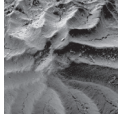


# Late Pennsylvanian fish assemblage from the Robledo Mountains and new records of Paleozoic chondrichthyans in New Mexico, USA

ALEXANDER O. IVANOV & SPENCER G. LUCAS



We describe a very diverse and rich assemblage of fossil fishes from the Upper Pennsylvanian (Missourian) interval of the Horquilla Formation in the Robledo Mountains of southern New Mexico, USA. The assemblage includes bransonelliiforms, symmoriiforms, a ctenacanthiform, a jalodontid, euselachians, neoselachians, an orodontiform, a helodontiform, an eugeneodontiform, a petalodontiform, a psephodontid, an acanthodian and actinopterygians. For the first time, the vascularization system of the teeth of *Adamantina*, *Bransonella*, *Helodus* and *Agassizodus* has been studied using a micro-CT. Besides the diverse fish assemblage from the Robledo Mountains, some other new records of Paleozoic chondrichthyans in New Mexico are documented. • Key words: fishes, Late Devonian–early Permian, New Mexico.

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Fossils of fishes are known from Pennsylvanian strata at several localities across New Mexico, USA (Zidek & Kietzke 1993; Lucas & Estep 2000; Ivanov *et al.* 2009; Lucas *et al.* 2011; Hodnett & Lucas 2015, 2017; Itano & Lucas 2018). But, despite extensive field study, extremely diverse assemblages of fossil fishes with numerous isolated micro- and rare macroremains have proven to be elusive. This has been changed by the discovery of fish fossils in a conglomerate bed (so called “shark bed”) of the Horquilla Formation in the Robledo Mountains of Doña Ana County, southern New Mexico, USA (Fig. 1).

The chondrichthyan remains here described from this bed are isolated teeth of bransonelliiforms, symmoriiforms, a ctenacanthiform, a jalodontid, a euselachian, indeterminate protacrodontid and hybodontiform, anachronistid neoselachians, an orodontiform, a helodontiform, a eugeneodontiform, indeterminate petalodontiform, psephodontid and euchondrocephalian; as well as the buccopharyngeal denticles of symmoriiforms; and scales of various types. Rare acanthodian scales, and several actinopterygian teeth and scales also occur in this assemblage.

Besides the diverse fish assemblage from the Horquilla Formation of the Robledo Mountains, some new records

of Paleozoic chondrichthyans in New Mexico that were not included in recent reviews (Hodnett & Lucas 2015, 2017) are also documented here. These new occurrences increase the taxonomic diversity in the fish assemblages, and represent some taxa that are recorded in New Mexico for the first time: the fin spine of *Ctenacanthus* in the Upper Devonian and the teeth of *Bransonella* and *Sphenacanthus* in the Middle Pennsylvanian.

## Geological context

The Robledo Mountains are an isolated fault-block mountain range northwest of Las Cruces in southern New Mexico, USA (Fig. 1). Most of the strata exposed in the Robledo Mountains belong to the lower Permian Hueco Group (Lucas *et al.* 2015). However, on the northern tip of the range, below its summit at Robledo Mountain, an ~300 m thick section of Pennsylvanian marine strata of the Horquilla Formation is exposed (Krainer *et al.* 2015). Krainer *et al.* (2015) divided this section of the Horquilla Formation into five informal members (A–E, in ascending order) and documented fusulinids and conodonts that indicate the section ranges

in age from Early Pennsylvanian (Morrowan) to early Permian (Wolfcampian). Member B is ~24m thick and consists of shallowing upward cycles of shale-limestone (Fig. 2). Near the top of member B is a 0.1m-thick bed of conglomerate composed of limestone and chert clasts. This conglomerate is crossbedded, clast supported, and its clasts are subrounded to subangular and up to 5 cm in diameter. It contains the fish fossils documented here at NMMNH locality 12253. Conodonts from the conglomerate represent the *Idiognathodus cancellosus* conodont Zone, of early Missourian (early Kasimovian) age (Rosscoe & Barrick 2013, Barrick *et al.* 2013, Krainer *et al.* 2015).

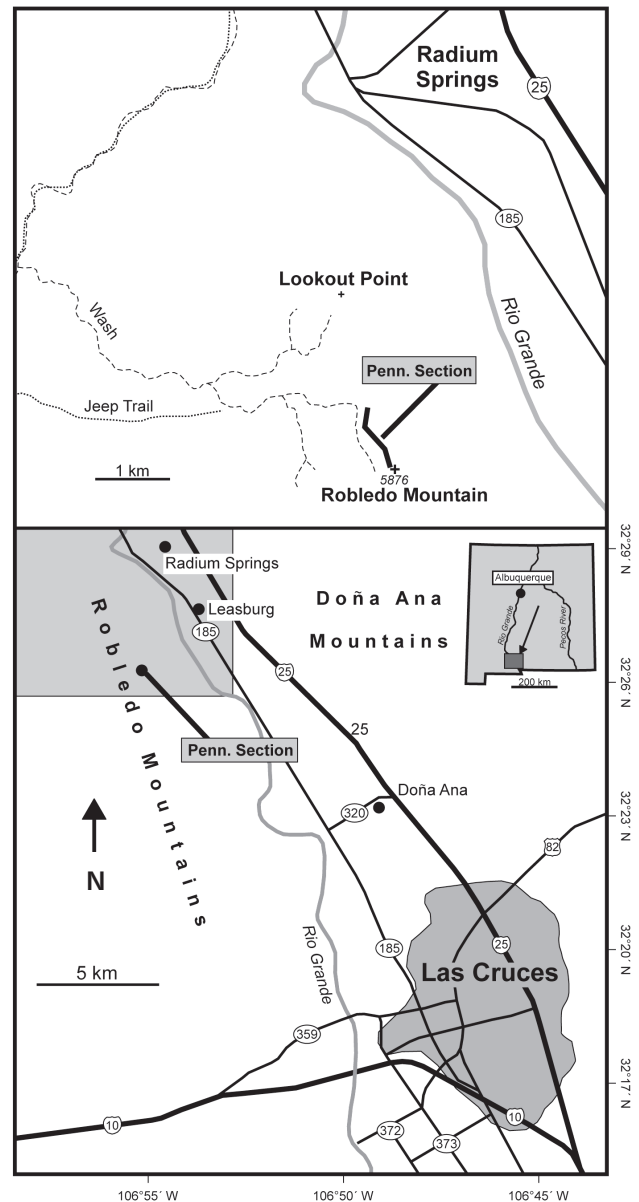
## Material and methods

Acetic acid was utilized to recover vertebrate micro- and rare macroremains from the samples of carbonate-cemented rocks. The microremains were microphotographed using the scanning electron microscopes Hitachi S-3400N, Cambridge CamScan-4 and Tescan VEGA-II XMU. The internal structure of some teeth was scanned with a SkyScan 1172 Bruker-microCT (Centre for X-ray Diffraction Studies of Research Park of the St. Petersburg State University) at a voltage of 55–96 kV and 104–167 mA, with an aluminium/copper or aluminium filter and a 180° rotation at the highest camera resolution with an average rotation step of 0.4°. The virtual cross-section images were generated from the 3D reconstruction using the software DataViewer, CTVox, and CTAn. The transparent mode of skeletal tissues was used for the reconstruction of the canal system.

The specimens described here are deposited in the collections of the New Mexico Museum of Natural History and Science, under specimens numbers NMMNH P-72263–72341.

## Fish assemblage from the Robledo Mountains

The assemblage includes diverse isolated teeth, tooth plates and scales (Figs 3–10) of chondrichthyans, rare scales of acanthodians, and actinopterygian microremains such as teeth, scales and fragments of skull bone. The preservation of fish microremains from the Horquilla Formation of the Robledo Mountains is variable, but most of the fossils are incomplete, and broken parts sometimes have abraded surfaces of differing degrees. Some groups of fishes such as petalodontiforms, orodontiforms, eugeneodontiforms, and actinopterygians, are represented by very fragmentary remains that mainly are parts of tooth crowns. The sections (Fig. 5O) and micro-CT images



**Figure 1.** Index maps showing the location of the Pennsylvanian (Penn.) section on the northern end of the Robledo Mountains, New Mexico, USA. Modified from Krainer *et al.* (2015).

(Figs 3L, M; 5P, Q) demonstrate the presence of fracture recrystallization of skeletal minerals and secondary deposition in the vascular canals. Some remains bear traces of bioerosion. A few specimens (for example, some teeth of *Adamantina* and *Helodus*, Figs 5E–H, 8E–K) are complete, with well preserved skeletal tissue.

## Chondrichthyans

A list of chondrichthyan taxa from the Horquilla Formation in the Robledo Mountains shows Tab. 1.

**Tab 1.** Chondrichthyan taxa from the Horquilla Formation in the Robledo Mountains.

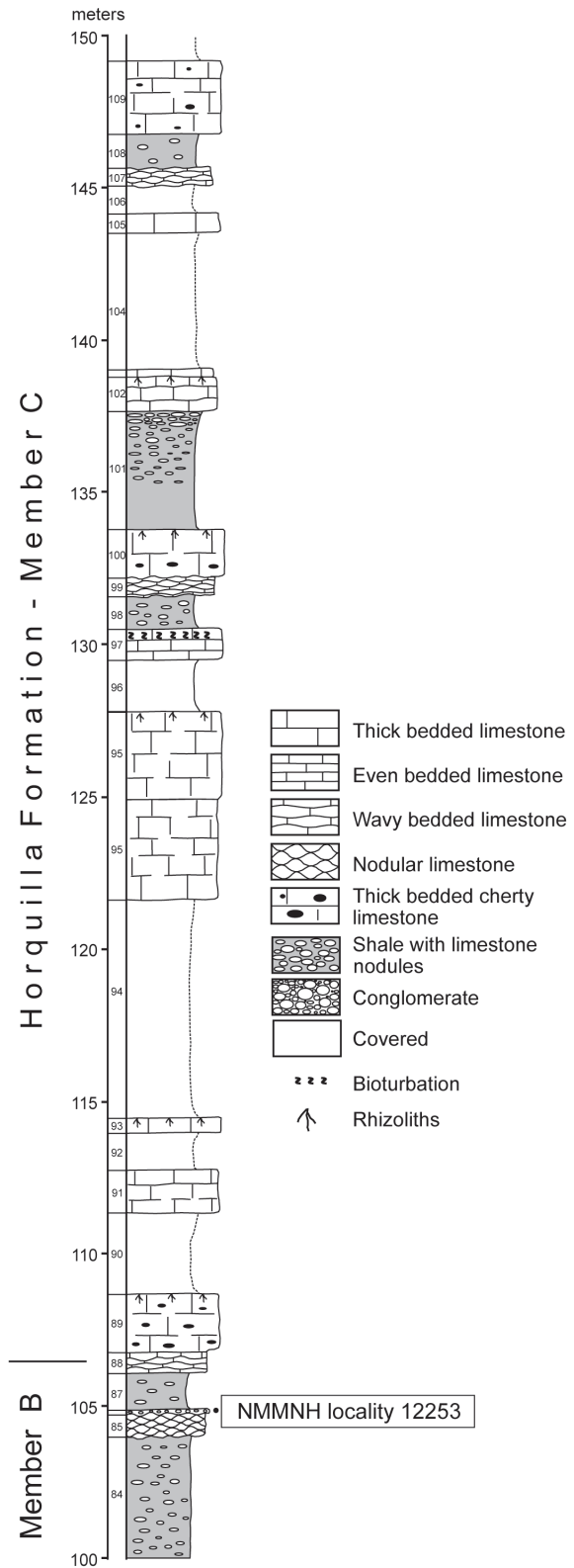
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Class Chondrichthyes Huxley, 1880

