps that slightly differ from the more rounded cusps shown by some of our specimens. In addition, the development on the labial face of cristae that thicken around the crown-base interface (Fig. 3J–L) and the development of cusplets between the lateral cusps (Fig. 3F–I) are not usual features within the species. Therefore, although the general morphology fits well within the normal range of intraspecific variation of *P. serra*, due to the low number of specimens and their poor preservation, more material is needed in order to describe properly the morphological variation of this taxa.

Occurrence—Protacrodus serra* has been recorded from the middle–late Famennian (*Late marginifera–*Middle *praesulcata* conodont zones). *Protacrodus serra* has been found in several Upper Devonian localities of Morocco (Anti-Atlas), France (Montagne Noire), Poland (Holy Cross Mountains), central Iran (Ginter et al., 2010), and Western Australia (Roelofs et al., 2015).
**DISCUSSION AND CONCLUSIONS**

Herein, we report a comparatively diverse assemblage of chondrichthyan remains from a new upper Famennian locality in northeast Sonora, Mexico. Although specimens are rare and the abundance relatively low, we have identified at least four different taxa belonging to three orders (Phoebodontiformes, Ctenacanthiformes, and Hybodontiformes). This constitutes the first Devonian paleoichthyological record from Mexico and the oldest formally described gnathostome remains of the country. The microichthyolith assemblage includes the chondrichthyans *Phoebodus limpidus*, *Thrinacodus tranquillus*, *Cladodoideus* sp., and *Protacrodus serra*, showing some similarities to the Upper Devonian (Frasnian–Famennian) assemblages of neighboring regions such as Utah and New Mexico (Ginter, 2001; Hodnett and Lucas, 2015). In addition to the chondrichthyan tooth remains, an isolated dental denticle, characterized by a monocuspidated, posteriorly recurved conical crown (Fig. 3R), conodonts, and indeterminated actinopterygians fragments (scales and teeth) were also recovered.

The relatively abundant chondrichthyan assemblage herein described most likely represents an ecologically diverse community including the three morphoeological categories of sharks defined by Ginter et al. (2002): (1) fast-swimming and eurytopic surface hunters with cladodont tooth crowns (e.g., *Cladodoideus* like spp.); (2) demersal species with crushing or grinding teeth living in well-oxygenated photic waters (e.g., *Protacrodus* spp.); and (3) pelagic species with clutching or grasping phoebodont teeth preying upon comparatively soft prey (e.g., *Phoebodus* and *Thrinacodus*). Moreover, the relative abundance of such ecological groups has been demonstrated as a useful tool for approximating water paleodepth. In this sense, Ginter (2000, 2001) proposed three chondrichthyan assemblages or biofacies for the late Famennian based on the relative abundance of different shark micromains: (1) the *Jalodus* biofacies, representing deep-water environments; (2) the *Phoebodus* biofacies, representing open shelves environments, of intermediate bathymetric conditions, mainly below the shallow subtidal zone; and (3) the *Protacrodus* biofacies, characteristic of the shallow subtidal zone representing shallow-water conditions. Both *Th. tranquillus* and *P. limpidus* in our sample are rather indicators of the intermediate *Phoebodus* biofacies, which, together with the presence of *Protacrodus*, could indicate relatively shallow conditions. This assumption is supported by the conodont and sedimentological data. The conodont assemblage recovered in the section indicates a late Famennian age (from the Late postera Zone to the praesulcata Zone). More precisely, the sample PI-36, which contains the microichthyolithes remains, has yielded a typical Middle–Late expansa zone, with a conodont fauna represented by *Icriodus* darbysiensis, *Polygnathus extralobatus*, and *Polygnathus obliquocostatus*. This conodont assemblage corresponds to the polygnathid-crioïdï conodont biofacies III of Sandberg and Dreesen (1984), typical of outer-shelf (‘backshore’) shoal environments. Moreover, the shallow-water shelf environment inferred from conodonts and chondrichthys is also in agreement with paleogeographic and geological data obtained in other outcrops of northeastern Sonora, suggesting that the northwestern part of Mexico represented an extensive epicontinental sea placed in a subequatorial latitude associated with the passive continental margin of southern Laurentia (Ortega-Gutiérrez et al., 2000; Poole et al., 2005).

Finally, our study suggests that the lack of Paleozoic fossil fish record in Mexico could be mainly due to low sampling effort more than biological or taphonomic biases, stressing the necessity of focussing our efforts in this region in order to increase our knowledge on the biodiversity and biogeographic distribution of the Mexican Paleozoic vertebrates.

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