Chondrichthyans from the Devonian–Early Carboniferous of Belarus

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Abstract. Diverse remains of chondrichthyans were found in several stratigraphic levels in 18 cores of the Devonian and Lower Carboniferous of Belarus. Most of the taxa were first reported in that territory. A new species of ctenacanthiform shark, *Tamiobatis elgae*, is described. The internal structure of teeth of this species is reconstructed for the first time using microtomography. The distribution of chondrichthyan taxa is analysed.

Key words: Chondrichthyes, Lower Devonian–Lower Carboniferous, Belarus.

INTRODUCTION

Chondrichthyans are poorly known from the Palaeozoic of Belarus. They are mentioned occasionally in the lists of Devonian–Lower Carboniferous vertebrates from that territory (Esin et al. 2000; Mark-Kurik 2000; Plax 2008, 2011, 2012, 2013). The scales of *Lugalepis* cf. *multispinata* Karatajūtė-Talimaa have been reported from the Narva Regional Stage (Eifelian, Middle Devonian) of Belarus (Karatajūtė-Talimaa 1997), but other chondrichthyan remains have not been studied or described yet.

The Devonian shallow-water deposits of Belarus as a part of the East European Platform are very varied including different facies types depending on the stratigraphic intervals and structural-tectonic units (Kruchek et al. 2001, 2010; Obukhovskaya et al. 2005). The Early Devonian, Emsian strata are represented by terrigenous deposits dominated by sandstones, more rarely carbonate sediments such as marls and limestones. The Eifelian (Middle Devonian) deposits include marls and dolomites in the lower part and clays and siltstones in the upper part. The Givetian sediments are represented by sandstones, siltstones and clays with rare interlayers of marls and dolomites. The Frasnian deposits are mostly carbonates with clays and evaporates in the upper part. The thickening Famennian sediments include organogenic limestones, dolomites with the interbedding of clays, marls and with massive sulphate- and salt-bearing beds. The Lower Carboniferous strata are represented by clayey deposits with intercalations of limestones, sandstones and marls.

The descriptions of chondrichthyan microremains collected from several stratigraphic levels of the Devonian and Lower Carboniferous of Belarus are presented in this paper. The chondrichthyan teeth and scales were found from the drill cores in the Lower Devonian, Emsian Vitebsk Regional Stage; the Middle Devonian, Eifelian Gorodok and Kostyukovichi regional stages and the Givetian Polotsk Regional Stage; the Upper Devonian, Famennian Kuzmichi, Drozdy, Petrikov, Starobin and Borovoe regional stages; the Lower Carboniferous, Lower Tournaisian Malevka, Upa and Cherepet regional stages (see Table 1). The Devonian and Lower Carboniferous subdivisions of Belarus are presented in the most recent stratigraphic chart (Kruchek et al. 2010). The chondrichthyan remains were recorded from 18 cores drilled in different regions of Belarus (Fig. 1). These cores were located in several structural-tectonic units: the Pripyat Trough – Berzhetsy-475, Brinev-6, Glusk-1, Knyshevichi-7, Krasnoselskaya-215, Ostashkovichi-2R, Pinsk-26, Starobin-239, Turov-5,

Table 1. List of drill cores and samples containing the described chondrichthyan remains

Drill core	Depth (m)	Sample	Stratigraphical level	Lithology
Buda Dalnyaya-35	231.7	6	L. Devonian, U. Emsian, Vitebsk R.S., Lepel B.	Marl light grey, thick-bedded
Bykhov-151	141.3	3a	M. Devonian, Eifelian, Narva R.SS., Gorodok R.S.	Marl dolomitic, light grey, massive
Pinsk-26	415.7	6b	M. Devonian, Eifelian, Narva R.SS., Kostyukovichi R.S.	Dolomite argillaceous, light grey
Lepel-1	175.4	3	Givetian, Polotsk R.S., Goryn B.	Sandstone grey, fine-grained
	194	19	M. Devonian, Eifelian, Narva R.SS., Kostyukovichi R.S.	Clay grey
Berdyzh-1	230.8	35	M. Devonian, Givetian, Polotsk R.S., Stolin B.	Siltstone argillaceous, light grey
Turov-5	2042.2	49	U. Devonian, L. Famennian, Zadonsk R.SS., Kuzmichi R.S.	Limestone grey, organogenic
Ostashkovichi-2R	2637–2641	27	U. Devonian, L. Famennian, Elets R.SS., Drozdy R.S.	Limestone light grey, massive
Knyshevichi-7	1989.9	4	U. Devonian, L. Famennian, Petrikov R.S.	Limestone grey, organogenic
	2060.3	10	U. Devonian, L. Famennian, Elets R.SS., Drozdy R.S.	Limestone grey, coquinoid
	2081.7	–	U. Devonian, L. Famennian, Elets R.SS., Turov R.S.	Limestone grey, organogenic
Glusk-1	1347–1351	16a	U. Devonian, L. Famennian, Petrikov R.S.	Limestone grey, massive
Brinev-6	446.7	1a	U. Devonian, L. Famennian, Petrikov R.S.	Limestone light grey
Krasnoselskaya-215	3176–3184	16a	U. Devonian, L. Famennian, Petrikov R.S.	Limestone argillaceous, dark grey
Starobin-239	1043.8–1047.6	37a	U. Devonian, L. Famennian, Petrikov R.S.	Limestone light grey, massive
482	423	–	U. Devonian, U. Famennian, Polese R.SS., possibly Starobin R.S.	Marl light grey
506	241.6	56b	U. Devonian, U. Famennian, Polese R.SS., Borovoe R.S.	Clay dark grey
331	225–227	2	L. Carboniferous, L. Tournaisian, Cherepet R.S.	Clay dark grey
	276–277	12	L. Carboniferous, L. Tournaisian, Upa R.S.	Clay dark grey, coaly
	278–282	13d		Clay grey
	292.2	16a	L. Carboniferous, L. Tournaisian, Malevka R.S.	Limestone light grey, thin-bedded
441	280	25v	L. Carboniferous, L. Tournaisian, Malevka R.S.	Clay grey
	304–307	30v	L. Carboniferous, L. Tournaisian, Malevka R.S.	Mudstone greenish-grey
Turov-106	207	2b	L. Carboniferous, L. Tournaisian, Malevka R.S.	Clay dark grey
Berzhetsy-475	166	8	L. Carboniferous, L. Tournaisian, Upa R.S.	Clay dark grey

Abbreviations: B., Beds; L., Lower; M., Middle; R.S., Regional Stage; R.SS., Regional Superstage; U., Upper.

Fig. 1. Location of the studied drill core sections (grey circles) in Belarus: 1, Pinsk-26; 2, Turov-5; 3, Berzhetsy-475; 4, 441; 5, Turov-106; 6, Brinev-6; 7, 506; 8, 331; 9, Starobin-239; 10, Glusk-1; 11, 482; 12, Knyshevichi-7; 13, Ostashkovichi-2R; 14, Krasnoselskaya-215; 15, Berdyzh-1; 16, Bykhov-151; 17, Lepel-1; 18, Buda Dalnyaya-35.

Turov-106, 331, 441, 482, 506; the Zhlobin Saddle – Berdyzh-1; Orsha Depression – Bykhov-151; the Belarus Anteclise – Buda Dalnyaya-35, Lepel-1.

MATERIAL AND METHODS

The chondrichthyan microremains are represented by isolated teeth, scales and small fragments of the prismatic cartilage. The remains were micrographed using the scanning electron microscopes Cambridge CamScan-4, Tescan VEGA-II XMU and JEOL JSM–5610 LV. The internal structure of the teeth of the new taxon was studied with a SkyScan 1172 Bruker-microCT (Center for Geo-Environmental Research and Modeling 'GEOMODEL', Research park of St Petersburg State University), and were reconstructed using NRecon, DataViewer, CTAnalyzer softwares.