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Subclass: Elasmobranchii Bonaparte, 1838  
 Superorder Xenacanthomorpha Nelson, 1976  
 Order Bransonelliformes Hampe & Ivanov, 2007  
 Family indet.  
 Genus *Bransonella* Harlton, 1933  
     *Bransonella lingulata* Ivanov & Ginter, 1996  
     *Bransonella nebraskensis* (Johnson, 1984)  
 Superorder Cladodontomorphi Ginter, Hampe & Duffin, 2010  
 Order Symmoriiformes Zangerl, 1981  
 Family Symmoriidae Dean, 1909  
 Genus *Stethacanthus* Newberry, 1889  
     *Stethacanthus* sp.  
 Family Falcataidae Zangerl, 1990  
 Genus *Denaëa* Pruvost, 1922  
     *Denaëa* sp.  
 Symmoriiformes indet.  
 Order Ctenacanthiformes Glikman, 1964  
 Family Hesslerodidae Maisey 2010  
 Genus *Glikmanius* Ginter, Ivanov & Lebedev, 2005  
     *Glikmanius* sp.  
 Elasmobranchii incertae sedis  
 Order indet.  
 Family Jalodontidae Ginter, Hairapetian & Klug 2002  
 Genus *Adamantina* Bendix-Almgreen, 1993  
     *Adamantina foliacea* Ivanov, 1999  
 Cohort Euselachii Hay, 1902  
 Superfamily Protacrodontoidea Zangerl, 1981  
 Family Protacrodontidae Cappetta, Duffin & Zidek, 1993  
 Genus *Protacrodus* Jaekel, 1925  
     *Protacrodus* sp.  
 Protacrodontidae indet.  
 Order Hybodontiformes Maisey, 1975  
 Hybodontiformes indet.  
 Euselachii indet.  
 Subcohort: Neoselachii Compagno, 1977  
 Division Neoselachii Compagno, 1977  
 Order indet.  
 Family Anachronistidae Duffin & Ward, 1983  
 Genus *Cooleyella* Gunnell, 1933  
     *Cooleyella amazonensis* Duffin, Richter & Neis, 1996  
     *Cooleyella* cf. *fordi* (Duffin & Ward, 1983)  
     *Cooleyella* sp.  
 Subclass Euchondrocephali Lund & Grogan, 1997  
 Infraclass Paraselachii Grogan & Lund, 2000  
 Order Orodontiformes Zangerl, 1981  
 Family Orodontidae De Konnick, 1878  
     *Orodus* sp.  
 Order Eugeneodontiformes Zangerl, 1981  
 Superfamily Edestoidea Hay, 1929  
 Family Agassizodontidae Zangerl, 1981  
 Genus *Agassizodus* St. John & Worthen, 1875  
     *Agassizodus* sp.  
 Eugeneodontiformes indet.  
 Order Petalodontiformes Zangerl, 1981  
 Petalodontiformes indet.  
 Superorder Holocephali Bonaparte, 1832–1841  
 Order Helodontiformes Patterson, 1965  
 Family Helodontidae Patterson, 1965  
 Genus *Helodus* Agassiz, 1838  
     *Helodus* sp.  
 Order Cochliodontiformes Obruchev, 1953  
 Family Psephodontidae Zangerl, 1981  
 Psephodontidae indet.  
 Euchondrocephali indet.

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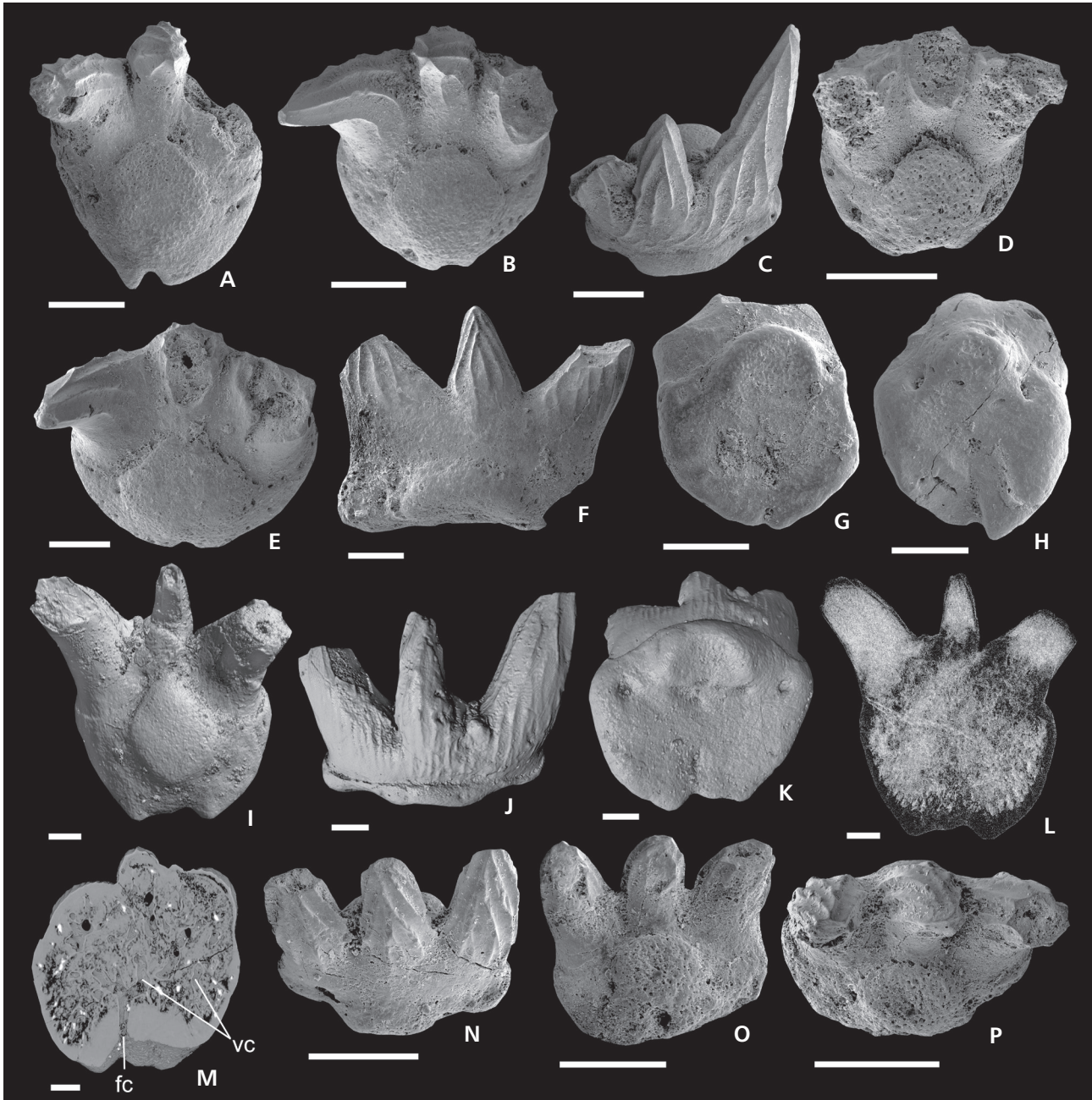
**Figure 2.** Part of the Pennsylvanian stratigraphic section at Robledo Mountain showing the location (bed 86) of NMMNH locality 12253, from which the fossil fishes reported here were collected. Modified from Krainer *et al.* (2015), where the complete Pennsylvanian section is illustrated.

### Bransonelliforms

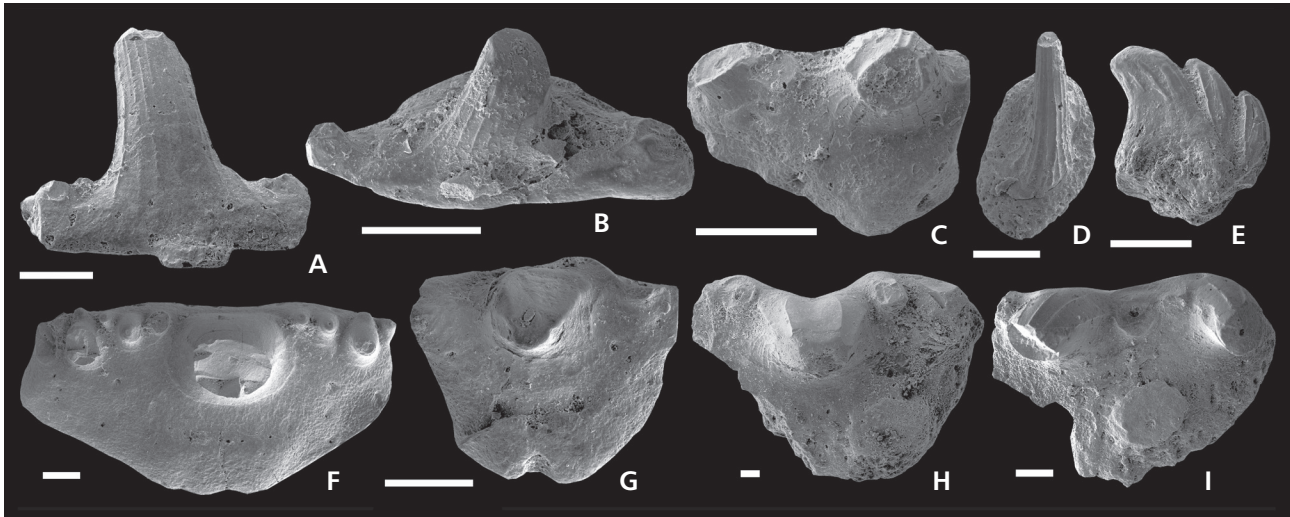
The assemblage contains numerous isolated teeth of *Bransonella*, among them 64 teeth of *B. lingulata* Ivanov & Ginter, 1996 and 6 teeth of *B. nebraskensis* (Johnson, 1984). The bransonelliform teeth of both species are

incomplete (Fig. 3), with poorly preserved dental tissue, and secondary deposition into the vascular canals and fractures (Fig. 3L, M).

The teeth of *Bransonella lingulata* Ivanov & Ginter, 1996 (Fig. 3A–M) possess a tricuspid, diplodont crown with higher and wider lateral cusps than the central one. The



**Figure 3.** Teeth of the xenacanthimorph *Bransonella*, Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian (A–H, N–P – scanning electron micrographs; I–M – micro-CT images). • A–M – *Bransonella lingulata* Ivanov & Ginter, 1996; A – NMMNH P-72263, occlusal view; B, C – NMMNH P-72264, occlusal (B) and labial (C) views; D – NMMNH P-72265, occlusal view; E – NMMNH P-72266, occlusal view; F – NMMNH P-72267, labial view; G – NMMNH P-72268, basal view; H – NMMNH P-72269, basal view; I–M – NMMNH P-72270, oblique occlusal (I), labial (J) and basal (K) views, view with transparent dental tissue (L) and virtual section of tooth base (M). • N–P – *Bransonella nebraskensis* (Johnson, 1984), NMMNH P-72271, labial (N), lingual (O) and occlusal (P) views. Scale bars = 0.3 mm. Abbreviations: fc – foramen of vascular canal; vc – vascular canal.



