Fish Microremains from the Cutoff Formation (Roadian, Middle Permian) of the Guadalupe Mountains, West Texas, USA

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ABSTRACT: A new assemblage of diverse fish microremains from the Roadian Williams Ranch Member of the Cutoff Formation in the Guadalupe Mountains, West Texas is described. The chondrichthyan remains comprise symmoriiforms *Stethacanthulus decorus*, *Kungurodus* sp. and indeterminate taxa; ctenacanthiform *Glikmanius myachkovensis*; euselachian *Sphenacanthus* sp. and Hybodontiformes indet.; anachronistids *Cooleyella amazonensis*, *Cooleyella* sp. and *Reifella lata* Ivanov, n. gen., n. sp.; jalodontids *Adamantina foliacea*, *Isacrodus marthae* and *Isacrodus* sp.; indeterminate euchondrocephalian and chondrichthyans. Actinopterygian remains include the elonichthyid *Alilepis texasensis* Bakaev, n. sp., indeterminate platysomids and acrolepidids, indeterminate taxa and other osteichthyans. The assemblage includes the widely geographically distributed taxa *Cooleyella amazonensis, Stethacanthulus decorus* and *Adamantina foliacea.* The occurrence of last two species in the Cutoff Formation represents their youngest record in the world. Possible migration paths are proposed for *Alilepis.*

INTRODUCTION

Fish microremains from the Wordian - Capitanian (Bell Canyon Formation) of Texas are known from a number of localities and strata: from the Rader Limestone Member (Capitanian) in the "Rader Slide" section, Guadalupe Mountains (Ivanov et al. 2015b); from the Hegler/Pinery Members (upper Wordian) in the PI section, Guadalupe Mountains (Ivanov et al. 2020); from the "McKittrick Canyon Limestone", Lamar Limestone and Reef Trail Members (Capitanian) in the Patterson Hills, Guadalupe Mountains (Ivanov et al. 2020); and from strata equivalent in age to the Lamar Limestone and Reef Trail Members (Capitanian) in the EF and M sections, Apache Mountains (Ivanov et al. 2013). Some fish remains have been reported from the Shumard (uppermost Kungurian) and El Centro (Kungurian/Roadian) Members of the Cutoff Formation, from the Pipeline Shale (lower Roadian) of the Brushy Canyon Formation and from the Getaway Member (upper Roadian - lowest Wordian) of the Cherry Canyon Formation (Ivanov et al. 2015a).

The new assemblage of Roadian chondrichthyan and actinopterygian fishes described herein are recorded in the first time from the Williams Ranch Member of the Cutoff Formation in the Quarry section of the Guadalupe Mountains, West Texas (text-fig. 1). Chondrichthyans are represented by the symmoriiform teeth and denticles; ctenacanthiform, sphenacanthid, hybodontiform, anachronistid and jalodontid teeth; euchondrocephalian tooth plate; and chondrichthyan scales. The microremains of bony fishes include lonichthyid, platysomid and acrolepidid scales; actinopterygian teeth, tooth plates, fragments of jaw bones and denticles; and osteichthyans postcranial elements.

GEOLOGICAL SETTING

The microremains were collected at the so-called Quarry section of the Guadalupe Mountains area (text-fig. 1). There are two road cuts with strata of the Williams Ranch Member of the Cutoff Formation (Roadian) located on the both sides of US Highway 62/180 about 3 km northeast of its junction with Texas Highway 54 (31°49'0.2"N, 104°49'48"W) (text-figs. 1, 2). Approximately 4 m of dark gray to black thin-bedded spiculitic limestone (wackestone/packstone) and mudstone with beds of calcareous shale and with wavy bedding are exposed on the southeastern side of the road in the Q1 outcrop (Nestell and Nestell 2020). Fish microremains occur in the samples Q-1 and Q1-3. Opposite to the Q1 outcrop, a small quarry (Quarry section) with poorly exposed limestone beds is located on the northwestern side of the highway (text-fig. 3). The deposits there are represented by thin-bedded black carbonate mudstone with small black lenses of packstone (Nestell and Nestell 2020). The lower part of this outcrop correlates with the Q1 outcrop. The upper part of the Quarry section contains a several meters thick sequence of quarry debris with beds of laminated black carbonate mudstone and with lenses of mollusk-bearing packstone outcropping in some places (see Nestell and Nestell 2020 for a detail discussion of the general geological setting and stratigraphy of the Quarry section). In addition to the mollusks, the packstone lenses include a diverse invertebrate fauna of foraminifers, radiolarians, ammonoids, ostracodes, scolecodonts, holothurian sclerites, and conodonts. The diverse fish microremains were collected from the mollusk-bearing packstone (samples CQF-1, CQF-2, CQF-3, CQF-4, Q-20), and a few remains - from the carbonate laminated mudstone (sample CWR-6).

MATERIAL AND METHODS

The fish microremains were recovered from conodont residues extracted from limestone rock matrix by standard processing of the samples with formic acid and heavy liquid separation. Micrographs of the specimens were obtained under the scanning electron microscopes Hitachi S-3400N (Research Park of the St. Petersburg State University, Russia), Cambridge CamScan-4 and Tescan VEGA-II XMU (Borissiak Paleontological Institute, Moscow, Russia), and JEOL T-300 (University of Texas at Arlington, Arlington, USA). The internal structure of the microremains such as the teeth of *Glikmanius myachkovensis*, *Reifella lata* Ivanov, n. gen., n. sp., *Isacrodus marthae*, the euchondrocephalian tooth plate, and the scale of *Alilepis texasensis* Bakaev, n. sp. were reconstructed non-destructively with a SkyScan 1172 Bruker micro-CT device (Center for Geo-Environmental Research and Modelling "GEOMODEL", Research Park of St. Petersburg State University, Russia). Micro-CT scanning of the specimens was utilized with an aluminium filter and a 180° rotation at the highest camera resolution with an average rotation angle step of 0.4°, and with electric parameters of 59–74 kV and 100–155 mA. The virtual cross-sections were generated from the 3D reconstruction using software DataViewer, CTVox, and CTAn.

Thin sections of the actinopterygian scales were prepared at the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia. All material to be sectioned was first embedded in polymethylmethacrylate thermoplastic Glass Fil (Print Product). When making the ground sections, the specimen was first glued to a glass slide using the same embedding thermoplastic. The opposite surface of the specimen was then ground down until the desired area was well exposed and polished. Subsequently, the polished surface was glued to another glass slide with "Top Coat" (nail polish). Finally, the rough, unpolished side was ground down on waterproof sanding paper Mirka WPF with grit sizes ranging from P800 to P2000 until the section was at the desired thinness for observation under a transmitted light microscope. The thin sections were photographed with an AXIOPLAN-2 microscope equipped with a Leica DFC420 digital camera.

The terminology of Esin (1990, 1995b) was adopted to describe the topographical variability of scales on the body of actinopterygian fishes. This scheme has been successfully applied to the description of the scale cover of the basal bony fishes *Ligulalepis* (Burrow 1994), *Psarolepis* (Qu et al. 2013), *Guiyu* (Cui et al. 2019), *Andreolepis* (Chen et al. 2012), *Sparalepis* (Choo et al. 2017) and basal actinopterygian *Moythomasia* (Trinajstic 1999a, b), *Mimipiscis* (Trinajstic 1999b; Choo 2011), *Donnrosenia* (Long et al. 2008), *Gogosardina* (Choo et al. 2009), and *Burguklia* (Bakaev and Kogan 2020). A significant range of such well-described squamation of distinct taxa has allowed us to identify similar patterns of topographical variability within the studied material. Modified versions of this scheme based on geometric morphometrics of scales have been proposed in two papers (Chen et al. 2012; Cui et al. 2019). However, the use of geometric morphometry and statistical processing requires a larger sample of undamaged scales than we have available. Unfortunately, Esin's methodology is not useful for the deep-bodied fishes, such as Platysomidae, because of their different proportions and topographical variability patterns. In this case, a more generic topographical terminology was utilized in this paper.

The scale morphology (text-fig. 4) has been described using the terminology proposed by Schultze (1966) and subsequently modified by several authors (Esin 1990; Burrow 1994; Qu et al. 2013; Bakaev and Kogan 2020). The terminology of the scale surface ultrasculpture is from Märss (2006) and the histological terms - from Sire et al. (2009), Schultze (2016, 2018) and Qu et al. (2016).

The preservation of the fish microremains is variable: from fine to poor, sometimes with traces of bioerosion (Pl. 10, fig. 9), and with abraded surfaces of various degrees. The micro-CT images demonstrate the well-preserved dental tissues (Pl. 2, figs. 1d-1f), as well as the presence of fractures and secondary deposition of minerals within the vascular canals (Pl. 5, figs. 7a, 7b).

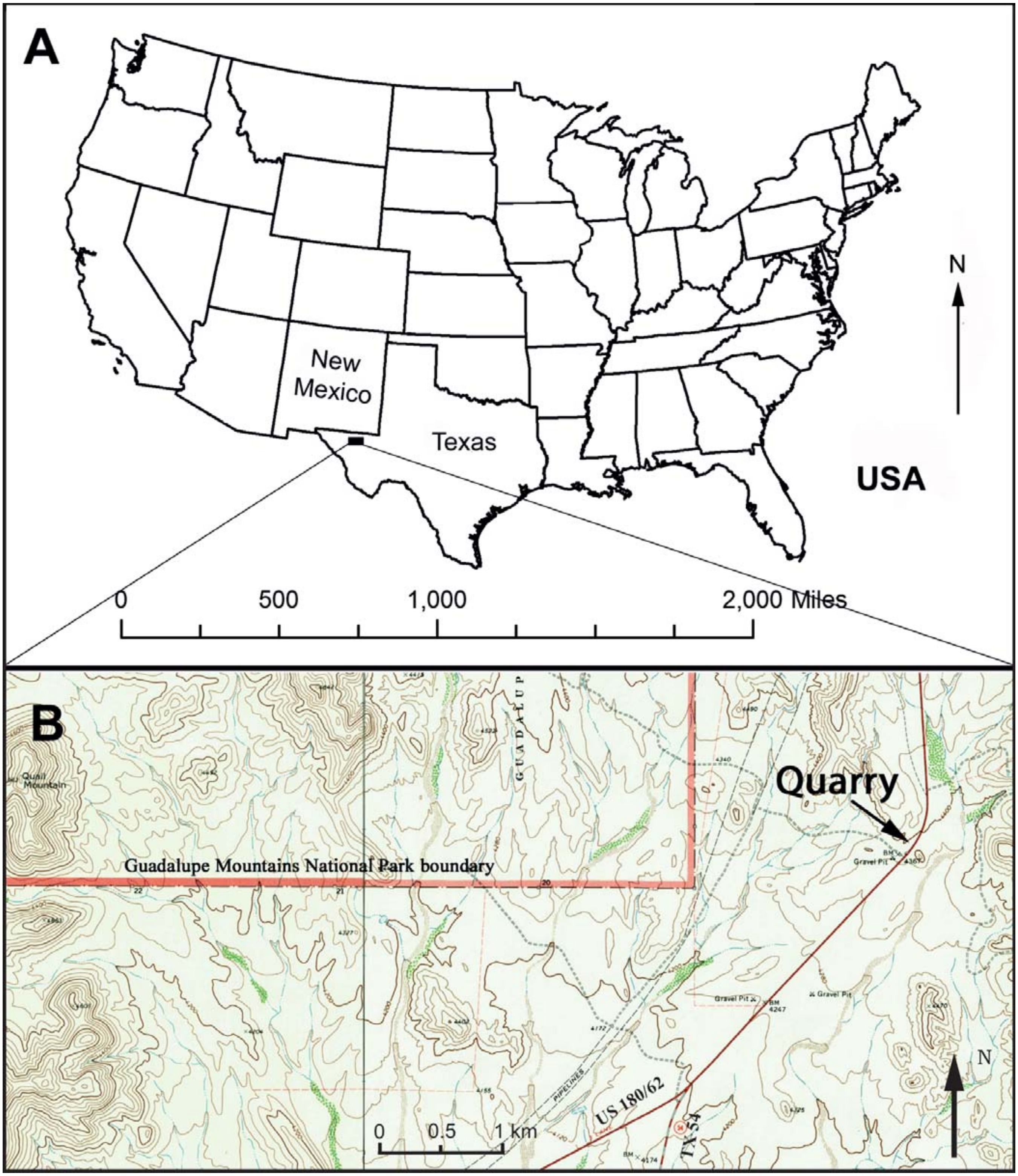
SYSTEMATIC PALEONTOLOGY

The specimens described herein are housed in the New Mexico Museum of Natural History and Science, Albuquerque (abbreviation - NMMNHS) under collection no. 80888, 81460-81582, 81586, 81587, and the thin sections of actinopterygian scales and comparative specimens of the actinopterygian are at the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (abbreviation - PIN) under collection no. 5799 and 5803.

Class CHONDRICHTHYES Huxley 1880
Subclass ELASMOBRANCHII Bonaparte 1838
Superorder CLADODONTOMORPHI Ginter, Hampe and Duffin 2010
Order SYMMORIIFORMES Zangerl 1981
Family SYMMORIIDAE Dean 1909
Genus *Stethacanthulus* Zangerl 1990
Type species: *Denaea meccaensis* Williams 1985.

Stethacanthulus decorus (Ivanov 1999)
Plate 1, figures 1-10

Description: The teeth have a three- to seven-cusped cladodont crown including three main cusps, central and lateral (or outer intermediate), and one or two pair of cusplets. The cusps are inclined lingually, sigmoidal incurved, round in cross sections, and distinctly separated from each other. A delicate lateral carina is present on all cusps. The boundary between the crown and base is well marked. The tooth base is thin, considerably extended lingually, trapezoidal in occlusal view, and without any articulation button or projection on the occlusal and basal sides. The base has a narrow flat part behind the crown/base boundary and a wide, sloped part with a triangular depression at the midline. This depression begins from a large foramen of the main vascular canal and extends to the lingual edge. The sloped parts on each side of the depression are penetrated by numerous tiny foramina of small vascular canals (Pl. 1, figs. 1, 2b, 2c). These foramina are concentrated along the boundary of the flat part. Sometimes papilla-like structures are formed around foramina (Pl. 1, figs. 9b, 9c, ps). The basal surface of the base has a prominent median part with two lateral depressions on each



TEXT-FIGURE 1
A– Location of Texas in the USA map; B– Location of the studied Quarry section along U.S. Highway 62/180 in the Guadalupe Mountains, West Texas (modified after Nestell and Nestell 2020).

side. The foramen of the main vascular canal is located at the labio-basal edge, below the central cusp.

The teeth are represented by three morphotypes. The first one has a narrow crown with five thin, smooth cusps including three main cusps and one pair of intermediate cusplets (Pl. 1, figs. 1, 2). The central cusp is slightly higher and wider than the lateral ones. The spoon-like tooth base of this morphotype has a narrow labial and wide lingual parts, and parallel or divergent lateral edges. The second morphotype has a crown with three to five ornamented cusps (Pl. 1, figs. 3, 4). The central cusp is higher than the lateral cusps. The tooth base is almost of the same width as the crown, rounded or rectangular in shape, sometimes with a triangular extension. The lateral edges of the tooth base are slightly divergent. The third morphotype has a wide crown with five to seven ornamented cusps (Pl. 1, figs. 5-9). The crown with seven cusps consists of the main central cusp, pairs of main outer intermediate cusps, inner intermediate cusplets and lateral accessory cusplets (Ivanov 1999, fig. 2B). The central cusp is higher and considerably wider than other ones. The tooth base of this morphotype has a wide labial and narrow lingual parts, is of trapezoid shape in the occlusal view, and has an arched transverse prominence on the basal side. The lateral edges of the base are concave, considerably divergent to the center of the lingual edge. The cusps of the second and third morphotypes are ornamented with distinct cristae. The ornamentation on the labial side of the central cusp consists of two to three long, curved cristae forming a lanceolate structure with short cristae located below this structure. The lateral cusps have the same ornamentation but with one lanceolate crista. The lingual ornamentation includes thin, straight, long and short cristae. The number of the cusps, the width and height of the cusps, the depth of lingual depression, and the outline of the base vary within one morphotype.

Material: 48 teeth.

Remarks: The presence of papilla-like structures situated around the tiny foramina have been reported in the teeth of *Kungurodus obliquus* (Ivanov 2005) at the occlusal depression surrounding the apical button (Ivanov 2016). These structures were possibly formed as the result of the deposition and growth of a mineral into and around the vascular canal during fossilization.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1, CQF-2, CQF-3, CQF-4, CWR-6, Q1-3, Q-20; Carboniferous, Mississippian, Serpukhovian and lower Permian, Cisuralian, Asselian - Artinskian of Nearpolar and South Urals, Russia; Carboniferous, Mississippian, Serpukhovian – Pennsylvanian, Bashkirian of the Gissar Mountains, Uzbekistan (Ivanov 2013).

Family INCERTAE SEDIS
Genus *Kungurodus* Ivanov 2016
Type species: *Cobelodus obliquus* Ivanov 2005.

Kungurodus sp.
Plate 1, figure 13

Description: The small teeth have a tricuspid crown with central and lateral cusps. The central cusp is slightly higher and wider than the lateral ones. The cusps are incurved, inclined lingually, rounded in cross section. The central cusp is slightly dislocated labially. The lateral cusps strongly diverge from the central one. The lateral carina is well developed on the upper part of the cusps, but is barely traceable on the lower part and between the cusps. A continuous carina connects all the cusps between each other. The cusps are ornamented with distinct cristae on both lingual and labial faces. The labial surface is covered with long cristae, which form a lanceolate structure on the central cusp. The lingual surface of the cusps is covered in slightly wavy long and short cristae that do not reach the cusp apex.

The tooth base is almost rhomboid in shape, with a short lingual torus, acuminate lateral parts, convex occlusal and concave basal faces. A single, prominent and wide apical button is located on the lingual rim and occupies most of the occlusal surface. The button is separated from the crown by shallow depressions on both lateral sides and by a narrow groove. The lingual notch at the center of the button is formed by the main vascular canal opening basally. The labio-basal projection is thick and wider than the base of the central cusp.

Material: Two teeth.

Remarks: The teeth differ from those of *Kungurodus obliquus* (Ivanov 2005) by the smaller central cusp, larger apical button and wider labio-basal projection (Ivanov 2016). The teeth of *K. obliquus* have a more pronounced cladodont crown with higher and wider central cusp than the lateral ones. Two morphotypes of *K. obliquus* teeth have been described, those with tricuspid and those with five-cusped crowns (Ivanov 2005, 2016).

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4.