The described specimens are housed at the Palaeontological Museum of St Petersburg State University (abbreviation PM SPU), in the State Enterprise 'Scientific and Production Center for Geology' (abbreviation SPCG) and in the Department of Geology, Tallinn University of Technology (abbreviation GIT, collection of Elga Mark-Kurik).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order PHOEBODONTIFORMES Ginter, Hairapetian & Klug, 2002
Family PHOEBODONTIDAE Williams in Zangerl, 1981
Genus *Phoebodus* St. John & Worthen, 1875

Phoebodus cf. *typicus* Ginter & Ivanov, 1995
Figure 2A–C

Material. One complete (SPCG 95/16a-1) and two incomplete (SPCG 106/49-3 and 70/4-1) teeth.

Occurrence. Sample 49, depth 2042.2 m, Turov-5 core, Kuzmichi Regional Stage; sample 4, depth 1989.9 m, Knyshevichi-7 core, sample 16a, depth 1347–1351 m, Glusk-1 core, Petrikov Regional Stage, Lower Famennian, Upper Devonian.

Description and remarks. The teeth have a five-cuspid crown with large central and lateral cusps and small intermediate cusps. The cusps bear a weakly developed lateral carina, straight and long striae on the labial side and short and delicate striae on the lingual surface. The tooth base is elongated mesio-distally, with a distinct apical button extended mesio-distally and located centrally. One tooth (Fig. 2B) displays features typical for the species: a subrectangular base with rounded corners and oval apical button. The base of a second tooth (Fig. 2C) is narrow, with a small button. A third tooth (Fig. 2A) possesses a trapezoid-shaped base and oval apical button resembling some teeth of *Phoebodus fastigatus* Ginter & Ivanov and *Phoebodus latus* Ginter & Ivanov (Ginter & Ivanov 1992, 1995). The tooth of *P. typicus*, with a similar trapezoid base but with a small rounded button, has been described from the Famennian of Morocco (Ginter et al. 2002).

Phoebodus turnerae Ginter & Ivanov, 1992
Figure 2D–F

Material. One complete tooth (SPCG 97/1a-1), one incomplete (SPCG 101/10-1) tooth and one tooth fragment (SPCG 101/10-3).

Occurrence. Sample 1a, depth 446.7 m, Brinev-6 core; sample 16a, depth 3176–3184 m, Krasnoselskaya-215 core, Petrikov Regional Stage, Lower Famennian, Upper Devonian.

Description and remarks. The tooth crown includes three main cusps sigmoidally incurved, with a distinct lateral carina. The cusps may be covered by a few cristae on both preserved surfaces. The tooth (Fig. 2F) has one broken intermediate cusp. The tooth base is almost oval or has pentagonal shape with rounded corners. The prominent and round apical button lies close to the lingual rim. The tooth bases of typical teeth of *P. turnerae* are pentagonal with an obtuse angle in the lingual rim (Ginter & Ivanov 1992, 2000; Hairapetian & Ginter 2009) but some teeth described from the Famennian of Armenia (Ginter et al. 2011) and of Iran (Hairapetian & Ginter 2010) possess an oval tooth base.

Phoebodus sp.
Figure 2G

Material. One incomplete tooth (SPCG 99/27-1).
Occurrence. Sample 27, depth 2637–2641 m, Ostashkovichi-2R core; Drozdy Regional Stage, Elets Regional Superstage, Lower Famennian, Upper Devonian.

Description and remarks. The tooth has a tricuspid crown with short cusps. The cusps bear several coarse cristae on the lingual and labial surfaces. The tooth base is oval, elongated mesio-distally, with a short lingual part and wide labio-basal projection. The apical button

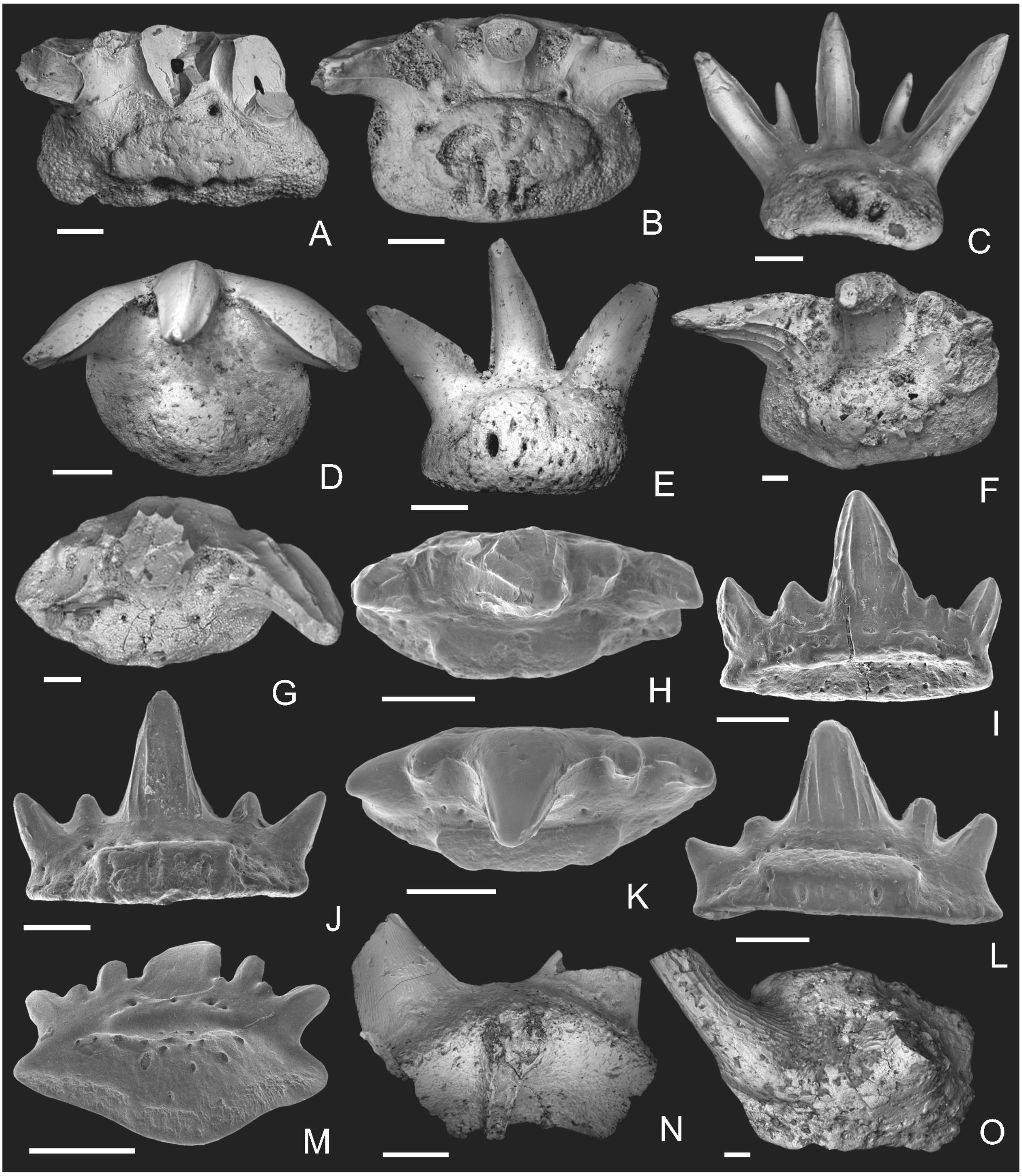
Fig. 2. Teeth of *Phoebodus*, *Cladodoides* and *Karksiodus* from the Devonian and Carboniferous of Belarus. **A–C**, *Phoebodus* cf. *typicus* Ginter & Ivanov, 1995. A, SPCG 106/49-3, occlusal view, Turov-5 core, depth 2042.2 m, sample 49, Lower Famennian, Kuzmichi Regional Stage; B, SPCG 70/4-1, occlusal view, Knyshevichi-7 core, depth 1989.9 m, sample 4, Lower Famennian, Petrikov Regional Stage; C, SPCG 95/16a-1, lingual view, Glusk-1 core, depth 1347–1351 m, sample 16a, Lower Famennian, Petrikov Regional Stage. **D–F**, *Phoebodus turnerae* Ginter & Ivanov, 1992. D, E, SPCG 97/1a-1, occlusal and lingual views, Brinev-6 core, depth 446.7 m, sample 1a, Lower Famennian, Petrikov Regional Stage; F, SPCG 101/10-3, occlusal view, Krasnoselskaya-215 core, depth 3176–3184 m, sample 16a, Lower Famennian, Petrikov Regional Stage. **G**, *Phoebodus* sp., SPCG 99/27-1, occlusal view, Ostashkovichi-2R core, depth 2637–2641 m, sample 27, Lower Famennian, Drozdy Regional Stage. **H–M**, *Cladodoides* cf. *wildungensis* (Jaekel, 1921). H, I, K–M, 331 core, depth 292.2 m, sample 16a, Lower Tournaisian, Malevka Regional Stage; H, I, PM SPU 82-1, occlusal and labial views; K, L, PM SPU 82-3, occlusal and lingual views; M, PM SPU 82-4, oblique basal view; J, PM SPU 82-2, lingual view, 441 core, depth 304–307 m, sample 30v, Lower Tournaisian, Malevka Regional Stage. **N**, **O**, *Karksiodus mirus* Ivanov & Märss, 2011; Lepel-1 core, depth 194 m, sample 19, Eifelian, Kostyukovichi Regional Stage. N, SPCG 47/19-26, oblique basal view; O, SPCG 47/19-26a, occlusal view. Scale bars A–C, F, G, O – 100 µm; D, E, H–N – 500 µm.

