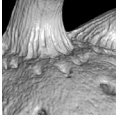


New late Carboniferous chondrichthyans from the European Russia

ALEXANDER O. IVANOV



Three new genera *Heslerodoides* gen. nov., *Gzhelodus* gen. nov., and *Samarodus* gen. nov. were erected on the basis of numerous isolated teeth found in the late Carboniferous of European part of Russia. The teeth of the ctenacanthiform *Heslerodoides* resemble the teeth of *Heslerodus* and demonstrate the morphological variations of teeth in their dentition. The protacrodontid euselachian *Gzhelodus* is closely related to *Deihim* and *Tiaraju*. The peculiar teeth of *Samarodus* possess a combination of features previously unknown in the Palaeozoic chondrichthyans. The new taxa contribute to the knowledge of the variety of dentitions in the Carboniferous shark. • Key words: chondrichthyans, Carboniferous, Pennsylvanian, Russia.

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Chondrichthyan remains from the early Carboniferous (Mississippian) of European part of Russia are common, rather diverse and have been quite well studied (Romanowsky 1864, Trautschold 1874, Khabakov 1941, Obruchev 1977, Ivanov & Ginter 1996, Lebedev 1996, and others). The chondrichthyan assemblages from the Bashkirian–Moscovian (Pennsylvanian) of this territory have also been described in many publications (e.g. Trautschold 1879, Khabakov 1939, Obruchev 1951, Lebedev 2001, and others). However, chondrichthyan fishes are poorly known from the Kasimovian–Gzhelian of this area.

The remains of diverse chondrichthyans were recently found in the Kasimovian–Gzhelian deposits of the Moscow, Samara and Volgograd regions, and in the Bashkirian–Moscovian of the Republic of Bashkortostan. The remains are represented by isolated teeth and scales of various chondrichthyan groups and mostly belong to known taxa. However, three new taxa presented by teeth occurred in these stratigraphical intervals and regions, and are described in this paper.

Geological setting

The teeth of the new taxa described in the present paper have been found in four regions of Russia (Fig. 1): Moscow, Samara and Volgograd regions, and the Republic of Bashkortostan. The most numerous specimens come from

the Moscow Region (Fig. 1B) and occur in the following localities, stratigraphical levels, and samples:

1) Vodniki-2/3 borehole, Moscow City, near railroad station, town of Dolgoprudny, depth 93.5–94.0 m, sample V-2/3-10; Mescherino Formation, Dorogomilovian Regional Stage, Kasimovian.

2) Mytischki-17 borehole, Mytischki District, depth 43.0–47.0 m, sample 17/1-2; Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian.

3) Moscow-1832 borehole, Moscow City, Academician Sakharov Avenue, depth 56.25–56.40 m, sample 1832/70; Neverovo Formation, Khamovnikian Regional Stage, Kasimovian (Alekseev *et al.* 1998, 2015a).

4) Rusavkino Quarry, Balashikha District, near the village of Rusavkino-Popovschino, sample PC-054; Kosherovo Formation, Dobryatinian Regional Stage, *Idiognotodus simulator* Zone, Gzhelian (Alekseev *et al.* 2015a).

5) Gzhel section, Ramenskoe District, near railroad station, historical stratotype of the Gzhelian; Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian (Alekseev *et al.* 2009b).

6) Myachkovo section, Ramenskoe District, on the left bank of the Moscow River, near village of Turaevo, sample M7-34; Voskresensk Formation, Krevyaktion Regional Stage, Kasimovian (Makhlina *et al.* 2001).

7) Domodedovo Quarry, Domodedovo District, on the right bank of the Pakhra River, 15 km south of Moscow City, beds 39, sample D-8C; Suvorovo Formation, Krevyaktion Regional Stage, Kasimovian (Goreva *et al.* 2009).

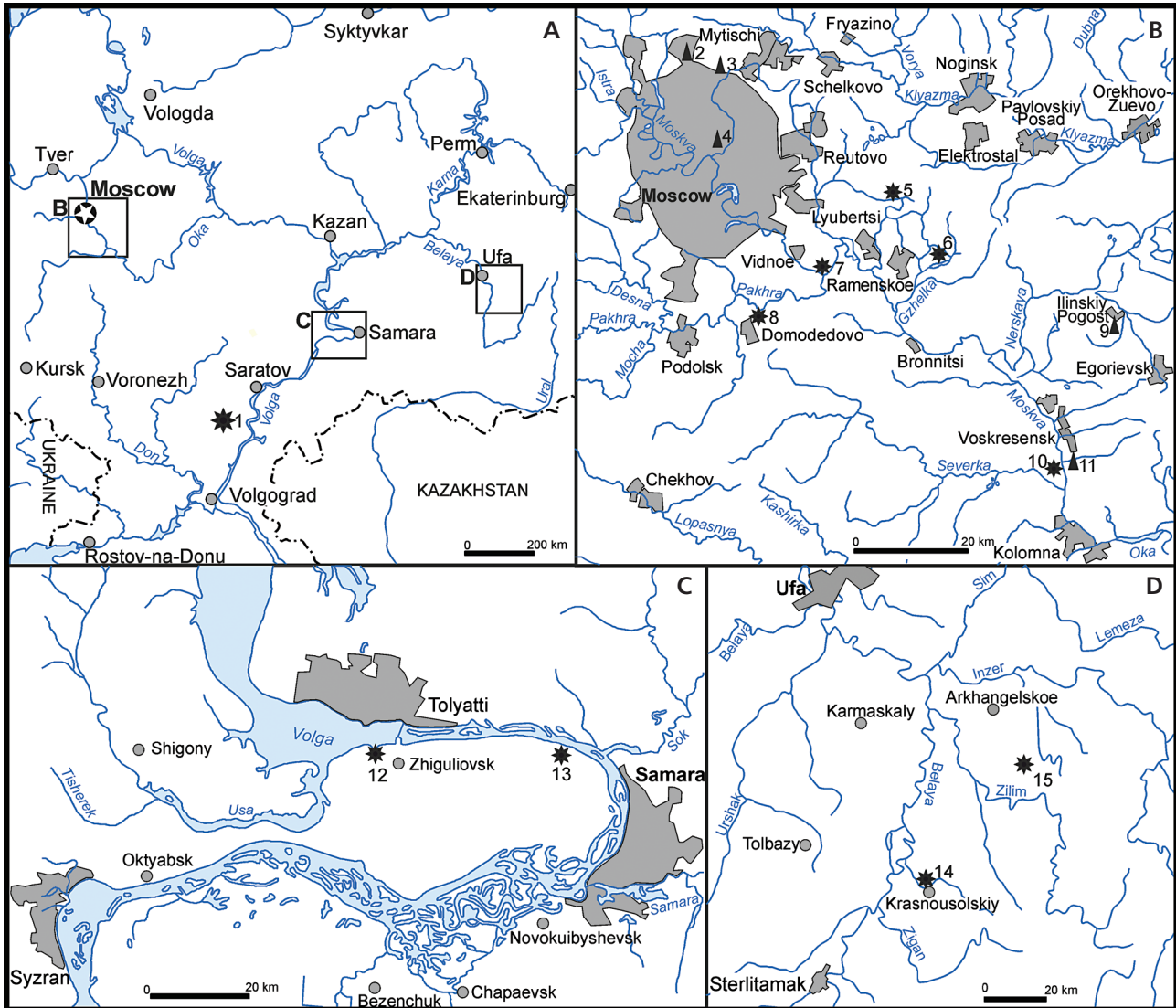


Figure 1. Sketch-map showing the position of localities (black asterisk – outcrop or quarry, black triangle – borehole) with described teeth in the European part of Russia (A), in the Moscow Region (B), in the Samara Region (C), and in the Republic of Bashkortostan (D). Legend: 1 – Zhirnovsk (Volgograd Region); 2 – Vodniki-2/3 borehole; 3 – Mytishi-17 borehole; 4 – Moscow-1832 borehole; 5 – Rusavkino Quarry; 6 – Gzhel section; 7 – Myachkovo section; 8 – Domodedovo Quarry; 9 – Ilinskiy Pogost-89 borehole; 10 – Afanasievo Quarry; 11 – Perhurovo-1 borehole; 12 – Yabloneviy Ravin Quarry; 13 – Shiryaevo-31a borehole; 14 – Dalniy Tyulkas section; 15 – Askyn section.