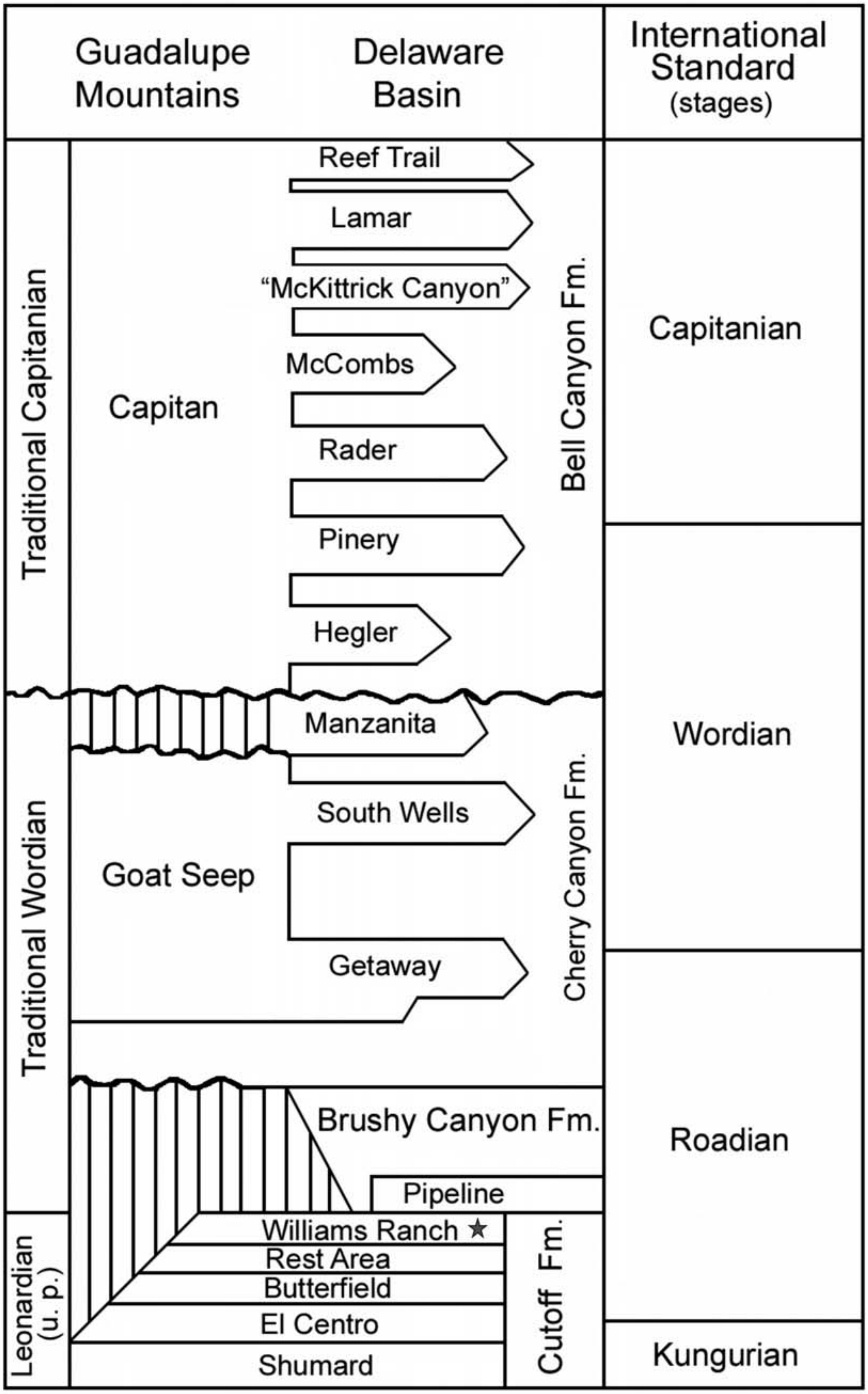
Symmoriiformes indet.
Plate 1, figures 11, 12

Description: The teeth have a cladodont crown with three to six cusps. The cusps are inclined lingually, slightly incurved, oval in cross section and covered in straight, long and short cristae on both the labial and lingual sides. The central cusp is considerably higher than the lateral ones. The lateral carina is weakly developed along the entire crown. The tooth base is extended lingually, with slightly convex occlusal and concave basal surfaces. The apical button and labio-basal projection are absent. One tricuspid tooth (Pl. 1, fig. 12) has a triangular extension of a lingual torus. Some foramina of the vascular canal open at the lingual rim, around the base of the central cusp and in the depression of the basal surface.

Material: Four teeth.

Remarks: The teeth are similar to the teeth of *Denaea* Pruvost 1922, but the latter have two or three pairs of intermediate cusps, a well-developed apical button and labio-basal tubercles.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4.



TEXT-FIGURE 2
Stratigraphic units of the Guadalupian in the Delaware Basin area (modified from Wardlaw 2004). Asterisk – position of studied fish assemblage. Abbreviations: u. – upper, p. – part, Fm. – formation (modified after Nestell and Nestell 2020).

Order CTENACANTHIFORMES Glikman 1964
Family CTENACANTHIDAE Dean 1909
Family HESLERODIDAE Maisey 2010
Genus *Glikmanius* Ginter, Ivanov and Lebedev 2005
Type species: *Cladodus occidentalis* Leidy 1860.

Glikmanius myachkovensis (Lebedev 2001)
Plate 2, figures 1-3

Description: The teeth have a cladodont crown with a long central cusp, moderate lateral cusps, one to three pairs of intermediate cusplets, and one pair of lateral cusplets. The cusps are oval in cross section, flattened labio-lingually, and incurved lingually. All cusps and cusplets are arranged in one line. The inner cusplet can be located on the lateral side of the central cusp (Pl. 2, fig. 1c). The central and lateral cusps bear the lateral carina that extends into the middle part and does not reach the cusp base. Straight cristae cover the labial and lingual faces of the main cusps. The cristae on the lingual face are the coarsest. The labial ornamentation of the cusplets is poorly expressed. The tooth base is trapezoid with rounded corners or almost semicircular in shape, with the lingual part folded downwards. The two small apical buttons are rounded, located almost intermediate between the crown and the lingual rim, and rather far from each other. A shallow labio-basal depression is developed at the base of the central cusp and on the labial edge of the base. Two prominent, oval labio-basal tubercles (projections) are located on each side of this depression.

The occlusal surface of tooth base is penetrated by a few large and numerous small foramina of the vascular canals. Two large canals open on the basal side of the base. The central cusp is composed of osteodentine at its lower part; all other cusps consist of orthodentine (Pl. 2, fig. 1e). The internal vascularization system of the teeth includes a dense network of strongly branched canals occupying the entire base and distributed to the crown (Pl. 2, fig. 1d-f). A few large horizontal main canals run across the tooth base. The same sized, moderate secondary canals form a network. The ascending canals and their ramifications fill the lower part of the central cusp and are connected to the pulp canal.

Material: Seven teeth.

Remarks: There are several differences between the smaller and larger teeth of *Glikmanius myachkovensis* (Lebedev 2001) as noted earlier by Ginter et al. (2005). The smaller teeth have more cusplets than the larger teeth, with one pair of intermediate cusplets. However, the lateral cusps of the larger teeth are considerably higher than the lateral ones of the smaller teeth. The collection of teeth from the Quarry section includes only one quite small tooth with several pairs of cusplets (Pl. 2, fig. 1).

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4; Carboniferous, Pennsylvanian, Moscovian - Kasimovian of Moscow Syneclise, Russia, Donetsk Basin, Ukraine, and USA, Nebraska; lower Permian, Cisuralian, Kungurian (Leonardian) of Arizona, USA (Ginter et al. 2005; Hodnett et al. 2012).

Cohort EUSELACHII Hay 1902
Order HYBODONTIFORMES Patterson 1966

Hybodontiformes indet.
Plate 2, figure 8

Description: The tooth has a crown with three cusps that are triangular in labial and lingual views and fused at the base. The central cusp is higher and wider than the lateral ones, inclined laterally. A distinct lateral carina divides the strongly convex lingual and almost flat labial surfaces. The cusps bear coarse ridges on the labial and lingual faces. The ridges are wavy and sometimes branched at the cusp base, not reaching the cusp apex. The tooth base is lingually extended, wider than the crown, subtriangular in shape, with convex, smooth occlusal and concave basal surfaces. The labio-basal projection is weakly developed. The large foramina of vascular canals open at the lingual rim, but a few small foramina are located along the crown/base junction, on the occlusal side.

Material: One tooth.

Remarks: The tooth resembles the teeth of *Lamarodus triangulus* Ivanov 2020, but the *Lamarodus* teeth differ in wider cusps considerably fused in the crown, and a shorter tooth base with large foramina present on the occlusal and basal sides (Ivanov et al. 2020). The tooth described herein is similar to some tricuspid teeth of *Protacrodus serra* Ginter, Hairapetian and Klug 2002, but these teeth are distinguished by a high central cusp and strongly fused cusps on the pyramidal crown (Ginter et al. 2002).

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, sample CQF-3.

Order INCERTAE SEDIS
Family SPHENACANTHIDAE Maisey 1982
Genus *Sphenacanthus* Agassiz 1837 (in 1843)
Type species: *Sphenacanthus serrulatus* Agassiz 1837 (in 1843).

Sphenacanthus sp.
Plate 2, figures 4-7

Description: The teeth have a monolithic, pyramidal protacrodont crown and euselachian-type base. The width of the crown and base is the same and the crown overhangs the base. The crown has up to ten low, conical cusps, rounded in cross section, triangular in the labial or lingual views, often slightly inclined mesially or distally. The cusps are fused to each other near the base but separated by shallow triangular depressions. The cusps are gradually arranged by their height mesially and distally, from highest central to smallest lateral. The number of cusps in the asymmetrical crown vary from three to five on one side on the tooth. The central cusp is extended labially (Pl. 2, figs. 4d, 6d). The cusps bear coarse cristae that join at the apex and bifurcate at the crown/base junction. The long cristae are located on the labial and lingual faces of the cusps. The cristae on the mesial and distal sides of each cusp connect to each other and form a linear structure similar to the occlusal crest. The short cristae diverge from the cusp apex and long crista. The crown/base junction is marked by a groove on the lingual and labial faces.

TEXT-FIGURE 3
Panoramic view of the Quarry section located on the northwestern side of U.S. Hwy 62/180 (after Nestell and Nestell 2020).

The tooth base is extended lingually, considerably vascularized, with a convex occlusal surface. The basal concave surface has a flat lingual part and a depressed middle part with a distinct labial ledge. Numerous foramina of various diameters open on the occlusal and basal depressed sides of the base and are arranged in longitudinal rows (Pl. 2, figs. 4c, 5c, 6c). One small tooth with a poorly developed base has more separated cusps bearing tuberculated cristae (Pl. 2, fig. 7). The cristae are not interconnected along the midline.

Material: Five teeth.

Remarks: The teeth described herein closely resemble the teeth of *Sphenacanthus delepinei* Fournier and Pruvost 1928, but the later differs in having a higher central cusp, more separated lateral cusps, and ornamentation only consisting of long cristae (Ivanov and Derycke 2005). The teeth from the Quarry section are distinguished from the teeth of *Sphenacanthus carbonarius* (Giebel 1848) (Soler-Gijón 1997) and *S. serrulatus* Agassiz 1837 (Dick 1998) by possessing a shorter central cusp, more fused lateral cusps, and numerous short cristae in the ornamentation. The teeth of *Sphenacanthus tenuis* Ginter 2016 differ from the teeth described herein by presenting higher central cusp, acuminated lateral cusps, numerous ridges on the cusps, and a base with a very narrow lingual part.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1, CQF-2, and CQF-4.

Subcohort NEOSELACHII Compagno 1977
Order INCERTAE SEDIS
Family ANACHRONISTIDAE Duffin and Ward 1983

Remarks: The family includes the genera *Amaradontus* Hodnett and Elliott 2018, *Cooleyella* Gunnell 1933, *Ginteria* Duffin and Ivanov 2008, and *Reifella* Ivanov, n. g.

Genus *Cooleyella* Gunnell 1933
Type species: *Cooleyella peculiaris* Gunnell 1933.

Remarks: Besides the type species, the genus includes the species *Cooleyella amazonensis* Duffin, Richter and Neis 1996, *C. duffini* Ivanov 2015, and *C. fordi* (Duffin and Ward 1983). *Cooleyella platera* Hodnett and Elliott 2018 is very similar to one morphotype of *C. amazonensis* and probably junior synonym of that species.

Cooleyella amazonensis Duffin, Richter and Neis 1996
Plate 3, figures 1-17

Description: The anachronistid teeth are small (0.4–0.8 mm mesiodistally) with crown wider than the base. The crown is smooth, overhangs labially the base, with a distinct occlusal crest dividing the extended, sloping labial part and the short, inclined lingual part bent under the crest. The labial surface is flat or slightly concave, trapezoidal in shape, with a labial flange. The occlusal crest is lingually placed, mainly bears a prominent central cusp. This cusp is triangular, acuminated (Pl. 3, figs. 6, 13, 15, 17) or obtuse (Pl. 3, figs. 3-5, 11), sometimes inclined mesially or distally. The cusp is separated by a triangular depression from the extended lateral blades. Some teeth have no developed cusp in the crown (Pl. 3, figs. 2, 7). The labial flange is terminated, the labial surface is short and straight, commonly wide but rounded triangular in a few teeth (Pl. 3, figs. 3, 5). The crown/base junction is very noticeable in the narrowest part of the tooth.

The tooth base is oval in basal view, mainly with extended, convex lingual and very narrow labial faces. A few teeth (Pl. 3, figs. 5, 12) have a weakly developed base considerably smaller than the crown. The lingual edge of the base is rounded, often with a small median notch and surrounding button-like thickening in the center of the lingual rim. A notch is formed by the main vascular canal, which opens on the basal side of the base. The small basal tubercle is circular, located beneath the labial flange. The basal face of the base is drop-like in shape, with a slightly convex lingual part. A narrow transversal groove separates the basal tubercle and lingual part of the base. A round pit of the pulp cavity is located in that groove. This wide and short pulp cavity continues into a thin pulp canal (Pl. 3, figs. 15, 17). Numerous tiny dentine tubules are present on the abraded labial flange (Pl. 3, fig. 16).

Material: 52 teeth.

Remarks: The variation in the tooth morphology of *Cooleyella amazonensis* is not as noticeable as in the teeth of *C. fordi* (Duffin and Ward 1983). The proportion of crown and base, height and inclination of central cusp, and the length of the lateral blades vary in the teeth from the diverse collection of the Quarry section.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1, CQF-2, CQF-3, CQF-4, Q1-3; Carboniferous, Pennsylvanian, Moscovian of Brazil and Oklahoma, USA; Kasimovian (Missourian) of New Mexico, USA; Gzhelian of Kansas, USA; lower Permian, Cisuralian, Artinskian of South Urals, Russia; middle Permian, Guadalupian, Roadian (Kazanian) of the East European Platform, Russia; Capitanian of Texas, USA (Ivanov et al. 2017, 2020; Ivanov and Lucas 2019).

Cooleyella sp.
Plate 3, figures 18, 19

Description: The anachronistid teeth have a crown shorter and narrower than the base. The crown is trapezoid in shape, slightly overhanging the base labially, and has a short labial flange, rounded lateral blades and occlusal crest. The central cusp is undeveloped. The crown/base junction is deep. The tooth base is considerably extended lingually, with a round lingual edge and with a small median notch of the main canal opening. The basal tubercle is circular, located beneath the labial flange. The large pit of the pulp cavity is oval and penetrates the depression near the basal tubercle.

Material: Three teeth.

Remarks: The teeth described herein are distinguished from the teeth of most *Cooleyella* species in having a shorter labial flange, rounded occlusal crest without a central cusp and shallower basal depression without a basal groove. The teeth of *C. amazonensis* differ from the described teeth by a larger crown than tooth base, the longer labial flange and lateral blades, deeper basal depression of the base with a narrow groove. The teeth from the Quarry section are similar to the tooth of *Cooleyella peculiaris* Gunnell 1933 illustrated by Gunnell (1933, pl. 31, figs. 65, 66), but differ in the obtuse labial flange and large tooth base. Hansen (1986) redescribed this species and mentioned that the teeth of *C. peculiaris* have a narrow and deep basal groove surrounding the basal tubercle.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-2 and CQF-4.

Genus ***Reifella*** Ivanov, **n. gen.**
Type species: *Reifella lata* Ivanov, n. sp.

Diagnosis: Anachronistid teeth, elongated mesiodistally, with almost the same sizes of the crown and base; smooth, elongated semicircular crown; with rounded lateral blades and short, semioval labial flange; occlusal crest placed almost on the midline of the crown; low, triangular central cusp displaced labially; crown lingual surface curved to a deep lingual groove; vertical protrusions on distal and mesial crown parts; shallow, low crown/base junction; oval base extended lingually with a triangular thickening in the middle part; deep groove of a transversal canal in the lingual part; oval or rhomboid, prominent basal tubercle placed under the slightly overlapping labial flange; central and six ascending vascular canals connect the mesiodistally elongated pulp cavity.

Etymology: Named in honor of the outstanding palaeoichthyologist and ichthyologist Professor Wolf-Ernst Reif in recognition of his work on fossil and modern chondrichthyans.

Remarks: The teeth of the new genus *Reifella* are distinguished from the teeth of known anachronistids including *Cooleyella* Gunnell 1933 and *Ginteria* Duffin and Ivanov 2008, in the wider, sloped lingual part of the crown; the middle position of occlusal crest; lower central cusp; weakly developed lateral blades and labial flange; shallower and lower crown/base junction; the presence of vertical protrusions in the distal and mesial parts, a triangular thickening in the middle part of the base, deep groove of a transversal canal in the lingual part; six ascending canals and long pulp cavity in the vascularization system. The teeth of *Amaradontus* differ from the described teeth in well-developed central and lateral cusps, very narrow basal tubercles and shallow basal face of the tooth base (Hodnett and Elliott 2018).

Range: Middle Permian, Guadalupian, Roadian.