**Figure 4.** Microremains of symmoriiforms (A–G) and ctenacanthiforms (H, I), Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian. • A–C – teeth of *Denaea* sp.; A – NMMNH P-72272, labial view; B – NMMNH P-72273, oblique labial view; C – NMMNH P-72274, occlusal view. • D – symmoriiform monocuspid denticle, NMMNH P-72278, crown view. • E – symmoriiform buccopharyngeal denticle (“*Stemmatias*” type), NMMNH P-72277, lateral view. • F, G – teeth of *Stethacanthus* sp., occlusal views: F – NMMNH P-72275; G – NMMNH P-72276. • H, I – teeth of *Glikmanius* sp., occlusal views; H – NMMNH P-72279; I – NMMNH P-72280. Scale bars = 0.2 mm.

lateral cusps are almost round in cross section, but the central cusp is compressed mesio-distally. The well preserved cusps are acuminate and bear an inverted “V”-nested ornamentation on the labial side and a straight crista on the lingual side. The labial ornamentation can reach the crown/base boundary (Fig. 3C, J) but sometimes the cristae cover only the upper part of the crown (Fig. 3F). One tooth bears a tiny intermediate cusplet between the central and lateral cusps (Fig. 3J). The lingually extended tooth bases range from oval to circular in shape, and vary in width. The base possesses a prominent apical button occupying almost the entire occlusal surface and a semilunar labio-basal tubercle at the labial rim. The apical button varies from oval to round in shape. The width of the button and of the labio-basal tubercle corresponds to the width and shape of the base. The foramen of the main vascular canal perforates the linguo-basal part of the base, forming a distinct notch at the lingual rim. The small foramina of the secondary vascular canals surround the apical button (Fig. 3D, E). Two foramina of the lateral canals open on both sides of the labio-basal tubercle (Fig. 3H, K).

The teeth of *Bransonella nebraskensis* (Johnson, 1984) (Fig. 3N–P) have a tricuspid crown with a central cusp that is just a little shorter than the lateral ones. All cusps are rounded in cross section and the same size at the crown/base junction. The inverted “V”-nested ornamentation of the cusps is slightly twisted. The oval tooth base bears a prominent, circular apical button that does not reach the lingual rim (Fig. 3O). The foramen of the main vascular canal opens between the button and the lingual rim. The distinct labio-basal tubercle is semilunar and does not extend labially (Fig. 3N).

### Symmoriiforms

The symmoriiform remains include 24 isolated, fragmentary teeth of *Denaea* sp., four isolated, incomplete teeth of *Stethacanthus* sp., and several denticles. The poorly preserved teeth of *Denaea* (Fig. 4A–C) possess the cladodont crown with high central and moderate lateral cusps. The intermediate cusplets are not preserved. The cusps are round in cross section. The central cusp is lingually inclined, slightly incurved and covered by straight tiny cristae on both the labial and the lingual sides. The tooth base is triangular in shape, with a pointed part of the lingual rim. The distinct, rounded apical button is located at the lingual rim. The labio-basal tubercle is prominent, oval in shape, and extends mesio-distally.

The incomplete teeth of *Stethacanthus* sp. (Fig. 4F, G) have a crown consisting of a large central cusp and nine small cusps and cusplets. The central cusp is compressed labio-lingually, and the other cusps are round in cross section. One pair of cusps is higher and wider than the other intermediate ones. One accessory cusplet is placed labial to the line of cusps. The cusp ornamentation is not preserved. The tooth base is subtriangular in shape, with an extended lateral part that is prominent on the labial edge of the lateral parts of the crown. The large apical button is rectangular in outline, located at the lingual rim and separated from the central cusp by a shallow depression.

The symmoriiform denticles contain the monocuspid (Fig. 4D) and multicuspid, spiral-like (Fig. 4E) denticles. The first one has a high, conical cusp flattened laterally, inclined posteriorly and covered by straight cristae. The prominent denticle base is oval in shape, with a prominent

basal side. Such denticles belong to denticles from the spine-brush complex of some symmoriiforms (e.g., Coates & Sequeira 2001). The multicuspoid denticles (Fig. 4E) have three to five recurved, elongate cusps consecutively overlapping each other. The cusps bear coarse cristae. The base is extended basally and anteriorly. These denticles are buccopharyngeal or mucous membrane denticles (Zangerl & Case 1976, Williams 1985, Coates & Sequeira 2001), and were described as the formal taxon “*Stemmatias (Stemmatodus)*” (St. John & Worthen 1875).

### *Ctenacanthiformes*

Six isolated teeth of the ctenacanthiform *Glikmanius* (Fig. 4H, I) are fragmentary and poorly preserved. They possess cladodont crowns with large central and moderate-sized lateral cusps separated by one or two small intermediate cusps. The main cusps are compressed labio-lingually, and bear a few distinct, straight cristae. The tooth base is semicircular in shape, elongated mesiodistally, and extended lingually. Two rounded apical buttons are located at a considerable distance from each other on the occlusal side of the base. The deep labial depression is separated by two oval, labio-basal tubercles.

### *Jalodontids*

The jalodontid remains include 56 isolated teeth and tooth fragments of *Adamantina foliacea* Ivanov, 1999 in varying preservation (Fig. 5). The teeth possess a crown consisting of three to five cusps and a lingually extended base. The cusps are wide, triangular in shape, slightly labio-lingually compressed and inclined lingually. They bear strong, lanceolate ornamentation on the labial side and rare, straight cristae on the lingual side. There are two or three lanceolate ridges. The short, straight or incurved additional ridges are placed inside the lanceolate ridges. The cusps in the tricuspid crown are equal in height and fused in their basal part (Fig. 5A–F). The upper parts of the lateral cusps can diverge from the central cusp. The crown with four cusps has three almost equal cusps and an accessory lateral cusp, sometimes inclined mesially or distally. This lateral cusp can be tiny (Fig. 5H, J) or moderate in size but lower than the main cusps (Fig. 5K–M). The lanceolate ridges on such crowns are common in main and accessory lateral cusps, and one ridge is traced on both cusps (Fig. 5K, L). The five-cusped crown has a high central, moderate intermediate and small lateral cusps forming a fan-shaped structure (Fig. 5N). The intermediate cusps are shorter than the central one but they have the same width. The cusps in a five-cusped crown are separated by deep notches. The crown/base junction is poorly developed in tricuspid teeth, and narrow in multicuspoid ones.

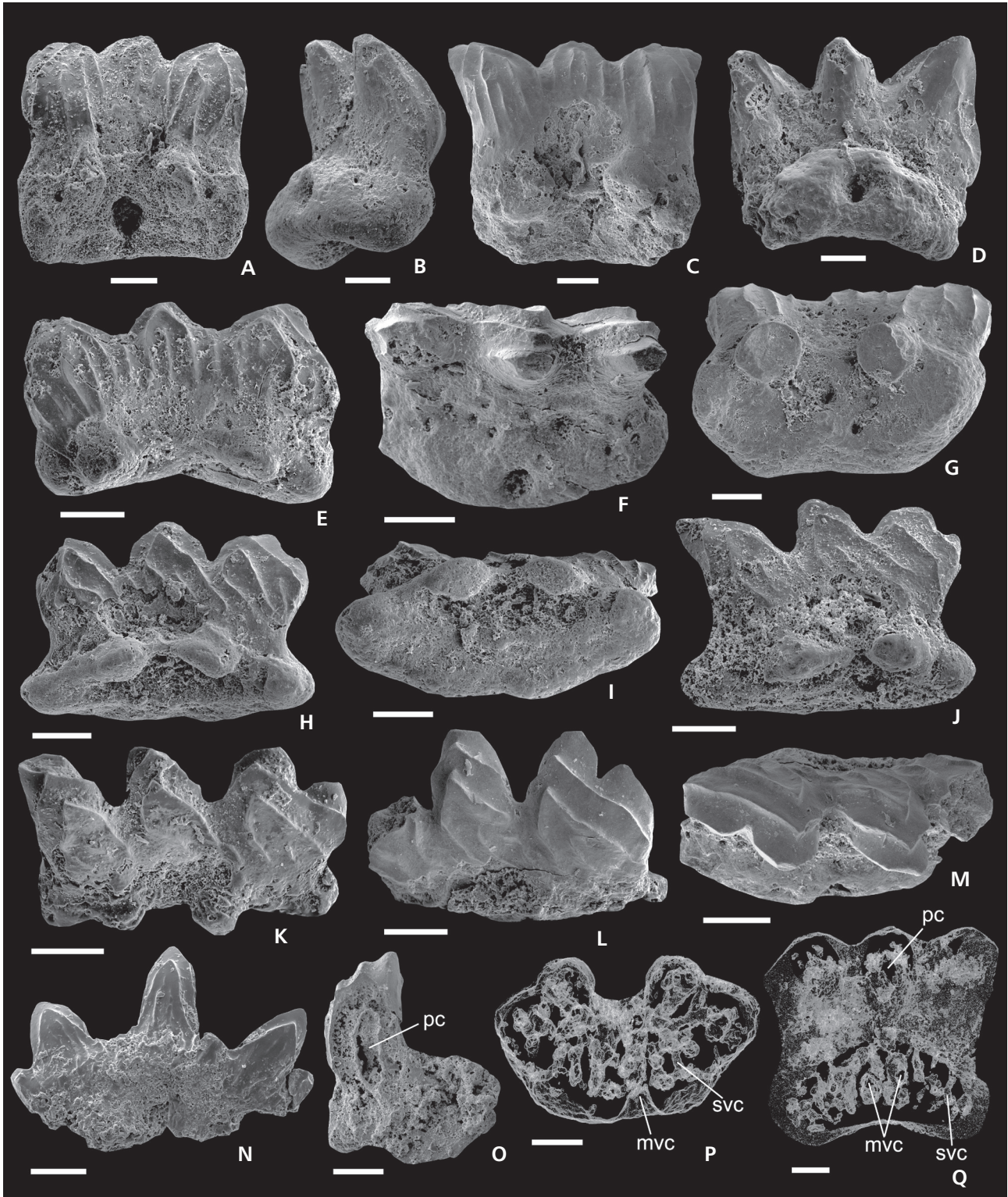
The tooth base is thick, with smooth, convex occlusal and slightly concave basal surfaces, and is arched, especially in tricuspid teeth. Two labio-basal tubercles are prominent, round or oval, and separated from each other by a wide depression (Fig. 5E, K). Their shape and size, as well as the distance between them vary: the circular tubercles can be placed far apart (Fig. 5A–G), or the oval tubercles are nearly in contact with each other (Fig. 5H–J). The large foramina of the main vascular canal penetrate the occlusal surface, at the lingual rim (Fig. 5D, F) and in the concave part of the basal side (Fig. 5A, G). The numerous tiny foramina open in the shallow groove on the occlusal side, near the crown/base junction.

The vascularization system of the *Adamantina* teeth contains the main, secondary and pulp canals (Fig. 5O–Q). The large main canal passes across the tooth base, from the lingual rim to the labial depression. The numerous short and narrow secondary canals are branched from the main one, and extended on the new branch. Two long canals open on the outside of the basal tubercles. The pulp canals are very wide and their width does not change on almost the entire height of the cusp (Fig. 5O).

### *Euselachians*

The assemblage contains the isolated teeth of protacrodontids, hybodontiforms and an undetermined euselachian. Protacrodontid remains are represented by nine incomplete teeth of *Protacrodus* sp. and 16 fragmentary teeth of an undetermined protacrodontid. They mainly include fragments of the tooth crown. The teeth of *Protacrodus* (Fig. 6A–F) possess a pyramidal crown that is labio-lingually compressed. The cusps are gradually arranged by their height, fused basally, often inclined mesially or distally, and covered by coarse cristae. The cristae diverge from the cusp apex, and are wavy and bifurcate. The accessory cusplets may occur between lateral cusps (Fig. 6C). The base is slightly lingually extended and arched. The rows of canal foramina occur on the labial and occlusal sides. Most of the *Protacrodus* teeth have two to four pairs of lateral cusps, and a wide central cusp that is slightly higher than the lateral ones (Fig. 6A–C, F). These teeth are very similar to the teeth of *Protacrodus vetustus* Jaekel, 1925 (e.g., Ginter *et al.* 2010). But, several teeth possess a very high and wide central cusp, and only one pair of small lateral cusps (Fig. 6D, E). Such teeth resemble the tooth morphotype 1 of *Protacrodus serra* Ginter, Hairapetian & Klug, 2002 (Ginter *et al.* 2002, text-fig. 11a–e, pl. 11, fig. a).

