

Late Devonian (Famennian) chondrichthyans from Mexico

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RH: MARTÍNEZ-PÉREZ ET AL.—DEVONIAN SHARKS FROM MEXICO

The Paleozoic vertebrate fossil record from Mexico is very scarce and strongly biased by rock exposure, comprised mainly by 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 semiarticulated symphyseal tooth whorls 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 semiarticulated symphyseal 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 symphyseal 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 micro-ichthyoliths have been described, first by Brunner (1987) and later by Derycke-Khatir et al. (2005), from the Late Pennsylvanian and early Permian Patlanoaya Formation (Puebla, central Mexico). The few studied dermal denticles have been identified as belonging to *Cooperella typicalis*, *Moreyella typicalis*, “*Sturgeonella*” *quineloba* and probably an Hybodontidae shark. To day, these studies represent the complete record of vertebrates remains known from the Paleozoic rocks of Mexico, emphasizing its scarcity and hence the importance of expanding our knowledge of its 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 the neighbours regions.

GEOLOGIC SETTING AND AGE

The study area lies in the east 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 that range from the Proterozoic eon, represented by the Mesteñas Granite ($1,589 \pm 3$ Ma) and the Pinal Schist (1,640 Ma), to 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 studied section, in the northeast area of Cerro Las Pintas (Fig. 1C), is mainly composed by a carbonate sequence of limestone and sandy limestone, 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 $109^{\circ}44'43''\text{W}$, $30^{\circ}58'31''\text{N}$ and $109^{\circ}44'36''\text{W}$, $30^{\circ}58'34''\text{N}$), belonging to the Martin Limestone and dated as Famennian (Late Devonian), upper part of the Lower *postera* to the Upper *expansa* zones (equivalent to the lower part of the *Bi. ultimus* Zone) based on the

occurrence of *Polygnathus experplexus*, *Palmatolepis perlobata postera*, *Palmatolepis rugosa rugosa* transitional to *Palmatolepis rugosa ampla*, and “*Icriodus*” *darbyensis*. From the 43 carbonate rock samples taken (≈ 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. The studied teeth were photographed using a scanning electron microscope at the University of Valencia, Spain and stored at the Paleontological collection of the Estación Regional del Noroeste (ERNO) of the Instituto de Geología, UNAM, under the institutional abbreviation (ERNO NP-PI).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES 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

(Figs. 2A–D)

Referred Material — one specimen (ERNO NP-PI-36-1) 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 cusps on the crown. The cusps are slightly inclined lingually, with the main lateral cusps diverging mesio-distally (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 mesio-distally, with a subelliptical or slightly triangular base and a slight apical button. As stated by Ginter et al. (2002), *Ph. limpidus* has been associated to deep-water environments in several localities, indicating their open marine preferences.

Occurrence — *Phoebodus limpidus* shows a Late Devonian (late Famennian) stratigraphical range, from the Early *expansa* to Early/Middle *praesulcata* zones (Ginter, 2010), upper part of the *expansa* zone in Mexico. In addition, according to Ginter et al. (2010), *Ph. limpidus* occurs in USA (Nevada), Morocco (Anti-Atlas), France (Montagne Noire), Italy (Carnic Alps, Sardinia), Germany (Thuringia), Poland (Holy Cross Mts.), 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)

(Figs. 2E-M)

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

Description —Teeth are large, more than 1 mm length labio-lingually 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 (non-sigmoidal) cusps slightly recurved lingually, and in some cases laterolingually. The cusps show size variation and on one of them (Fig. 2I, ERNO PI-36-3) 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 towards the distal margins. At least a single foramen opens in their middle part (Fig. 2F).

Remarks — *Thrinadocus tranquillus*, as other species of the genus, shows a clear asymmetry of their crown with a wide range of tooth morphotypes, probably representing different position in the jaw (monognathic heterodonty), varying from almost symmetrical specialised 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 lateral areas of the jaws (bicuspidate teeth) and remaining the anterior teeth tricuspid (Ginter and Turner, 2010). The specimen NP-PI-36-4 (Figs. 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 (Figs. 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 Mts.), 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.