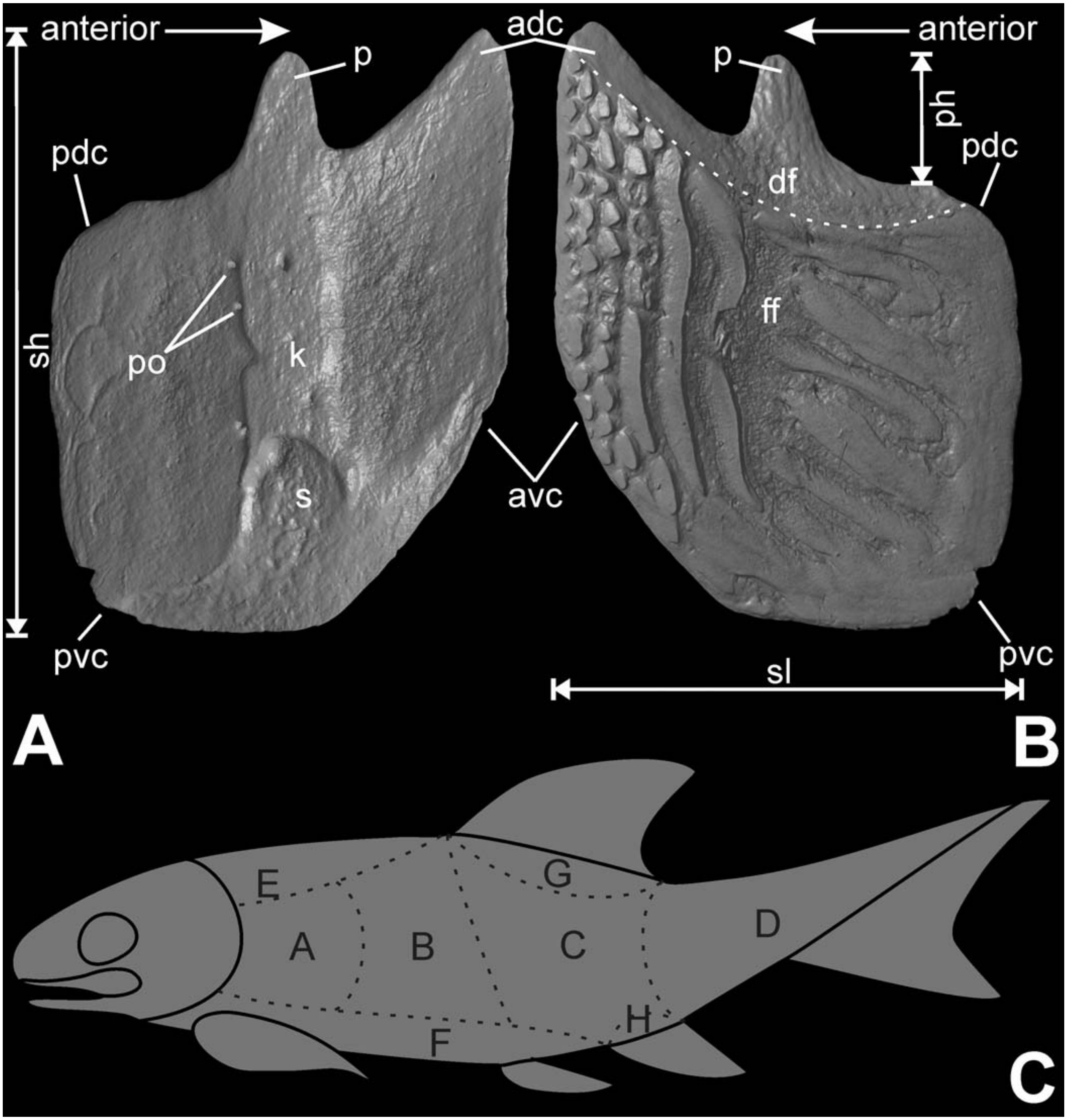
Reifella lata Ivanov, **n. sp.**
Plate 4, figures 1-5

Diagnosis: As for the genus.

Description: The teeth possess the anachronistid design of crown and base. The teeth are elongated mesiodistally, small (measuring from 0.7 to 1.1 mm mesiodistally). The crown is about the same size as the tooth base. The smooth crown is slightly convex, elongated semicircular in occlusal view, with rounded lateral blades, and slightly overhangs the base labially. A distinct occlusal crest is located almost in the midline of the crown, bears a central cusp, and separates the sloping labial and lingual surfaces. The labial surface is slightly convex, terminated by a short, semioval labial flange. The lingual surface is flat, curved to a deep lingual groove. The occlusal crest in a well-preserved specimen is delicately serrated (Pl. 4, fig. 2d). The central cusp is low, triangular, slightly inclined and displaced labially from the crest line. The lingual groove is limited by vertical protrusions on both the distal and mesial parts of the crown (Pl. 4, fig. 1a, 1e, pr). The crown/base junction is shallow and low.

The tooth base is elongated oval in shape, extended lingually. The occlusal face of the base is convex, with a triangular thickening in the middle part and the small notch of a transversal canal (Pl. 4, figs. 1e, 2b, 4b). The basal face is flat in the lingual part and depressed in the middle part (Pl. 4, fig. 1d). The deep groove of a transversal canal is located in the lingual part. A large pit of the central canal is located in the center of the depressed part, closed to the basal tubercle. The tubercle is prominent, oval or rhomboid in shape, elongated mesiodistally, and located under the slightly overlapping labial flange.

The vascularization system of the teeth includes transversal, central and six ascending canals, and a pulp cavity (Pl. 4, fig. 1d, 1h-1k). The transversal canal runs across the basal surface of the base in the lingual part. A short central canal starts from the foramen at the basal tubercle, extends upward and connects the pulp cavity. Six ascending canals are located in the base and connect with the pulp cavity. These canals are of different length: the longer ones are located in the extended mesial and



TEXT-FIGURE 4
Terminology used for morphological description of actinopterygians. A, B - The holotype of *Alilepis texasensis* Bakaev, n. sp. (NMMNHS-81548), area B scale: A - internal surface (visceral view); B - external surface (crown view). C - reconstructed squamation of *Alilepis texasensis* Bakaev, n. sp. and distribution of scale morphotypes on the fish body. Body areas A–H follow Esin (1990). Abbreviations: adc – antero-dorsal corner, avc – antero-ventral corner, df – depressed field, ff - free field, k – keel, p – peg, pdc – postero-dorsal corner, ph - peg height, po – pore, pvc - postero-ventral corner, s – socket, sh - scale height, sl - scale length.

distal parts. The long pulp cavity is elongated mesiodistally in the lower part of the crown. Bundles of dentine tubules are concentrated in the lateral blades of the crown.

Designation of types: Complete tooth (Pl. 4, fig. 1), Holotype, no. NMMNHS-81499, sample CQF-1, Williams Ranch Member, Cutoff Formation, Roadian, Guadalupian, middle Permian; Quarry section, Guadalupe Mountains, West Texas, USA.

Etymology: From the Latin *latus*, meaning wide.

Material: Four teeth.

Remarks: See remarks to the genus.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4.

Superorder and order INCERTAE SEDIS
Family JALODONTIDAE Ginter, Hairapetian and Klug 2002

Remarks: Included genera: *Jalodus* Ginter 1999; *Adamantina* Bendix-Almgreen 1993; *Isacrodus* Ivanov, Nestell and Nestell 2012; *Texasodus* Ivanov, Nestell and Nestell 2012.

Genus *Adamantina* Bendix-Almgreen 1993
Type species: *Adamantina benedictae* Bendix-Almgreen 1993.

Adamantina foliacea Ivanov 1999
Plate 5, figures 1-3

Description: The teeth possess mainly three or rarely two cusps in the massive crown. The cusps are wide and thick, almost rounded in cross section or slightly labio-lingually flattened. They are strongly fused above the tooth base and form a compact crown in the basal part. The cusps in the tricuspid crown have an almost equal height. The lateral cusps are closely packed in some tricuspid crowns (Pl. 5, figs. 2, 3); sometimes they are divergent from the central one and incurved mesially and distally in bicuspid and some tricuspid teeth (Pl. 5, fig. 1). The labial face of the crown bears strong ornamentations from two or three coarse lanceolate and short cristae. The short straight cristae can be branched from the long lanceolate ones (Pl. 5, fig. 1) or placed separately in the lower part of crown labial face (Pl. 5, figs. 2, 3). The lingual face of the crown is covered by a few short cristae reaching the cusp apex. The bicuspid crown instead the central cusp has a small prominence formed of two closely placed cristae (Pl. 5, fig. 1e). The basal part of the crown often bears a network of imprints on the lingual and labial sides. These imprints of the cells are isometric polygonal, most developed in the depressions at the crown/base junction (Pl. 5, figs. 1a, 2a).

The tooth base is thick, with prominent occlusal and slightly concave basal faces, and with a quite short lingual part. The crown/base junction is marked with a shallow groove bearing a row of small foramina. Two labio-basal tubercles are massive, rounded and prominent behind the labial and basal faces of the base. They are separated from each other by a deep and wide depression that can be traced from the basal part of the crown to the basal surface of the tooth base. The large foramina of a few main vascular canals open on the lingual rim and in the concave part of the basal side, closed to labio-basal tubercles.

Material: Four isolated teeth.

Remark: The teeth of *Adamantina foliacea* Ivanov are known with three to five cusps (Ivanov 1999; Ivanov et al. 2012). The multicuspid crown has a fan-shaped structure in the cusp arrangement. The occurrence of the *Adamantina* tooth with a bicuspid crown and undeveloped central cusp is a first record for the genus.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4; Carboniferous, Mississippian, Tournaisian of the South Urals, Russia; lower Permian, Cisuralian, Asselian of the Polar Urals, and Artinskian of the Middle Urals, Russia (Ivanov 1999); Carboniferous, Pennsylvanian, Moscovian of North Greenland (Cuny and Stemmerik 2018); Kasimovian of Iowa and New Mexico, USA (Tway and Zidek 1983; Ivanov and Lucas 2019).

Genus *Isacrodus* Ivanov, Nestell and Nestell 2012
Type species: *Isacrodus marthae* Ivanov, Nestell and Nestell 2012.

Isacrodus marthae Ivanov, Nestell and Nestell 2012
Plate 5, figures 4-7

Description: For the full description of the species based on the material from the Quarry section, see Ivanov et al. (2012, p. 14).

The teeth of *Isacrodus* have three massive cusps in the crown with labial lanceolate ornamentation and delicate cristae on the lingual face. Reticular and sinuous cristae occur on the lingual side in the lower part of cusps (Pl. 5, fig. 4b). A network of cell imprints is present on the lower part of the tooth crown, at the crown/base junction, on both the lingual and labial faces (Pl. 5, figs. 4b, 6). These imprints are up to 10 µm in size, isometric penta- or hexagonal polygons in shape.

The internal vascularization system of the teeth includes a dense network of vascular canals occupying the entire tooth base (Pl. 5, fig. 7a, b). A large horizontal main canal crosses the base from the lingual rim to the labial edge, and opens on the basal surface, at the labio-basal tubercle. The ascending canals of the base pass into the wide pulp canal of the cusps.

All the teeth from the Quarry section include three morphotypes: 1) narrow crown and base with a single oval labio-basal tubercle; 2) crown with straight cusps, slightly wider base with two rounded tubercles closely placed; and 3) lateral cusps curved sideward, with a wide base with two large, widely spaced oval tubercles.

Material: 43 teeth.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1, CQF-2, CQF-4, CWR-6, Q1-3, and Q-20.

***Isacrodus* sp.**
Plate 5, figure 8

Description: The teeth have a tricuspid crown flattened labio-lingually. The cusps are narrow, straight, with acute apexes, far placed from each other and separated by a very wide space. All of the cusps are the same in width and height. The labial ornamentation of the cusps consists of coarse and strongly lanceolate cristae in the upper part and curved, branched cristae in the lower part of the cusp. The lanceolate cristae are formed by a peculiar wavy, stepped lateral edge; the top part of the cusp is narrower than first lanceolate crista. The tooth base is thick and wide, oval in shape, with extended lateral parts and a strongly convex occlusal surface. The two labio-basal tubercles are wide, oval, widely spaced, oriented at an obtuse angle to each other.

Material: Two teeth.

Remarks: The teeth of *Isacrodus marthae* Ivanov, Nestell and Nestell differ from the described teeth in having massive cusps, narrow spaces between cusps, narrower central cusp, and non-stepped lateral edge of the cusps. The described teeth are similar to the third morphotype of *I. marthae*, but the latter have considerably divergent lateral cusps from the central one.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, sample Q-20.

Subclass EUCHONDROCEPHALI Lund and Grogan 1997

Euchondrocephali indet.
Plate 5, figure 9

Description: The tooth plate is symmetric, elongated labio-lingually, arched, semispherical in lateral view, extended basally, with convex occlusal and concave basal faces. The occlusal surface bears a narrow, compressed laterally, elevated crown with three transversal ridges. The ridges are separated by shallow depressions. Small foramina of the vascular canal open on lingual part of ocular surface, on the basal surface. Numerous secondary canals are concentrated in the crown, under the transversal ridges, and are connected by the long ascending canal (Pl. 5, fig. 9b).

Material: One tooth plate.

Remarks: The tooth plate is slightly similar to the tooth plates of *Arcuodus* Itano and Lambert 2018, but the latter has a wide occlusal surface compounded of tubular dentine (Itano and Lambert 2018).

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, sample CQF-4.

Chondrichthyan denticles and scales

The chondrichthyan denticles from the Quarry section include monocuspid, tricuspid and multicuspid types (Pl. 6, figs. 1-7). The monocuspid denticles have a long, acuminate crown, curved posteriorly, flattened laterally, ornamented with straight cristae (Pl. 6, fig. 1). The base is extended basally, slightly wider than the crown, with a porous surface. Similar denticles have been described from the cranial cap or spine-brush complex in some representatives of symmoriiforms (Lund 1974, 1985, 1986; Zidek 1993; Coates and Sequeira 2001). One denticle is a series of monocuspid denticles with fused bases, but the boundary of a denticle can be traced on the lateral edges (Pl. 6, fig. 7).

The multicuspid denticles have a crown consisting of four overlapping cusps arranged in a spiral row (Pl. 6, figs. 2, 3). The cusps increase in size posteriorly; they are pyramidal, incurved and inclined posteriorly, ornamented with curved cristae. Some denticles bear distinct lateral carinae on the flattened cusps (Pl. 6, fig. 3). The denticle base is slightly concave and bears numerous pores on the external surfaces. These denticles have been described as the form-taxon *Stemmatias* Hay 1899 and determined as the mucous membrane or buccopharyngeal denticles of symmoriiforms (Zangerl and Case 1976; Coates and Sequeira 2001).

The tricuspid denticles have two small anterior cusps and one large posterior cusp on the crown (Pl. 6, figs. 4-6). The cusps are located separately (Pl. 6, fig. 4) or fused basally (Pl. 6, fig. 5). They are pyramidal, acuminate, curved posteriorly, with flattened anterior and convex posterior faces, covered by a few straight cristae. The base is larger than the crown, is subtriangular in occlusal view, with convex occlusal and almost flat basal surfaces. One denticle has two separated crowns and partly fused bases (Pl. 6, fig. 6). Such denticles have been defined as probably gill-arch denticles of *Stethacanthulus meccaensis* (Williams 1985).

The fish assemblage from the Quarry section contains very diverse chondrichthyan scales. They include 10 morphotypes, some of which are significantly varied. The scales of morphotype 1 are very few in number, and have a flat, low, monolithic crown, low neck and hemispherical, convex base (Pl. 6, figs. 8-10). The crown possesses a compact odontocomplex including a central odontode that is surrounded by elongate, narrow lateral odontodes. The odontodes in some scales were fused partly (Pl. 6, fig. 9) or completely, without distinct boundaries (Pl. 6, fig. 10). One scale has a central odontode placed anteriorly that is surrounded by lateral odontodes postero-laterally (Pl. 6, fig. 8). The external surface of the crown (Pl. 6, fig. 10) or the anterior part of the scale neck (Pl. 6, fig. 9) have a network of polygonal cellular imprints. Similar scales have been described as protacrodontid (Gross 1938; Ørvig 1967) or orodontid (Ivanov and Nilov 2017).

The scales of morphotype 2 (Pl. 6, figs. 11-13) are quite scarce in the assemblage. They have a polyodontode complex crown, narrow, weakly developed neck and a low, flat base. The crown is curved and inclined backward, often asymmetric, consists of triangular central and long, narrow lateral fused odontodes. They are closely spaced, arranged subparallel to each other, separated by narrow grooves, and ornamented with branched ridges. The scale base is larger than the crown, with a concave basal side. The foramina of vascular canals open in the anterior surface of the neck and in the basal surface of the base. Such scales belong to the ctenacanthid type (e.g., Turner 1993; Ivanov and Nilov 2017). However, similar scales have also been found in the xenacanthiform *Diplodoselache* (Dick 1981) and the euselachian *Sphenacanthus* (Dick 1998).

The scales of morphotype 3 are abundant in the assemblage. They have a high, elongated crown, well-developed narrow neck, low and small base (Pl. 6, figs. 14-17). The crown is inclined posteriorly, bears long and prominent longitudinal ridges separated by wide and deep grooves. The crown of some scales is terminated by an acuminated posterior process (Pl. 6, fig. 14); other scales have a serrated posterior edge of the crown (Pl. 6, figs. 15, 17). The longitudinal ridges of the crown are often serrated and sometimes have a striated lateral face process (Pl. 6, fig. 16). The scale base has convex external and flat basal surfaces. These scales are usually assigned to hybodontid type (e.g., Reif 1978) and were named as the formal taxon *Cooperella* (Gunnell 1933). The scales of such type have been described for some euselachian sharks (Böttcher and Duffin 2000; Wang et al. 2009).

The scale morphotype 4 is rare among the scales in the Quarry section, has a spiked crown, poorly developed neck, low and wide base (Pl. 6, figs. 18, 19). The acuminate cusps of different length are arranged in a medial longitudinal row and on both lateral edges. The cusps are inclined posteriorly, microstriated and ornamented with small, elongated tubercles at the crown/base junction. The external surface of the scale base is corrugated and penetrated by foramina of vascular canals. The basal face of the base is slightly concave, with numerous foramina.

The very scarce scales of morphotype 5 have a large crown, very narrow neck and moderate base (Pl. 6, fig. 20). The crown bears anastomosing, branched ridges with rare cristae and three posterior processes. The scale base is oval in shape, with smooth, convex external and flat basal surfaces. Numerous foramina of the vascular canals open on the external face.

The scales of morphotype 6 (Pl. 6, figs. 21, 22) are rare in the assemblage and have a small crown and large, pyramidal base. The crown is tiny, tuberculated, conical (Pl. 6, fig. 21) or larger than the crown/base junction, inclined posteriorly and has two lateral ridges (Pl. 6, fig. 22). The fluted base bears prominent ridges diverging from the crown and terminated in processes. These marginal processes are separated by deep notches. The basal surfaces of the base are strongly concave. The similar scales have been illustrated by Reif (1978) as the scales of *Hybodus delabechei* Charlesworth 1839.

The scales of morphotype 7 are most abundant in the fish assemblage from the Quarry section. The scales have a rhomboid, inclined crown, well-developed, narrow neck and base with short processes (Pl. 6, figs. 23-27). The crown is almost smooth with a small anterior ridge (Pl. 6, figs. 24-26) or bears straight lateral and triangular medial ridges separated by wide grooves and notches in the anterior edge (Pl. 6, fig. 27). The crown varies in the width and pointedness of the apex. The scale base has ridges diverging from the crown and terminated in short processes (Pl. 6, fig. 23). The foramina of the neck canal open in the groove between these ridges. The basal face of the base is slightly concave. These scales have been described as the formal taxon *Moreyella* (Gunnell 1933) and they belong to the neoselachians (e.g., Reif 1985; Campbell 2003).