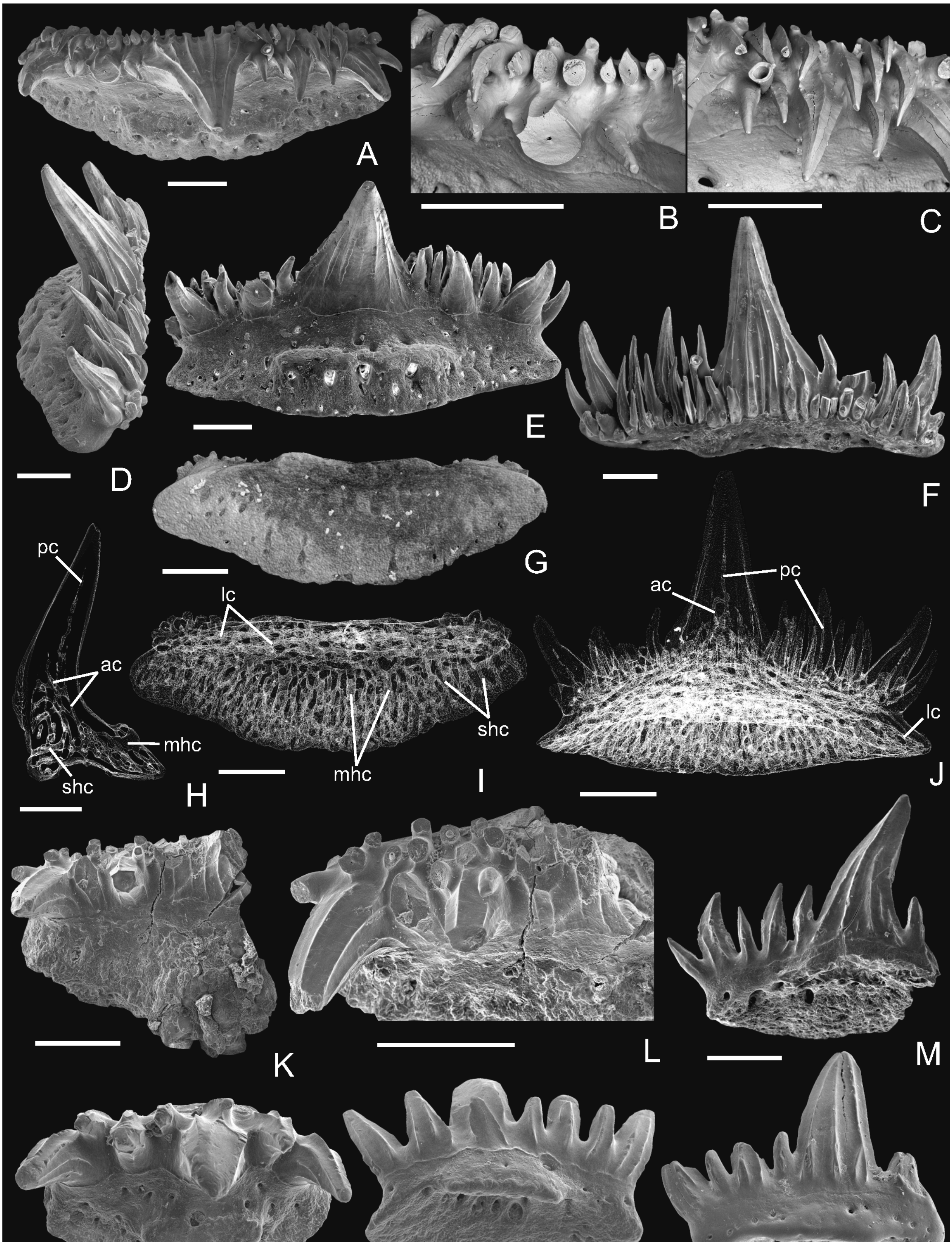
is oval, large and occupies almost the entire occlusal surface. This tooth is similar to the teeth of *Phoebodus* aff. *turnerae* from the Famennian of Iran (Hairapetian & Ginter 2009) in the crown structure with short cusps covered by several coarse cristae. However, the teeth from Iran have a more extended lingual part of the base and the apical button is placed centrally.

Order CTENACANTHIFORMES Glikman, 1964
Family CTENACANTHIDAE Dean, 1909
Genus *Tamiobatis* Eastman, 1897

Tamiobatis elgae Ivanov sp. nov.
Figure 3A–L

Derivation of name. Named in honour of the outstanding palaeoichthyologist, Elga Mark-Kurik.

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Holotype. GIT 783-1, isolated complete tooth (Fig. 3A–J).

Type locality and horizon. Sample 2b, depth 207 m, Turov-106 core, Belarus; Malevka Regional Stage, Lower Tournaisian, Lower Carboniferous.

Material. One complete tooth (holotype) and two incomplete teeth (PM SPU 82-5, 82-29).

Occurrence. Sample 56b, depth 241.6 m, 506 core, Borovoe Regional Stage, Upper Famennian, Upper Devonian; sample 2b, depth 207 m, Turov-106 core, Belarus; Malevka Regional Stage, Lower Tournaisian, Lower Carboniferous.