8) Ilinskiy Pogost-89 borehole, Orekhovo-Zuevo District, depth 43.7 m, sample 89-16-6; Perkhurovo Formation, Dorogomilovian Regional Stage, Kasimovian (Goreva & Alekseev 2018).

9) Afanasievo Quarry, Voskresensk District, on the right bank of the Moscow River, about 5 km southwest of town of Voskresensk, samples AF5-54, AF5-56, AF5-57, AF5-59, AF5-60, AF5-74; Neverovo Formation, Khamovnikian Regional Stage, Kasimovian (Alekseev *et al.* 2009a, Goreva & Alekseev 2019).

10) Perhurovo-1 borehole, Voskresensk District, sample PKh-17; Neverovo Formation, Khamovnikian Regional Stage, Kasimovian (Goreva & Alekseev 2019).

The studied teeth were found also at two localities of the Samara Region (Fig. 1C). A first one is the Yabloneviy Ravin Quarry, Zhiguli Mountains, Samara Bend of the Volga River, right bank, sample 8.1.2'; *Idiognathodus simulator* Zone, Gzhelian (Ermakova *et al.* 2012, Alekseev *et al.* 2015b). The other locality is the Shiryaevo-31a borehole, near village of Shiryaevo, depth 76.7–83.2 m, sample Sh31a/34; *Streptognathodus firmus* Zone, Dorogomilovian Regional Stage, Kasimovian (Alekseev *et al.* 2015b).

The teeth in the Volgograd Region (Fig. 1A) were recorded in the Zhirnovsk Quarry, Zhirnovsk District, right bank of the Medveditsa River, near town of Zhirnovsk;

Khamovnikian Regional Stage, Kasimovian (Petukhov *et al.* 2011).

The described specimens found in the Republic of Bashkortostan, on the western slope of the South Urals (Fig. 1D) come from two localities: the Askyn section, Askyn River, near village of Solontsy, sample 25/2, Askynbashian Regional Stage, Bashkirian (Sinitsyna *et al.* 2002) and sample 47/2, Zilimian Regional Stage, Moscovian; and the Dalniy Tyulkas section, near town of Krasnousolskiy, Usolka River, samples DT-1, DT-11, DT-14, DT-36; Zilim Formation, Podolskian Regional Stage, Moscovian (Alekseev & Goreva 2012, 2015).

Material and methods

The teeth described here were extracted from conodont residues and donated to the author by A.S. Alekseev, L.I. Kononova and A.N. Reimers (Department of Paleontology, Geology Faculty, Lomonosov Moscow State University, Moscow, Russia), N.V. Goreva (Geological Institute of the Russian Academy of Science, Moscow, Russia), and an amateur palaeontologist, T.A. Artemova. Acetic and formic acids were utilized to recover the microremains from the samples of carbonate-cemented rocks. The shark teeth were microphotographed using the scanning electron microscopes Cambridge CamScan-4, Hitachi S-3400N, and Tescan VEGA-II XMU.

The internal structure of some teeth was 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 40–65 kV and 153–222 mA. The virtual cross-sections were generated from the 3D reconstructions using the DataViewer, CTVox, and CTAn softwares. The transparent mode of skeletal tissues was used for the reconstruction of the canal system.

The specimens described herein are housed in the Palaeontological Museum of the St. Petersburg State University (abbreviation PM SPU).

Systematic paleontology

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Superorder Cladodontomorphi Ginter, Hampe & Duffin, 2010
 Order Ctenacanthiformes Glikman, 1964
 Family Heslerodidae Maisey, 2010

Genus *Heslerodoides* gen. nov.

Type species. – *Heslerodoides triangularis* sp. nov.

Etymology. – Greek “Like *Heslerodus*”.

Diagnosis. – Small teeth with fan-shaped crown from five to nine incurved cusps: three to five main cusps, and two to four intermediate and lateral cusplets; central cusp almost equal in size with lateral or intermediate cusps; intermediate and lateral cusps diverging mesially and distally from the center; straight cristae on both cusp sides not reaching apex; long crista on cusp lateral side instead lateral carina; triangular tooth base with pointed central part; one or two closely placed prominent apical buttons in the central part; small labial depression on the labial side below central cusp; wide projection or one to small two tubercles on the labio-basal rim; orthodontine cusps with very thin pulp canals; main and secondary horizontal canals with lacuna-like cavities; wide longitudinal canal connecting pulp canals.

Occurrence. – Carboniferous, Pennsylvanian, Bashkirian–Gzhelian; Moscow Region, Republic of Bashkortostan, Russia, Brazil.

Heslerodoides triangularis sp. nov.

Figures 2, 5H–O

Holotype. – Tooth, PM SPU 77-1 (Figs 2A–D, 5H–O).

Type horizon and locality. – Zilim Formation, Podolskian Regional Stage, Moscovian, Pennsylvanian, Carboniferous. Dalniy Tyulkas section, Usolka River, Republic of Bashkortostan, South Urals, Russia; sample DT-1.

Material. – Two teeth from the Vodniki-2/3 borehole, depth 93.5–94.0 m, sample V-2/3-10, Mescherino Formation, Dorogomilovian Regional Stage, Kasimovian; one tooth from the Moscow-1832 borehole, depth 56.25–56.40 m, sample 1832/70, Neverovo Formation, Khamovnikian Regional Stage, Kasimovian; one tooth from the Myachkovo section, sample M7-34, Voskresensk Formation, Krevyaktion Regional Stage, Kasimovian; one tooth from the Domodedovo Quarry, beds 39, sample D-8C, Suvorovo Formation, Krevyaktion Regional Stage, Kasimovian; one tooth from the Ilinskiy Pogost-89 borehole, depth 43.7 m, sample 89-16-6, Perkhurovo Formation, Dorogomilovian Regional Stage, Kasimovian; 12 teeth from the Afanasievo Quarry, samples AF5-54, AF5-56, AF5-57, AF5-59, AF5-60, AF5-74, Neverovo Formation, Khamovnikian Regional Stage, Kasimovian; three teeth from the Perhurovo-1 borehole, sample PKh-17, Neverovo Formation, Khamovnikian Regional Stage,

Kasimovian; one tooth from the Askyn section, samples 25/2, Askynbashian Regional Stage, Bashkirian; four teeth from the Dalniy Tyulkas section, sample DT-1, Zilim Formation, Podolskian Regional Stage, Moscovian.

Etymology. – From the Latin *triangularis*, triangular.

Diagnosis. – As for the genus.

Description. – The teeth are small in size (measuring from 0.25 to 0.65 mm mesio-distally). The crown includes nine to five cusps and cusplets. The number of main cusps varies from three to five. They include one central, paired intermediate and lateral cusps. The cusps and cusplets are incurved, round in the cross section, inclined lingually, acute at the top, and situated separately from each other. The central cusp is almost equal in height and width with the lateral ones in the pentacuspoid crown (Fig. 2X, Y, AA, CC) or with the intermediate cusps in the multicuspoid crown (Fig. 2A–R). The intermediate and lateral cusplets are different in their size but smaller than the main ones. The one or rarely two cusplets (Fig. 2O) are placed between the main cusps. The tiny cusplets can be located on the lateral inner side of the main cusp (Fig. 2B, T). The intermediate and lateral cusps diverge mesially and distally from the crown center forming a fan-shaped structure in the multicuspoid teeth. All cusps and cusplets are covered by straight cristae on both sides. The cristae often do not reach the cusp apex. The labial ornamentation includes two or three long cristae which occasionally formed the inverted “V”-nested structure (Fig. 2L, M, V). The cristae on lingual side are shorter but numerous. The long crista is placed on the lateral side of the cusp instead of the lateral carina. The crown is usually symmetrical, but sometimes, the slight asymmetry is due to the different heights of cusps or cusplets, or an additional cusplet (Fig. 2A, O, T). The strong asymmetry in rare teeth is expressed in the mesial or distal inclination of the cusps (Fig. 2U–W).

