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New data on *Karksiodus* (Chondrichthyes) from the Main Devonian Field (East European Platform)

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Abstract. New teeth belonging to *Karksiodus mirus* Ivanov & Märss (Chondrichthyes) were found together with putative chondrichthyan scales in five new localities of the Leningrad Region, northwestern Russia, within the Aruküla and Burtnieki regional stages, Givetian, Middle Devonian. The teeth exhibit variability in the number of cusps, angles between the lateral cusps, base curvature, length of lateral parts and the prominence of the wall of the transversal basal canal. *Karksiodus* tooth material collected from these sites suggests that this taxon possesses an heterodont dentition and a specific, complex vascularization system affecting the dental base and the crown. Enameloid tissue seems to be absent, thus the surface striations on the cusps are presumably made up by orthodentine. The fish fauna from these localities is listed.

Key words: *Karksiodus*, Chondrichthyes, Aruküla Regional Stage, Burtnieki Regional Stage, Givetian, Middle Devonian, Leningrad Region, Estonia.

INTRODUCTION

Chondrichthyan remains are very rare in the Devonian shallow-water deposits of the northwestern region of the East European Platform, on the territory called the Main Devonian Field (Borisyak 1922). This territory with the large exposure area of Devonian deposits includes parts of Estonia, Latvia and Lithuania and the northern region of Belarus (the western part of the Main Devonian Field), as well as the northwest of Russia: Leningrad, Pskov, Novgorod and Vologda regions (the eastern part of the Main Devonian Field). Scarce chondrichthyan scales have been reported from the Middle Devonian Narova (= Narva) and Burtnieki regional stages of Estonia and northwestern Russia (Karatajūtė-Talimaa 1997; Märss et al. 2008). A few chondrichthyan teeth are also known from the Middle (Aruküla and Burtnieki regional stages) and Late Devonian (Kursa and Mūri regional stages) of Latvia, Estonia and northwestern Russia (Ivanov & Lukševičs 1994; Mark-Kurik & Karatajūtė-Talimaa 2004; Ivanov et al. 2011). *Karksiodus mirus* Ivanov & Märss, 2011 (in Ivanov et al. 2011) is so far the best-known, dentition-based chondrichthyan taxon from the Main Devonian Field. The five teeth ascribed to this species have been recorded in the Givetian Aruküla deposits of the Aruküla cave (Mark-Kurik & Karatajūtė-Talimaa 2004) and Burtnieki deposits of the Karksi outcrop, Estonia (Ivanov et al. 2011). The additional teeth from the Karksi outcrop and the new specimens from the Givetian of the localities from the Leningrad Region, Russia, are described in this paper.

MATERIAL AND METHODS

The teeth of *Karksiodus* collected to date are usually incomplete, with broken cusps and bases, exposing the walls of the transverse basal vascular canal; they also often show abraded surfaces. However, some teeth bear well-preserved striations on the cusps.

Most of the sandstone layers containing chondrichthyan remains were very weakly cemented and did not require acid preparation. Samples of the sandstone were fractioned and sieved. Vertebrate microremains were then manually picked under an optical microscope. Acetic acid was utilized to recover vertebrate microremains from the samples of dense, carbonate-cemented sandstone from the Kemka locality. The tooth microstructure was examined in thin section; the images were photographed at the different stages of polishing using the optical microscope Nikon ECLIPSE 50i and digital camera Nikon DS-Fi1. One tooth cusp was polished and etched for 10 sec in 5% HCl. The microremains were micrographed using the scanning electron microscopes Cambridge CamScan-4, Tescan VEGA-II XMU and Zeiss EVO MA15.

The described specimens are housed at the Paleontological Museum of St. Petersburg State University (collection number PM SPU 70) and in the Institute of Geology at Tallinn University of Technology (collection number GIT 383 with specimen numbers 47–49).

LOCALITY DATA

The new teeth of *Karksiodus mirus* Ivanov & Märss were found in five distinct localities within the Leningrad Region, northwestern Russia (Fig. 1): Lemovzha (Volosovo District), Siverskij, Zaitsevo and Novinka (Gatchina District) and Kemka (Luga District).

Lemovzha locality

The outcrop is located on the right bank of the Lemovzha River (right tributary of the Luga River), 4.5 km upstream from the river mouth and 2.5 km from Khotnezha village (Fig. 1B). The Middle Devonian beds are well exposed in a cliff about 20 m high and 40 m long. The section includes the deposits of the Narova (Narva) Regional Stage in the lower part of the outcrop