The scales belonging to the morphotype 8 are common in the assemblage of the Quarry section. They are characterized by a low, polygonal crown with flat or slightly inclined, smooth external and vertical lateral faces, and rounded corners (Pl. 6, figs. 28, 29). The crown/base boundary is marked by a distinct, narrow groove. The base is extended basally, round or polygonal in the basal view, higher and narrower than the crown, with vertical or slightly sloping lateral and almost flat basal faces. The lateral surface is perforated with numerous foramina of vascular canals opening in the vertical grooves. A large foramen opens in the center of basal surface. This morphotype of scales has been named as *Kirkella* (Gunnell 1933).

PLATE 1

Symmoriiform teeth from the Williams Ranch Member, Cutoff Formation,
Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains.
All SEM microphotograph images. Abbreviations: fvc – foramen of vascular canal, ps – papilla structure.

1-10 – *Stethacanthulus decorus* (Ivanov 1999).

1 NMMNHS-81582, occlusal view; sample CQF-4; scale bar 200 µm

2 NMMNHS-81460; 2a, oblique lateral view, scale bar 200 µm; 2b, occlusal view, scale bar 200 µm; 2c, enlarged occlusal view, scale bar 20 µm; sample CQF-4

3 NMMNHS-81461, oblique labial view; sample CQF-1; scale bar 200 µm

4 NMMNHS-81462, occlusal view; sample CQF-3; scale bar 200 µm

5 NMMNHS-81463, oblique lateral view; sample CQF-3; scale bar 200 µm

6 NMMNHS P-81464, occlusal view; sample CQF-1; scale bar 200 µm

7 NMMNHS P-81465, occlusal view; sample Q-20; scale bar 200 µm

8 NMMNHS-81466, labial view; sample CQF-4; scale bar 200 µm

9 NMMNHS-81467; 9a, labial view; 2b, occlusal view; 2c, enlarged occlusal view; sample CQF-1; scale bar 200 µm; (9c) scale bar 20 µm

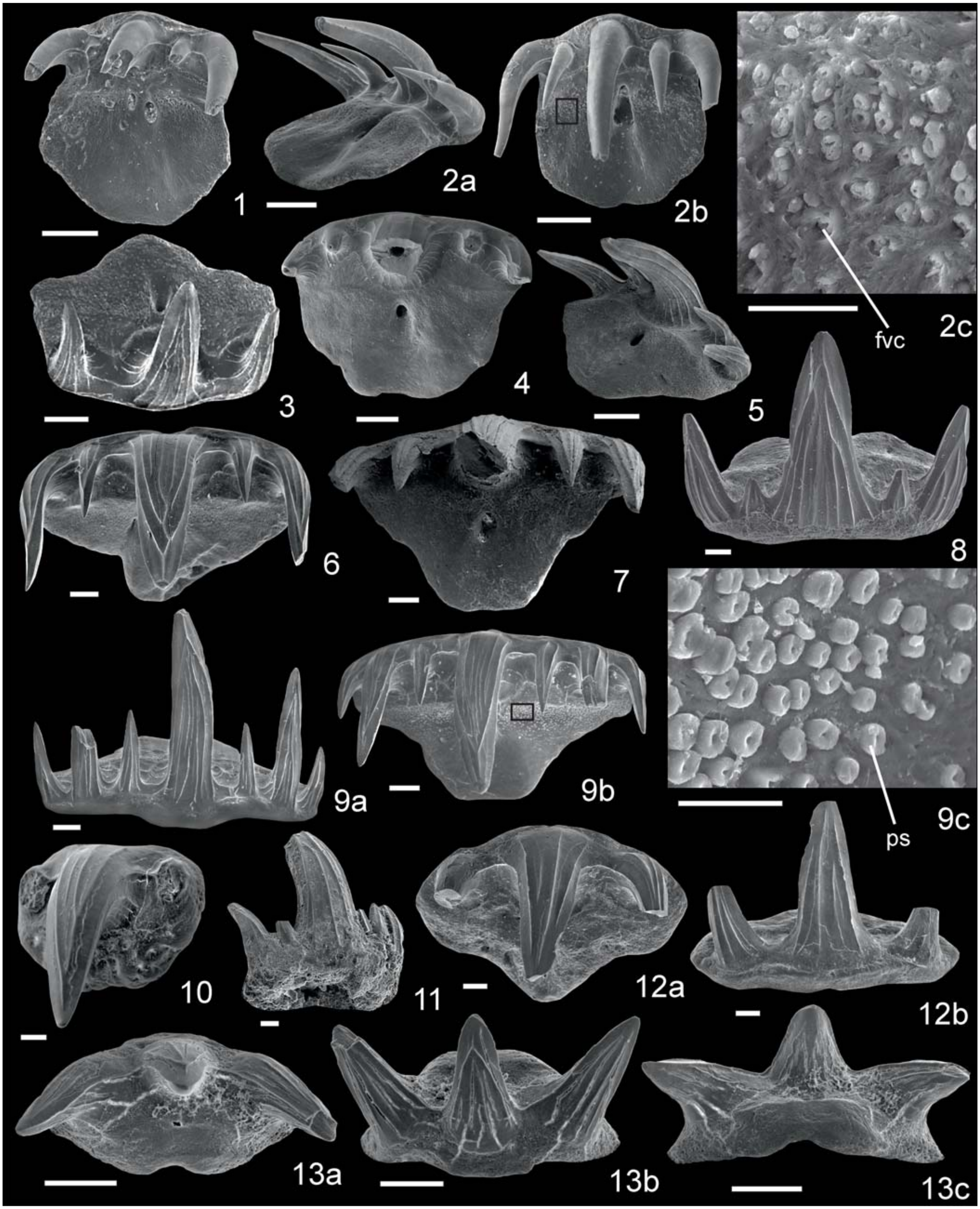
10 NMMNHS-81468, oblique occlusal view; sample CQF-1; scale bar 200 µm

11, 12 – Symmoriiformes indet.

11 NMMNHS-81469, oblique labial view; sample CQF-1; scale bar 200 µm

12 NMMNHS-81470; 12a, occlusal view; 12b, labial view; sample CQF-4; scale bar 200 µm

13 – *Kungurodus* sp., no. NMMNHS-81471; 13a, occlusal view; 13b, labial view; 13c, lingual view; sample CQF-4; scale bar 200 µm


1
2a
2b
2c
fvc
3
4
5
6
7
8
9a
9b
9c
ps
10
11
12a
12b
13a
13b
13c

The scales of morphotype 9 occur rarely in the section. These scales have a small crown, very narrow neck and base with four long processes (Pl. 6, fig. 30). The crown is smooth, conical, slightly inclined posteriorly, with distinct lateral edges. The processes in the base are separated by wide notches, formed in a cross-like shape. The basal face of the base is concave in the middle part. Such scales are known in the squamation of some neoselachians (e.g., squalids or heterodontids, Reif 1985).

The scales of morphotype 10 are common in the assemblage and have a hemispherical, ornamented crown and polygonal base (Pl. 6, figs. 31–34). The crown bears anastomosing, curved, bifurcated, coarse ridges separated by distinct grooves. The grooves can cover only the crown (Pl. 6, figs. 31, 32) or penetrate until the base forming the anastomosing edge of the crown (Pl. 6, fig. 33). The scale base is larger than the crown, with slightly convex external and flat basal faces. A few foramina of vascular canals open along the crown/base junction and in the center of the basal surface. Tessera-like scales can develop in this morphotype when the scale bases fuse, but the crowns remain separate (Pl. 6, fig. 34). Such scales are often determined as possible head scales (e.g., Burrow et al. 2009).

Superclass OSTEICHTHYES Huxley 1880
Class ACTINOPTERYGII Cope 1887
Family ELONICHTHYIDAE Aldinger 1937

Genus *Alilepis* Yankevich 1998
Type species: *Alilepis elegans* Yankevich 1998.

Remarks: Besides the type species, the genus includes the following species: *Alilepis esini* A. Minich 2006, *A. secunda* A. Minich 2006, *A. kolguevensis* A. Minich 2006, and *Alilepis texasensis* Bakaev, n. sp.

Alilepis texasensis Bakaev, **n. sp.**
Plate 7, figures 1-9; Plate 8, figures 1-12, Plate 9, figures 1-3

Alilepis sp. - IVANOV et al. 2020, p. 249-250, figs. 8 E, F.
Varialepis sp. – IVANOV et al. 2013, p. 157-158, figs. 6 A-C. – IVANOV et al. 2015b, p. 311, pl. 2, fig 17. – IVANOV et al. 2020, p. 250, figs. 8 H, I.
Elonichthyid scale - IVANOV et al. 2020, p. 250, fig. 8 D.
Haplolepid scale - IVANOV et al. 2015b, p. 311, pl. 2, fig. 15. – IVANOV et al. 2020, p. 250, fig. 8 G.

Diagnosis: (based on the scales from areas A and B). Small actinopterygian fish with thin rhomboidal ganoid scales. Depressed field is very small; there is a narrow band along the anterior margin. Anterior and posterior margins are straight. The anterior margin of the free field consists of subvertical rows of small, roundly triangular, slightly elevated postero-ventrally ridges. Rows are replaced by long subvertical, triangular in section, ridges caudally, also slightly elevated posteriorly. These ridges extend ventrally and then turn posteriorly. The middle part of free field consists of ridges that extend postero-ventrally and can fuse into a smooth surface. A few pores open along the anterior margin of the free field and between the ridges, in grooves or furrows.

Description: Area A scales (Pl. 7, figs. 5, 6). The scales are 1.5-2 times higher than longer. Anterior and posterior margins

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PLATE 2

Ctenacanthiform and euselachian teeth from the Williams Ranch Member,
Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains.
SEM microphotograph (1a, 1c, 2–8) and microtomographic (1b, 1d-f) images in transparent model.
Abbreviations: ac – ascending canal, mhc – main horizontal canal, pc – pulp canal, shc – secondary horizontal canal.

1-3 – *Glikmanius myachkovensis* (Lebedev 2001).

1 NMMNHS-81472; 1a, occlusal view; 1b, basal view; 1c, oblique labial view; 1d, frontal view; 1e, sagittal view; 1f, transversal view; virtual sections; sample CQF-1; scale bar 200 µm

2 NMMNHS-81473; 2a, labial view; 2b, occlusal view; sample CQF-1; scale bar 200 µm

3 NMMNHS-81474, occlusal view; sample CQF-1; scale bar 200 µm

4-7 – *Sphenacanthus* sp.

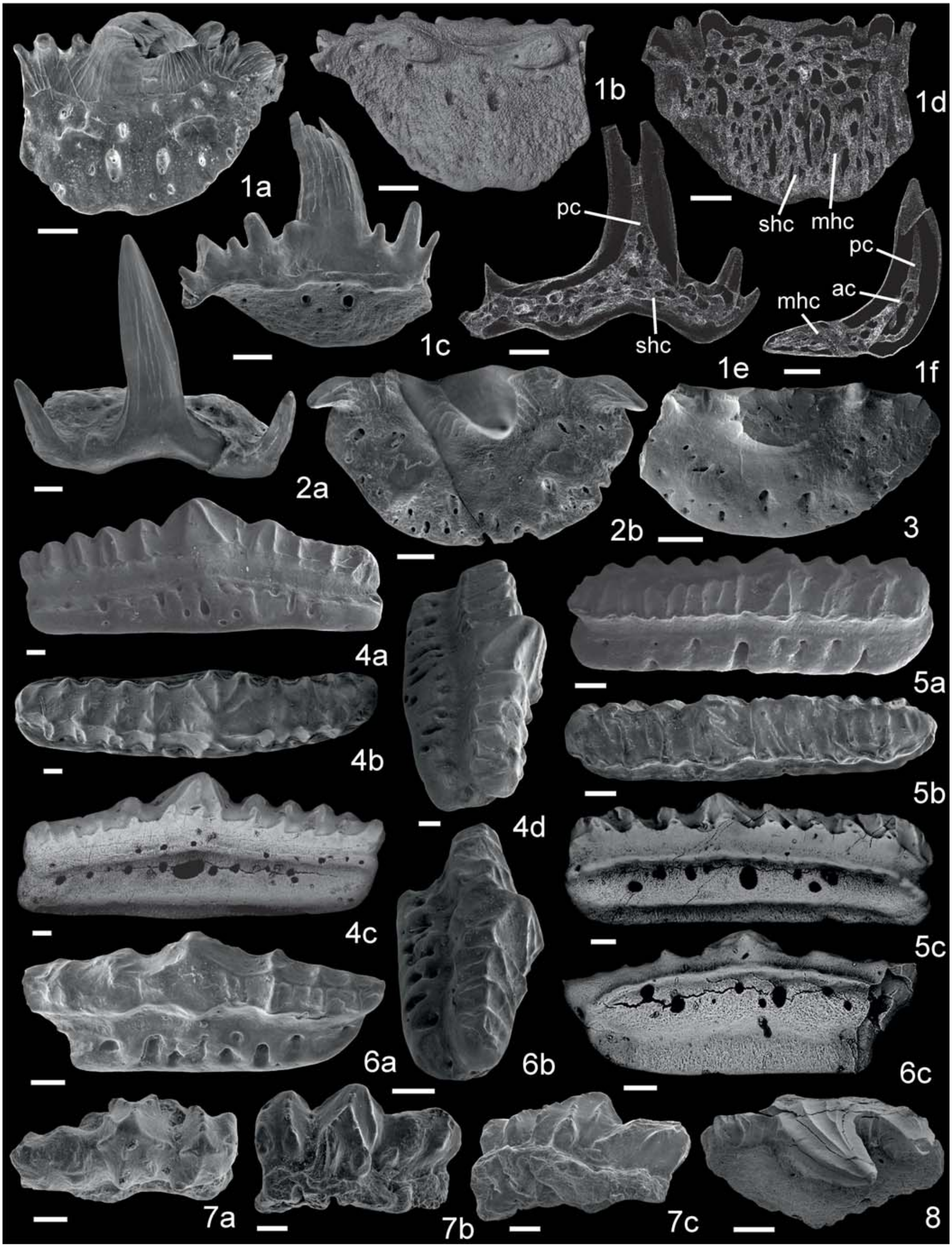
4 NMMNHS-81475; 4a, lingual view; 4b, occlusal view; 4c, labial view; 4d, oblique lateral view; sample CQF-1; scale bar 100 µm

5 NMMNHS-81476; 5a, lingual view; 5b, occlusal view; 5c, oblique labial views; sample CQF-2; scale bar 100 µm

6 NMMNHS-81477; 6a, oblique lingual view; 6b, oblique lateral view; 6c, basal view; sample CQF-2; scale bar 100 µm

7 NMMNHS-81478; 7a, occlusal view; 7b, labial view; oblique basal view; sample CQF-4; scale bar 100 µm

8 Hybodontiformes indet., no. NMMNHS-81479, occlusal view; sample CQF-3; scale bar 100 µm


1a
1b
1c
1d
pc
shc
mhc
1e
pc
ac
mhc
1f
2a
2b
3
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8

are straight. Dorsal edge is concave, ventral edge - slightly convex. Antero-ventral and postero-ventral corners are slanting. Antero-dorsal corner is high and pointed. Peg and socket are well developed, reaching a third of the scale height, located midway along the scale length. The peg has a wide base. Keel is well developed, flat, and closer to the peg- and -socket midline. There are narrow depressed fields along the anterior and dorsal margins. The free field consists of high ridges, separated by wide grooves. Anterior ridges are short and subvertical, whereas posterior ridges are nearly horizontal. The scale (Pl. 8, fig. 6, no. NMMNHS-81560) probably comes from the ventral part of area A and is not as high as the scale (Pl. 7, fig. 5, no. NMMNHS-81550) that comes from the anterior part of area A.

Area B scales (Pl. 7, figs. 1-3, 9). Subrectangular scales are similar to those of area A but thicker; the scale height is nearly equal the scale length. Antero-ventral and postero-ventral corners are slanted less than in the scales from area A. Peg and socket are well developed, but smaller than scales in area A, reaching one quarter of the scale height, located midway along the scale length. Anterior margin of the free field consists of three or four subvertical rows of small, roundly triangular, slightly elevated postero-ventrally ridges. Rows are replaced by two or three long subvertical ridges caudally. The middle part of free field consists of low ridges that extend postero-ventrally and fuse into a smooth surface.

The scale (Pl. 7, fig. 9, no. NMMNHS-81554) has all of the features of a juvenile scale (Esin 1995b): very small size; well-developed ornamentation; few ridges; lacks of a keel and peg and socket; not pronounced antero-dorsal corner; and elongate tubercles on the ganoine surface. This scale belongs to area B, based on its ornamentation. This specimen is the only scale with preserved denticles.

Area C scales (Pl. 7, fig. 7; Pl. 8, fig. 9). Scales are subrectangular, 1.5–2 times longer than higher. Anterior and posterior margins are straight, dorsal and ventral margins are slightly convex or straight. Antero-ventral and postero-ventral corners are less slanted than in area B scales, or form an obtuse angle. Peg and socket are very short or lack. Keel is flat. Anterior margin of the free field consists of three to five long subvertical ridges. The middle part of the free field is dissected by furrows. The ganoine cover in the posterior part converges on the continuous surface. The scale (Pl. 8, fig. 9, no. NMMNHS-81563) comes from the posterior part of area C, based on the absence of articular elements (peg and socket).

PLATE 3

Anachronistid teeth of *Cooleyella* from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains.
All SEM microphotograph images. Scale bar – 100 µm.
Abbreviations: dt – dentine tubule, en – enameloid layer, pc – pulp canal, pca – pulp cavity.