The incomplete teeth of an undetermined protacrodontid (Fig. 6G–J) have a monolithic, slightly pyramidal crown with an occlusal crest. Coarse ridges diverge from the crest on the labial and lingual sides of the crown. The ridges on the labial side are terminated in the prominent



**Figure 5.** Teeth of the jalodontid *Adamantina foliacea* Ivanov, 1999; Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian (A–O – scanning electron micrographs; P, Q – micro-CT images in transparent model); A – NMMNH P-72302, oblique labial view; B, P, Q – NMMNH P-72303, lateral view (B), virtual sections of base (P) and tooth in lingual view (Q); C – NMMNH P-72304, oblique labial view; D – NMMNH P-72305, lingual view; E – NMMNH P-72306, labial view; F – NMMNH P-72307, occlusal view; G – NMMNH P-72308, basal view; H, I – NMMNH P-72309, labial (H) and basal (I) views; J – NMMNH P-72310, labial view; K – NMMNH P-72311, labial view; L, M, NMMNH P-72312, labial (L) and occlusal (M) views; N – NMMNH P-72313, labial view; O – transversal cross-section of tooth, NMMNH P-72314. Scale bars = 0.1 mm. Abbreviations: mvc – main vascular canal; pc – pulp canal; svc – secondary vascular canal.

projection separated by deep notches (Fig. 6G, H). These projections become wider in the direction of the crown center (Fig. 6G). The tooth base is extended lingually and perforated by large foramina on the occlusal surface (Fig. 6G, I). These teeth resemble the teeth of *Deihim mansur- eae* Ginter, Hairapetian & Klug, 2002 from Iran and Armenia (Ginter *et al.* 2010), from Australia (Roelofs *et al.* 2015, 2016), and especially the teeth of that species from New Mexico (Ivanov & Lucas 2011). But the tooth crown of *Deihim* is pyramidal with prominent cusps and without an occlusal crest, but bears the distinct labial cusplets unrelated to the crown ornamentation. These protacrodontid teeth described here probably belong to a new genus.

Two isolated tooth crowns of an undetermined hybodontiform (Fig. 6N) possess a triangular central cusp, prominent labial peg and ridges on the labial and lingual sides. The ridges are extended basally and form the projections separated by depressions. The short ridges occur on the labial peg. These tooth crowns resemble some Paleozoic lonchidiid teeth attributed to “*Lissodus*” sp. (e.g., Duncan 2004, Ivanov & Lebedev 2014). However, lonchidiid teeth possess a well-developed occlusal crest and extended labial peg.

The isolated tooth of a peculiar undetermined euselachian (Fig. 6K–M) has a tricuspid smooth crown with large, triangular central and small, rounded lateral cusps. The crown is compressed labio-lingually and partly separated from the base by a shallow depression (Fig. 6L). The tooth base is considerably extended lingually and slightly labially (Fig. 6M), with a sloped lingual part. The large foramina of the vascular canals perforate the lingual and basal surfaces.

### Neoselachians

The neoselachians are represented by teeth of the anachronistids *Cooleyella amazonensis* Duffin, Richter & Neis, 1996, *Cooleyella cf. fordi* (Duffin & Ward, 1983) and *Cooleyella* sp. The assemblage contains 20 isolated teeth and tooth fragments of *C. amazonensis* Duffin, Richter & Neis, 1996 (Fig. 7A–E). These small teeth possess a smooth crown that is wider than the base. The crown bears a distinct occlusal crest separating the trapezoidal, sloping labial and short, almost vertical lingual faces (Fig. 7E). The small to moderate central cusp is placed on the crest. The crown has a short and wide labial flange, and rounded lateral blades (Fig. 7A, C). The crown/base junction is deep, and the crown overhangs the base laterally and labially. The narrow tooth base is semilunar in shape, with extended, convex lingual and very narrow labial surfaces (Fig. 7D). The rounded lingual edge is perforated by the foramen of the main vascular canal. The convex basal surface bears a small, round basal tubercle and an oval pit of the pulp cavity (Fig. 7D).

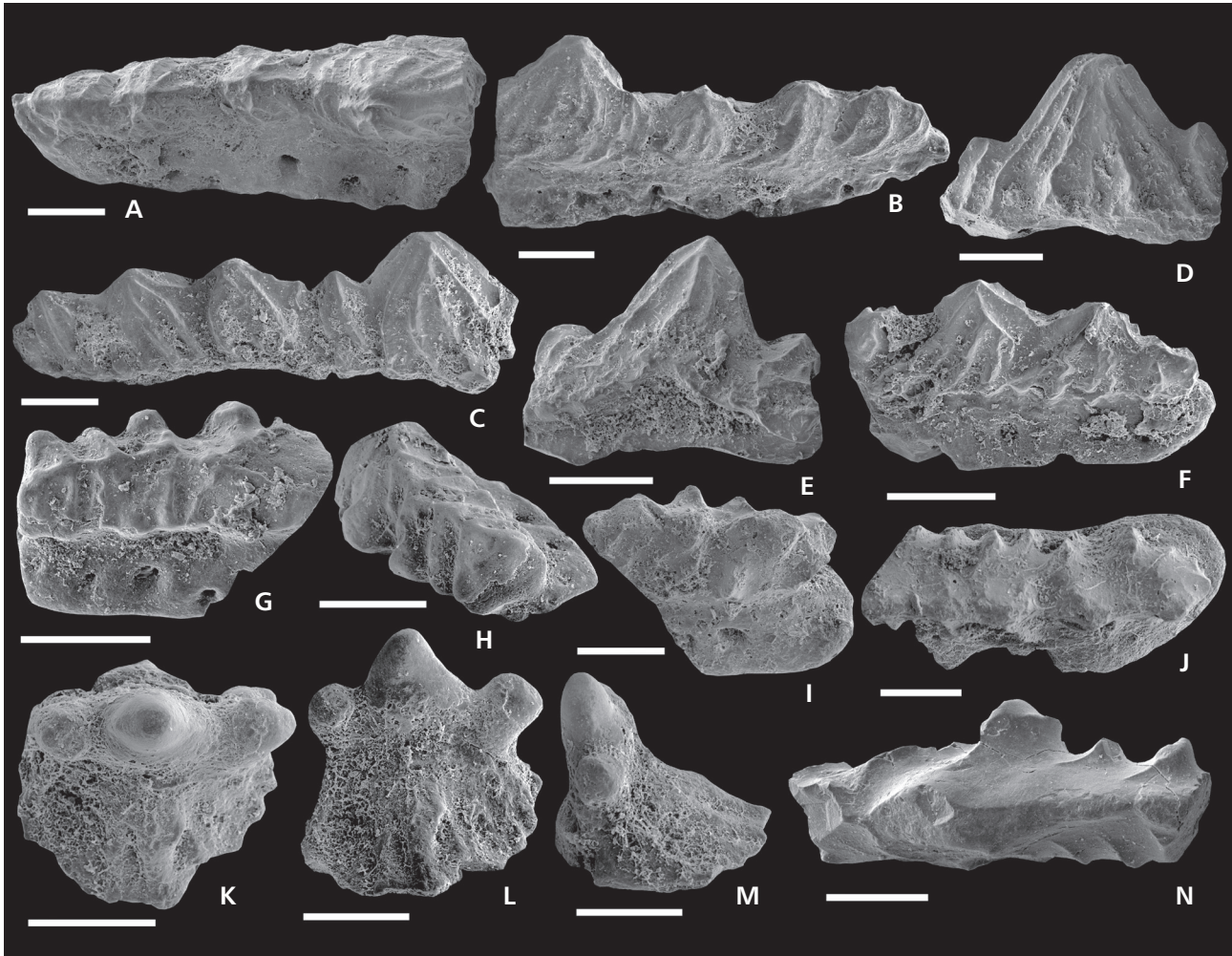
The microremains of *Cooleyella cf. fordi* (Duffin & Ward, 1983) include 14 isolated teeth and tooth fragments (Fig. 7H–M). These teeth are extended mesio-distally, and have a crown narrower than the base. The crown has three cusps separated by depressions (Fig. 7I); long, sloping labial and short lingual faces; a long, almost triangular labial flange (Fig. 7K); acuminate lateral blades (Fig. 7H, K); and a discontinuous occlusal crest. The central cusp is prominent, larger than the lateral ones (Fig. 7I, J), and rounded in cross section. The crown/base junction is incised and narrow, with a distinct labial and lingual groove. The tooth base is oval in shape, considerably extended lingually and laterally, and has a convex lingual, very short labial and concave basal surfaces. The foramen of the main vascular canal is perforated along the lingual rim, often forming a small notch. A basal tubercle is oval in shape, and placed beneath the labial flange (Fig. 7I). The convex basal surface bears a large pit of the pulp cavity and a narrow depression surrounding the basal tubercle.

Five isolated teeth of *Cooleyella* sp. (Fig. 7F, G) possess the crown and base of the same size or the crown slightly wider than the base. The crown of some teeth is asymmetrical. The crown has a prominent central and small lateral cusps; tiny tubercle-like cusplets are placed between the cusps (Fig. 7F). The occlusal crest is poorly developed and discontinued by a narrow depression that surrounds the central cusp. The labial flange and lateral blades of the crown are acuminate (Fig. 7F). The crown/base junction is rather narrow. The tooth base has a lingual extension and rounded basal tubercle. These teeth differ from the teeth of *Cooleyella amazonensis* Duffin, Richter & Neis, 1996 in their long, acuminate labial flange, tubercle-like cusplets, and larger base with a wide basal tubercle; the teeth of *Cooleyella cf. fordi* (Duffin & Ward, 1983) are distinguished from the teeth of *Cooleyella* sp. in the considerably shorter base; longer labial flange; and round shape of the basal tubercle.

### Euchondrocephalians

The diverse euchondrocephalians (Figs 8, 9) include orodontiforms, helodontiforms, cochliodontiforms, eugeneodontiforms, petalodontiforms and unidentified euchondrocephalians. Most of the euchondrocephalian remains, such as those of petalodontiforms, orodontiforms, and eugeneodontiforms, are very fragmentary and include the incomplete tooth crowns; but some teeth are complete and well preserved. Two isolated and incomplete tooth crowns of an unidentified euchondrocephalian are present in the assemblage (Fig. 8L). They are considerably elongated mesio-distally, with prominent central and sloped lateral parts, and with a small, triangular lingual peg slightly dislocated from the central prominence. These tooth crowns are slightly similar to the crown of some *Helodus*,





**Figure 6.** Teeth of euselachians; Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian. • A–F – *Protacrodus* sp.; A, B – NMMNH P-72281, occlusal (A) and labial (B) views; C – NMMNH P-72282, tooth crown, labial view; D – NMMNH P-72283, tooth crown, labial view; E – NMMNH P-72284, labial view; F – NMMNH P-72285, labial view. • G–J – Protacrodontidae indet.; G, H – NMMNH P-72286, oblique occlusal (G) and lateral (H) views; I – NMMNH P-72287, oblique occlusal view; J – NMMNH P-72288, occlusal view. • K–M – Euselachii indet., NMMNH P-72289, occlusal (K), lingual (L) and lateral (M) views. • N – Hybodontiformes indet., NMMNH P-72288, tooth crown, occlusal view. Scale bars = 0.2 mm.