(Figs. 2N–P)

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

Description — Specimen approximately 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 outwards, meanwhile the intermediate cusps are very poorly developed. The main cusps are slightly arched lingually and are subcircular (slightly compressed linguo-labially) in cross section. A marked longitudinal crista 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 labio-basal 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, that together with its general cladodont morphology, makes difficult to identify it. As stated by Ginter (2010), there are numerous small isolated Devonian cladodont teeth that have been usually identify as *Stethacanthus* sp. or *Symorium* sp., if not included in Stethacanthidae indet. Most of these teeth, as our specimen, show the cusps connected by the enameloid layer, have flattened median cusps and wide labio-basal shelves that, according to Ginter (2010), are features of Ctenacanthids. Similar specimens to ERNO NP-PI-36-5 (Figs. 2N-P) have been assigned in the literature to *Stethacanthus*, see 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 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 PROTACRODONTOIDEA 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

(Figs. 3A-Q)

Referred Material — one complete and five incomplete teeth (ERNO NP-PI-36-6 to ERNO NP-PI-36-11) 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 mesio-distal elongated, crowns formed by pyramidal to bulbous cusps labio-lingually compressed (ornamented by distinct wavy cristae on both, lingual and labial sides), and a distinct occlusal blade that connect all the cusps (Fig. 3F,L). The central cusp seems to be the bigger, 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 (Fig. 3J), the crista on the labial face thicken around the crown base interface resembling like small cusplets. The bases are laterally elongated and perforated with numerous horizontal canals that cross the base labio-lingually.

Remarks — Almost all the specimens are broken and slightly abraded, but it is possible to determine the pyramidal to bulbous cusp in shape and the mesio-distally tooth elongation typical from protacrodontids. Our specimens are characterized by crown composed by three to seven cusps connected by an occlusal blade. All these features are typical of *P. serra*, representing our teeth examples of the Morphotype M1 (Figs. 3A-B,M-O), M2 (Fig. 3J-L) and M4 (Figs. 3D,I) described by Ginter et al. (2002) from Iran and Morocco. However, morphologies as 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 showed by some of our specimens. In addition, the development on the labial face of cristae thickens 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). *P. serra* has been found in several Upper Devonian localities of Morocco (Anti-Atlas), France (Montagne Noire), Poland (Holy Cross Mts.), central Iran (Ginter et al., 2010), and Western Australia (Roelofs et al., 2015).

DISCUSSION AND CONCLUSIONS

Herein we report a comparatively diverse association 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 association includes the chondrichthyans *Phoebodus limpidus*, *Thrinacodus tranquilus*, *Cladodoides* sp., and *Protacrodus serra*, showing some similarities with the Upper Devonian (Frasnian-Famennian) of neighbour regions such as Utah and New Mexico (Ginter, 2001; Hodnett and Lucas 2015). In addition to the chondrichthyan teeth remains, an isolated dermal denticle, characterized by a monocuspidated conical crown posteriorly recurved (Fig. 3R), conodonts, and not diagnostic actinopterygians fragments (scales and teeth) were also recovered.

The relatively abundant chondrichthyan assemblage herein described most likely represents an ecologically diverse community including three morphoecological categories of sharks according to Ginter et al. (2002): (1) fast-swimming and eurytopic surface hunters with cladodont tooth-crowns (e.g., *Cladodoides*-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 microremains: (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 *Ph. 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 Upper *postera* Zone to the *praesulcata* zones). More precisely, the sample PI-36, which contains the microichthyolites remains, has yielded a typical Middle-Upper *expansa* zones, with a conodont fauna represented by “*Icriodus*” *darbyensis*, *Polygnathus extralobatus* and *Polygnathus obliquicostatus*. This conodont association corresponds to the polygnathid-“icriodid” 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 chondrichthyans, is also in agreement with palaeogeographic 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 focus our attempts in this region in order to increase our knowledge on the biodiversity and biogeographical distribution of the Mexican Paleozoic vertebrates.