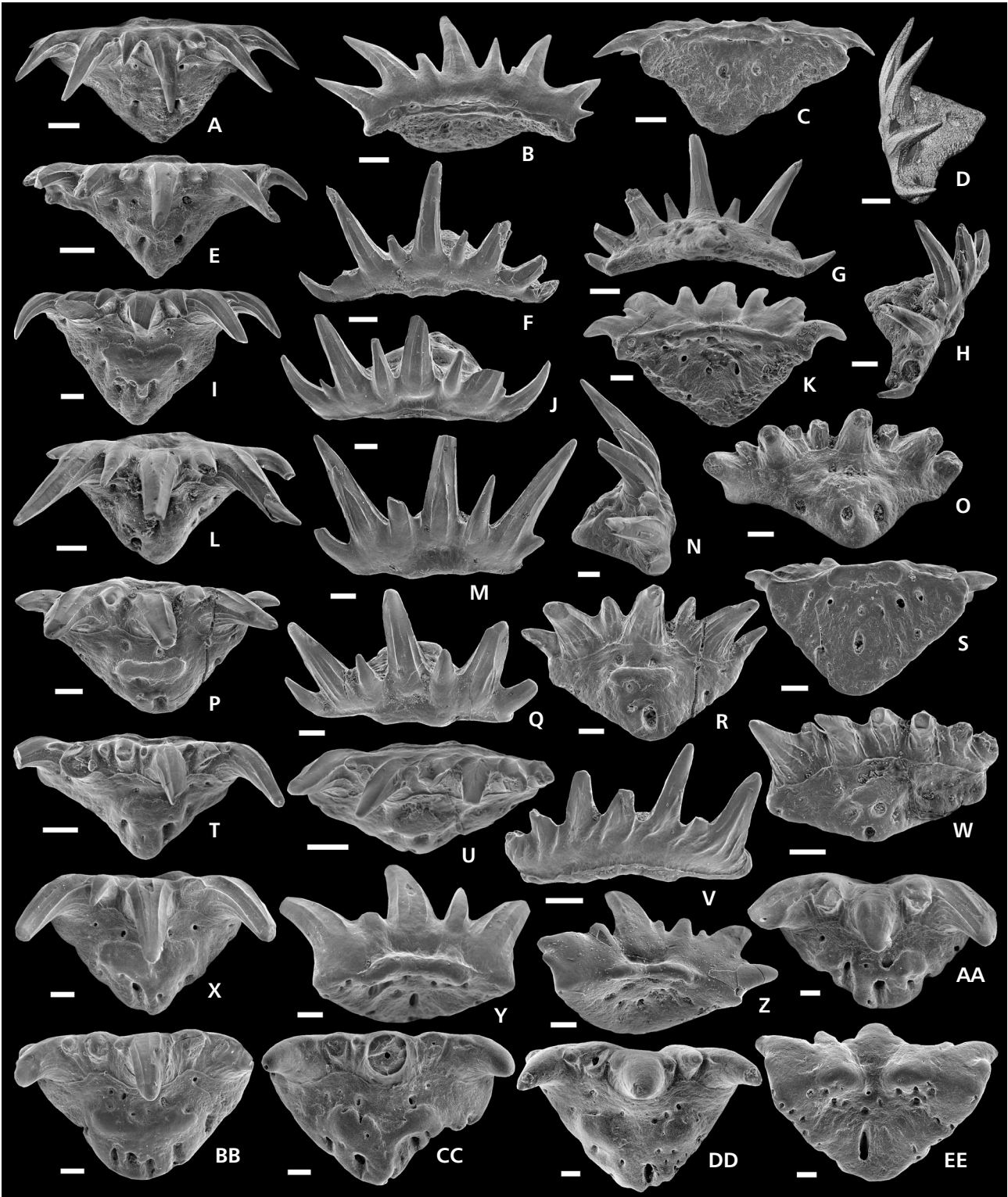
The tooth base is triangular in shape, slightly arched, extended lingually, with a pointed central part of the lingual rim, with a convex occlusal side and a slightly concave basal side. The skewed latero-lingual edges are straight, slightly concave or convex curved. The central part of the base occlusal face bears one or two apical buttons. The button is oval (Fig. 2A), rounded (Fig. 2DD) or subtriangular (Fig. 2I) in shape. Two buttons are closely placed, even

in contact with each other (Fig. 2BB) or situated at some distance (Fig. 2DD) or fused in the middle parts (Fig. 2X, AA, CC). The button surrounds numerous large foramina of vascular canals. The labio-basal rim possesses a prominent, wide shelf-like projection in the teeth with five main cusps (Fig. 2C, K) or oval tubercle (Fig. 2S) or two round tubercles (Fig. 2EE) in the teeth with three main cusps and two buttons. The shelf-like projection is extended beneath the most part of the crown: from one to other intermediate cusps (Fig. 2B, C). The distinct oval tubercle is located below central cusp and intermediate cusplets. The round tubercles are placed closely and beneath the intermediate cusp. The small labial depression is located on the labial side of the base, below the central cusp and above the labio-basal projection or single tubercle. This depression within the teeth with two buttons and tubercles is continued within the basal side of the base and separated two tubercles from each other (Fig. 2EE). The teeth with fused buttons in the middle part (Fig. 2AA, CC) possess the oval tubercle with the middle waist (Fig. 2Z). The foramina of the canals penetrate the concave part of basal side.

The cusps consist of orthodentine and contain very thin pulp canals (Fig. 5J, L, O, M). The internal vascularization system of the tooth base includes a longitudinal, main and secondary horizontal, and ascending canals (Fig. 5K, N). The longitudinal canal is wide and long, ranging from one lateral cusp to others, connecting all pulp canals. The main horizontal canals (mhc) extend as lacuna-like cavities. The short secondary horizontal canals connect the main horizontal canals in the network and with a longitudinal canal. The short ascending canals open along the crown/base junction on the occlusal side and along the labio-basal rim on the basal side (Fig. 5L, M, O).

The teeth of *Heslerodoides* show several morphological variations. They vary in the number of cusps and cusplets, height of cusps, shape, size and number of apical buttons and labio-basal tubercles, with distances between them, and sizes of labial depressions. The first morphotype possesses the crown with five main cusps and seven to nine cusps and cusplets, subtriangular or oval apical button and long labio-basal projection. The second morphotype has a crown with three main cusps and five to seven cusps and cusplets, two round apical buttons and two labio-basal tubercles. There are several variations with combination of mentioned features between these two terminal morphotypes.

Figure 2. Teeth of ctenacanthiform *Heslerodoides triangularis* gen. et sp. nov., Republic of Bashkortostan (A–D) and Moscow Region (E–EE); Pennsylvanian, Carboniferous. • A–D – Dalniy Tyulkas section, sample DT-1; Zilim Formation, Podolskian Regional Stage, Moscovian. Holotype, PM SPU 77-1, occlusal (A), oblique labial (B), basal (C) and oblique lateral (D) views. • E–H, O – Perhurovo-1 borehole, sample PKh-17; Neverovo Formation, Khamovnikian Regional Stage, Kasimovian; E–H – PM SPU 77-2, occlusal (E), labial (F), lingual (G) and oblique lateral (H) views; O – PM SPU 77-5, oblique lingual view. • I–K, P–S, X, Y, AA–EE – Afanasievo quarry; Neverovo Formation, Khamovnikian Regional Stage, Kasimovian; I–K – PM SPU 77-3, sample AF5-54, occlusal (I), labial (J), and oblique basal (K) views; P–S – PM SPU 77-6, sample AF5-54, occlusal (P), labial (Q), oblique lingual (R) and basal (S) views; X, Y – PM SPU 77-9, sample AF5-59, occlusal (X) and oblique labial (Y) views; AA – PM SPU 77-11,



sample AF5-59, occlusal view; BB – PM SPU 77-12, sample AF5-60, occlusal view; CC – PM SPU 77-13, sample AF5-60, occlusal view; DD, EE – PM SPU 77-14, sample AF5-56, occlusal (DD) and oblique basal (EE) views. • L–N – Myachkovo section, sample M7-34; Voskresensk Formation, Krevyakian Regional Stage, Kasimovian; PM SPU 77-4, occlusal (L), labial (M), and oblique lateral (N) views. • T – Vodniki-2/3 borehole, depth 93.5–94.0 m, sample V-2/3-10; Mescherino Formation, Dorogomilovian Regional Stage, Kasimovian; PM SPU 77-7, occlusal view. • U–W – Moscow-1832 borehole, depth 56.25–56.40 m, sample 1832/70; Neverovo Formation, Khamovnikian Regional Stage, Kasimovian; PM SPU 77-8, occlusal (U), labial (V), and oblique lingual (W) views. • Z – Domodedovo Quarry, beds 39, sample D-8C; Suvorovo Formation, Krevyakian Regional Stage, Kasimovian; PM SPU 77-10, oblique labial view. Scale bar = 100 μ m.