1-17 – *Cooleyella amazonensis* Duffin, Richter and Neis 1996

1 NMMNHS-81480, occlusal view; sample CQF-2

2 NMMNHS-81481, occlusal view; sample CQF-3

3 NMMNHS-81482; 3a, occlusal view; 3b, basal view; sample Q1-3

4 NMMNHS-81483, oblique occlusal view; sample CQF-3

5 NMMNHS-81484; 5a, occlusal view; 5b, basal view; sample CQF-4

6 NMMNHS-81485, occlusal view; sample Q1-3

7 NMMNHS-81486, occlusal view; sample Q1-3

8 NMMNHS-81487; 8a, oblique occlusal view; 8b, lingual view; sample Q1-3

9 NMMNHS-81488; 9a, lateral view; 9b, oblique labial view; sample CQF-1

10 NMMNHS-81489, oblique lateral view; sample Q1-3

11 NMMNHS-81490, lateral view; sample Q1-3

12 NMMNHS-81491, basal view; sample CQF-1

13 NMMNHS-81492, labial view; sample CQF-4

14 NMMNHS-81493, occlusal view; sample CQF-1

15 NMMNHS-81494, oblique labial view, with broken labial part of the crown; sample CQF-4

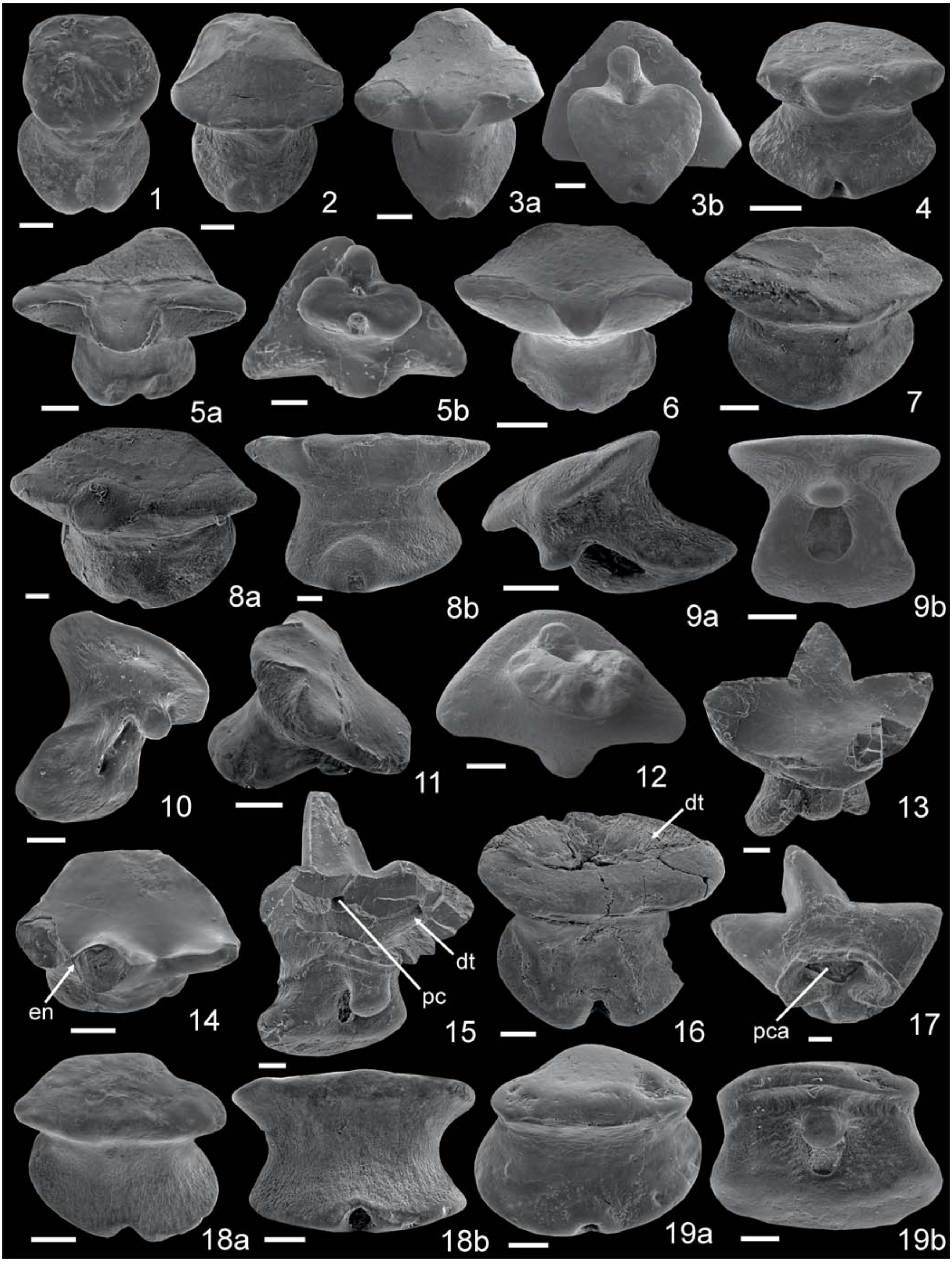
16 NMMNHS-81495, oblique occlusal view, with abraded labial part of the crown; sample CQF-2

17 NMMNHS-81496, basal view, with broken base; sample CQF-4

18, 19 – *Cooleyella* sp.

18 NMMNHS-81497; 18a, oblique occlusal view; 18b, lingual view; sample CQF-2

19 NMMNHS-81498; 19a, oblique occlusal view; 19b, oblique labial view; sample CQF-4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3b
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5a
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7
8a
8b
9a
9b
10
11
12
13
dt
en
14
pc
dt
15
16
pca
17
18a
18b
19a
19b

Area D scales (Pl. 8, figs. 7, 8, 10-12). The scales are almost rectangular, relatively thick, height slightly exceeds than length. Margins are relatively straight. Antero–dorsal corner is slightly acute, antero-ventral and posterio-dorsal corners are obtuse, posterio-ventral corner is pointed. Keel, peg and socket are lacking. Depressed fields are narrow, occur along both the anterior and dorsal margins in posterior scales. The free field has a well-developed ganoine layer. Its anterior margin is straight, consists of one or two subvertical ridges or lacks them. Middle and posterior parts of the free field consist of a flat surface with a few narrow furrows or without them. Posterior margin bears two dentices or is smooth. The scale (Pl. 8, fig. 12, no. NMMNHS-81566) can be a juvenile and has features similar to those of scale illustrated in Plate 7, fig. 9 (no. NMMNHS-81554).

Area F scales (Pl. 8, figs. 1-6). The scales are very long, 2-5 times longer than high. Anterior and posterior margins are straight, dorsal and ventral margins are slightly concave and convex respectively. Antero-ventral corner is slanting. Antero–dorsal corner is pointed. Peg and socket are well developed in the anterio-dorsal part of area (Pl. 8, figs. 1, 4), and very short or absent in the postero-ventral part (Pl. 8, figs. 5, 6). Keel is flat. Anterior margin of the free field consists of three to five long subvertical ridges. Free field sculpture is well developed in the anterior part of the area (Pl. 8, figs. 3, 4) and weakly developed in the posterior part (Pl. 8, figs. 5, 6). Area F scales are similar to scales of A, B, C areas.

Ridge scale (Pl. 7, fig. 8). The scale is bilaterally symmetrical, arrowhead-shaped, with a deeply invaginated margin anteriorly. Anterior “horns” lack a ganoine cover. Depressed field is wide anteriorly (along the invaginated margin) and narrow posteriorly; it is triangular in shape. Anterior border of the free field is dissected by narrow and short furrows. Peg, socket, keel and serration are absent.

Other types of scales reliably referred to *Alilepis texasensis* have not been discovered yet.

Scale surface ultrasculpture. The ganoine’s external surface of *Alilepis texasensis* has numerous small microtubercles. It is a characteristic feature of basal ray-finned fishes (Reissner 1859; Ermin et al. 1971; Schultze 1966, 1968, 1977, 2016, 2018; Bakaev and Kogan 2020). The tubercles are present in the center of the epidermal cells, and indicate a different secretion process of the basal layer of the epidermis in actinopterygians (Sire et al. 1987; Schultze 2016). Esin (1995b) observed that these tubercles are rounded on the ganoine surface of adult fishes, whereas they are elongated in juveniles. It has been previously suggested that the rounded or elongated shape of the tubercles reflects the shape of the epidermal cells (Bakaev and Kogan 2020), and that the elongated tubercles on the scale surface of young individuals correspond to the stretched epidermal cells of a fast-growing organism. A stretched appearance of the original epidermal cells can also be assumed for the areas with more substantial ganoine cover and where the ganoine sculpture is considerably thicker than in areas where this tissue is thinner.

Scale histology. A histological study has been performed on the scales from area C. The palaeoniscoid-type scale (Sire et al. 2009; Schultze 2016) is composed of three types of tissue (from outer to inner surfaces): ganoine, orthodentine and lamellar bone with osteocyte lacunae. The ganoine is relatively thick and

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PLATE 4

Anachronistid teeth of *Reifella lata* Ivanov, n. gen., n. sp. from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains. SEM microphotograph (1a-1g, 1f, 2–5) and microtomographic (1h, 1j-1k) images. Scale bar – 100 µm. Abbreviations: ac – ascending canal, cc – central canal, fcc – foramen of central canal, pca – pulp cavity, pr – crown protrusion, tc – transversal canal.

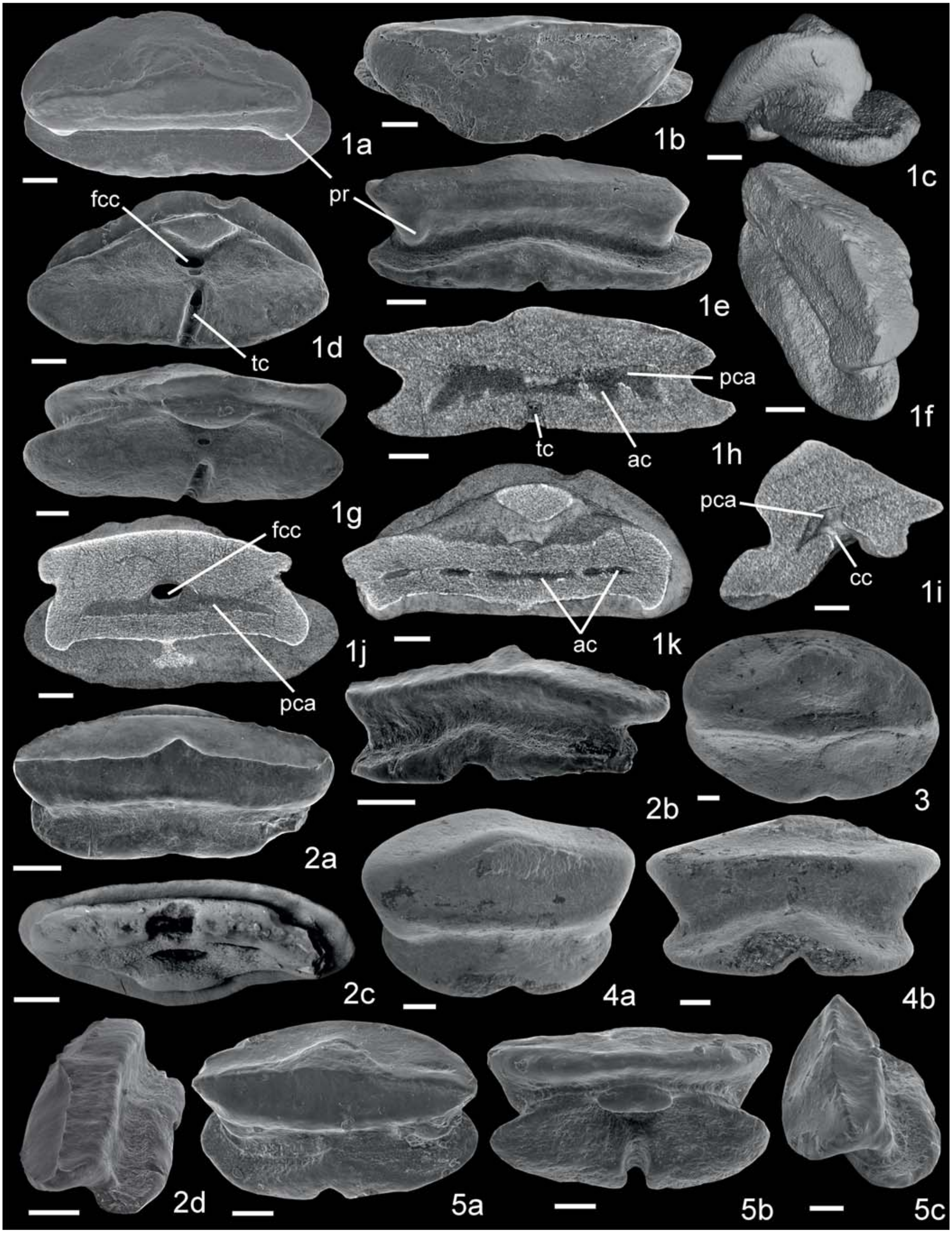
1 NMMNHS-81499, holotype; 1a, occlusal view; 1b, labial view; 1c, lateral view; 1d, basal view; 1e, lingual view; 1f, oblique lateral view; 1g, oblique basal view; 1h, sagittal view; 1i, transversal view; 1j, frontal in occlusal view; 1h, frontal in basal view, virtual sections; sample CQF-1

2 NMMNHS-81500; 2a, occlusal view; 2b, lingual view; 2c, basal view; 2d, oblique lateral view; sample CQF-1

3 NMMNHS-81501, occlusal view; sample CQF-1

4 NMMNHS-81502; 4a, occlusal view; 4b, lingual view; sample CQF-1

5 NMMNHS-81503; 5a, occlusal view; 5b, oblique basal view; 5c, oblique lateral view; sample CQF-4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1b
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fcc
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consists of numerous distinctive and superimposed layers (Pl. 9, fig. 3). Each individual layer is associated with odontodes of the same and developmental generation (Pl. 9, fig. 3b, gl). This feature is the result of the overlapping growth of several ganoine layers during the ontogenetic development. The ganoine layer is penetrated by vertical vascular canals (Pl. 9, fig. 3b, vc), associated with pore cavities at the surface of the scale (Qu et al. 2016). The dentine extends into the pores and inserts between the ganoine layers. The dentine layer is relatively thin (Pl. 9, fig. 3). The odontodes are organized side by side; the series is defined as odontocomplex. The shape of the odontodes indicates partial resorption of dentine, preceding the formation of a new odontode. Horizontal canals of the vascular system lie at the base of the odontodes (Pl. 9, fig. 3b, hc) and represent the homolog of pulp cavities (Qu et al. 2016). Numerous dentine tubules penetrate the dentine layer, as typical for the orthodentine of early osteichthyans (Sire et al. 2009). The scale base is thick and formed by pseudolamellar bone with many osteocyte lacunae enclosed between the bone lamella (Pl. 9, fig. 3b, arrowheads). Scale-anchoring Sharpey's fibers are abundant in the keel (Pl. 9, fig. 2), dorsal and ventral margins (Pl. 9, fig. 3b, sh), and extend toward the center of the scale. This system is similar to that observed in the scales of recent *Polypterus* (Gemballa and Bartsch 2002), where collagen fibers of the *stratum compactum* (paraserial and interserial) are anchored to the keel, whereas two neighboring scales in single row are connected by fibers between the peg and socket (dorsal and ventral margins, respectively).

The longitudinal cross section of the scale of *Alilepis texasensis* n. sp. resembles that of a scale of *Elonichthys punctatus?* Aldinger 1937 (Dias et al. 2010, fig. 6) and, especially, *Elonichthys punctatus* Aldinger (Aldinger 1937, text-fig. 3, taf. 2).

Designation of types: Scale from area B, from transition zone with area A (Pl. 7, fig. 3; Pl. 9, fig. 1), Holotype, Pl. 7, fig. 3, no. NMMNHS-81548, sample CQF-4, Williams Ranch Member, Cutoff Formation, Roadian, Guadalupian, middle Permian; Quarry section, Guadalupe Mountains, West Texas, USA.

Etymology: After the state of Texas, USA.

Material: 180 well or moderately preserved scales.

Discussion: *Alilepis texasensis* n. sp. differs from all other species of the genus in the combination of small, roundly triangular ridges placed cranially, and long subvertical ridges placed caudally in the anterior part of free field. Additionally, the new species is distinguished from *A. elegans* Yankevich 1998 by the absence of numerous large pores on the free field, higher antero-dorsal corner and lower peg, more dissected free field, small ridges slightly elevated postero-ventrally, and less pronounced serration. *A. texasensis* differs from *A. esini* A. Minich 2006 (A. Minikh 2006, pl. 11, figs. 4-6; Esin 1990) in a higher antero-dorsal corner, more dissected free field, smaller depressed field, and less pronounced serration. The new species is distinguished from *A. secunda* A. Minich 2006 by a higher antero-dorsal corner and lower peg and less number of small ridged rows. *A. texasensis* differs from *A. kolguevensis* A. Minich 2006 in the presence of small ridged rows along the anterior margin of the free field, and less pronounced serration.

PLATE 5

Jalodontid teeth and euchondrocephalian tooth plate from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains.
SEM microphotograph (1–6, 8, 9a, 9c, 9d) and microtomographic (7, 9b) images.
Abbreviations: ac – ascending canal, mhc – main horizontal canal, pc – pulp canal, sc - secondary canal, shc – secondary horizontal canal.