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FIGURE CAPTIONS

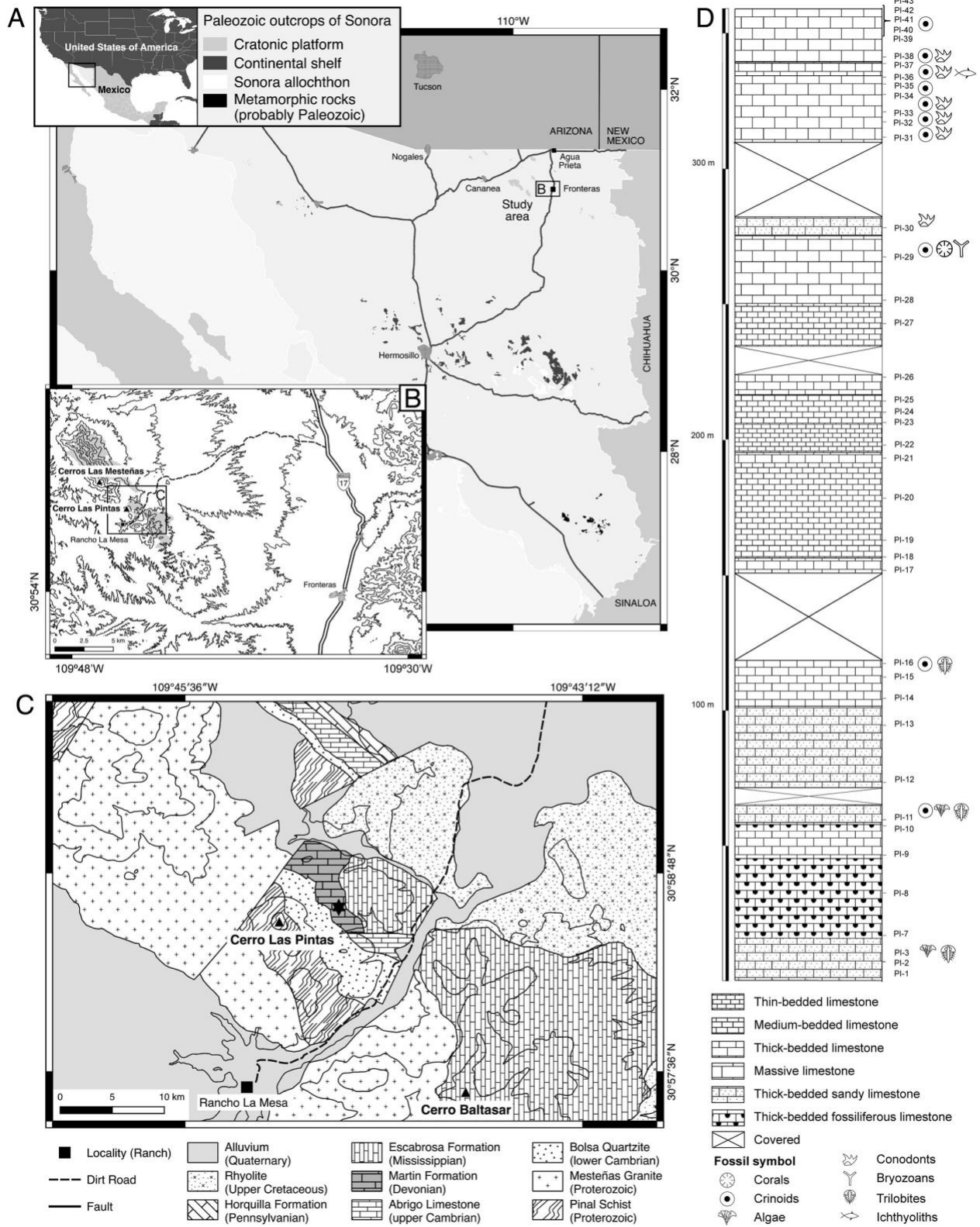


FIGURE 1. A, map of Sonora, north of Mexico, showing Paleozoic outcrops and the location of

the studied section east of the Cerro Las Pintas; **B**, map of the study section related with the closer locality, Fronteras; **C**, Geological map of the Cerro Las Pintas area, modified from Peiffer-Rangin, 1988, and exact location of the study section; **D**, Stratigraphic column of the study section with location of samples and distribution of fossils. [planned for 2/3 page width]