Diagnosis. Teeth with multicuspid cladodont crown; central cusp twice as high and three times more broad than the lateral and intermediate cusps; pair of high accessory cusplets placed outside the lateral cusps; two rows of numerous high and small accessory cusplets placed labially; intermediate cusps and cusplets differently directed and incurved; labial cristae on the central cusp extended and prominent at the base; sublenticular base very elongated mesio-distally; ridge-like apical button considerably elongated, placed close to the lingual rim; shelf-like wide labio-basal projection; dense network of vascular canals occupying the entire tooth base.

Description. The teeth possess a multicuspid cladodont crown made up of the main central, intermediate and lateral cusps and numerous intermediate and accessory cusplets. The central cusp is triangular, flattened labio-lingually, twice as high and three times as broad at the base as the lateral and largest intermediate cusps. The lateral cusps are slightly flattened labio-lingually, wider than the highest intermediate cusps. Some intermediate cusps reach the heights of the lateral cusps. Two quite high accessory cusplets are placed outside the lateral cusps. The row of numerous rather high accessory cusplets is located labially. Some of those cusplets are more labially displaced than others. The cusplets of that row bear small accessory cusplets or denticles that form a third external row. The accessory cusplets may be situated on the high accessory cusplets, on the main cusps and between them. All cusps and cusplets except the central and lateral ones are round in cross section or slightly flattened mesio-distally. All cusps and cusplets are acuminate, inclined lingually and incurved. Their curvature and direction vary: most of them are incurved to the crown centre, but some cusplets are twisted mesially or distally, or sometimes sigmoidally curved. The ornamentation consisting of distinct cristae is coarser on the labial side of the crown than on the lingual side. The cristae on the labial side are long, slightly incurved, almost reaching the cusp tip and sometimes bifurcating at the base. The cristae on the labial face of the central cusp are considerably extended and prominent at the cusp base. Short cristae are present only on the lingual surface of the main cusps. The lateral carina is well developed on the central and lateral cusps. The boundary between the crown and base is distinct.

The tooth base is sublenticular in outline, very elongated mesio-distally, with a short lingual part, gently curved lingual rim and overhanging, rounded lateral parts. The occlusal surface is slightly convex and the basal one, slightly concave. The apical button is prominent, ridge-like, short and considerably elongated, placed close to the lingual rim. The edge of the button is penetrated by the foramina of the main vascular canals. The labio-basal projection is shelf-like, wide, separated from other basal surface of the base by a longitudinal groove. The projection is of the same width as the button. A shallow labial depression is weakly developed in the labial edge of projection.

The base bears numerous large and small foramina of the vascular canals concentrated on the occlusal surface around the button, on the lateral parts, and in the labial depression and on the basal side. The crown is composed of orthodentine apart from the lower part of the central cusp which consists of trabecular dentine. The vascularization system compounds a very dense network of vascular canals occupying the whole of the tooth base (Fig. 3H–J). This network consists of wide, main and narrow, secondary transverse horizontal canals, their small ramifications and ascending canals rising to the crown. The long longitudinal canals are connected to this network and the pulp canals of the cusps.

Fig. 3. Teeth of *Tamiobatis* from the Devonian and Carboniferous of Belarus. **A–L**, *Tamiobatis elgae* Ivanov sp. nov. A–J, GIT 783-1, holotype; Turov-106 core, depth 207 m, sample 2b, Lower Tournaisian, Malevka Regional Stage. A–L, SEM images; A–C, occlusal (B, C – details of crown), D, oblique lateral, E, lingual, F, labial and G, basal views. H–J, microtomographic images; H, virtual sagittal section of tooth, I, virtual frontal section of tooth base, J, lingual view in transparent mode. **K**, **L**, PM SPU 82-5, occlusal view (L – detail of crown), 506 core, depth 241.6 m, sample 56b, Upper Famennian, Borovoe Regional Stage. **M–P**, *Tamiobatis* sp. M–O, 506 core, depth 241.6 m, sample 56b, Upper Famennian, Borovoe Regional Stage. M, PM SPU 82-6, oblique labial view; N, O, PM SPU 82-7, N, occlusal and O, labio-basal views; P, PM SPU 82-8, oblique labial view, 331 core, depth 276–277 m, sample 12, Lower Tournaisian, Upa Regional Stage. Abbreviations: ac, ascending canal; lc, longitudinal canal; mhc, main horizontal canal; pc, pulp canal; shc, secondary horizontal canal. Scale bars 500 µm, besides M, N – 250 µm.

Remarks. Ginter et al. (2010) correctly remarked that the genus *Tamiobatis* should be revised based on type collections and clarified the validity of the species. However, the teeth of the new species differ from the teeth of all other species of *Tamiobatis* in the greater number of cusplets and the unique morphology of the crown comprising two rows of accessory high cusplets differently directed and incurved. The teeth of *T. vetustus* Eastman and *T. succinctus* St. John & Worthen are most similar to the teeth of the new species but they possess one row of short accessory cusplets and a more developed labial depression (St. John & Worthen 1875; Williams 1998; Ginter et al. 2010). The teeth of the new species resemble some teeth described as *Cladodus thomasi* Turner from the Tournaisian of Australia (Turner 1982; Roelofs et al. 2016) but the latter has one row of accessory cusplets and a base trapezoid in outline, more extended lingually.

Tamiobatis sp.
Figure 3M–P

Material. One complete (PM SPU 82-7) and two incomplete (PM SPU 82-6, 82-8) teeth.

Occurrence. Sample 56b, depth 241.6 m, 506 core, Borovoe Regional Stage, Upper Famennian, Upper Devonian; sample 12, depth 276–277 m, 331 core, Upa Regional Stage, Lower Tournaisian, Lower Carboniferous.

Description and remarks. The teeth have a cladodont crown with large central, moderate lateral and short intermediate cusps. The central cusp is twice as high as the lateral ones but the width varies from twice as wide to almost the same width. The number of intermediate cusps varies from one to three on either side of the tooth crown. The accessory cusplets can be occasionally placed outside the lateral cusps and labially from the main cusps. The intermediate cusps are labially displaced from the central and lateral ones. The cusps and cusplets are inclined lingually, sometimes incurved mesially or distally and covered by coarse long and short cristae. The tooth base is oval in outline, with an oval, prominent apical button and a distinct, rather thick labio-basal projection.

The described teeth are similar to the teeth of *Tamiobatis* sp. from the Tournaisian of China (Ginter & Sun 2007) and to some teeth of *T. wachsmuthi* St. John & Worthen from the Tournaisian of Iowa, USA (St. John & Worthen 1875) but differ from the latter in the oval, more extended lingually base.

Family *incertae sedis*
Genus *Cladodoides* Maisey, 2001

Cladodoides cf. *wildungensis* (Jaekel, 1921)
Figure 2H–M

Material. Four complete (PM SPU 82-1–82-4) and four incomplete (PM SPU 82-30–82-33) teeth.

Occurrence. Sample 16a, depth 292.2 m, 331 core; sample 30v, depth 304–307 m, 441 core, Malevka Regional Stage; sample 13d, depth 278–282 m, 331 core, Upa Regional Stage, Lower Tournaisian, Lower Carboniferous.

Description. The teeth possess a cladodont five-cuspid crown with large triangular central, moderate lateral and small intermediate cusps. The intermediate cusps of some teeth are of the same height as the lateral ones but they are narrower than the latter. One tooth (Fig. 2M) has tiny additional cusplets between the lateral and intermediate cusps. The lingually inclined cusps are oval in cross section and flattened labio-lingually. The lateral cusps diverge mesially or distally from the central axis of the crown. The central cusp bears a weakly developed lateral carina. The labial and lingual faces of the cusps are ornamented with straight, coarse cristae unevenly covering the cusp surface. The middle part of the central cusp is smooth or bears short tiny cristae. The tooth base is trapezoidal in shape, extended mesio-distally, with short lingual and acuminate lateral parts. The occlusal surface of the base is slightly convex, with a very prominent, wide, rectangular apical button. The button occupies most of the occlusal face and is placed at the lingual rim. The labio-basal projection is wide, extended mesio-distally, separated from the rest of the base by a groove containing a row of foramina. The basal surface is concave and bears numerous openings of the vascular canals. One tooth has an acuminate lingual part of the base (Fig. 2M).