Remarks. – The teeth of new taxon, especially the second morphotype, resemble the teeth of ctenacanthiform *Heslerodus*. However, the latter possesses the three main cusps and two intermediate cusplets; the central cusp slightly thicker than the lateral ones; the lateral cusps strongly divergent mesio-distally; the well-developed lateral carina; the rounded base with deep labio-basal depression; two prominent round apical buttons placed closely to the lingual rim; and two round, wide labio-basal tubercles (Ginter 2002, Hodnet *et al.* 2012).

The incomplete tooth from the late Pennsylvanian of Brazil described as *Denaeta?* sp. (Duffin *et al.* 1996, fig. 7a–c) as well as the undescribed shark tooth from the lower–middle Pennsylvanian of Brazil (Moutinho *et al.* 2016, fig. 12g) are very similar to the teeth of *Heslerodoides* and should thus, belong to this genus.

Occurrence. – Carboniferous, Pennsylvanian, Bashkirian–Gzhelian; Moscow Region, Republic of Bashkortostan, Russia, Brazil.

Cohort Euselachii Hay, 1902
Superfamily Protacrodontoidea Zangerl, 1981
Family Protacrodontidae Cappetta, Duffin & Zidek, 1993

Genus *Gzhelodus* gen. nov.

Type species. – *Gzhelodus serratus* sp. nov.

Etymology. – From the Gzhel locality, and the Greek “*odous*”, meaning tooth.

Diagnosis. – Euselachian teeth with central cusp, three to five intermediate and lateral cusplets in the pyramidal, elongated mesio-distally crown; triangular prominent central cusp; crenulated occlusal crest; coarse transversal ridges and prominent projections with hook-like apices on both labial and lingual sides of the crown; long labial peg with bulb-shaped tubercle; highly vascularized tooth base with prominent central part of occlusal face; dense network of vascular canals occupying lower part of the crown and whole base; longitudinal canal connecting short pulp canals.

Occurrence. – Carboniferous, Pennsylvanian, Kasimovian–Gzhelian; Moscow, Samara and Volgograd regions, Russia.

***Gzhelodus serratus* sp. nov.**

Figures 3, 5P–V

Holotype. – Tooth, PM SPU 77-15 (Figs 3A–E, 5P–V).

Type horizon and locality. – Khamovnikian Regional Stage, Kasimovian, Pennsylvanian, Carboniferous. Zhirnovsk

Quarry, right bank of the Medveditsa River, Volgograd Region, Russia.

Material. – One tooth from the Rusavkino Quarry, sample PC-054, Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; five teeth from the Gzhel section, Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; one tooth from the Yabloneviy Ravin Quarry, sample 8.1.2', *Idiognathodus simulator* Zone, Gzhelian; one tooth from the Zhirnovsk Quarry, Khamovnikian Regional Stage, Kasimovian.

Etymology. – From the Latin *serratus*, serrated.

Diagnosis. – as for the genus.

Description. – The euselachian teeth have a width of base from 1.4 to 1.7 mm mesio-distally. They possess the pyramidal crown with triangular central cusp, three to five intermediate and lateral cusplets. The crown is compressed labio-lingually, elongated mesio-distally, and almost symmetrical or asymmetrical. The prominent central cusp is larger than other cusplets. They are separated by notches from deep (Fig. 3J–L) to weakly developed (Fig. 3M–O). The crown asymmetry is expressed in different numbers of cusplets, ridges and projection on mesial and distal parts, in distally inclined central cusp. The crenulated occlusal crest is better developed on the central cusp and in the notches between cusplets. The coarse transversal ridges are presented on the labial and lingual sides of the crown. The long ridges diverge from the apices of cusps or cusplets. The lingual face of central cusp bears from one (Fig. 3O) to six short ridges (Fig. 3K). The one long ridge on the labial face of central cusp passes into the labial peg. The peg is very prominent, well-developed in the lower part of the crown, and extended below the crown-base junction, at the labio-basal rim forming the bulb-shaped tubercle. This tubercle is surrounded with depression. The prominent projections are located on most long ridges on both labial and lingual sides of the crown. The projections are long and rather narrow, being oval or drop-like in shape in the labial and lingual views, being irregular in size, sometimes serrated (Fig. 3D, L) or with pointed hook-like apices (Fig. 3E). They are shorter than the labial peg, and narrowed and disappeared above the crown-base junction. The more prominent projections are associated with the cusplets but some small projections are situated on the lingual face of central cusp (Fig. 3G) or between long projections (Fig. 3L). The number of projections on one side of the crown varies from two to ten. The projections are separated by deep depressions of different width. The crown-base junction is marked by the groove or a distinct line (Fig. 3K, O).

The tooth base is oval in basal view, elongated mesio-distally, with convex occlusal and flat basal faces. The