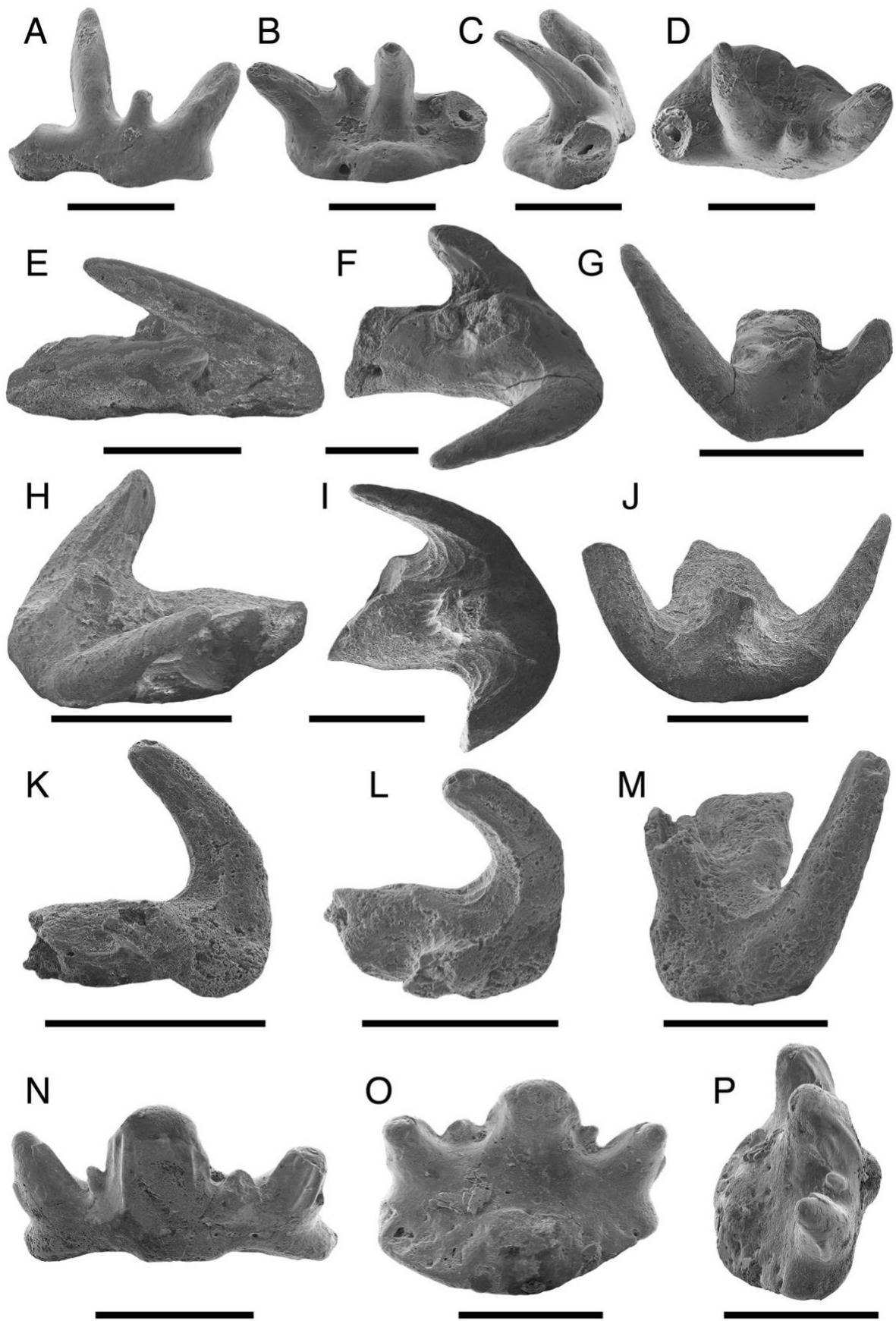


FIGURE 2. Chondrichthyan teeth remains from Cerro de Las Pintas Section (sample PI-36), Famennian (Late Devonian). **A–C**, *Phoebodus limpidus* (ERNO-NP-PI-36-1) in labial, lingual, lateral and occlusal views; **D–M**, Teeth of *Thrinacodus tranquilus*, **E–G**, Specimen ERNO-NP-PI-36-2 in lateral, occlusal and labial view; **H–J**, Specimen ERNO-NP-PI-36-3 in lateral, occlusal and labial view; **K–M**, Specimen ERNO-NP-PI-36-4 in lateral, occlusal and labial view; **N–P**, *Cladodoides* sp. (ERNO-NP-PI-36-5) in labial, lingual, and lateral view. Scale bars: A-D 200 μ m, E,F,M 300 μ m, G-L,, N-P 500 μ m. [planned for page width]