Remarks. *Cladodoides wildungensis* (Jaekel) was described from the Upper Frasnian of Bad Wildungen, Germany (Gross 1938). Ginter et al. (2010) described the teeth of that species based on rubber casts of the type material. The preservation of the teeth in the type specimens does not allow detailed comparison with isolated teeth from others regions of the world. Nevertheless, the teeth described here differ from the Wildungen teeth in possessing higher intermediate cusps and the irregular placement of cristae on the cusps.

The genus *Cladodoides* was referred to the order Ctenacanthiformes (Ginter et al. 2010). However, this assignment as well as the family attribution need to be specified.

Cohort EUSELACHII Hay, 1902
Superfamily PROTACRODONTOIDEA Zangerl, 1981
Family PROTACRODONTIDAE Cappetta, Duffin & Zidek, 1993
Genus *Protacrodus* Jaekel, 1925

Protacrodus aequalis Ivanov, 1996
Figure 4A–C

Material. Two almost complete teeth (SPCG 101/10-2 and PM SPU 82-9).

Occurrence. Sample 16a, depth 3176–3184 m, Krasnoselskaya-215 core, Petrikov Regional Stage, Lower Famennian; sample 56b, depth 241.6 m, 506 core, Borovoe Regional Stage, Upper Famennian, Upper Devonian.

Description and remarks. The tooth crown consists of three separate, basally fused cusps. The cusps are round in cross section and bear distinct ridges on the labial and lingual faces. The ridges diverge basally from the cusp tip, and some bifurcate basally. The cusps are equal in size in one tooth (Fig. 4A) but the central and one lateral cusp are higher and wider than the other lateral one in the second tooth (Fig. 4B). The cusps in the second tooth (PM SPU 82-9) are asymmetrically inclined. The

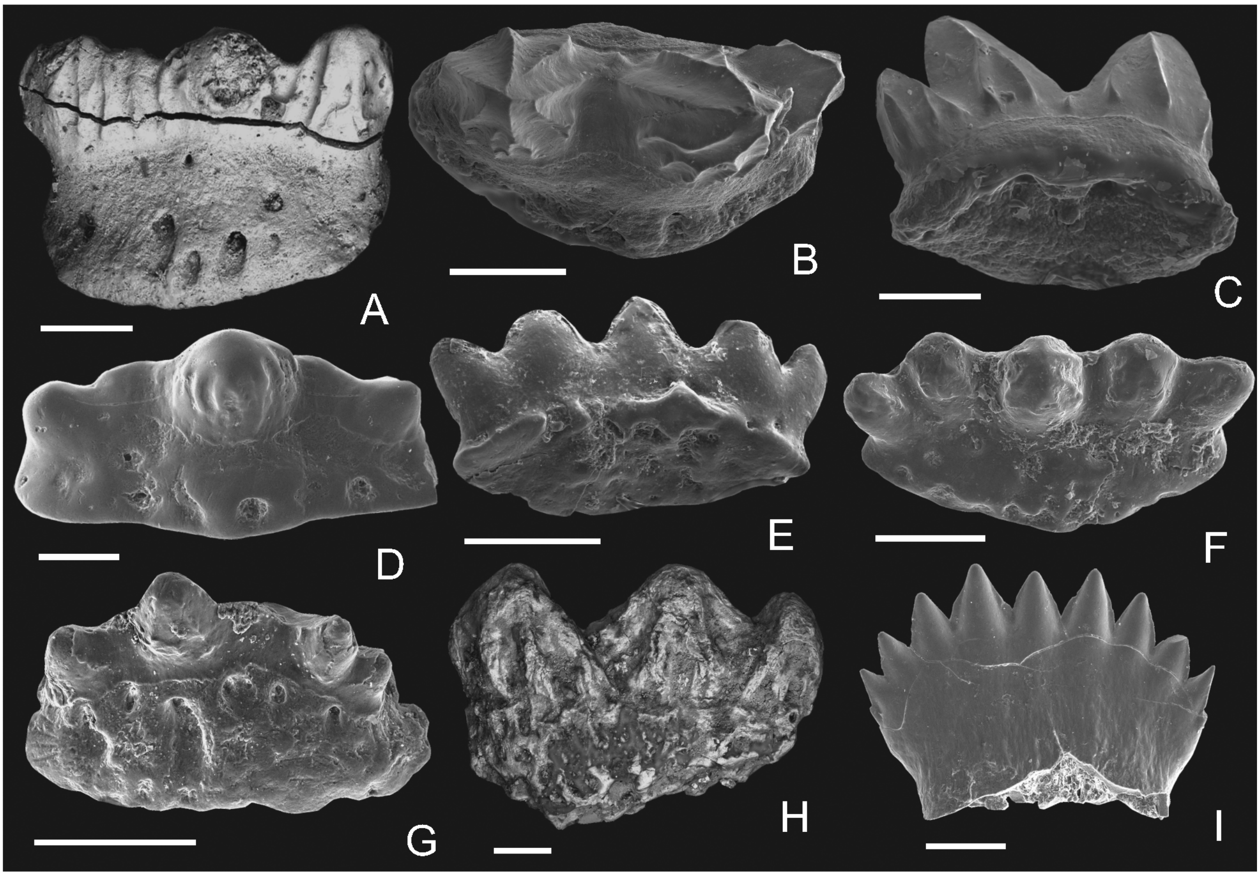


Fig. 4. Teeth of protacrodontids and *Ageleodus* from the Devonian and Carboniferous of Belarus. **A**–**C**, *Protacrodus aequalis* Ivanov, 1996. A, SPCG 101/10-2, lingual view, Krasnoselskaya-215 core, depth 3176–3184 m, sample 16a, Lower Famennian, Petrikov Regional Stage; B, C, PM SPU 82-9, B, occlusal and oblique labial views, 506 core, depth 241.6 m, sample 56b, Upper Famennian, Borovoe Regional Stage. **D**–**F**, *Protacrodus* sp. D, PM SPU 82-10, oblique lingual view, Berzhetsy-475 core, depth 166 m, sample 8, Lower Tournaisian, Upa Regional Stage; E, F, PM SPU 82-11, E, oblique labial and F, occlusal views, 331 core, depth 225–227 m, sample 2, Lower Tournaisian, Cherepet Regional Stage. **G**, **H**, Protacrodontidae indet. G, PM SPU 82-12, oblique lingual view, 441 core, depth 304–307 m, sample 30v, Lower Tournaisian, Malevka Regional Stage; H, SPCG 86/35-1c, labial view, Berdyzh-1 core, depth 230.8 m, sample 35, Givetian, Polotsk Regional Stage. **I**, *Ageleodus* sp., PM SPU 82-13, ?lingual view, 506 core, depth 241.6 m, sample 56b, Upper Famennian, Borovoe Regional Stage. Scale bars 200 µm.

tooth base is subtriangular, elongated mesio-distally, slightly extended lingually, with convex occlusal and concave basal surfaces.