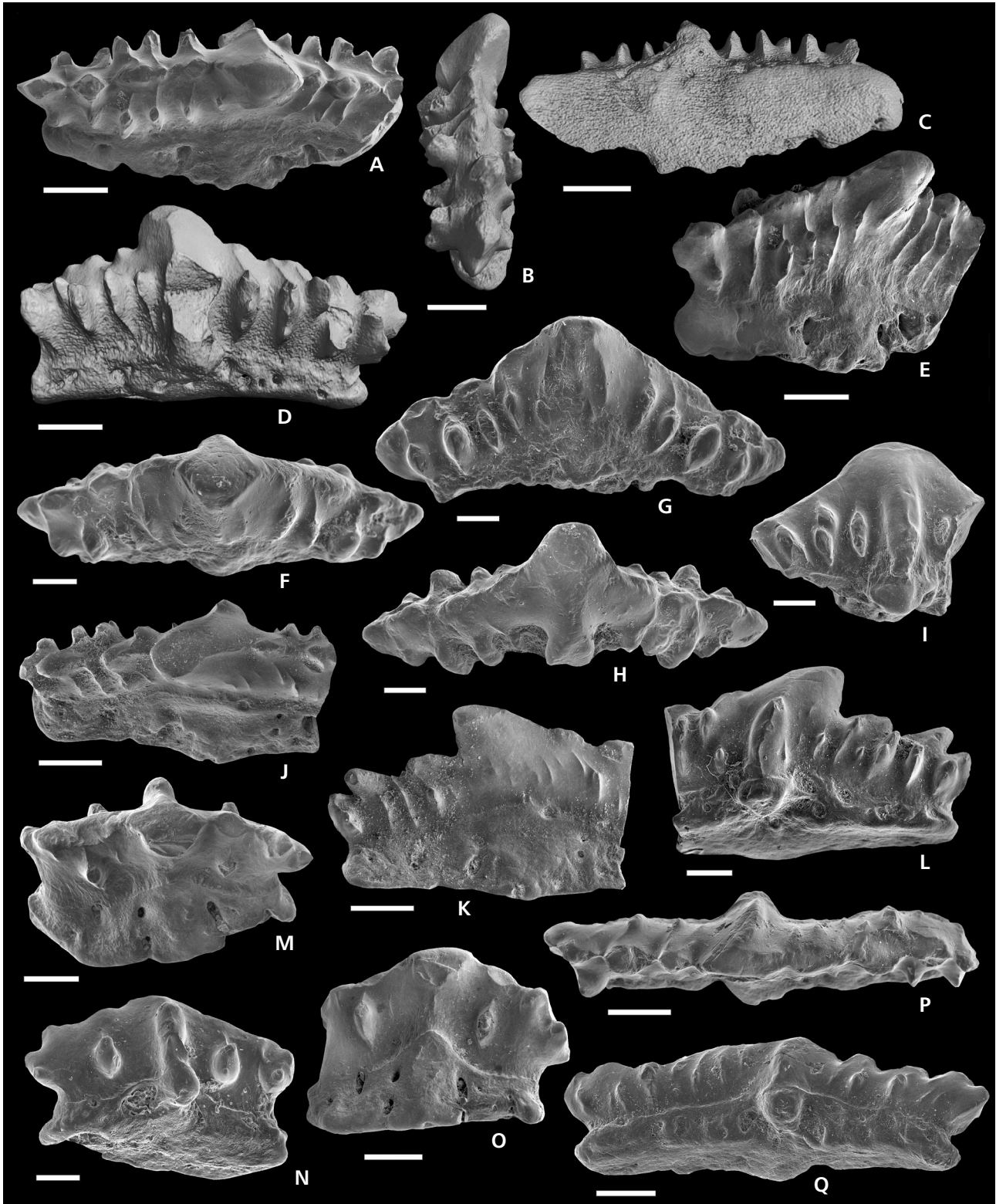


Figure 3. Teeth of euselachian *Gzhelodus serratus* gen. et sp. nov., Volgograd (A–E) and Moscow (F–Q) regions; Pennsylvanian, Carboniferous. • A–E – Zhirnovsk Quarry; Khamovnikian Regional Stage, Kasimovian; holotype, PM SPU 77-15, occlusal (A), lateral (B), basal (C), labial (D) and oblique lingual (E) views. • F–L, P, Q – Gzhel section; Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; F–H – PM SPU 77-16, occlusal (F), lingual (G) and labial (H) views; I – PM SPU 77-17, labial view; J–L – PM SPU 77-18, occlusal (J), lingual (K) and oblique labial (L) views; P, Q – PM SPU 77-20, occlusal (P) and oblique labial (Q) views. • M–O – Rusavkino Quarry; Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; PM SPU 77-19, oblique occlusal (M), labial (N) and lingual (O) views. Scale bar = 300 μ m.

extended lingual part of the base is triangular (Fig. 3A, I) or oval (Fig. 3M) in the occlusal view, with a prominent central part. The large and small foramina of vascular canals penetrate the occlusal face of the base. The rows of foramina open on the labial surface, mesially and distally from the labial peg (Fig. 3D, L, Q).

The vascularization system contains a dense network of canals occupying the lower part of the crown and the whole tooth base (Fig. 5R–V). The network includes the transverse main and secondary horizontal, longitudinal, narrow ascending and secondary, short pulp canals. The horizontal canals run across the base from the lingual torus to the labio-basal edge (Fig. 5S, T). The ascending and secondary canals are connected to the horizontal canals. The ascending canals are vertical or inclined from the vertical axis. The longitudinal canal connects the pulp canals. The straight dentine tubules were observed into the large cusps (Fig. 5R).

The teeth vary in the number of cusplets, projections and ridges; in the height and inclination of central cusp; in the size of projections and labial peg; in the depth of notches between the cusp and cusplets; and in the shape of tooth base.

Remarks. – The *Gzhelodus* teeth are similar to the teeth of some taxa such as *Deihim mansureae* Ginter, Hairapetian & Klug, 2002 from the Late Devonian and early Carboniferous of Iran, Armenia, Australia, New Mexico (USA) and Kuznetsk Basin, Russia (Ginter *et al.* 2010; Ivanov & Rodina 2010; Ivanov & Lucas 2011; Roelofs *et al.* 2015, 2016); *Roogodus phijani* Hairapetian & Ginter, 2009 from the Late Devonian of Iran (Hairapetian & Ginter 2009); *Reesodus pectinatus* (Lebedev 1996) from the early Carboniferous of Belgorod Region, Russia (Lebedev 1996); and *Tiaraju tenuis* Richter, 2007 from the middle Permian of Brazil (Richter 2007). However, the teeth of new taxon differ from the teeth of above mentioned taxa in the prominent projections on both labial and lingual surfaces; well-developed, long labial peg; crenulated occlusal crest and flat basal face of the base.

Occurrence. – Carboniferous, Pennsylvanian, Kasimovian–Gzhelian; Moscow, Samara and Volgograd regions, Russia.

Order and family incertae sedis

Genus *Samarodus* gen. nov.

Type species. – *Samarodus flexus* sp. nov.

Etymology. – From the Samara Region, and the Greek “*odous*”, meaning tooth.

Diagnosis. – Small teeth with three cusps in the crown; cusps sigmoidally curved, with smooth labial face and small nodes in the upper part; central cusp slightly higher and wider than the lateral ones; lingual cusp surface ornamented by numerous straight, slightly wavy cristae; lateral carina in the upper part of the cusp; triangular or semicircular base with a smooth occlusal face; two small labio-basal tubercles with a shallow depression only on the basal face; pulp canals slightly extended at the cusp node; large foramina of three wide main horizontal vascular canals.

Occurrence. – Carboniferous, Pennsylvanian, Moscovian–Gzhelian; Samara and Moscow regions, Republic of Bashkortostan, Pechora Sea, Russia.

Samarodus flexus sp. nov.

Figures 4, 5A–G

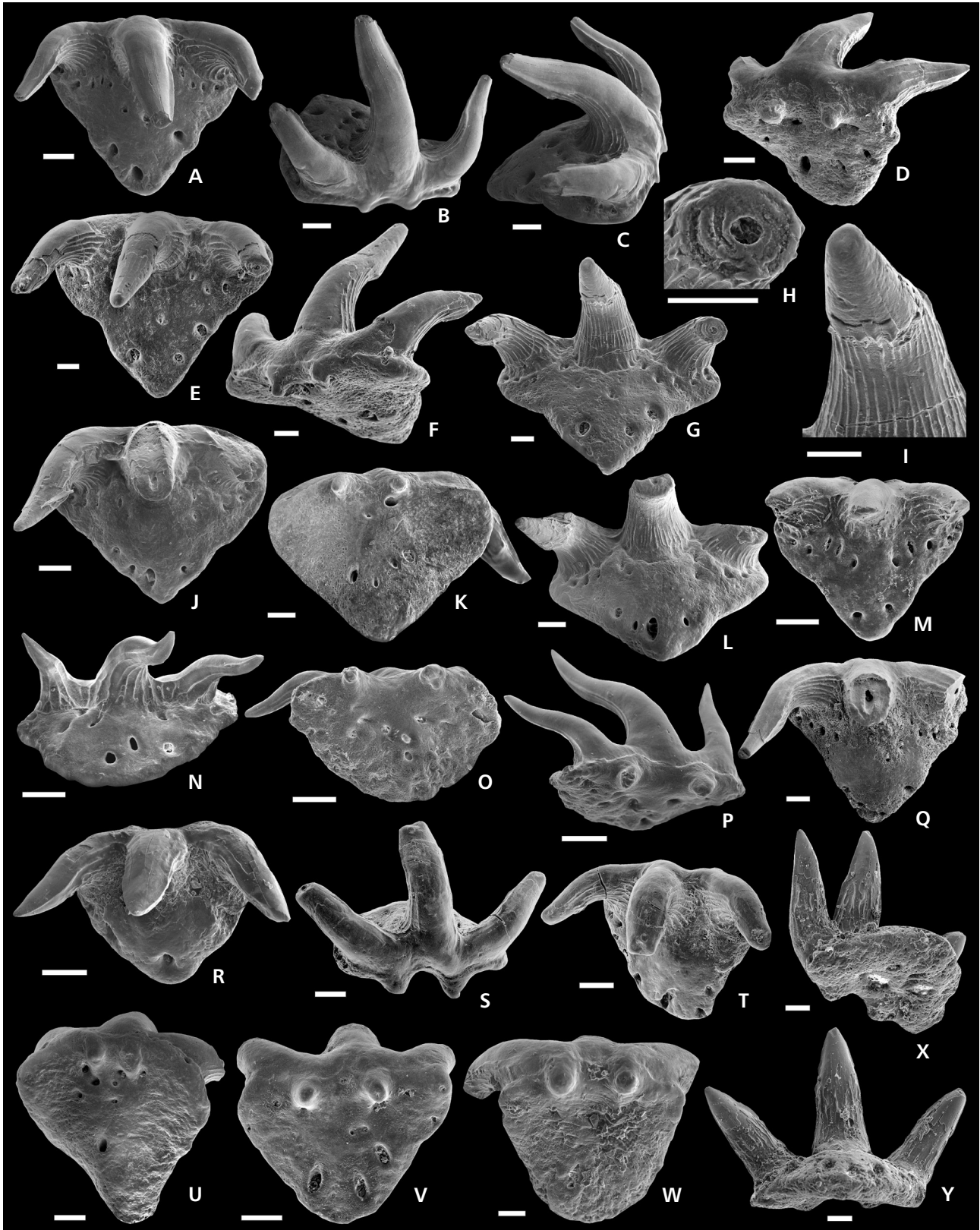
1999 ‘*Cladodus*’ *divergens* Trautschold, 1879. – Ivanov, pp. 276, 277 (*partim*), fig. 3a, pl. 7, fig. 1 (*non* fig. 3b–e).