1-3 – *Adamantina foliacea* Ivanov 1999

1 NMMNHSS P-80888; 1a, oblique labial view; 1b, lingual view; 1c, occlusal view; 1d, basal view; 1e, enlarged labial view of the crown central part; sample CQF-4; scale bar 100 µm

2 NMMNHS-81504; 2a, labial view; 2b, lingual view; 2c, basal view; sample CQF-4; scale bar 100 µm

3 NMMNHS-81505, labial view; sample CQF-4; scale bar 100 µm

4-7 – *Isacrodus marthae* Ivanov, Nestell and Nestell 2012

4 NMMNHS-81506; 4a, occlusal view; 4b, oblique lateral view; sample Q1-3; scale bar 100 µm

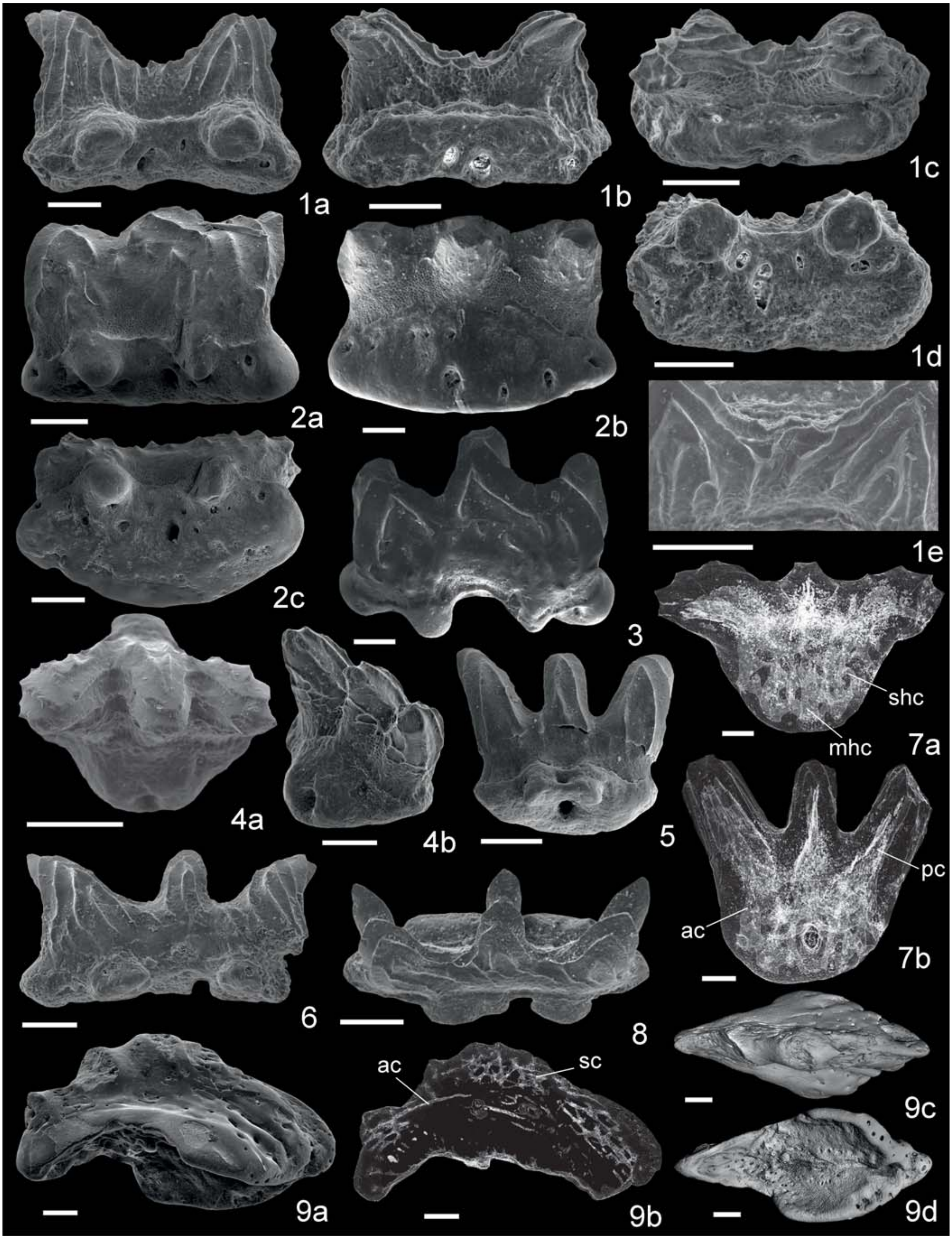
5 NMMNHS-81507, oblique labial view; sample CQF-3; scale bar 100 µm

6 NMMNHS-81508, labial view; sample Q1-3; scale bar 100 µm

7 NMMNHS-81509, 7a, occlusal; 7b, lingual views in transparent model; sample CQF-4; scale bar 100 µm

8 – *Isacrodus* sp., no. NMMNHS-81510, oblique labial view; sample Q-20; scale bar 100 µm

9 – Euchondrocephali indet., no. NMMNHS-81511; 9a, lateral view; 9b, virtual sagittal section; 9c, occlusal view; 9d, basal view; sample CQF-4; scale bar 500 µm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ac
sc
9c
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PLATE 6

Chondrichthyan microremains from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains. All SEM microphotograph images.

1 – Monocuspid denticle, no. NMMNHS-81512, lateral view; sample CQF-2; scale bar 300 µm

2, 3 – Multicuspid denticles
- 2 NMMNHS-81513, lateral view; sample CQF-4; scale bar 100 µm
- 3 NMMNHS-81514, anterior view sample CQF-4; scale bar 100 µm

4-6 – Tricuspid denticles
- 4 NMMNHS-81515, oblique anterior view; sample CQF-1; scale bar 300 µm
- 5 NMMNHS-81516, oblique crown view; sample CQF-1; scale bar 100 µm
- 6 NMMNHS-81517, oblique crown view; sample CQF-1; scale bar 300 µm

7 – Series of monocuspid denticles, no. NMMNHS-81518, oblique crown view; sample CQF-1; scale bar 100 µm

8-10 – Scales of morphotype 1
- 8 NMMNHS-81519, oblique crown view; sample CQF-1; scale bar 100 µm
- 9 NMMNHS-81520, oblique crown view; sample CQF-3; scale bar 100 µm
- 10 NMMNHS-81521, crown view; sample CQF-3; scale bar 100 µm

11-13 – Scales of morphotype 2
- 11 NMMNHS-81522, lateral view; sample CQF-4; scale bar 300 µm
- 12 NMMNHS-81523, anterior view; sample CQF-4; scale bar 100 µm
- 13 NMMNHS-81524, oblique crown view; sample CQF-2; scale bar 100 µm

14-17 – Scales of morphotype 3
- 14 NMMNHS-81525, crown view; sample CQF-4; scale bar 300 µm
- 15 NMMNHS-81526, oblique anterior view; sample CQF-1; scale bar 100 µm
- 16 NMMNHS-81527, lateral view; sample CQF-1; scale bar 100 µm
- 17 NMMNHS-81528, lateral view; sample CQF-4; scale bar 100 µm

18, 19 – Scales of morphotype 4
- 18 NMMNHS-81529, lateral view; sample CQF-1; scale bar 100 µm
- 19 NMMNHS-81530, crown view; sample CQF-4; scale bar 300 µm

20 –Scale of morphotype 5, no. NMMNHS-81531, crown view; sample CQF-1; scale bar 300 µm

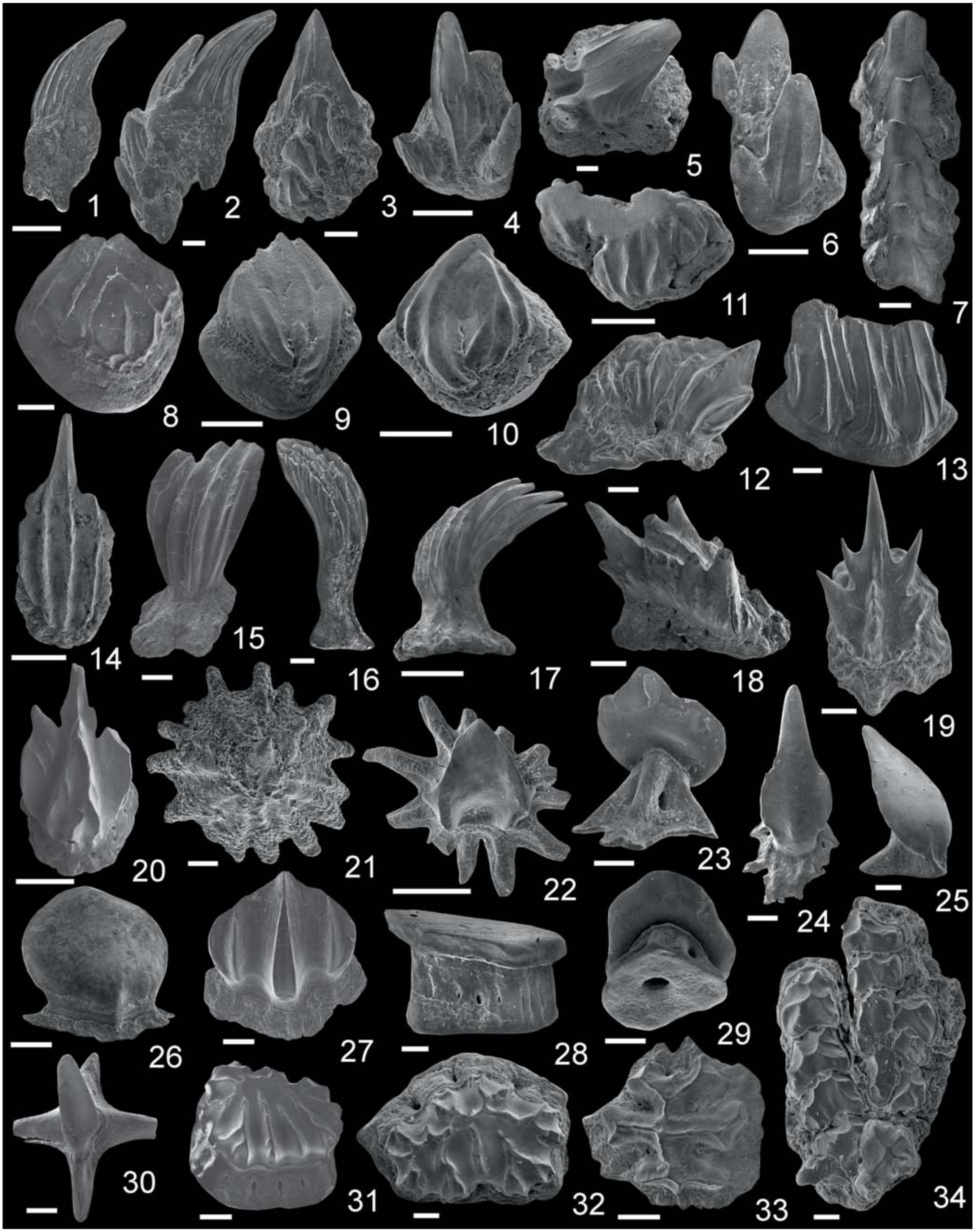
21-22 – Scales of morphotype 6
- 21 NMMNHS-81532, crown view; sample CQF-4; scale bar 100 µm
- 22 NMMNHS-81533, crown view; sample CQF-3; scale bar 100 µm

23-27 – Scales of morphotype 7
- 23 NMMNHS-81534, oblique posterior view; sample Q1-3; scale bar 100 µm
- 24 NMMNHS-81535, oblique crown view; sample CQF-3; scale bar 100 µm
- 25 NMMNHS-81536, oblique anterior view; sample CQF-4; scale bar 100 µm
- 26 NMMNHS-81537, oblique anterior view; sample CQF-3; scale bar 100 µm
- 27 NMMNHS-81538, crown view; sample Q1-3; scale bar 100 µm

28-29 – Scales of morphotype 8
- 28 NMMNHS-81539, lateral view; sample CQF-2; scale bar 100 µm
- 29 NMMNHS-81540, oblique basal view; sample CQF-3; scale bar 100 µm

30 – Scale of morphotype 9, no. NMMNHS-81541, oblique crown view; sample CQF-2; scale bar 100 µm

31-34 – Scales of morphotype 10
- 31 NMMNHS-81542, oblique crown view; sample CQF-2; scale bar 100 µm
- 32 NMMNHS-81543, crown view; sample CQF-3; scale bar 300 µm
- 33 NMMNHS-81544, crown view; sample Q1-3; scale bar 100 µm
- 34 NMMNHS-81545, crown view; sample CQF-4; scale bar 100 µm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Almost all scales of *A. texasensis* in our collection have no denticles in the posterior margin, possibly due to small and thin, fragile denticles; those could have been broken in the process of fossilization, on one hand, and high flow energy, on other hand. Both variants are also possible.

Remarks: The genus *Alilepis* Yankevich 1998 belongs to family Elonichthyidae nominally. *Elonichthys germari* Giebel 1848 (Štamberg 2016, fig. 11) has some similarity with *Alilepis* in scale shape and sculpture pattern, but complete cranial material of *Alilepis* is needed for more reliable conclusions.

The species closest to *A. texasensis* n. sp. is *A. kolguevensis* from the Urzhumian and Severodvinian (Wordian and Capitanian) strata of Kolguev Island (Afanasieva et al. 2006). *A. esini* (previously identified as *Acentrophorus varians* Esin 1995a) from coeval Kazanian (Roadian) deposits of the Volga and Kama River region and Kanin Peninsula (Esin 1995a; Afanasieva et al. 2006; Minikh and Minikh 2009) is less close to the new species. The largest differences are observed between *A. texasensis*, on one hand, and *A. secunda* from Urzhumian and Severodvinian deposits of Kolguev Island (Afanasieva et al. 2006) and *A. elegans* from the Ufimian (Kungurian) deposits of the Pechora Coal Basin (Yankevich and Minikh 1998), on other hand. In our opinion, *"Rhadinichthys" flexosus* Yankevich 1998 and *"R." silvensis* Yankevich 1998 from Ufimian (Kungurian) deposits of the Pechora Coal Basin (Yankevich and Minikh 1998) should be assigned to the genus *Alilepis* because of great similarities in the patterns of the free field sculpture, especially with species *A. kolguevensis* and, to a lesser degree, *A. texasensis*.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4; Capitanian, Bell Canyon Formation, strata equivalent in age to the Lamar Limestone and Reef Trail Members of the Apache Mountains (Ivanov et al. 2013); Wordian - Capitanian, Bell Canyon Formation, Hegler, Pinery, and Rader Members of the Guadalupe Mountains (Ivanov et al. 2015b; Ivanov et al. 2020).

Family PLATYSOMIDAE Young 1866

Platysomidae gen. indet.
Plate 10, figures 1-3

Description: The flank scales (Pl. 10, figs. 1-2) are nearly 5 times higher than they are long. Anterior and posterior margins are straight. Ventral margin is convex. Antero-dorsal and postero-dorsal corners are not pronounced because they are fused with very wide peg. Antero-dorsal and postero-dorsal corners are nearly straight. Peg and socket are triangular, high and well developed. Depressed field is narrow. Free field consists of three or four subhorizontal roll-shaped, hollow, nearly parallel, inclined anteriorly ridges with rounded ends. Pores open between the ridges in the grooves. Uppermost ridges are subvertical in the anterior part and beginning along the dorsal margin of the free field, but then they turn posteriorly. The ridges of several (maximum five) previous generations are traced inside the broken ridges of the last generations. There is no observable ultrasculpture on the surface of free field.

The scale (Pl. 10, fig. 3, no. NMMNHS-81569) can be determined as a ridge scale. The scale is V-shaped, symmetrical, pos-

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PLATE 7

Actinopterygian scales of *Alilepis texasensis* Bakaev, n. sp. from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains, crown (outside) views. All SEM microphotograph images.

1 NMMNHS-81546, area B scale from transition zone with area A; sample CQF-4; scale bar 500 µm

2 NMMNHS-81547, area B scale from transition zone with area A. Sample CQF-4; 2a, normal view, scale bar 500 µm; 2b, enlarged view, detail of sculpture, scale bar 100 µm

3 NMMNHS-81548, holotype, area B scale from transition zone with area A; sample CQF-4; scale bar 500 µm

4 NMMNHS-81549, area B scale, from posterodorsal part; sample CQF-4; scale bar 500 µm

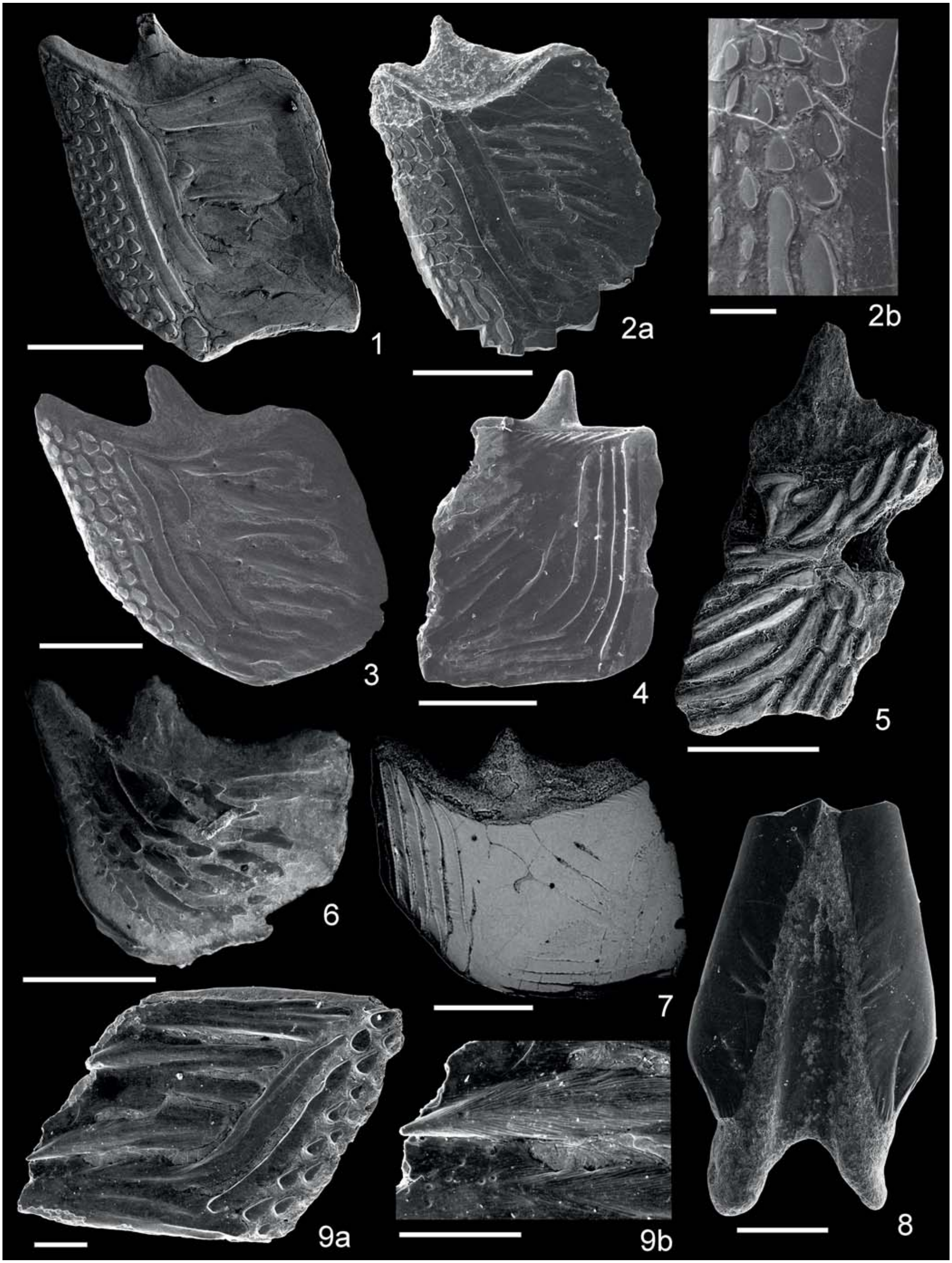
5 NMMNHS-81550, area A scale from anterior part, with lateral line opening; sample CQF-3; scale bar 500 µm

6 NMMNHS-81551, area A scale from transition zone with area F; sample CQF-4; scale bar 500 µm

7 NMMNHS-81552, area C scale from transition zone with area B; sample CQF-2; scale bar 500 µm

8 NMMNHS-81553, ridge scale posterior of the dorsal fin; sample CQF-4; scale bar 500 µm

9 NMMNHS-81554, area B scale, juvenile; 9a, normal view, scale bar 500 µm; 9b, enlarged view, detail of sculpture; sample CQF-1; scale bar 100 µm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9b

sibly lacks a ganoine cover. Point of scale bears several ridges. Several pores are located irregularly on the depressed field. The articulation areas are located on the sides of the scale.