*Leiodus* and *Fadenia* (Stahl 1999, Ginter *et al.* 2010), but the preservation of the teeth prevents their genus-level identification.

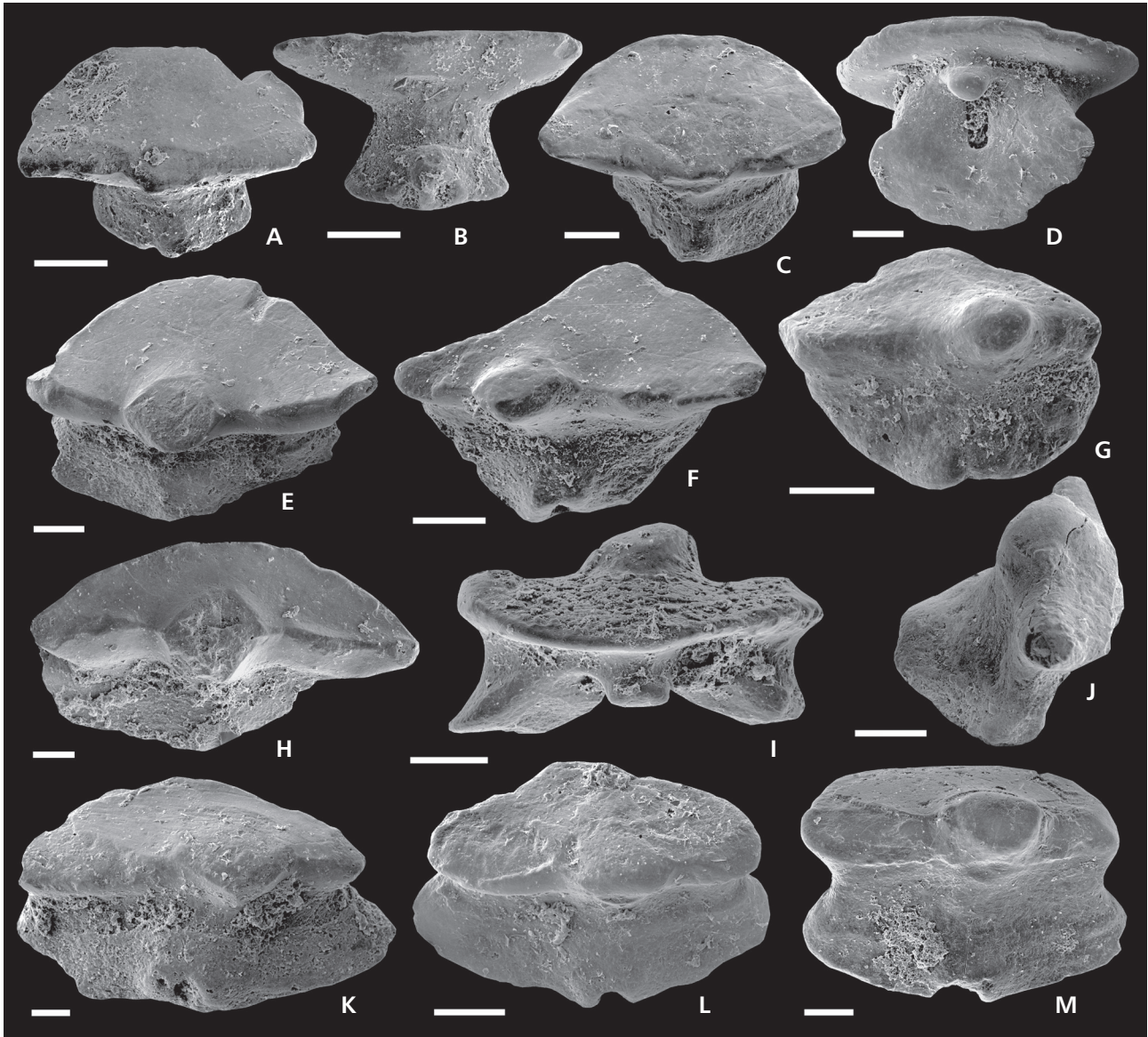
### Orodontiforms

The microremains of *Orodus* sp. are represented by three isolated tooth crowns with only small fragments of the tooth base preserved (Fig. 8A–C). The tooth crown is pyramidal, elongated mesio-distally, with a prominent central cusp. The crown is covered by anastomosing, incurving coarse ridges, sometimes dividing on different levels. The ridges diverge from the tip of the central cusp. The central cusp is round in cross section, and separated from the remaining crown by narrow but shallow grooves. The teeth resemble some morphotypes of *Orodus mammillaris*

Newberry & Worthen, 1866 from the Upper Devonian and Mississippian of the USA (Ginter *et al.* 2010).

### Helodontiforms

The assemblage includes seven isolated teeth and tooth crowns of *Helodus* sp. (Fig. 8D–K). Some of the tooth crowns and teeth are very well preserved. The teeth possess a crown that is elongated mesio-distally, with a prominent central part, sloped mesial and distal parts, an extended, pointed labial peg, and large tubule openings on the occlusal surface. The small teeth have a weakly developed occlusal crest (Fig. 8D). The crown is wider than the tooth base, and overhangs the base on the labial side. The crown is separated from the base by a deep groove on the lingual and labial sides. This groove is not developed in



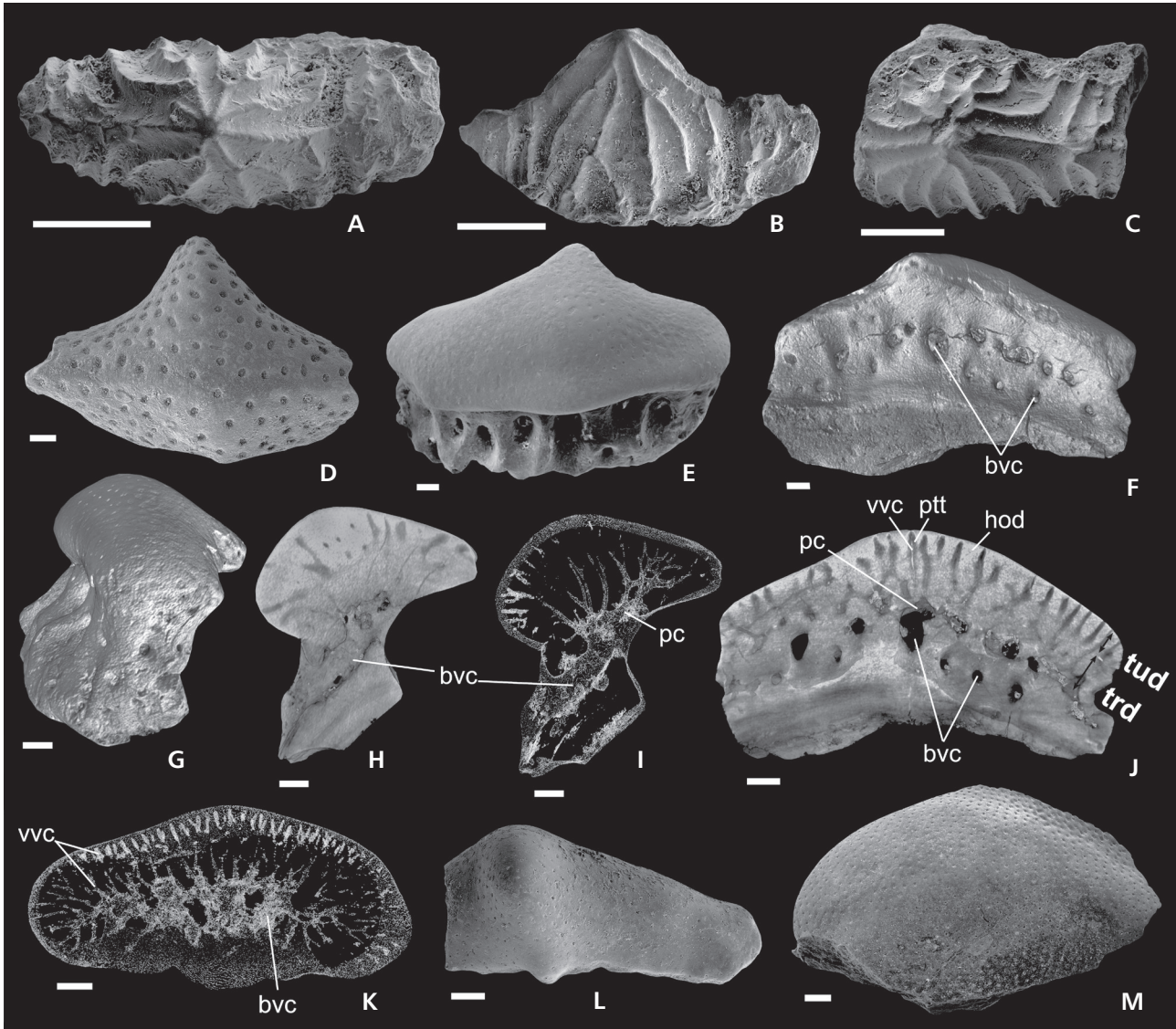
**Figure 7.** Teeth of the neoselachian *Cooleyella*; Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian. • A–E – *Cooleyella amazonensis* Duffin, Richter & Neis, 1996; A, B – NMMNH P-72290, occlusal (A) and lingual (B) views; C – NMMNH P-72291, occlusal view; D – NMMNH P-72292, oblique labial view; E – NMMNH P-72293, occlusal view. • F, G – *Cooleyella* sp., occlusal views; F – NMMNH P-72294; G – NMMNH P-72295. • H–M – *Cooleyella* cf. *fordi* (Duffin & Ward, 1983); H – NMMNH P-72296, occlusal view; I – NMMNH P-72297, labial view; J – NMMNH P-72298, lateral view; K – NMMNH P-72299, occlusal view; L – NMMNH P-72300, occlusal view; M – NMMNH P-72301, oblique occlusal view. Scale bars = 0.1 mm.

the lateral corners. The tooth base is extended lingually and arched, with slightly convex, ridged occlusal and almost flat basal surfaces. The base is perforated by numerous large foramina of vascular canals. They form rows on the lingual and labial sides. The tooth crown consists of the tubular dentine with a hypermineralized layer in the upper part and trabecular dentine in the basal part (Fig. 8H–K). The divided vertical vascular canals in the crown are surrounded by peritubular trabeculine. These canals rise into the hypermineralized layer of the crown (Fig. 8J). The lower part of the tooth base is composed of solid lamellar

tissue. The wide and short basal vascular canals penetrate across the tooth base and branch in the lower part of the crown, connecting the vertical canals and weakly developed pulp cavity (Fig. 8I). The basal canals are connected with each other by short ramifications (Fig. 8K).

#### *Cochliodontiforms*

The cochliodontiform remains include five isolated incomplete tooth plates of unidentified psephodontids (Fig. 8M). They are the poorly preserved, thick, central part of



**Figure 8.** Euchondrocephalian teeth and tooth plate; Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian (A–E, L, M – scanning electron micrographs; F–K – micro-CT images). • A–C – *Orodus* sp., tooth crowns; A, B – NMMNH P-72315, occlusal (A) and labial (B) views; C – NMMNH P-72316, occlusal view. • D–K – *Helodus* sp.; D – NMMNH P-72317, tooth crown, occlusal view; E–K – NMMNH P-72318, tooth, oblique occlusal (E), labio-basal (F) and lateral (G) views, transverse (H, I in transparent mode) and sagittal (J) virtual sections of tooth, frontal virtual section of crown (K in transparent mode). • L – Euchondrocephali indet., NMMNH P-72319, tooth crown, occlusal view. • M – Psephodontidae indet., NMMNH P-72320, tooth plate, occlusal view. Scale bars = 0.5 mm. Abbreviations: bvc – basal vascular canal; hod – hypermineralized orthodontine; pc – pulp cavity; ptt – peritubular trabeculine; trd – trabecular dentine; tud – tubular dentine; vvc – vertical vascular canal.

the tooth plate with broken edges. The preserved part of the tooth plates is arched, with a very prominent, hemispherical central part on the occlusal side, and concave on the basal side. Numerous small foramina penetrate the occlusal surface.