Holotype. – Tooth, PM SPU 77-21 (Figs 4A–C, 5A–G).

Type horizon and locality. – *Idiognathodus simulator* conodont Zone, Gzhelian, Pennsylvanian, Carboniferous. Yabloneviy Ravin Quarry, Volga River, right bank, Samara Region, Russia; sample 8.1.2’.

Material. – One tooth from the Mytitschi-17 borehole, depth 43.0–47.0 m, sample 17/1-2, Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; one tooth from the Rusavkino Quarry, sample PC-054, Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; one tooth from the Gzhel section, Kosherovo Formation, Dobryatinian Regional Stage, Gzhelian; Samara Region: 10 teeth from the Yabloneviy Ravin Quarry, sample 8.1.2’, *Idiognathodus simulator* Zone, Gzhelian; five teeth from the Shiryaevo-31a borehole, depth 76.7–83.2 m, sample Sh31a/34; Dorogomilovian Regional Stage, Kasimovian; one tooth from the

Figure 4. Teeth of *Samarodus flexus* gen. et sp. nov., Samara (A–L, Q–V) and Moscow (M) regions, Republic of Bashkortostan (N–P, W), Pechora Sea (X, Y); Pennsylvanian, Carboniferous. • A–D, Q, U, V – Yabloneviy Ravin Quarry, sample 8.1.2’; *Idiognathodus simulator* Zone, Gzhelian; A–C – holotype, PM SPU 77-21, occlusal (A), oblique labial (B) and oblique lateral (C) views; D – PM SPU 77-22, oblique basal view; Q – PM SPU 77-27, occlusal view; U – PM SPU 77-30, basal view; V – PM SPU 77-31, basal view. • E–L, R–T – Shiryaevo-31a borehole, depth 76.7–83.2 m, sample Sh31a/34; Dorogomilovian Regional Stage, Kasimovian; E–I – PM SPU 77-23, occlusal (E), oblique lateral (F), lingual (G) views, detail of broken lateral cusp (H), detail of central cusp in lingual view (I); J–L – PM SPU 77-24, occlusal (J), basal (K) and lingual (L) views; R – PM SPU 77-28, occlusal view; S, T – PM SPU 77-29, labial (S) and oblique occlusal (T) views. • M – Mytitschi-17 borehole, depth 43.0–47.0 m, sample 17/1-2; Kosherovo



Formation, Dobryatinian Regional Stage, Gzhelian; PM SPU 77-25, occlusal view. • N–P, W – Dalniy Tyulkas section; Zilim Formation, Podolskian Regional Stage, Moscovian; N–P – PM SPU 77-26, sample DT-1, lingual (N), basal (B) and oblique labial (P) views; W – PM SPU 77-32, sample DT-14, basal view. • X, Y – Gulyaevskaya borehole, depth 2710 m; Gzhelian–Asselian boundary beds; PM SPU 77-32, oblique lateral (X) and lingual (Y) views. Scale bars: A–G, I–Y = 100 μ m; H = 50 μ m.

the Askyn section, sample 47/2, Zilimian Regional Stage, Moscovian; eight teeth from the Dalniy Tyulkas section, samples DT-1, DT-11, DT-14, DT-36, Zilimian Regional Stage, Moscovian; one tooth from the Gulyaevskaya borehole, depth 2710 m, Gzhelian–Asselian boundary beds.

Etymology. – From the Latin *flexus*, curved.

Diagnosis. – as for the genus.

Description. – Small teeth have a width of base from 0.45 to 0.95 mm mesio-distally. The crown consists of three cusps: central and paired lateral. The central cusp is slightly higher and wider than the lateral ones. The lateral cusps diverge mesially and distally from the central one. The cusps are thin, acuminate, sigmoidally curved, inclined in the lingual direction, round in cross section (Fig. 4H), and with smooth labial and ornamented lingual faces. The lingual face in the lower two thirds bears numerous straight, distinct cristae, which are sometimes slightly wavy and bifurcated at the base. The upper third part of the lingual face is smooth (Fig. 4G, I, Y). The short cristae are sometimes present between the cusps (Fig. 4M, N, Q). The cusps are thickened at the boundary of the smooth and ornamented lingual parts formed the distinct node (Fig. 4C, F–I, 5C). The lateral carina is well-developed in the upper part of the cusps especially at that node (Fig. 4C), and disappears in the lower part and between the cusps. The bases of the central and lateral cusps are placed along a straight line along the labial edge. A narrow groove marks the crown/base boundary.

The tooth base is rather thin, directed lingually, triangular or semicircular in shape, with acuminate triangular or rounded lingual part. The occlusal surface is smooth, slightly convex, the basal one is almost flat. The base bears two small, round, prominent labio-basal tubercles. The tubercles are separated by a shallow depression which is weakly developed only on the basal face (Fig. 4D, F, K, O, P, U–X). The large foramina of the main vascular canals are located at the lingual edge on the occlusal surface and on the basal surface of the base. The numerous small foramina of canals open around the cusp base.

The cusps comprise orthodentine (Fig. 4H) with thin pulp canals (Fig. 5G). The pulp canals are slightly extended

at the cusp node (Fig. 5D, F, G). The vascularization system of the tooth base consists of three large main horizontal, moderate secondary horizontal, and short ascending canals. The wider horizontal canal transverses the tooth base from the mid lingual rim to the pulp canal of central cusp (Fig. 5F). Two lateral main horizontal canals run along the lingual edges to the pulp canals of lateral cusps. The secondary horizontal canals connect these main canals in the network. The ascending canals penetrate the occlusal face near the crown/base junction and the basal face of the base (Fig. 5D, G).