Material: Three scales.

Remarks: The best description of the histology and microstructure of such scales was given for *Platysomus* sp. from the Wuchiapingian of East Greenland by Aldinger (1937). The scales are very distinct and easily distinguished from palaeoniscoid scales by the absence of ganoine and dentine (Aldinger 1937, text-fig. 48). The roll-shaped, hollow ridges consist of a single cellular bone lamella. Therefore, they lack surface ultrasculpture and have several superimposed generations of bone separated by hollow spaces in the fossilized material. The hollows in the ridges from different generations connect with each other and the external surface by a pore-channel system. The pores open along the ridges. The central ridges show more generations of superimposed bone layers than the ridges in the periphery. The number of ridges is determined ontogenetically (Aldinger 1937). The histological structure of these tall scales is probably more derived, compared to the ganoine-covered squamation of actinopterygians with fusiform bodies.

The direction of the ridges depends on the position of the individual scale on the fish trunk in platysomids *Ebenaqua ritchiei* Campbell and Phuoc 1983 (Campbell and Phuoc 1983) and *Platysomus biarmicus* Eichwald 1857 (Bakaev, unpublished data): the ridges are inclined posteriorly in the upper part of the body, whereas the ridges are inclined anteriorly in the lower part of the body. Based on that observation, it can be assumed that scales (Pl. 10, figs. 1-2, no. NMMNHS-81567 and no. NMMNHS-81568) come from the ventral half of the fish trunk.

The scales of Platysomidae gen. indet. from the Quarry section are similar to the scales of *Platysomus biarmicus* Eichwald 1857 (Pl. 11, figs. 1-3) from the Biarmian and Tatarian (Guadalupian and lower Lopingian; see Davydov et al. 2020) of the European part of Russia (Minikh and Minikh 2009; Bakaev et al. 2017). There are several generations of the same roll-shaped ridges (Pl. 11, fig. 3b) that prove the similar growth pattern. However, there is a similar sculpture pattern in different members of the Platysomidae: *Platysomus gibbosus* (=*P. striatus*) (Blainville 1818) (Haubold and Schaumberg 1985; Campbell and Phuoc 1983); *P. schultzei* Zidek 1992 (Zidek 1992); *P. swaffordae* Mickle and Bader 2009 (Mickle and Bader 2009); *P. solikamskensis* Yankevich and Minikh 1998 (Yankevich and Minikh 1998); *Ebenaqua ritchiei* Campbell and Phuoc 1983 and *Bobasatrania mahavavica* White 1932 (Campbell and Phuoc 1983); Platysomidae gen. indet. (Schultze 1985, fig. 7.10). The latter taxon from the Wolfcampian (Cisuralian) of Kansas may be an ancestor of the platysomid from the Cutoff Formation. However, there are ganoine and dentine layers in the scales and dermal bones of two taxa, *Paranaichthys longianalis* Dias 2012 (Dias 2012) and *Kargalichthys efremovi* Minich 2009 (Bakaev 2019), previously belonging to the Platysomidae. It

PLATE 8

Actinopterygian scales of *Alilepis texasensis* Bakaev, n. sp. from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains. Crown (outside) views. All SEM microphotograph images.

1 NMMNHS-81555, area F scale from transition zone with area C; sample CQF-4; scale bar 100 µm

2 NMMNHS-81556, area F scale from anteroventral part; sample CQF-4; scale bar 100 µm

3 NMMNHS-81557, area F scale from anterior part; 3a, normal view; 3b, enlarged view, detail of sculpture; sample CQF-4; scale bar 100 µm

4 NMMNHS-81558, area F scale from transition zone with area A; sample CQF-4; scale bar 100 µm

5 NMMNHS-81559, area F scale; sample CQF-3; scale bar 100 µm

6 NMMNHS-81560, area A scale; sample CQF-4; scale bar 100 µm

7 NMMNHS-81561, area D scale, from epaxial caudal lobe; 7a, normal view; 7b, enlarged view, detail of sculpture; sample CQF-4; scale bar 100 µm

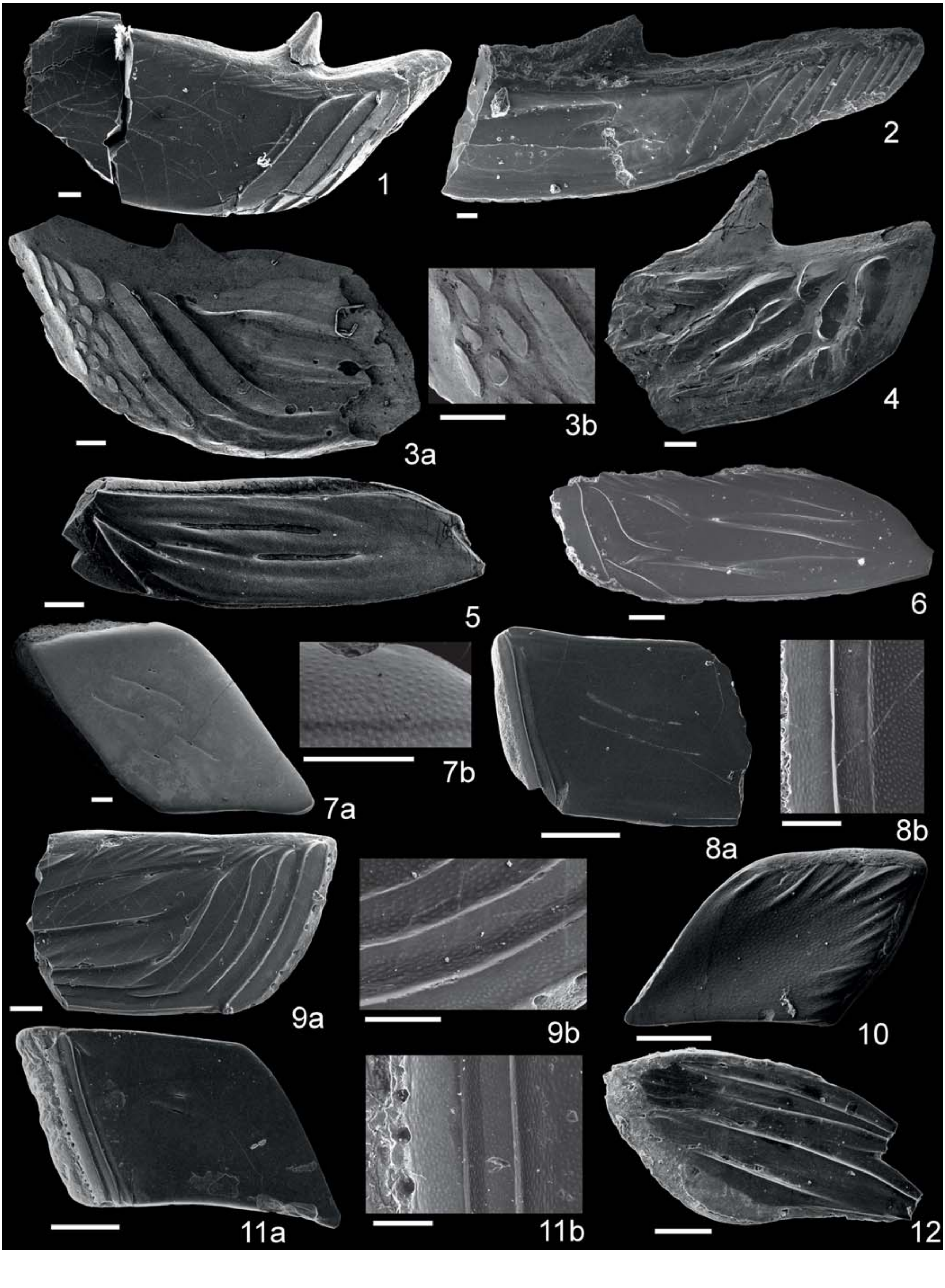
8 NMMNHS-81562, area D scale from transition zone with area C; 8a, normal view, scale bar 500 µm; 8b, enlarged view, detail of sculpture; sample CQF-4; scale bar 100 µm

9 NMMNHS-81563, area C scale, from transition zone with area D; 9a, normal view ; 9b, enlarged view, detail of sculpture; sample CQF-4; scale bar 100 µm

10 NMMNHS-81564, area D scale; sample CQF-3; scale bar 500 µm

11 NMMNHS-81565, area D scale; 11a, normal view, scale bar 500 µm; 11b, enlarged view, detail of sculpture; sample CQF-4; scale bar 100 µm

12 NMMNHS-81566, area D scale; sample CQF-3; scale bar 100 µm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can be supposed that these taxa should be excluded from the family Platysomidae, but retained in the order Bobasatraniformes, as more plesiomorphic members than the genera *Platysomus, Ebenaqua* and *Bobasatrania.*

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, samples CQF-1 and CQF-4.

Family ACROLEPIDIDAE Aldinger 1937

Acrolepididae gen. indet.
Plate 10, figure 4

Description: The scale is nearly 1.5-2 times higher than long. The anterior and lower margins are straight. The upper and posterior margins, peg and socket are broken. The antero-dorsal corner is damaged. The depressed fields reach 1/4 length of the scale. The free field consists of high diagonal, subparallel ridges, separated by wide grooves with pores. There is no evidence that the ridges are fused.

Material: One scale.

Remarks: The one poorly preserved scale is not enough for reliable conclusions about a determination and phylogenetic relationships. However, this scale is distinguished from almost all Acrolepididae (Aldinger 1937; Schaumberg 1996; Minikh and Minikh 2009) by separated posterior parts of the ridges. However, there are two exceptions: Acrolepididae gen. indet. (type D, Schaumberg 1996, abb. 16-18) from the Zechstein and Marl-Slate (Lopingian) of Germany and Britain, and the palaeoniscoid scale (Schultze 1985, fig. 7. 5) from the Wolfcampian (Cisuralian) of Kansas, USA. This acrolepidid is distinguished from the described scale by narrower ridges. Therefore, the acrolepidid from the Wolfcampian is morphologically closer to the scale from the Quarry section than to other acrolepidids. That may be evidence of the continuity of North America bony fish faunas in the Permian.

Occurrence: Middle Permian, Guadalupian, Roadian, Cutoff Formation, Williams Ranch Member; West Texas, Guadalupe Mountains, Quarry section, sample CQF-4.

Other actinopterygian and osteichthyan remains

In additional to scales, the actinopterygian remains include isolated teeth, tooth plates and fragments of jawbones (Pl. 10, figs. 5-10). Unfortunately, such elements are poorly described for the majority of Paleozoic ray-finned fishes. The assemblage from the Quarry section includes possible gill-raker (pharyngeal) denticles (Pl. 10, fig. 11). The denticle has a hook-like, incurved toward, pointed crown and a low-conical, hollow base. Similar denticles have been described from several samples in the PI-section and Patterson Hills sections of the Guadalupe Mountains (Ivanov et al. 2020, fig. 8L).

The actinopterygian jaw fragments (Pl. 10, figs. 9, 10) possibly represent dentalosplenial or maxilla/premaxilla of *Alilepis texasensis* n. sp. based on the presence simultaneously of ganoine cover and tooth replacement pit. However, the evidence for this conclusion is tenuous.

PLATE 9

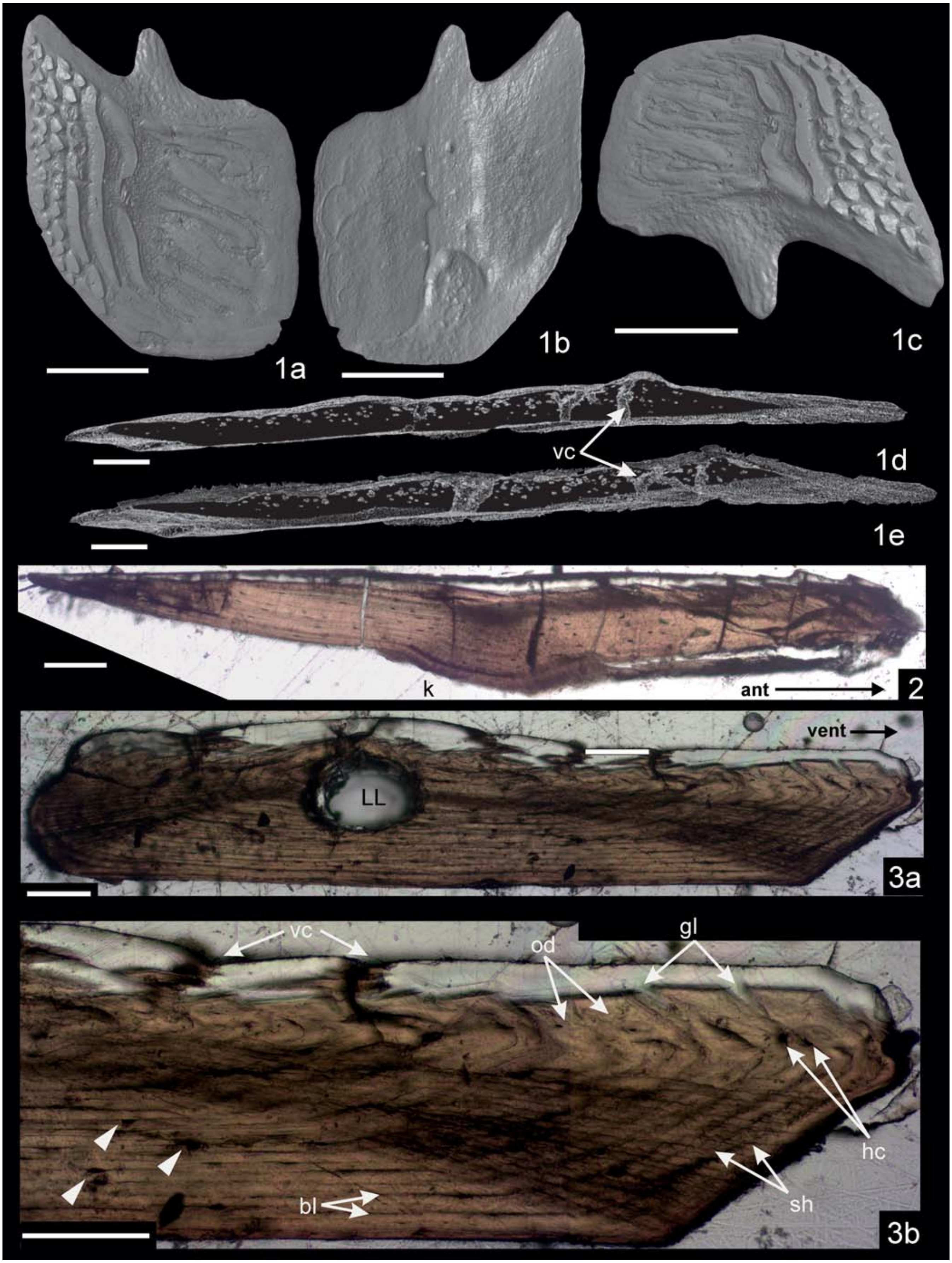
Histological details of *Alilepis texasensis* Bakaev, n. sp. scales from the Williams Ranch Member, Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains, sample CQF-4. Arrows point to osteocyte lacunae. Abbreviations: bl – cellular bone layers, d – dentine, gl – ganoine layers, LL – lateral line channel, k – keel, hc – horizontal vascular canals, od – odontode, sh – Sharpey's fibres, vc – vertical vascular canals.

1 – Microtomographic images, no. NMMNHS-81548, area B scale from transition zone with area A (holotype)

- 1a crown view, scale bar 500 µm
- 1b basal view, scale bar 500 µm
- 1c lateral-crown view, scale bar 500 µm
- 1d-f dorso-ventral sections, scale bar 100 µm

2-3 – Light micrographs of thin sections of area C scales under linear polarized light

- 2 PIN 5803/7, anteroposterior section; scale bar 100 µm
- 3 PIN 5803/8, dorsoventral section. 3a, normal view; 3b, enlarged view; scale bar 100 µm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Most isolated teeth of actinopterygians from the Quarry section are conical, straight, circular in cross-section, and bear an acrodin cap. Some teeth (Pl. 10, fig. 5) are mushroom-shaped that indicates the durophagous specialization. Similar teeth are known in some acrolepidids (Esin 1997). However, this evidence is not enough to reach taxonomical conclusions.

The tooth plate (Pl. 10, fig. 8, no. NMMNHS-81574) is strongly abraded for taxonomical determination. The preservation of specimens (Pl. 10, figs. 6, 7, no. NMMNHS-81572 and no. NMMNHS-81573) is much better. They are spongy and have numerous pores opening on the external surface. These bones bear the same small, short, closely placed, conical teeth, with a small blunt acrodin cap, which has a smooth external surface. The tooth surface under the cap is covered by very small, elongated tubercles, arranged in vertical rows (Pl. 10, fig. 6b). This feature characterizes the ganoine of primitive ray-finned fishes (Schultze 2016, 2018). The teeth of primitive actinopterygians are covered by a collar ganoine (Richter and Smith 1995), and the elongated tubercles are typical feature of that tissue. Similar elongated tubercles have been found also in some Paleozoic ray-finned fishes (Štamberg 2016). However, the basal part of the teeth is covered by small, rounded, irregularly arranged pustules (Pl. 10, fig. 6b). There is no information on the distribution of the corresponding ultrasculpture pattern in the known ray-finned fishes. The shape and arrangement of teeth on those tooth plates are similar to the type 3 teeth, located on some palatal bones (entopterygoid, dermometapterygoid and parasphenoid) of recent fishes *Polypterus* (Clemen et al. 1998), but the observed teeth have a smaller acrodin cap (less than half of tooth height). The specimen illustrated in Plate 10, fig. 7 (no. NMMNHS-81573) is bilaterally symmetric, and may be a fragment of a parasphenoid, whereas the specimen (Pl. 10, fig. 6, no. NMMNHS-81572) is asymmetric and possibly belongs to the bone of a pterygoid series.

The assemblage includes several postcranial elements of undetermined osteichthyans such as the intercentrum, ventral element with haemal spine and possible hypural (Pl. 10, figs. 12-17). These elements are poorly known in some groups of the Late Paleozoic osteichthyans and could not be determined in detail.

DISCUSSION

The fish assemblage from the Quarry section comprises chondrichthyans such as the symmoriiforms *Stethacanthulus decorus*, *Kungurodus* sp. and undetermined taxa; the ctenacanthiform *Glikmanius myachkovensis*; the euselachian *Sphenacanthus* sp. and Hybodontiformes indet.; the

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PLATE 10

SEM micrographs of bony fish remains from the Williams Ranch Member,
Cutoff Formation, Roadian, early Guadalupian, middle Permian, Quarry section, Guadalupe Mountains.