### *Eugeneodontiforms*

The eugeneodontiforms are represented in the assemblage by 10 isolated crowns and fragments of *Agassizodus* lateral teeth, as well as two isolated tooth crowns of indeter-

minate eugeneodontiforms. The fragmentary teeth of *Agassizodus* sp. (Fig. 9A–H) possess the crown, which is strongly elongated mesio-distally and compressed labio-lingually. The crown bears a low central cusp (Fig. 9B), a wavy occlusal crest and long, serrated buttresses on the labial side (Fig. 9D, E). The ridges of differing lengths diverge from the occlusal crest on the labial and lingual sides: the long, serrated ridges – on the lingual side, from the central cusp and opposite of the buttress; the short ridges – on both the labial and lingual sides, between the buttresses and long ridges (Fig. 9B, D). The occlusal surface also bears small tubercles

that often form a row (Fig. 9C, D). The crown is composed of tubular dentine with a hypermineralized orthodontine layer (Fig. 9F–H). The numerous thin vertical canals are surrounded by a tiny layer of peritubular trabeculine (Fig. 9H). They diverge from the basal canal and rarely branch.

The tooth crowns of an indeterminate eugeneodontiform (Fig. 9I–L) are very elongate mesio-distally, and possess a central swollen part, the labial buttresses and a distinct, wavy occlusal crest. The labial buttress is long in the central part and short in the lateral parts (Fig. 9I). The wavy ridges are placed on the labial buttress and opposite of the lingual side (Fig. 9I). The vertical vascular canals are divided and strongly diverged (Fig. 9J), and arranged in two parallel rows (Fig. 9K, L). These tooth crowns slightly resemble the teeth of *Gilliodus* (Ginter *et al.* 2010).

### *Petalodontiforms*

Four isolated tooth fragments of unidentified petalodontiforms (Fig. 9M, N) are found in the assemblage. These poorly preserved fragments are a small part of the tooth crown near the cutting edge. One fragment is the top acuminate part with an abraded surface and visible vertical vascular canals (Fig. 9M). Other fragments are small pieces of the sloped part of the tooth crown with a sharp cutting edge and imbricated ridges (Fig. 9N).

### *Chondrichthyan scales*

The chondrichthyan scales in the assemblage include various morphotypes such as ctenacanthid, euselachian, protacrodontid and orodontid, as well as a tessera-like scale. The scales of ctenacanthid type (Fig. 10A–C) possess a polyodontode crown that is curved backward and serrated posteriorly. The crown consists of triangular central and long, narrow lateral odontodes arranged subparallel to each other and separated by narrow grooves. The odontodes are ornamented with thin ridges. The scale neck is narrow and shallow, or weakly developed. The base is oval or round in outline, with a concave basal side.

The tessera-like scales (Fig. 10D) have a low polyodontode crown and large oval base. The odontodes are triangular tubercles of different sizes, partly fused and form the compact crown. The base has flat external and convex basal surfaces. Similar scales are often determined as head scales (*e.g.*, Burrow *et al.* 2009), and similar scales were described as those of *Adamantina benedictae* Bendix-Almgreen, 1993.

The numerous euselachian scales have a crown that ranges from low, drop-like (Fig. 10F) to high, elongate (Fig. 10E). The crown is inclined and pointed posteriorly, and bears strong ridges of different sizes. The scale neck is well developed, narrow and deep. The base has convex

external and concave basal surfaces, and a serrated edge with projections of different length and small notches.

The scales of protacrodontid type possess a flat, low, monolithic, polyodontode crown, narrow neck and a prominent, hemispherical base slightly larger than the crown. These scales are represented by two morphotypes. The first one has a wide central part from fused odontodes, and elongate, narrow lateral odontodes (Fig. 10G). The boundaries of the odontodes in some parts of the crown are poorly distinguished. Such scales were described from a fragment of squamation in *Protacrodus vetustus* Jaekel, 1925 (Gross 1938). The second morphotype of scales (Fig. 10H) possesses a crown with a compact odontocomplex containing a central primordial odontode and surrounded by additional odontodes with distinct boundaries. Similar scales were described as *Holmesella* (Ørvig 1967) or orodontid scales (Ivanov & Nilov 2017).

Besides the scales, the assemblage contains two spine-like denticles (Fig. 10I). These denticles have a monocuspid crown with a long, laterally compressed cusp covered by strong ridges. The latter are extended at the anterior edge where the ridges are bifurcated. The base is flat on the basal side, larger than the crown, extended anteriorly and narrowed posteriorly.

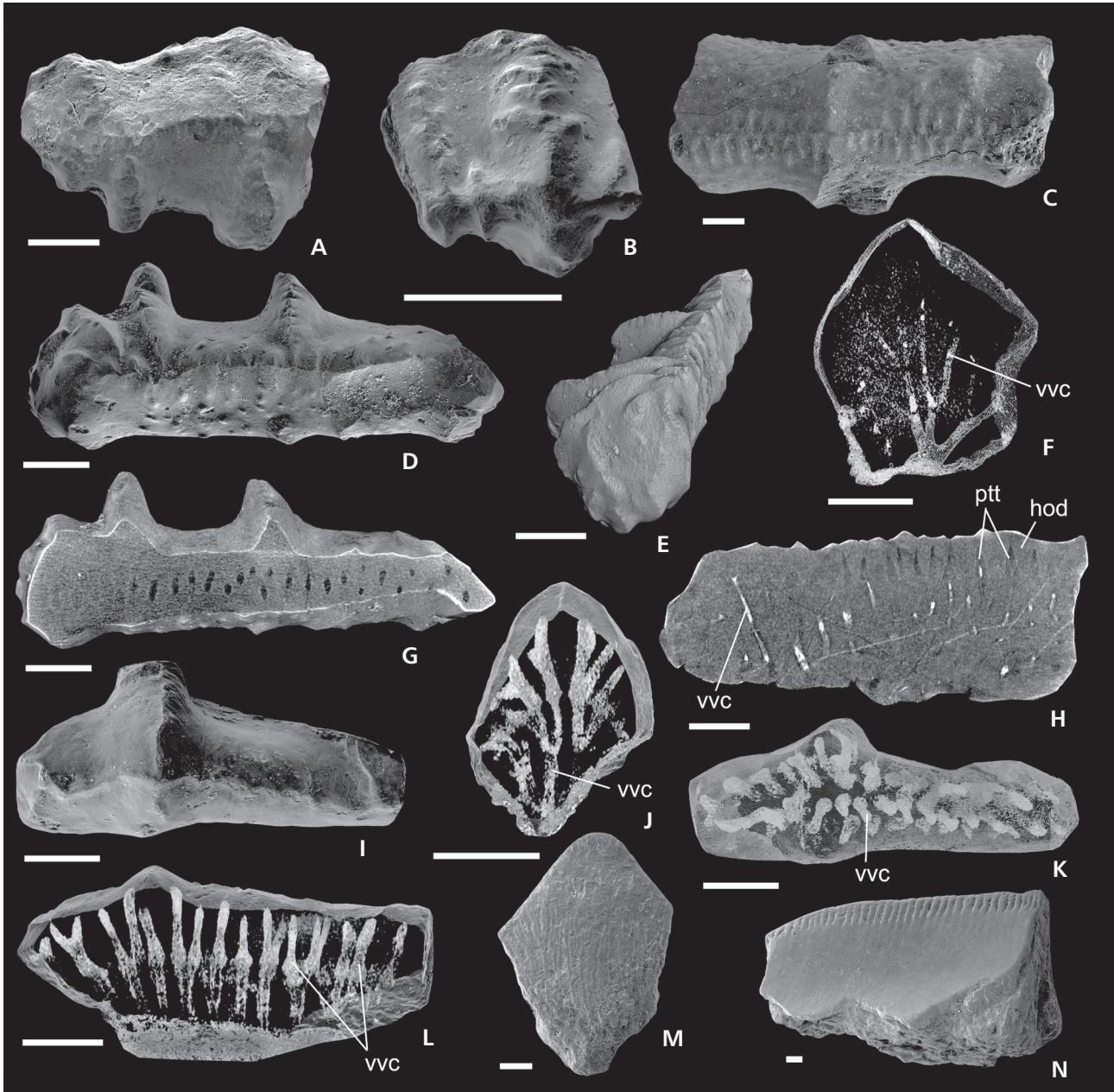
### Other fish remains

Apart from chondrichthyans, the assemblage from the Horquilla Formation of the Robledo Mountains contains rare remains of other fishes such as acanthodian scales and actinopterygian teeth and scales. The four acanthodian scales possess the flat, smooth, rhomboid-shaped crown, narrow neck and convex, rounded base (Fig. 10J). This type of scale belongs to the “*Acanthodes*” type, and is characteristic of all representatives of the order Acanthodiformes.

The actinopterygian teeth include three morphotypes. The common morphotype is high-conical, straight, smooth teeth that are circular in cross-section, with a pointed acrodin cap (Fig. 10L). The second morphotype is low teeth with a wide rounded acrodin cap (Fig. 10K). The teeth of the third type (Fig. 10M) possess an extended apex with a flat occlusal surface. This surface bears strong ridges diverging from the center. The rare fragment of actinopterygian bone (Fig. 10N) and incomplete scales (Fig. 10O) are poorly preserved, and covered by ganoine ridges of different width and length. Some scales resemble the scales of elonichthyiforms.

### Biostratigraphic distribution

Most of the chondrichthyan taxa found in the Robledo assemblage are widely distributed in the Carboniferous



**Figure 9.** Eucnondrocephalian teeth; Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian (A–D, I, M, N – scanning electron micrographs; E–H, J–L – micro-CT images). • A–H – *Agassizodus* sp., incomplete tooth crowns, occlusal views; A – NMMNH P-72321; B – NMMNH P-72322; C – NMMNH P-72323; D–H – NMMNH P-72324, occlusal (D) and oblique lateral (E) views, transverse (F in transparent mode), frontal (G) and sagittal (H) virtual sections. • I–L – Eugeneodontiformes indet., NMMNH P-72325, occlusal (I) view, transverse (J in transparent mode), frontal (K) and sagittal (L in transparent mode) virtual sections. • M, N – Petalodontiformes indet., fragments of teeth, possibly labial views; M – NMMNH P-72326; N – NMMNH P-72327. Scale bars = 0.5 mm. Abbreviations: hod – hypermineralized orthodontine; ptt – peritubular trabeculine; vvc – vertical vascular canal.

and Permian of many regions of the world and have long stratigraphic ranges.