The teeth of *Protacrodus aequalis* include two morphotypes: one with a symmetrical crown and equal cusps, and the other with an asymmetrical, inclined crown and a higher central cusp (Turner 1982; Ivanov 1996; Ivanov & Lucas 2011). However, the described tooth (PM SPU 82-9, Fig. 4B, C) with a considerably short one lateral cusp differs from all known specimens of that species.

Protacrodus sp.
Figure 4D–F

Material. Four complete, slightly abraded teeth (PM SPU 82-10, 82-11, GIT 783-2, 783-3) and two tooth fragments (PM SPU 82-34, 82-35).

Occurrence. Sample 2b, depth 207 m, Turov-106 core, Malevka Regional Stage; sample 8, depth 166 m, Berzhetsy-475 core, Upa Regional Stage; sample 13d, depth 278–282 m, 331 core, Upa Regional Stage; sample 2, depth 225–227 m, 331 core, Cherepet Regional Stage, Lower Tournaisian, Lower Carboniferous.

Description and remarks. The teeth have a pyramidal crown with five cusps. The cusps are fused basally, round in cross section and covered by coarse ridges where preserved. Most of the teeth possess cusps gradually arranged in their height and a semilunar, arched base with a short lingual part. However, one tooth (Fig. 4E, F) has intermediate cusps of the same size as the central one and a subtriangular, rather flat base with a considerably extended lingual part.

Protacrodontidae indet.
Figure 4G, H

Material. Two incomplete, abraded teeth (SPCG 86/35-1c and PM SPU 82-12).

Occurrence. Sample 35, depth 230.8 m, Berdyzh-1 core, Polotsk Regional Stage, Givetian, Middle Devonian; sample 30v, depth 304–307 m, 441 core, Malevka Regional Stage, Lower Tournaisian, Lower Carboniferous.

Description and remarks. The teeth are poorly preserved. The tooth from the Givetian (Fig. 4H) possesses cusps ornamented with coarse ridges divided at the cusp base. The small tooth from the Tournaisian (Fig. 4G) has an asymmetrical pyramidal crown and an arched base. The central cusp is separated from the two others by a wide depression. Probably this tooth is a growing replacement tooth from the tooth family.

Order *et* Family *incertae sedis*
Genus *Karksiodus* Ivanov & Märss, 2011

Karksiodus mirus Ivanov & Märss, 2011
Figure 2N, O

Material. Two incomplete teeth (SPCG 47/19-26, SPCG 47/19-26a).

Occurrence. Sample 19, depth 194 m, Lepel-1 core, Kostyukovichi Regional Stage, Eifelian, Middle Devonian.

Description and remarks. The teeth have a diplodont bicuspid or tricuspid crown and an arched base. The long lateral cusps are divergent mesio-distally, ornamented with numerous delicate, wavy striations on both labial and lingual sides. The tooth base is extended lingually and labio-basally, with convex occlusal and strongly concave basal surfaces and bears the prominent tube of the transversal basal canal. Most known teeth of *Karksiodus* possess a tricuspid crown, but two teeth with four cusps have also been found (Ivanov et al. 2011; Ivanov & Märss 2014). The teeth with a bicuspid crown occur extremely rarely. Besides the described tooth, such a specimen was illustrated by Mark-Kurik & Karatajūtė-Talimaa (2004) from the Givetian of Estonia.

Order *et* Family *incertae sedis*
Genus *Ageleodus* Owen, 1867

Ageleodus sp.
Figure 4I

Material. One incomplete tooth (PM SPU 82-13).

Occurrence. Sample 56b, depth 241.6 m, 506 core, Borovoe Regional Stage, Upper Famennian, Upper Devonian.

Description and remarks. The preserved tooth crown is flattened labio-lingually, bears nine conical, acuminate cusps and two tiny lateral cusplets. These cusps are arranged in a curved line forming a fan-like, zigzag structure. The cusps vary in height; the higher cusps are located on both sides of the central cusp. The crown is wider in the cuspid part and narrower towards the crown–base boundary. This tooth is very similar to some teeth of *Ageleodus pectinatus* (Agassiz) described from the Upper Famennian of Pennsylvania, USA (Downs & Daeschler 2001) and of *Ageleodus* sp. from the Tournaisian of the Tula Region, Russia (Lebedev 1996).

Chondrichthyan scales

A very diverse suite of chondrichthyan scales has been recovered from the Devonian and Carboniferous of Belarus. The scales resembling the scales of *Karksilepis parva* Märss were found in the Kostyukovichi Regional Stage (Eifelian) of the Lepel-1 core and the Vitebsk Regional Stage (Emsian) of the Buda Dalnyaya-35 core. These scales have a polyodontode crown consisting of elongated, acuminate odontodes of round cross section (Fig. 5A, B). The odontodes are separated from each other and bear fine striations on the lateral surfaces. The base is polygonal in outline, with a flat basal surface.

The scales of *Lugalepis* sp. collected from the Eifelian Gorodok Regional Stage of the Bykhov-151 core and the Givetian Polotsk Regional Stage of the Lepel-1 core, possess a crown with a compound odontocomplex. The elongated, spine-like odontodes bear a longitudinal groove in the middle part and striations on the extended part (Fig. 5C–E). The odontodes vary in size, and may overlap each other and merge laterally.

The scales of *Ohiolepis* type are recorded in the Malevka and Upa regional stages (Tournaisian) from the Berzhetsy-475 and 441 cores. They are polyodontodia with numerous narrow, spiniform odontodes compactly placed in the crown and sometimes diverging from the centre (Fig. 5F, G).

The scale of type A, occurring in the Eifelian Kostyukovichi Regional Stage of the Pinsk-26 core, has a rhomboid, flat crown and a small base (Fig. 5H). The distict ridges diverge apically from the base.

The scales of type B, found in the Drozdy (Famennian), Malevka and Upa (Tournaisian) regional stages of several cores, possess an inclined, acuminate crown with prominent ridges on the external surface, a narrow neck and a small, flat base (Fig. 5I, J). The crown consists of two or three partly merged odontodes.

The scales of protacrodontid type have a subrhomboid shape, a low, monolithic crown, a weakly developed neck and a convex, large base (Fig. 5K, L). The crown is formed by compactly placed odontodes surrounding each other, ranging from small central to elongated lateral ones. The odontodes may be fused either partially or completely. Such scales were found in the Drozdy and Petrikov regional stages (Lower Famennian) of the Knyshevichi-7 and Starobin-239 cores.

The tessera-like scales of type C from the Malevka and Upa regional stages of the 331 and Berzhetsy-475 cores have a low, compact crown consisting of odotodes–tubercles of different sizes and shapes (Fig. 5M, N). The odotodes bear the ridges diverging from the tubercle tip. The scale base is slightly convex.

Scales of ctenacanthid type are numerous and occur in the Turov, Borovoe, Petrikov (all Famennian), Malevka and Upa (Tournaisian) regional stages of several cores. These scales possess a polyodontode crown backwardly curved and include triangular central long and narrow lateral odontodes (Fig. 5O–R) which are closely spaced in a subparallel arrangement, separated by narrow and deep grooves. The scale base is rhomboid or round in outline, with a concave basal surface. The crown may be asymmetrical with an enlarged lateral part (Fig. 5P).

The hybodontid type scales from the Malevka and Upa regional stages of the 441 and Berzhetsy-475 cores have a cone-shaped, apically elongated crown with denticulate ridges separated by longitudinal grooves (Fig. 5S). The neck is quite well developed. The base is round or rhomboid, wider than the crown, flat on the basal side.

The diverse scales of euselachian type were found in the Starobin, Borovoe and Upa regional stages of the 441, 482 and 506 cores. These placoid scales have a drop-like, inclined, elongate crown, well-developed neck and small base with concave basal surface (Fig. 5T–W). The smooth crown in the anterior part bears the median ridge separated by grooves on both sides. The base possesses lateral and posterior projections of different length, sometimes accentuated by superficial ridges (Fig 5V).