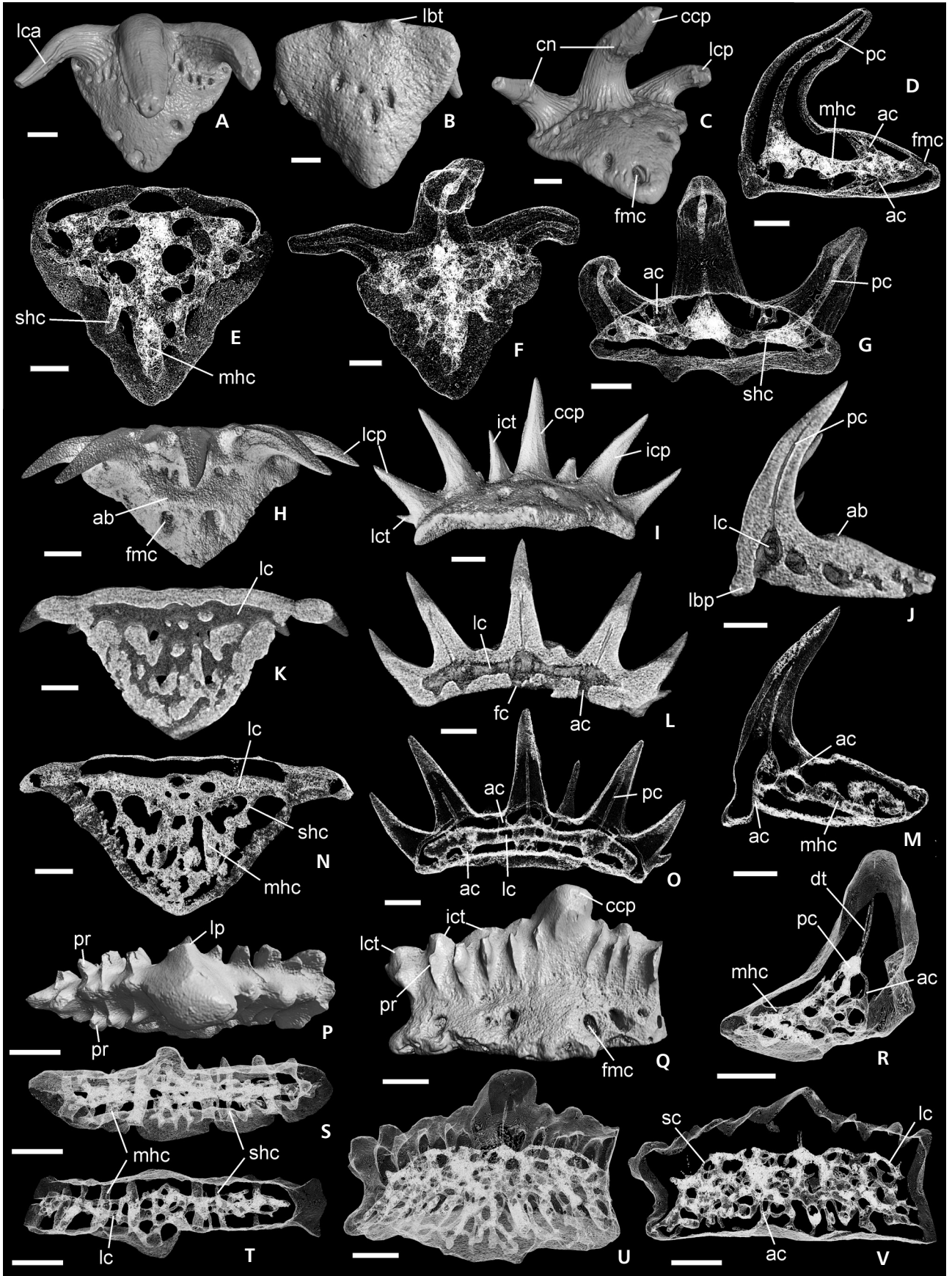
The teeth of the new taxon vary in the width of cusps, the degree of cusp sigmoidal curvature, the number of cristae on the cusp lingual face, the shape and length of tooth base, and the width of depression between labio-basal tubercles. The lingual part of the tooth base varies from acuminate triangular (Fig. 4A, E, M, U) to rounded (Fig. 4O, W). The smaller teeth in the collection (Fig. 4N–P, V) possess the thinner, strongly sigmoidally curved cusps, a lesser number of lingual cristae in the lingual ornamentation, the semicircular base with short lingual part and large foramina of the canals, and the wide-spaced labio-basal tubercles.

Remarks. – The tooth (Fig. 4X, Y) described earlier as ‘*Cladodus*’ *divergens* Trautschold, 1879 (Ivanov 1999) from the Gzhelian–Asselian boundary beds of the Gulyaevskaya borehole (Pechora Sea) is assigned to *Samarodus flexus* gen. et sp. nov.

The teeth of the new taxa differ from the teeth of Palaeozoic sharks in the cusps with a smooth labial face but with well-developed lingual ornamentation, and with a node in the upper part, two labio-basal tubercles at the base but occlusal surface without any articulation elements. The weakly-developed cladodont crown and proportion of cusps in the new taxon is rather similar to that of *Heslerodus* teeth but the latter is different in the presence of intermediate cusplets in the crown, two apical buttons on the occlusal side of the base and a deep labio-basal depression (Ginter *et al.* 2010).

Occurrence. – Carboniferous, Pennsylvanian, Moscovian–Gzhelian; Samara and Moscow regions, Republic of Bashkortostan, Pechora Sea, Russia.

Figure 5. Micro-CT images of the teeth. • A–G – *Samarodus flexus* gen. et sp. nov., holotype, PM SPU 77-21; occlusal (A), basal (B) and oblique lingual (C) views; oblique lingual view with translucent tooth (F); transversal (D), frontal (E) and sagittal (G) virtual sections with translucent tooth. • H–O – *Heslerodoides triangularis* gen. et sp. nov., holotype, PM SPU 77-1; occlusal (H) and lingual (I) views; transversal (J), frontal (K) and sagittal (L) virtual sections; transversal (M), frontal (N) and sagittal (O) virtual sections with translucent tooth. • P–V – *Gzhelodus serratus* gen. et sp. nov., holotype, PM SPU 77-15; occlusal (P) and lingual (Q) views; lingual view with translucent tooth (U); transversal (R), frontal (S, T) and sagittal (V) virtual sections with translucent tooth. Abbreviations: ab – apical button; ac – ascending vascular canal; ccp – central cusp; cn – cusp node; dt – dentine tubules; fc – foramen of vascular canal; fmc – foramen of main vascular canal; icp – intermediate cusp; ict – intermediate cusplet; lbp – labio-basal projection; lbt – labio-basal tubercle; lc – longitudinal vascular canal; lca – lateral carina; lcp – lateral cusp; lct – lateral cusplet; lp – labial peg; mhc – main horizontal vascular canal; pc – pulp canal; pr – crown projection; sc – secondary vascular canal; shc – secondary horizontal vascular canal. Scale bars: A–O = 100 µm; P–V = 300 µm.



Discussions

Heslerodoides

The teeth of a new taxon, especially first morphotype, possess some features in the structure of the crown similar to falcetid symmoriiformes such as *Stethacanthulus* and two species of *Danaea* (*D. saltsmani* Ginter & Hansen, 2010 and *D. wangi* Wang, Jin & Wang, 2004). These teeth have quite high intermediate and lateral cusps and cusplets but the central cusp is larger than other cusps. The structure of the tooth base in the falcetids is different to those of *Heslerodoides* teeth. The teeth of the mentioned *Danaea* species possess the base with weakly developed apical button placed at the lingual rim and labio-basal tubercle (Wang *et al.* 2004, Ginter & Hansen 2010). The tooth bases of *Stethacanthulus* teeth lack both an apical button and labio-basal tubercle but have an occlusal transverse depression and basal prominence (Williams 1985, Ivanov 1999).

The teeth of *Heslerodoides* closely resemble the teeth of ctenacanthiform *Heslerodus* (Ginter 2002) but are distinguished from these with a fan-shaped crown; the main cusps are almost equal in sizes; a small labial depression on the labial side below central cusp; a triangular tooth base with a pointed central part; one or two closely placed apical buttons in the central part of the crown; one labio-basal projection or one tubercle or two small, closely placed tubercles. The teeth of most ctenacanthiforms excepting *Heslerodus* and *Heslerodoides* are characterized by a typical cladodont crown with a strongly dominant central cusp (Ginter *et al.* 2010). The central cusp in the teeth of *Heslerodus* and *Heslerodoides* is almost equal in height to the lateral ones. However, the central cusp in *Heslerodus* teeth is usually wider than the lateral cusps. The large variation in the crown and base morphology suggests the heterodonty in the *Heslerodoides* dentition.