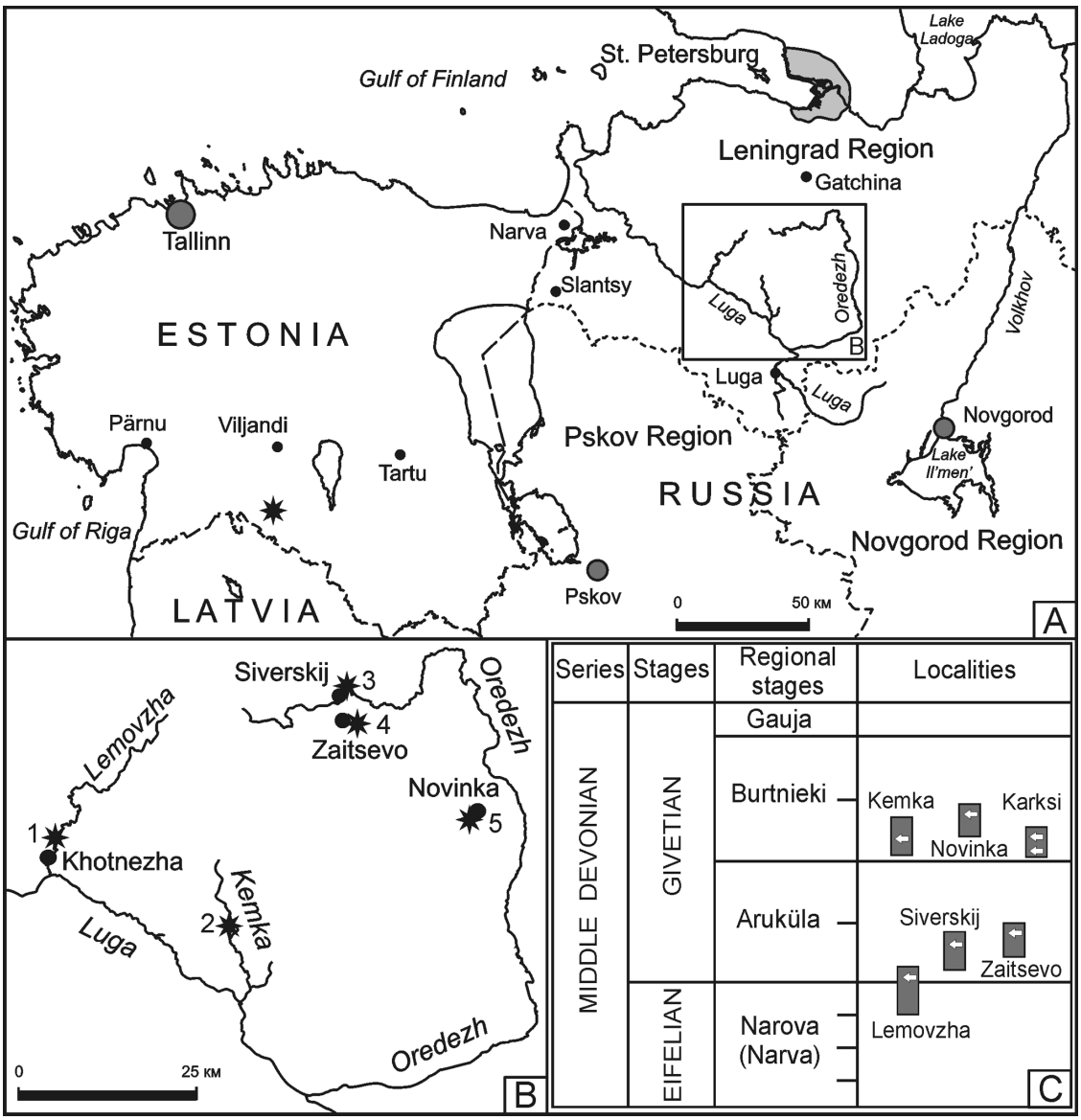

Fig. 1. A, **B**, location of the studied outcrops; the Karksi outcrop is shown by an asterisk in A; outcrops (localities) in the Leningrad Region are shown by asterisks in B: 1, Lemovzha; 2, Kemka; 3, Siverskij; 4, Zaitsevo; 5, Novinka. **C**, Stratigraphical interval of the studied outcrops (shown by grey rectangles) and levels of collected specimens (shown by a white arrow).

and the Aruküla Regional Stage (lower part of the Luga Regional Beds) in the upper part. The Narova deposits of the Lemovzha and Khotnezha members are represented by brownish or dappled marls with brownish-grey sandstones, bluish-grey siltstone and clay interlayers. Some marl levels downstream along the Lemovzha River contain well-preserved remains of agnathans and fishes (Ivanov & Lebedev 2011; Skutschas et al. 2011; Ivanov et al. 2012). The vertebrate assemblage occurring there includes the psammosteids *Schizosteus splendens* (Eichwald) and *S. striatus* (Gross); the placoderms *Holonema* sp., *Homostius* sp. and *Byssacanthus dilatatus* (Eichwald); the acanthodians *Archaeacanthus* sp., *Cheiracanthus longicostatus* Gross, *C. brevicostatus* Gross, *Diplacanthus*? sp., *Haplacanthus* sp., *Markacanthus costulatus* Valiukevičius, *Ptychodictyon* sp. and *P. distinctum* Valiukevičius; and the sarcopterygians *Glyptolepis*? *quadrata* Eichwald, Struniiformes indet., *Dipterus arenaceus* Eichwald, cf. *Gyroptychius* sp., *Thursius* sp. and Osteolepiformes indet. (Valiukevičius 1985; Ivanov et al. 2012, with additional data herein).