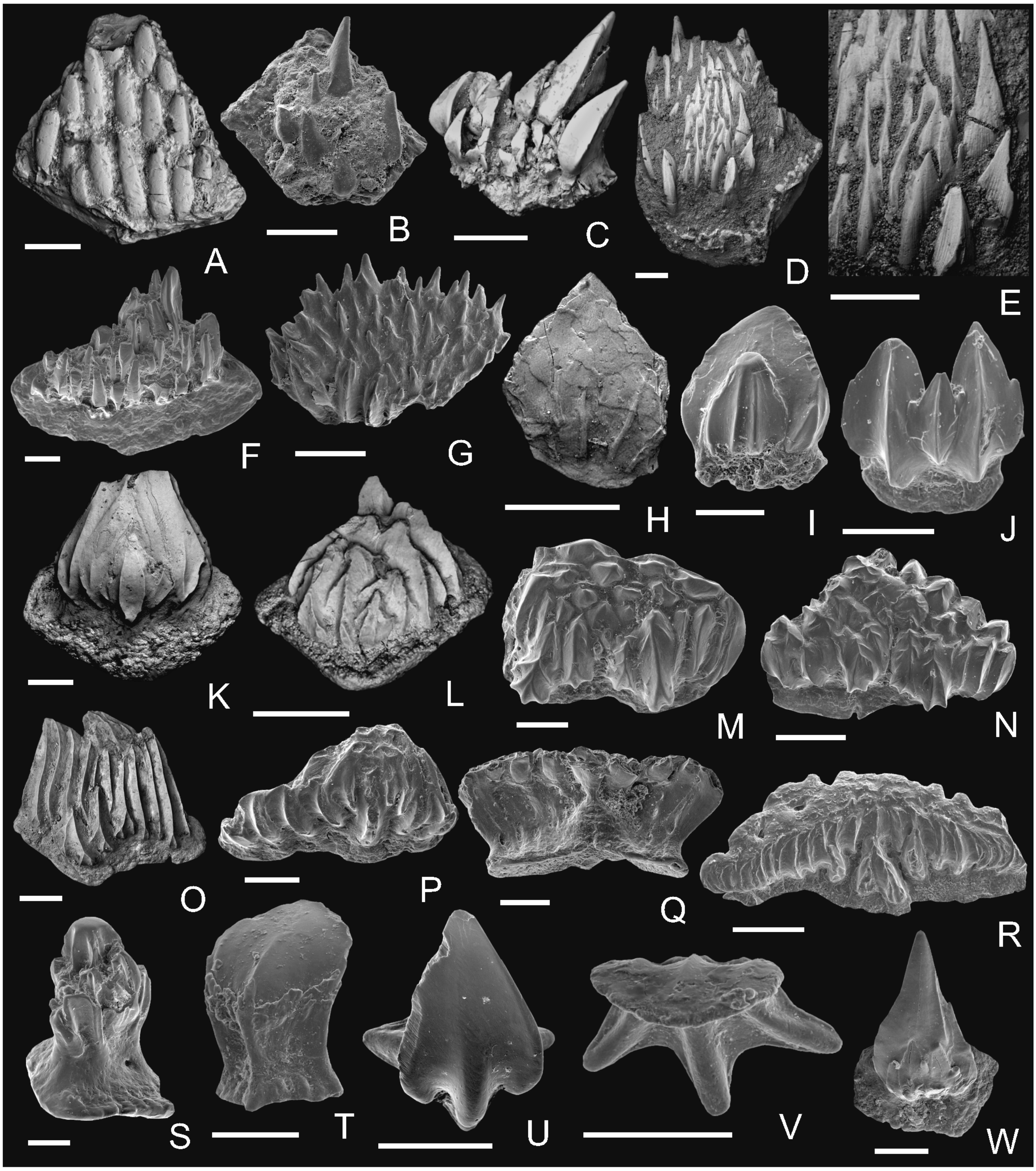
RESULTS

Assemblages of various chondrichthyans have been found in the Devonian–Lower Carboniferous of Belarus (Figs 6, 7). The only scales of *Karksilepis* cf. *parva* Märss were recorded in the Emsian Vitebsk Regional Stage. The Middle Devonian assemblages are more diverse. The Eifelian assemblage from the Gorodok and Kostyukovichi regional stages contains the teeth of *Karksiodus mirus* Ivanov & Märss, scales of *K.* cf. *parva*, *Lugalepis* sp. and type A. The Givetian chondrichthyans are rare and include protacrodontid teeth and *Lugalepis* scales.

Varied assemblages occur in the Lower and Upper Famennian. The tooth of *Phoebodus* cf. *typicus* Ginter & Ivanov and ctenacanthid type scales were found respectively in the Kuzmichi and Turov regional stages. The diverse assemblage from the Drozdy and Petrikov regional stages contains the teeth of *Phoebodus turnerae* Ginter & Ivanov, *P.* cf. *typicus*, *Phoebodus* sp. and *Protacrodus aequalis* Ivanov; scales of protacrodontid and ctenacanthid types and type B. The assemblage including the teeth of *Tamiobatis elgae* Ivanov sp. nov., *Protacrodus aequalis*, *Ageleodus* sp., scales of ctenacanthid and euselachian types are reported from the Borovoe Regional Stage.

The most diverse assemblage occurs in the Malevka and Upa regional stages (Lower Tournaisian, Lower Carboniferous). It contains the teeth of *Tamiobatis elgae*, *Tamiobatis* sp., *Cladodoides* cf. *wildungensis* (Jaekel), *Protacrodus* sp. and various scales (Fig. 7).

Most of the taxa occurring in Belarus are widely distributed in different regions of the world. *Phoebodus typicus* is known from the Lower Famennian of the Kuznets Basin (Russia); the Lower–Middle Famennian of Queensland (Australia), the South Urals (Russia), Morocco and Iran (Ginter et al. 2010; Ivanov & Rodina 2010). *Phoebodus turnerae* occurs in the Lower Famennian of Armenia and the Kuznets Basin (Russia); the Lower–Middle Famennian of the South Urals (Russia), Poland, Iran and Alaska (USA) (Ginter et al. 2010, 2011; Ivanov & Rodina 2010).



Global stage	Regional stage, Beds		Chondrichthyans
Givetian	Ubort		
Givetian	Polotsk	Moroch	
Givetian	Polotsk	Stolin	Protacrodontidae indet.
Givetian	Polotsk	Goryn	*Lugalepis* sp.
Eifelian	Kostyukovichi		*Karksiodus mirus, Karksilepis* cf. *parva*; type A scale
Eifelian	Gorodok		*Lugalepis* sp.
Eifelian	Osveya		
Eifelian	Adrov		
Emsian	Vitebsk	Lepel	*Karksilepis* cf. *parva*
Emsian	Vitebsk	Obol	
Emsian			

Fig. 6. Distribution of chondrichthyans in the Lower and Middle Devonian of Belarus (stratigraphic chart after Kruchek et al. 2010).