Currently, the order Ctenacanthiformes includes two families: Ctenacanthidae and Heslerodidae (Ginter *et al.* 2010, Maisey 2010). The family Heslerodidae primarily contains the genera *Heslerodus*, *Avonacanthus* and *Bythiacanthus* (Maisey 2010). Later, some authors suggested that the genera *Glikmanius*, *Kaibabvenator* and *Nanoskalme* should also have been included into this family (Hodnett *et al.* 2012) such as *Glencartius* (Ivanov & Lebedev 2014). Hodnett *et al.* (2021) described a new genus of ctenacanthiforms and proposed that this order should include four to five families or superfamilies. They presumed the combination the genera *Dracopristis*, *Glikmanius*, *Glencartius*, *Kaibabvenator*, *Nanoskalmae* and family Heslerodidae into one new superfamily (Hodnett *et al.* 2021). *Heslerodoides* is closely related to *Heslerodus* and can be assigned to the family Heslerodidae (Maisey 2010).

Gzhelodus

The teeth of *Gzhelodus* resemble the teeth of *Deihim*, *Roongodus*, *Reesodus pectinatus* and *Tiaraju*. The *Deihim* teeth differ from the teeth of new taxon in the row of short projections (cusplets) only on the labial face, projections covered with coarse cristae, an undeveloped occlusal crest, deeper notches between cusps, a concave basal surface of the base, and numerous large foramina on the occlusal and basal sides (Ginter *et al.* 2002, 2011; Roelofs *et al.* 2016). The various teeth with large variations in morphology were described as *Deihim*. Originally the teeth of *Deihim mansureae* included four tooth morphotypes which were rather distinguishable from each other (Ginter *et al.* 2002). However, the teeth described later differed from these four morphotype. One tooth (Hairapetian & Ginter 2010, text-fig. 3a) has a crown typical of *Protacrodus* with pyramidal cusps rounded in cross section and strongly separated from each other; ridges on the labial and lingual faces diverged basally from the cusp apex. This tooth has five labial projections. Other tooth (Roelofs *et al.* 2016, fig. 6.11, 12) possesses a monolithic pyramidal crown without a differentiation of cusps. The *Deihim* teeth do not commonly have a labial peg but two teeth possess a strongly prominent labial peg (Ginter *et al.* 2002, fig. 10g, i; Roelofs *et al.* 2015, text-fig. 6f). The tooth with a cladodont crown and weakly pronounced apical button but with a few small labial projections was described also as *D. mansureae* (Hairapetian & Ginter 2009, text-fig. 2d). These abovementioned teeth have only one feature in common: the presence of labial projections. Such large differences cannot be explained just by tooth variations in the heterodont dentition. It is obvious that the genus *Deihim* includes several species besides *D. mansureae*, and some teeth probably belong to other genera.

The incomplete and poorly preserved teeth from the late Pennsylvanian of New Mexico (USA) described as Protacrodontidae indet. resemble the teeth of *Deihim* and *Gzhelodus* but they have a low crown and weakly developed cusplets (Ivanov & Lucas 2019).

The teeth *Roongodus* in contradistinction to *Gzhelodus* teeth possess the lingual peg and the massive central cusp (Hairapetian & Ginter 2009). One tooth, the holotype of *Reesodus pectinatus* (Lebedev 1996, fig. 2d–f), is similar to the teeth of new taxon in the prominent labial projections and peg, but differs in the small, tubercle-like lingual projections and distinct, straight occlusal crest. Other teeth of this species are distinguished from the holotype and described taxon in the weakly developed projections, while some specimens have a monolithic crown without differentiated cusplets (Lebedev 1996).

The tooth of *Tiaraju* (Richter 2007) resembles the teeth of *Gzhelodus* with the presence of projections (buttresses) on both labial and lingual faces but differs in the short

central cusp; the well differentiated cusplets; the lacking labial peg; the regular arrangement of almost equal projections; the concave basal face of the base. The author assigned *Tiaraju* to eugeneodontiforms (Richter 2007). The teeth of eugeneodontiforms mainly have a fused cusp and cusplets in the crown consisting of tubular dentine, and a highly vascularized tooth base (Ginter *et al.* 2010). The *Tiaraju* tooth is strongly distinguished from the teeth of any known eugeneodontiforms and is very similar to that of euselachians such as *Gzhelodus* and *Deihim*, thus, probably belonging to this group.

Samarodus

The peculiar teeth of *Samarodus* are distinguished from the teeth of all known Palaeozoic chondrichthyans. The teeth of most Palaeozoic sharks possess the considerably developed ornamentation on the labial surface then that on the lingual side. The teeth of phoebodontiforms such as *Phoebodus depressus* Ginter, Hairapetian & Klug, 2002 and some species of *Thrinacodus* (Ginter *et al.* 2010) secondarily lost the labial ornamentation but have several short cristae on their lingual face. The *Samarodus* teeth have a smooth labial face but a well-developed ornamented lingual face. The node in the upper part of cusp related with the extinction of the pulp canal is an uncommon characteristic of Palaeozoic shark teeth. The lateral carina, if present in the known Palaeozoic teeth, is developed along the entire lateral edge of the cusp and often connects the cusps together in the crown. In contrast to this, the lateral carina in the *Samarodus* teeth is well-developed in the upper part of the cusps and extended at the node, whilst missing in the lower part and between the cusps. The teeth of Palaeozoic sharks bearing one or two labio-basal tubercles (projections) usually have one or two apical buttons (Ginter *et al.* 2010). However, the teeth of *Samarodus* have two prominent labio-basal tubercles and lack an apical button. The teeth of only one chondrichthyan group Jalodontiformes possess one to four labio-basal tubercles and lack an apical button (Ivanov *et al.* 2021).

Such a combination of features is unknown in the teeth of all Palaeozoic chondrichthyans. However, the teeth from the Early Cretaceous of Europe demonstrate a similar cusp design. The teeth of *Cretacladoides noricum* Feichtinger, Engelbrecht, Lukeneder & Kriwet, 2020 from Austria (Feichtinger *et al.* 2020) and especially the tooth described as *Falcatidae* indet. from France (Guinot *et al.* 2013) possess the sigmoidally curved cusps with one to two cristae in the lower part of a mostly smooth labial face, with numerous slightly wavy cristae in the lower two-thirds of the lingual face and smooth upper third part. *Cretacladoides* was tentatively assigned by authors as also belonging to the family *Falcatidae* of the order *Symmoriiformes*

(Feichtinger *et al.* 2020). These Cretaceous teeth slightly resemble the Palaeozoic falcatid teeth in their crown morphology but this resemblance is only superficial. The crowns of falcatid teeth possess cusps which are rounded in cross-section and separated from each other. The lateral carina is weakly developed or missing. The crowns of Cretaceous teeth have cusps with a biconvex cross-section and which are connected to each other with well-developed lateral carina (cutting edge). The structure of the tooth base in Cretaceous teeth differs considerably from that of the Palaeozoic falcatid teeth. The base of Cretaceous teeth has a transversal thickening on the central part of the occlusal face and flat basal face (Feichtinger *et al.* 2020). Such transversal thickening is common for several fossil and modern neoselachians (Cappetta 2012). In contrast, the base of falcatid teeth possesses the distinct apical button and labio-basal projection (Ginter & Hansen 2010) or an occlusal transverse depression and basal prominence (Williams 1985, Ivanov 1999). The Cretaceous teeth in the crown design are similar to those of the synechodontiform neoselachians especially the Permian synechodontid teeth (Ivanov 2005). However, the synechodontiform teeth have a strongly ornamented labial face of the crown and smaller lateral cusps (Thies 1983, Duffin & Ward 1993, Klug 2009). Apparently, all teeth described from the Early Cretaceous of Europe should be attributed to neoselachians.

Conclusions

The new taxa described here demonstrate the taxonomical diversity in the late Carboniferous chondrichthyans with various types of tooth morphology. These taxa occur in the Bashkirian–Gzhelian from numerous localities of Republic of Bashkortostan, Moscow, Samara and Volgograd regions of Russia. *Heslerodoides* has also been recorded in the Pennsylvanian of Brazil.

The ctenacanthiform *Heslerodoides* demonstrates variations in tooth morphology and has teeth resembling those of *Heslerodus*. The protacrodontid euselachian *Gzhelodus* is closely related with *Deihim* and *Tiaraju*. The peculiar teeth of the astonishing shark *Samarodus* possess a combination of features previously unknown in the teeth of Palaeozoic chondrichthyans but their cusps are similar to the peculiar teeth from the Early Cretaceous of Austria and France.

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