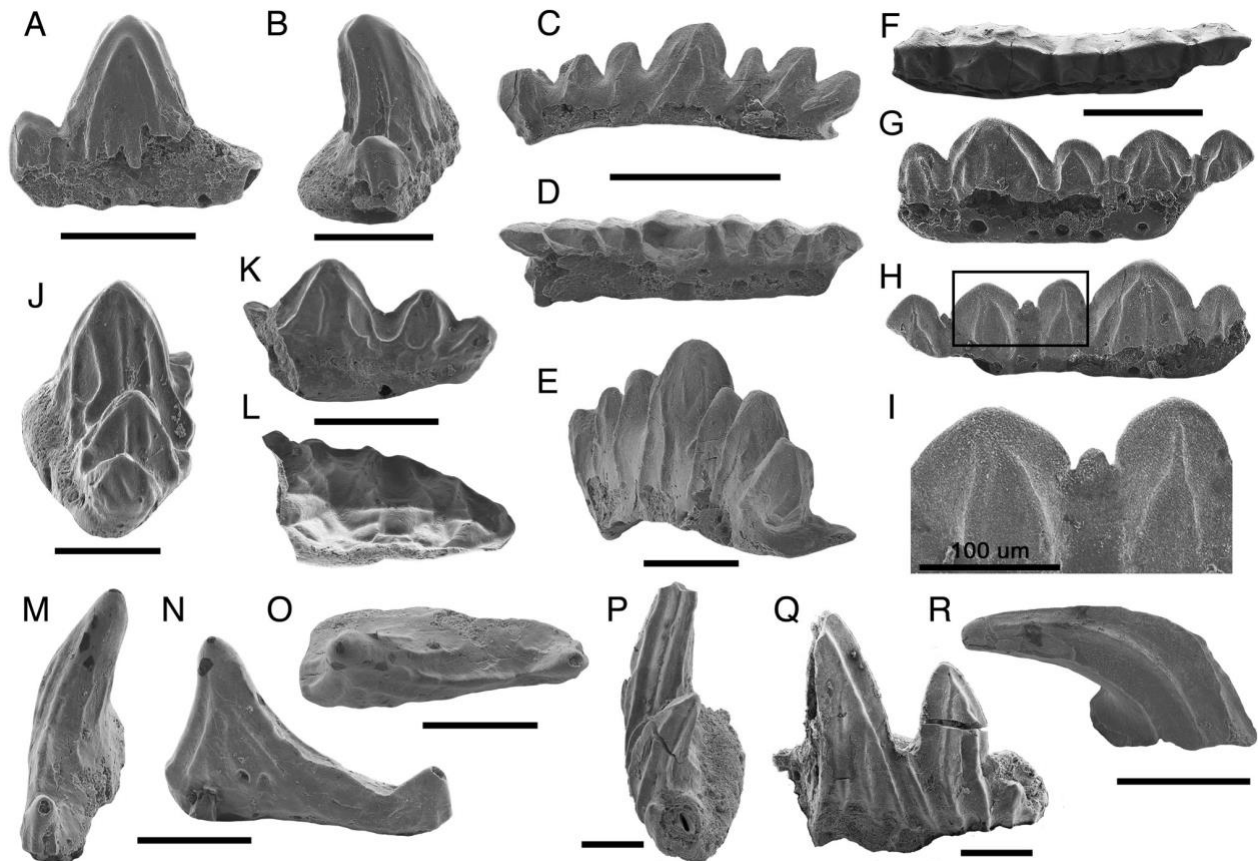


FIGURE 3. Teeth of the Protacrodontid *Protacrodus serra* from Cerro de Las Pintas Section (sample PI-36), Famennian (Late Devonian). **A–B**, *P. serra* (ERNO NP-PI-36-6) in labial and lateral views; **C–E**, *P. serra* (ERNO-NP-PI-36-7) in labial, occlusal and lateral views; **F–I**, *P. serra* (ERNO-NP-PI-36-8) in occlusal, lingual and labial views, and a detail of the lateral cusps; **J–L**, *P. serra* (ERNO-NP-PI-36-9); in lateral, lingual and occlusal views. **M–O**, *P. serra* (ERNO

NP-PI-36-10) in lateral, labial and occlusal views, **P-Q**, *P. serra* (ERNO-NP-PI-36-11) in lateral and labial views; **R**, Chondrichthyan dermical denticle (ERNO NP-PI-36-12) in lateral view. Scale bars: E, I, J 100 μm , A,B,F-H, K,L-R 200 μm , C,D, 300 μm . [planned for page width]