The species of the xenacanthimorph *Bransonella* are recorded in the lower Carboniferous–middle Permian. *B. lingulata* Ivanov & Ginter, 1996 has been found in the lower Viséan of the Kuznetsk Basin, Russia; the lower Serpukhovian of the Moscow Region, Russia (Hampe &

Ivanov 2007); the lower Bashkirian of the South Urals, Russia (Ivanov & Hampe 2015); and the Middle to Upper Pennsylvanian of Oklahoma, USA (Ivanov *et al.* 2017). Possible finds were described from the Bashkirian (Lower Pennsylvanian) of Arizona, USA (Johnson & Thayer 2009). *Bransonella nebraskensis* (Johnson, 1984) occurs in the Viséan of the Nearpolar and South Urals,

the Kaluga Region and the Kuznetsk Basin (Russia), the Holy Cross Mountains (Poland), England and the Dinantian Synclinorium (Belgium); in the Serpukhovian of Arizona (USA); in the lower Bashkirian and lower Moscovian of the South Urals (Russia); in the upper Moscovian of the Moscow Region (Russia); in the Gzhelian (Upper Pennsylvanian) of Nebraska and Kansas (USA); and the Sakmarian (lower Permian) of Kansas (USA) (Johnson 1984, Hampe & Ivanov 2007, Ginter *et al.* 2015, Ivanov & Hampe 2015, Hodnett & Elliott 2018). Possible occurrences of this species are recorded from the Tournaisian of England (Behan *et al.* 2012) and Iran (Habibi & Ginter 2011); and from the Bashkirian (Lower Pennsylvanian) of Arizona, USA (Johnson & Thayer 2009). Recently, *Bransonella* spp. was reported from the Moscovian of eastern North Greenland (Cuny & Stemmerik 2018).

The symmoriiform *Stethacanthus* is widely known from the Famennian (Upper Devonian) to the Kazanian (middle Permian) in many regions (Ginter *et al.* 2010, Ivanov & Lebedev 2014). The symmoriiform *Danaea* is widely distributed in the Carboniferous. *D. fourrieri* Pruvost, 1922 is known from the Viséan of Belgium; *D. saltsmani* Ginter & Hansen, 2010 occurs in the Pennsylvanian (Bashkirian–Gzhelian) of the USA (Ginter *et al.* 2010). *Danaea wangi* Wang, Jin & Wang, 2004 is found in the Viséan–Serpukhovian of Belgium, Germany, Poland and China (Wang *et al.* 2004, Ivanov & Derycke 2005, Ginter *et al.* 2010). *Danaea williamsi* Ginter & Hansen, 2010 is reported from the Viséan–Serpukhovian, lower Carboniferous of Illinois and Arizona, USA, England, Scotland, Poland and the Moscow Region, Russia (Ginter *et al.* 2010, Hodnett & Elliott 2018). Recently *Danaea* sp. was documented from the Moscovian, Pennsylvanian of eastern North Greenland (Cuny & Stemmerik 2018).

The ctenacanthiform *Glikmanius occidentalis* (Leidy, 1859) has been reported from the Pennsylvanian–lower Permian of the USA (New Mexico, Arizona, Kansas, Indiana, Illinois, Ohio, Colorado and Texas); the Moscovian, Pennsylvanian–Kazanian, middle Permian of the East European Platform and the Urals, Russia; the middle Permian of Japan (Ginter *et al.* 2005, Johnson 2008); and the upper Leonardian, Permian of Arizona, USA (Hodnett *et al.* 2012). *Glikmanius myachkovensis* (Lebedev, 2001) occurs in the upper Carboniferous of the Moscow Syncline, Donetsk Basin, and Nebraska (Ginter *et al.* 2005); the upper Leonardian, Permian of Arizona, USA (Hodnett *et al.* 2012); and probably the Wordian, middle Permian of Oman (Koot *et al.* 2013).

The euselachian *Protacrodus* is known from the Middle Devonian–Mississippian (Ginter *et al.* 2010). But, some protacrodontid teeth were found in the Pennsylvanian. For example, *P. sibiricus* Lebedev, 2001 was described from

the Moscovian of the Ryazan and Moscow regions, Russia (Lebedev 2001).

The species of the neoselachian genus *Cooleyella* occur from the early Carboniferous to the middle Permian (Ivanov 2011). *Cooleyella amazonensis* Duffin, Richter & Neis, 1996 was reported from the Moscovian of Brazil; the Upper Pennsylvanian of New Mexico, Oklahoma and Kansas, (USA); the Artinskian of the South Urals (Russia); the Roadian of Texas (USA); and the Kazanian of the Tatarstan, Vladimir and Kirov regions (Russia) (Robb 1992, Duffin *et al.* 1996, Ivanov 2011, Ivanov & Lucas 2014, Ivanov *et al.* 2012, Ivanov 2016). *Cooleyella fordi* (Duffin & Ward, 1983) occurs in the Viséan–Serpukhovian, lower Carboniferous of the Nearpolar Urals, Moscow and Novgorod regions (Russia), Belgium and England; in the Serpukhovian of Arizona (USA) (Hodnett & Elliott 2018); in the Moscovian, upper Carboniferous of North Timan (Russia); in the Gzhelian, Upper Pennsylvanian of Ohio (USA); in the Sakmarian–Artinskian, lower Permian of the South Urals (Ivanov 2011); and possibly in the middle Permian of Oman (Koot *et al.* 2013).

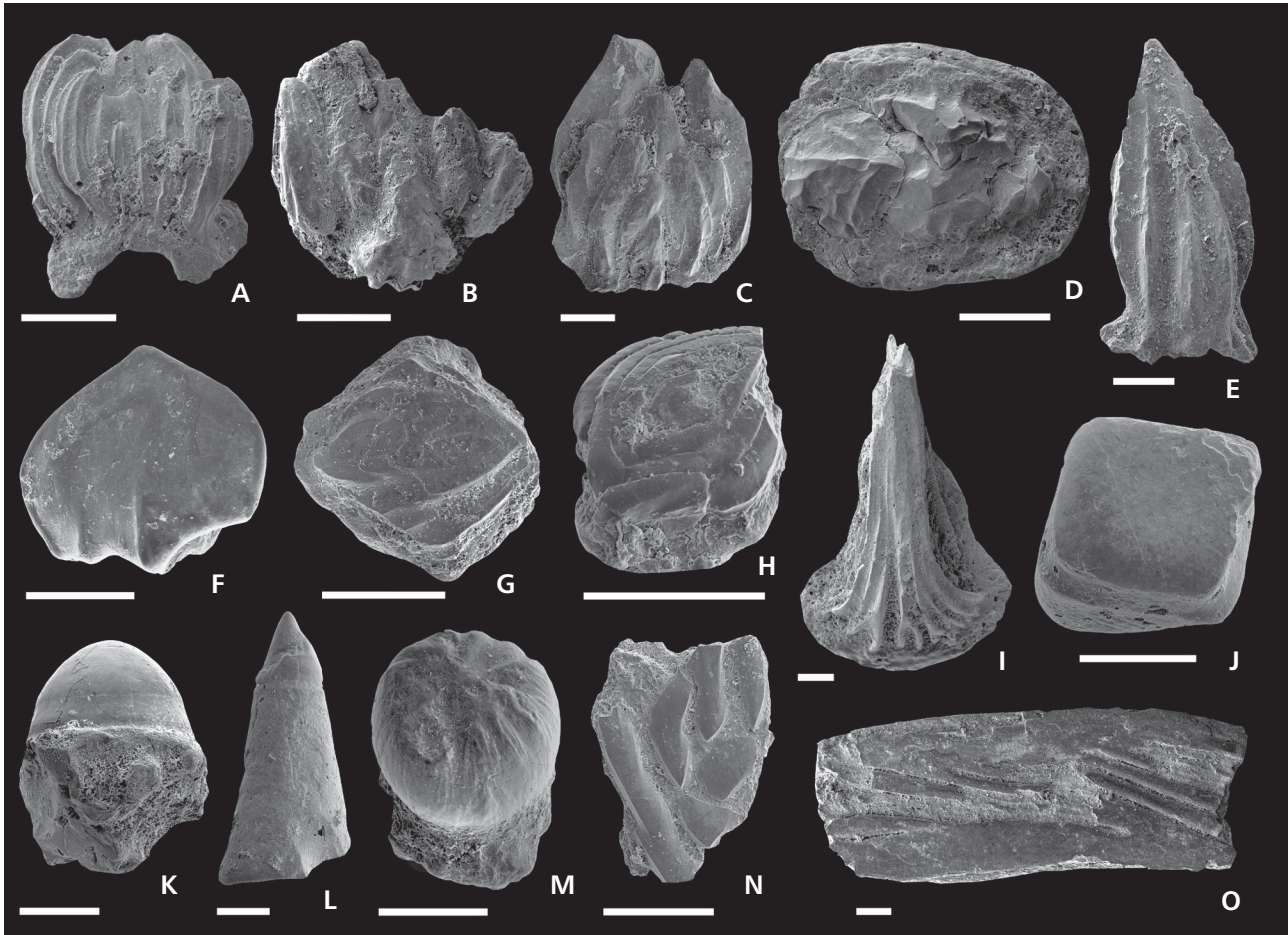
The jalodontid *Adamantina foliacea* Ivanov, 1999 has been recorded in the Tournaisian to the Roadian (Guadalupian, Permian): the Tournaisian of the South Urals, the Asselian of the Polar Urals, the Artinskian of the Middle Urals, Russia, the Moscovian of eastern North Greenland; the Upper Pennsylvanian of Iowa, USA; the Roadian of the Guadalupe Mountains, West Texas, USA (Ivanov 1999, Ivanov *et al.* 2012, Cuny & Stemmerik 2018).

The species of the euchondrocephalian *Orodus* are known from the Middle Devonian to Pennsylvanian (Moscovian) of different regions (Ginter *et al.* 2010). *Helodus* is common from the Upper Devonian to lower Permian of Australia, Eurasia and North America (Stahl 1999). The eugeneodontiform *Agassizodus* occurs in the Upper Pennsylvanian of the USA (Ginter *et al.* 2010).

The ranges for most fish taxa from the Robledo assemblage do not contradict the conodont data that indicate a Missourian (Kasimovian) age (see above). Only the protacrodontids and orodontids were not yet known from the Upper Pennsylvanian, and these are globally their youngest records.

## New finds of Paleozoic chondrichthyans in New Mexico

Here, we briefly document some new finds of Paleozoic chondrichthyans in New Mexico apart the fish assemblage from the Robledo Mountains, that were not included in the last reviews of Paleozoic fish occurrences in New Mexico (Hodnett & Lucas 2015, 2017). The age of the fish assemblage from the Sly Gap Formation is also discussed here.