1-3 – Platysomidae gen. indet., scales

1 NMMNHS-81567, flank scale, crown view; sample CQF-4; scale bar 100 µm

2 NMMNHS-81568, flank scale, crown view; sample CQF-1; scale bar 500 µm

3 NMMNHS-81569, ridge scale, anterior or posterior view;sample CQF-1; scale bar 100 µm

4 – Acrolepididae gen. indet., scale, crown view, no. NMMNHS-81570; sample CQF-4; scale bar 500 µm

5 – Durophagous actinopterygian tooth, lateral-crown view, no. NMMNHS-81571; sample CQF-4; scale bar 100 µm

6-8 – Actinopterygian tooth plates.

6 NMMNHS-81572; 6a, crown view, scale bar 500 µm; 6b, enlarged crown view, scale bar 100 µm; sample CQF-4

7 NMMNHS-81573, crown view; sample CQF-3; scale bar 500 µm

8 NMMNHS-81574, crown view; sample CQF-3; scale bar 100 µm

9 -10 – Actinopterygian jaw fragments

9 NMMNHS-81575, oblique lateral view; sample CQF-4; scale bar 100 µm

10 NMMNHS-81576, oblique medial view; sample CQF-4; scale bar 100 µm

11 – Actinopterygian possible gill-raker denticle, lateral view, no. NMMNHS-81577; sample CQF-4; scale bar 100 µm

12-17 – Postcranial elements of osteichthyans

12 NMMNHS-81578, centrum, anterior view; CQF-2; scale bar 100 µm

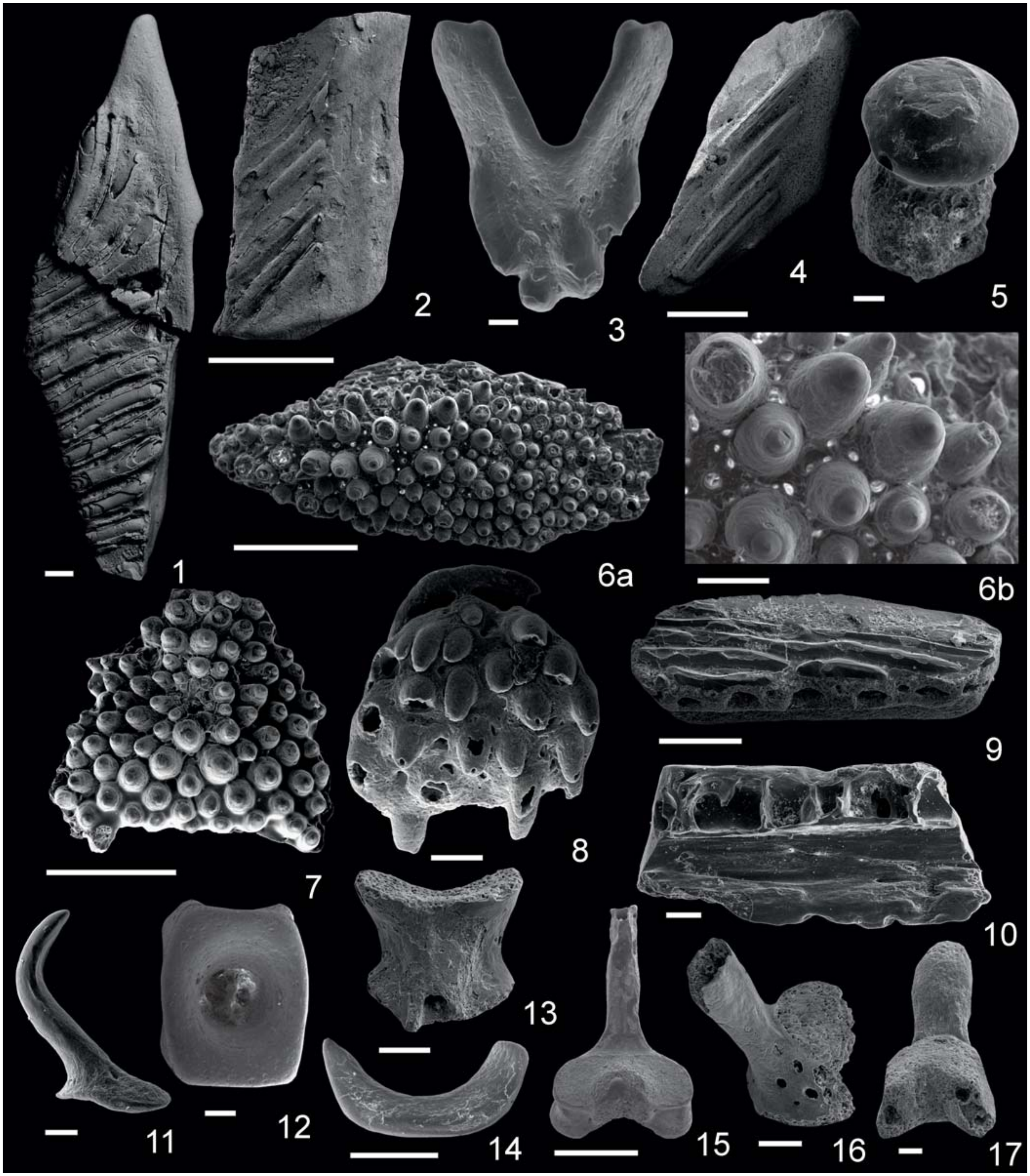
13 NMMNHS-81579, possible intercentrum, basal view; sample CQF-3; scale bar 100 µm

14 NMMNHS-81580, intercentrum, possible anterior view; sample CQF-4; scale bar 500 µm

15 NMMNHS-81581, possible hypural, anterior view; sample CQF-1; scale bar 500 µm

16 NMMNHS-81586, possible hypural, lateral view; sample CQF-3; scale bar 100 µm

17 NMMNHS-81587, ventral element with haemal spine, oblique anterior view; sample CQF-4; scale bar 100 µm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anachronistids *Cooleyella amazonensis*, *Cooleyella* sp. and *Reifella lata* Ivanov, n. gen. et sp.; the jalodontids *Adamantina foliacea*, *Isacrodus marthae* and *Isacrodus* sp.; undetermined euchondrocephalian and chondrichthyans, as well as actinopterygians such as the elonichthyid *Alilepis texasensis* Bakaev, n. sp., Platysomidae indet., Acrolepididae indet., and undetermined actinopterygians and osteichthyans. The microremains of *Alilepis texasensis* n. sp. are dominant among the other fishes, the teeth of *Stethacanthulus decorus, Cooleyella amazonensis* and *Isacrodus marthae* are abundant remains, but the remains of other fish taxa are minor in the assemblage.

The jalodontid *Isacrodus marthae* and anachronistid *Reifella lata* Ivanov n. gen., n. sp. are recorded only in the Roadian Williams Ranch Member, Cutoff Formation of the Guadalupe Mountains, West Texas. The symmoriiform *Kungurodus obliquus* has been reported from the Asselian – Kungurian of the South Urals (Ivanov 2005) and from the Artinskian of the Kazakhstanian Cisurals (Lebedev 2009).

The symmoriiform *Stethacanthulus decorus* has been found in the Serpukhovian, Mississippian, Carboniferous of Nearpolar Urals, the Asselian – Kungurian, Cisuralian, lower Permian of the Middle and South Urals, Russia (Ivanov 1999, 2005); Serpukhovian - Bashkirian of the Gissar Mountains, Uzbekistan (Ivanov 2013); and the Roadian, Guadalupian, middle Permian, Guadalupe Mountains, Texas, USA.

Besides the Roadian of the Guadalupe Mountains, the ctenacanthiform *Glikmanius myachkovensis* occurs in the Moscovian and Kasimovian, Pennsylvanian, Carboniferous of the Moscow and Ryazan regions, Russia; in the Moscovian of the Donetsk Basin, Ukraine, and Nebraska, USA (Ginter et al. 2005); in the Leonardian (Kungurian), Cisuralian, lower Permian of Arizona, USA (Hodnett et al. 2012). *Glikmanius* cf. *myachkovensis* has been described from the Wordian, Guadalupian, middle Permian of Oman (Koot et al. 2013).

The species of genus *Sphenacanthus* are known from the Viséan to Gzhelian, Carboniferous (Ginter et al. 2010), and also from the Artinskian, Cisuralian, lower Permian of Brazil (Chahud et al. 2010); from the Kazanian (Guadalupian), middle Permian of the East European Platform, Russia (Ivanov 2012). *Sphenacanthus carbonarius* (Giebel 1848) occurs in the Kasimovian – Gzhelian, Pennsylvanian, Carboniferous of Czech Republic, Germany, Spain, Nebraska and Pennsylvania, USA (Lund 1970; Soler-Gijón 1997; Ginter 2016); *S. delepinei* Fournier and Pruvost 1928 – in the Viséan of Belgium (Fournier and Pruvost 1928; Ivanov and Derycke 2005); *S. hybodoides* (Egerton 1853) - in the Westphalian (Bashkirian - Moscovian), Pennsylvanian, Carboniferous of England and Scotland (Egerton 1853; Maisey 1982); *S. serrulatus* Agassiz 1837 (in 1843) – in the Viséan - Namurian (Serpukhovian), Mississippian and Westphalian B/C (Moscovian), Pennsylvanian, Carboniferous of Scotland (Ginter et al. 2010); *S. tenuis* Ginter 2016 - in the Gzhelian, Pennsylvanian, Carboniferous of Nebraska, USA (Ginter 2016).

The anachronistid *Cooleyella amazonensis* is a widely geographically distributed species during the Pennsylvanian – Guadalupian, and has been reported from the Moscovian, Pennsylvanian, Carboniferous, of Brazil and Oklahoma, USA; the Missourian (Kasimovian) of New Mexico, USA; the Gzhelian of Kansas, USA; the Artinskian, Cisuralian, lower Permian of South Urals, Russia; the Kazanian (Roadian), Guadalupian, middle Permian of Tatarstan, Vladimir and Kirov regions, Russia; the Roadian and the Capitanian of Texas, USA (Ivanov et al. 2017, 2020; Ivanov and Lucas 2019).

The jalodontid *Adamantina foliacea* has been recorded in the Tournaisian, Mississippian, Carboniferous of the South Urals, the Asselian of the Polar Urals, the Artinskian, Cisuralian, lower Permian of the Middle Urals, Russia (Ivanov 1999); the Moscovian, Pennsylvanian, Carboniferous of North Greenland (Cuny and Stemmerik 2018); the Missourian (Kasimovian), Pennsylvanian of Iowa and New Mexico, USA (Tway and Zidek 1983; Ivanov and Lucas 2019); and the Roadian of Texas, USA. The occurrences of *Stethacanthulus decorus* and *Adamantina foliacea* in the Roadian of the Quarry section are the youngest record in the world.

Besides the Roadian part of the Cutoff Formation, the elonichthyiform *Alilepis texasensis* Bakaev, n. sp. occurs in the Wordian - Capitanian of the Apache and Guadalupe mountains (Ivanov et al. 2013, 2015b, 2020). Other species of *Alilepis* are widely distributed in the Permian (from the Kungurian to the Urzhumian) of the East European Platform and Cis-Urals (Minikh and Minikh 2009). *Alilepis elegans* has been known from the late Kungurian of the Pechora Coal Basin; *A. esini* - from the Kazanian and Urzhumian of the Kanin Peninsula and the north part of the East European Platform; *A. kolguevensis* - from the Kazanian, Urzhumian and possibly Tatarian of the north part of European Russia; *A. secunda* - from the possibly Tatarian of the north part of the East European Platform (Minikh and Minikh 2009).

The actinopterygian fauna of the Cutoff Formation has, on one hand, a continuity with the earlier Permian faunas of North America (for example, Platysomidae gen. indet. and Acrolepididae gen. indet. are closely related), and, on another hand, have a distinct relationship with coeval faunas of other biogeographic provinces. Four species of *Alilepis* have been previously described based on isolated scales from the Ufimian nearshore marine deposits of the Pechora Coal Basin (belongs to the Angaraland Province), the Kazanian nearshore marine deposits of the Volga and Kama River regions (belongs to the Subangara area), and the Urzhumian - Severodvinian marine deposits of Kolguev Island (Esin 1995a; Yankevich and Minikh 1998; Afanasieva et al. 2006; Minikh and Minikh 2009).

All continents in the Permian are subdivided into four biogeographic provinces (surrounded by ecotones): Angaraland (north-east of Eurasia), Cathaysia (China, Korea, Japan, Vietnam, Laos, Thailand, Indonesia, Malaysia) and Euramerica (Western and Central Europe, eastern North America, northern Africa), as well as Gondwana (South America, almost all of Africa, India, Australia, Antarctica) (for the paleogeographic zonation of the Permian see Zharkov 2004). The high degree of endemicity of some taxa is characteristic exclusively for the Gondwana. The European part of Russia is divided between Angaraland (northern part) and Subangara area (southern and central part; ecotone between Euramerica and Angaraland), whereas Texas was located in the western part of Euramerica.

Alilepis remains have not yet been discovered in the Cisuralian, lower Permian of the USA, therefore it can be assumed that representatives of this genus migrated from the Subangara area to the East European Platform at the end of the Early or at the beginning of the Middle Permian. *Alilepis* remains are unknown in freshwater sediments that may indicate that these fishes were an

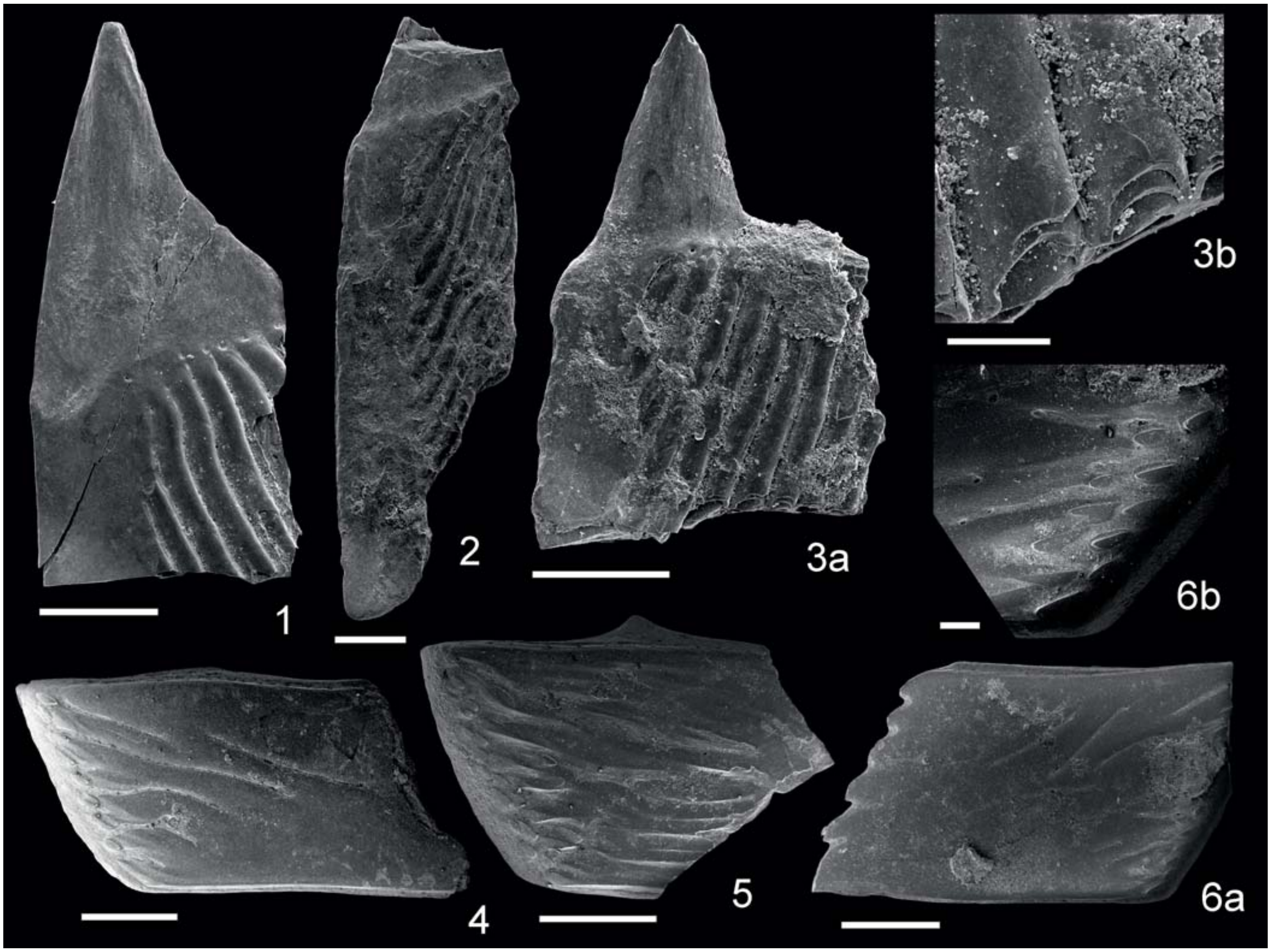

PLATE 11

Comparative actinopterygian scales from the Kamyshla Beds, Kazanian (Roadian) of the Sentyak locality (S5/6-8), Tatarstan, Russia. Scale bar is 100 µm.

1-3 – *Platysomus biarmicus* Eichwald 1857, scales
1 PIN 5799/6, crown view
2 PIN 5799/7, crown view
3 PIN 5799/8; 3a, crown view; 3b, enlarged crown view

4-6 – *Alilepis esini* A. Minich 2006, scales
4 PIN 5799/1, crown view
5 PIN 5799/2, crown view
6 PIN 5799/3; 6a, crown view; 6b, enlarged crown view

exclusively brackish water form. The Permian ray-finned fish faunas of China (Lu and Chen 2010) and East Kazakhstan (Kazantseva-Selezneva 1981) have no common genera or species with the Permian actinopterygian fauna of the East European Platform, making a migration of *Alilepis* through the Paleotethys unlikely. Their migration pathway may run along the border of the Boreal Ocean through modern Northern Europe, Spitsbergen, Greenland and Arctic Canada. During the Urzhumian stage, there were no seaways in the main part of the East European Platform and *Alilepis* seems to have disappeared from that region, although it is still found in the northern part of that platform. *Alilepis* remains have been discovered in the Middle Permian of the Northern European part of Russia and in Texas, whereas they have not been reported from the Upper Permian deposits of Germany and Britain. This distribution suggests that this genus almost disappeared during the end-Guadalupian mass extinction, as did many taxa of the chondrichthyans (Ivanov et al. 2020). This genus had a much more restricted distribution during the end-Guadalupian and may not have survived the mass extinction event that marks the end of the Guadalupian epoch, as did many taxa of the chondrichthyans (Ivanov et al. 2020).

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