Tamiobatis has been found in the Upper Famennian of Ohio (USA); the Tournaisian of Iowa (USA), China and Iran (St. John & Worthen 1875; Williams 1998; Ginter & Sun 2007; Ginter et al. 2010). *Cladodoides wildungensis* is recorded in the Upper Frasnian of Germany (Gross 1938) and China (Xia 1997); the Upper Frasnian–Middle Famennian of Poland (Moravia), Morocco, Iran, the South Urals and Kuznets Basin (Russia) (Ginter et al. 2010; Hairapetian & Ginter 2010; Ivanov & Rodina 2010); the Lower Famennian of France and Armenia (Riemann et al. 2002; Ginter et al. 2011); the Lower Famennian and Tournaisian of Western Australia (Roelofs et al. 2015, 2016). *Protacrodus aequalis* was reported from the Famennian of Queensland and the Tournaisian of Western Australia; the Early Famennian–Viséan of the Kuznetsk Basin, the South Urals and Timan-Pechora Province (Russia); the Early Famennian of Arctic Canada; the Middle Famennian of Latvia; the Tournaisian of Belgium (Ivanov & Lucas 2011; Roelofs et al. 2016).

The teeth of *Ageleodus* are known from the Upper Famennian of Pennsylvania (USA); the Tournaisian of the Tula Region (Russia); the Tournaisian–Viséan of Queensland and Victoria (Australia); the Viséan of

Fig. 5. Chondrichthyan scales from the Devonian and Carboniferous of Belarus. **A, B, D–G, K–P, R, U, W**, crown views; **C**, oblique lateral, **H–J, S, T,** anterior, **Q**, posterior and **V**, oblique posterior views. **A**, **B**, *Karksilepis* cf. *parva* Märss, 2008. A, SPCG 47/19-50t, Lepel-1 core, depth 194 m, sample 19, Eifelian, Kostyukovichi Regional Stage; B, PM SPU 82-14, Buda Dalnyaya-35 core, depth 231.7 m, sample 6, Upper Emsian, Vitebsk Regional Stage. **C**–**E**, *Lugalepis* sp. C, SPCG 47/3-3, Lepel-1 core, depth 175.4 m, sample 3; Givetian, Polotsk Regional Stage; D, E, SPCG 9/3a-1, Bykhov-151 core, depth 141.3 m, sample 3a, Eifelian, Gorodok Regional Stage. **F**, **G**, *Ohiolepis* type. F, PM SPU 82-15, Berzhetsy-475 core, depth 166 m, sample 8, Lower Tournaisian, Upa Regional Stage; G, PM SPU 82-16, 441 core, depth 280 m, sample 25v, Lower Tournaisian, Malevka Regional Stage. **H**, type A, SPCG 41/6b-1, Pinsk-26 core, depth 415.7 m, sample 6b, Eifelian, Kostyukovichi Regional Stage. **I**, **J**, type B. I, PM SPU 82-17, 331 core, depth 292.2 m, sample 16a, Lower Tournaisian, Malevka Regional Stage; J, PM SPU 82-18, 331 core, depth 278–282 m, sample 13d, Lower Tournaisian, Upa Regional Stage. **K**, **L**, protacrodontid type. K, SPCG 70/10-1, Knyshevichi-7 core, depth 2060.3 m, sample 10, Lower Famennian, Drozdy Regional Stage; L, SPCG 96/37a-2, Starobin-239 core, depth 1043.8–1047.6 m, sample 37a, Lower Famennian, Petrikov Regional Stage. **M**, **N**, Type C. M, PM SPU 82-19, 331 core, depth 292.2 m, sample 16a, Lower Tournaisian, Malevka Regional Stage; N, PM SPU 82-20, Berzhetsy-475 core, depth 166 m, sample 8, Lower Tournaisian, Upa Regional Stage. **O**–**R**, ctenacanthid type. O, SPCG 97/1a-4, Brinev-6 core, depth 446.7 m, sample 1a, Lower Famennian, Petrikov Regional Stage; P, PM SPU 82-21, 506 core, depth 241.6 m, sample 56b, Upper Famennian, Borovoe Regional Stage; Q, PM SPU 82-22, 441 core, depth 304–307 m, sample 30v, Lower Tournaisian, Malevka Regional Stage; R, PM SPU 82-23, same core and age. **S**, hybodontid type, PM SPU 82-24, Berzhetsy-475 core, depth 166 m, sample 8, Lower Tournaisian, Upa Regional Stage. **T**–**W**, euselachian type. T, PM SPU 82-25, 482 core, depth 423 m, Upper Famennian, possibly Starobin Regional Stage; U, PM SPU 82-26, same core and age; V, PM SPU 82-27, same core and age; W, PM SPU 82-28, 506 core, depth 241.6 m, sample 56b, Upper Famennian, Borovoe Regional Stage. Scale bars A, C–M, O–T, V, W – 200 μm; B, N, U – 500 μm.

Global stage	Regional stage	Chondrichthyans
Tournaisian	Kizel	*Protacrodus* sp.
	Cherepet	*Tamiobatis* sp., *Cladodoides* cf. *wildungensis*, *Protacrodus* sp.; ctenacanthid, hybodontid, euselachian, *Ohiolepis,* B and C type scales
	Upa	
	Malevka	*Tamiobatis elgae*, *Cladodoides* cf. *wildungensis*, *Protacrodus* sp., Protacrodontidae indet.; ctenacanthid, hybodontid, *Ohiolepis,* B and C type scales
Famennian	Kalinovo	
	Borovoe	*Tamiobatis elgae*, *Tamiobatis* sp., *Protacrodus aequalis, Ageleodus* sp.; ctenacanthid and euselachian type scales
	Stviga	
	Starobin	Euselachian type scales
	Streshin	
	Oressa	
	Lebedyan	*Phoebodus turnerae*, *Phoebodus* cf. *typicus*, *Protacrodus aequalis*; ctenacanthid and protacrodontid type scales
	Petrikov	
	Drozdy	*Phoebodus* sp.; protacrodontid type scales, type B scale
	Turov	Ctenacanthid type scales
	Visha	
	Tremlya	
	Tonezh	
	Kuzmichi	*Phoebodus* cf. *typicus*
	Domanovichi	

Fig. 7. Distribution of chondrichthyans in the Upper Devonan (Famennian) and Lower Carboniferous (Tournaisian) of Belarus (stratigraphic chart after Kruchek et al. 2010).

Scotland; the Pennsylvanian of Montana, Nevada, Ohio (USA), Nova Scotia (Canada), England, Netherlands, Belgium (Lebedev 1996; Down & Daeschler 2001; Garvey & Turner 2006; Ginter et al. 2010).

Karksiodus mirus has been found in the Givetian Aruküla and Burtnieki regional stages of Estonia and Leningrad Region, Russia (Ivanov & Märss 2014). The scales of *Karksilepis parva* Märss occur in the Givetian Aruküla and Burtnieki regional stages of Estonia and Leningrad Region, Russia (Märss et al. 2008; Ivanov & Märss 2014); the scales of *Lugalepis* – in the Ķemeri Regional Stage (Lower Devonian) of Latvia, the Eifelian Narva Regional Stage of Belarus, Lithuania, Latvia and Leningrad Region, Russia (Karatajūtė-Talimaa 1997).

Thus, the chondrichthyans are taxonomically diverse in the Devonian–Lower Carboniferous of Belarus. Most of the taxa were first reported in that territory.

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Klassi Chondrichthyes esindajate levikust Valgevene Devonis ja Alam-Karbonis

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Valgevene Devonit ja Alam-Karboni kivimeid avanud 18 puursüdamikus leiti mitmel stratigraafilisel tasandil mitmekesine fossiilsete kõhrkalade kooslus. Enamik määratud taksoneid olid sellel territooriumil esmaleiud. Kirjeldati uus ctenacanthiformne haikala liik *Tamiobatis elgae*. Selle liigi hammaste siseehitus rekonstrueeriti esmakordselt mikrotomograafi abil. Artiklis on selgitatud uuritud kõhrkalade levikut globaalselt.