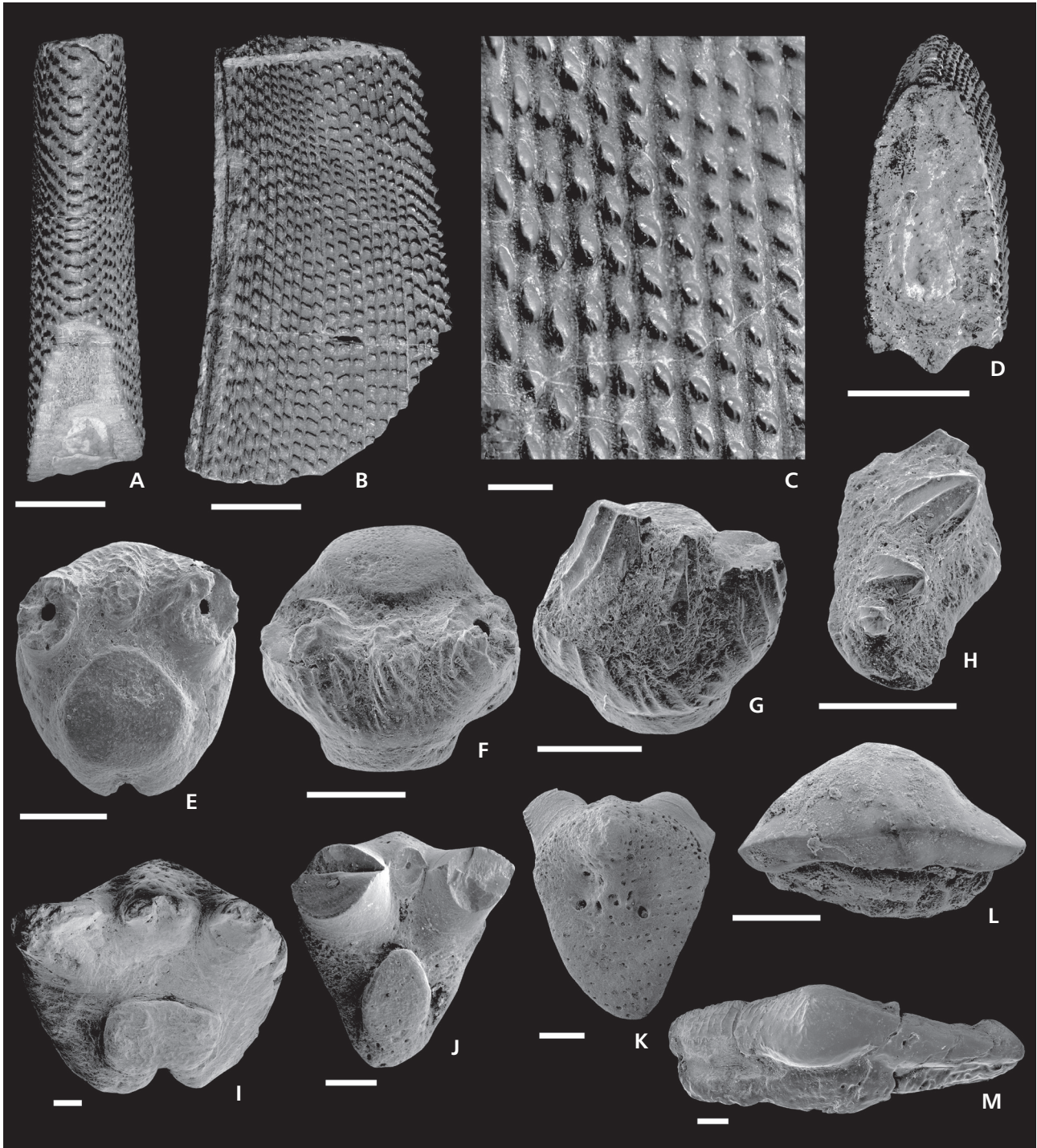
**Figure 10.** Fish microremains; Robledo Mountains, New Mexico, USA; Horquilla Formation, Missourian, Upper Pennsylvanian. • A–I – chondrichthyan scales; A–C – ctenacanthid type scales, crown views, NMMNH P-72328 (A), NMMNH P-72329 (B), NMMNH P-72330 (C). • D – tessera-like scale, NMMNH P-72331, crown view. • E, F – euselachian scales, anterior views; E – NMMNH P-72332, F – NMMNH P-72333. • G, H – protacrodontid type scale; G – NMMNH P-72334, crown view; H – NMMNH P-72335, oblique crown view. • I – spine-like denticle, NMMNH P-72336, crown view. • J – acanthodiform scale, NMMNH P-72337, crown view. • K–O – actinopterygian microremains; K–M – teeth, NMMNH P-72338 (K) lateral view, NMMNH P-72339 (L), lateral view, NMMNH P-72340 (M) oblique occlusal view; N – fragment of bone, NMMNH P-72342, external view; O – scale, NMMNH P-72341, external view. Scale bars = 0.2 mm.

## Devonian

The fin spine fragment of *Ctenacanthus* cf. *venustus* Eastman, 1902 (Fig. 11A–D) was found in the Box Member of the Percha Formation (Late Devonian) at the Percha type section (NMMNH locality 6945) in south-central New Mexico. This incomplete distal part of a fin spine is compressed laterally, incurved, with slightly convex lateral, narrow anterior and prominent posterior surfaces. The cross section is semioval, with a large central cavity (Fig. 11D). The ornamentation consists of longitudinal ridges separated by narrow grooves. The ridges bear the elongated tubercles oriented at different angles to the ridge axis (Fig. 11C). The tubercles are slightly striated and placed at different distances from each other. The tubercles form the slightly incurved transverse ridges at the anterior edge (Fig. 11A). The posterior surface bears a prominent

ridge separated by deep grooves from the posterior edges. The posterior denticles are not preserved. This incomplete fin spine differs from the fin spines of *Ctenacanthus venustus* Eastman, 1902 in the more rare location of tubercles on the longitudinal ridges (Maisey 1981).

Hodnett & Lucas (2015) observed that the fish assemblage from the Sly Gap Formation included the mixed taxa from the Devonian and Carboniferous and suggested that the age of the assemblage is Devonian, but the taxa earlier known only from the Carboniferous first appeared in New Mexico in the Devonian. This suggestion is not confirmed by the co-occurrence of Frasnian *Phoebodus latus* Ginter & Ivanov, 1995 and Famennian *P. gothicus* Ginter, 1990. *Phoebodus latus* and other Frasnian phoebodontids disappeared after the end-Frasnian mass extinction and did not exist in the Famennian interval of the *crepidapraesulcata* conodont zones when *P. gothicus* existed



**Figure 11.** Some Paleozoic chondrichthyans of New Mexico, USA. • A–D – *Ctenacanthus* cf. *venustus* Eastman, 1902, incomplete fin spine, NMMNH P-54783; Percha type section, locality NMMNH 6945; Box Member, Percha Formation, Upper Devonian; A – anterior; B – right lateral views; C – detail of ornamentation; D – section of distal part. • E–G – *Bransonella lingulata* Ivanov & Ginter, 1996, teeth; Talpa, locality NMMNH 1382, Taos Canyon; Flechado Formation, Desmoinesian, Middle Pennsylvanian; E, F – NMMNH P-14165a, occlusal (E) and oblique labial (F) views; G – NMMNH P-14165b, labial view. • H – *Sphenacanthus* sp., tooth, NMMNH P-12093, oblique lateral view; same locality and age. • I – *Orthacanthus* sp., tooth, NMMNH P-31823a, occlusal view; locality NMMNH 3390, Sandoval County; Atrasado Formation, Virgilian, Upper Pennsylvanian. • J, K – *Orthacanthus* cf. *texensis* (Cope, 1888), teeth, locality NMMNH 4706, Rio Arriba County; El Cobre Canyon Formation, Cutler Group, Wolfcampian, lower Permian; J – NMMNH P-34787a, occlusal view; K – NMMNH P-34787b, basal view. • L – “*Lissodus*” sp., tooth, NMMNH P-50544c, occlusal view; locality NMMNH 6826, East of Socorro; Busrum Formation, Wolfcampian, lower Permian. • M – “*Polyacrodus*” sp., tooth, NMMNH P-32058, oblique occlusal view; locality NMMNH 3423, Valencia; Red Tanks Member, Bursum Formation, Virgilian (Upper Pennsylvanian) – Wolfcampian (lower Permian). Scale bars: A, B, D = 10 mm; C = 2 mm; E–H = 0.5 mm; I–M = 1 mm.



(Ginter & Ivanov 1995). Thus, the age of assemblages is more believably Mississippian with reworked remains from the Frasnian and Famennian as discussed earlier (Ivanov & Lucas 2011).

## Middle Pennsylvanian

Teeth of *Bransonella lingulata* Ivanov & Ginter, 1996 and the tooth of *Sphenacanthus* sp. occur in the Flechado Formation (Desmoinesian) of Talpa (NMMNH locality 1382), Taos Canyon, northern New Mexico. The teeth of *B. lingulata* (Fig. 11E–G) are typical bransonellid teeth with a diplodont crown covered by the inverted “V”-nested ornamentation on the labial side, and with an oval tooth base bearing a prominent, oval apical button and semilunar labio-basal tubercle. Together with the Robledo fish fauna, this is the second record of *B. lingulata* in the Paleozoic in New Mexico.

The incomplete tooth of *Sphenacanthus* sp. (Fig. 11H) possesses the pyramidal protacrodont crown slightly inclined lingually. The cusps are rounded in cross section, gradually arranged by their height, and fused basally. The coarse, straight cristae cover all cusps, diverging from the cusp apex. The tooth base is slightly extended lingually, with prominent occlusal and flat basal surfaces. This tooth was illustrated by Kietzke (1990) for the first time as ichthyolith type A. Later, Zidek & Kietzke (1993) attributed this specimen to *Limnoselache*. But, this tooth closely resembles the teeth of *Sphenacanthus carbonarius* (Giebel, 1848) and *S. serrulatus* Agassiz, 1837 (Soler-Gijon 1997, Dick 1998).

## Upper Pennsylvanian–lower Permian

Teeth of *Orthacanthus* were found in the Atrasado Formation (Virgilian, Upper Pennsylvanian) of Sandoval County, NMMNH locality 3390, and in the El Cobre Canyon Formation of the Cutler Group (Wolfcampian, lower Permian) of Rio Arriba County, NMMNH locality 4706. The *Orthacanthus* teeth from the Atrasado Formation have a wide crown and base, two small central cusps, an almost rectangular apical button and a prominent basal tubercle (Fig. 11I). They are slightly similar to some teeth of *O. gibbosus* (Binney, 1840) and *O. platypternus* (Cope, 1884) (Hampe 2003, Johnson 2018). The teeth from the El Cobre Canyon Formation are attributed to *O. cf. texensis* (Cope, 1888) and possess large lateral cusps compressed linguo-labially, with serrated lateral carinae (Fig. 11J, K). The tooth base is elongated lingually and bears an oval apical button and a narrow basal tubercles.

A tooth of “*Polyacrodus*” sp. occurs in the Red Tanks Member, Bursum Formation (Virgilian, Upper Pennsyl-

vanian–Wolfcampian, lower Permian) of Valencia County, central New Mexico (NMMNH locality 3423). This tooth has an elongate, pyramidal crown with an extended central part and anostomosing cristae (Fig. 11M). The tooth is similar to the teeth of *P. ritchiei* Johnson, 1981 and ?*Acrodus sweetlacruzensis* Johnson, 1981 (Johnson 1981), although it is somewhat larger.

The fish assemblage from the early Permian (Wolfcampian) Bursum Formation NMMNH locality 6826 east of Socorro in central New Mexico includes the teeth of *Glikmanius* sp., “*Lissodus*” sp. and “*Polyacrodus*” sp. Most of the teeth are poorly preserved. The teeth of “*Lissodus*” (Fig. 11L) resemble the teeth of “*L. zideki*” (Johnson, 1981) from the lower Permian of Texas (Johnson 1981). The teeth of “*Polyacrodus*” are similar to the polyacrodontid teeth described from the upper Permian of Iran (Hampe *et al.* 2013).

## Conclusions

The fish assemblage from the Horquilla Formation of the Robledo Mountains, including numerous chondrichthyans, rare acanthodians and actinopterygians, is one of the most taxonomically diverse assemblages of Paleozoic fish in New Mexico. It contains chondrichthyan taxa such as *Bransonella*, *Adamantina*, *Cooleyella*, which, for the first time are reported from New Mexico. The occurrences of protacrodontids and orodontids in the Missourian are their youngest records.

Besides the Robledo fish fauna, the new discoveries of Paleozoic chondrichthyans augment the taxonomic diversity in the fish assemblages. *Ctenacanthus* is recorded for the first time in the Late Devonian of New Mexico, and the records of *Bransonella* and *Sphenacanthus* are their first occurrences in the Middle Pennsylvanian of New Mexico.

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