The deposits of the Aruküla Regional Stage are represented by brownish- and yellowish-grey, fine- to coarse-grained, cross-bedded sandstones with clay balls, lenses and interlayers. The sandstones are moderately cemented with weakly cemented interlayers. The Aruküla vertebrate assemblage known from the surroundings of Khotnezha village contains remains of the psammosteids *Pycnosteus palaeformis* Preobrazhensky, *P. pauli* Mark and *Schizosteus striatus*; the placoderms *Homostius* sp., *Actinolepis tuberculata* Agassiz, *Dickosteus* sp. and *Asterolepis estonica* Gross; the acanthodians *Archaeacanthus quadrisulcatus* Kade, *Haplacanthus marginalis* Agassiz, *Homacanthus gracilis* (Eichwald), *Diplacanthus carinatus* Gross, *D. gravis* Valiukevičius, *Diplacanthus* sp., *Markacanthus costulatus* Valiukevičius, *M. alius* Valiukevičius, *Minioracanthus laevis* Valiukevičius, *Cheiracanthus brevicostatus* Gross, *C. longicostatus* Gross, *C. talimae* Valiukevičius and *Ptychodictyon* sp.; and the sarcopterygians *Glyptolepis* sp., *Dipterus radiatus* (Eichwald) and Osteolepididae indet. (Valiukevičius 1985; Ivanov & Lebedev 2011, with additional data herein). The psammosteids and sarcopterygians are predominant among the vertebrate macroremains.

The precise position of the boundary between the Narova and Aruküla regional stages has not been determined in the Lemovzha section. The tooth of *Karksiodus mirus* Ivanov & Märss was found in the layer of brownish-grey, weakly cemented, fine- to medium-grained, cross-bedded sandstones, 1.5 m above the marls and sandstones boundary. This layer contains remains of the psammosteids *Schizosteus splendens*, *S. striatus* and *Pycnosteus pauli* (V. Glinskiy, pers. comm. 2013); the placoderms *Asterolepis* sp. and Coccosteidae indet.; the acanthodians *Cheiracanthus brevicostatus*, *Diplacanthus gravis*, '*Acanthodes*' sp., *Homacanthus* sp. and *Rhadinacanthus* sp.; and the sarcopterygians *Glyptolepis* sp. and Osteolepididae indet. The psammosteid taxa *S. striatus* and *P. pauli* occur in the Narova and Aruküla regional stages. However, *S. splendens* is only found within the Narova Regional Stage (Mark-Kurik 2000). On the other hand, the acanthodian species *Diplacanthus gravis* is only known to occur in the Aruküla Regional Stage (Mark-Kurik 2000; Valiukevičius 2000). For this reason, it is likely that the lower sandstone layer containing the *Karksiodus* tooth is of Aruküla age. Numerous and diverse acanthodian scales are also concentrated within this layer, as well as scales of *Karksilepis parva* Märss. The scale surface has four elongated odontodes that point sharply towards the posterior margin of the scale and a rhomboid, flat base (Fig. 2L). The slightly flattened, horizontally directed odontodes have a smooth surface, but their basal part bears fine striations (Fig. 2L, sc), as typical of *Karksilepis* (Märss et al. 2008). The central and largest of the odontodes extends across the entire base of the scale and projects beyond the posterior edge of the scale. Two small lateral odontodes are distributed in a row on either side of the central odontode and partly overlap.

Apart from the Karksi outcrop, the Lemovzha outcrop is the second locality where the teeth of *Karksiodus* and scale of *Karksilepis* occur jointly.

Fig. 2. Chondrichthyan remains from the Givetian of the Leningrad Region. **A**–**K**, teeth of *Karksiodus mirus* Ivanov & Märss, 2011. **A**, **B**, PM SPU 70-1, Siverskij locality; Aruküla Regional Stage; A, lingual and B, labial views. **C**, **D**, PM SPU 70-2, Lemovzha locality; Aruküla Regional Stage; C, lateral and D, oblique lingual views. **E**, PM SPU 70-3, Kemka locality; Burtnieki Regional Stage; oblique basal view. **F**, PM SPU 70-4, Novinka locality; Burtnieki Regional Stage; occlusal view. **G**–**I**, PM SPU 70-5, Zaitsevo locality; Aruküla Regional Stage; G, oblique basal and H, occlusal views, I, detail of a broken lateral cusp showing the vascular canals in the bottom of pulp cavity. **J**, **K**, PM SPU 70-6, Siverskaya locality; Aruküla Regional Stage; J, occlusal and K, oblique lingual views. **L**, *Karksilepis parva* Märss, 2008; PM SPU 70-7; scale in oblique crown view; Lemovzha locality; Aruküla Regional Stage. Scale bars for all figures equal 200 μm except I, which is 100 μm.

Abbreviations: ant., anterior; cc, central cusp; dt, dentine tubules; ic, intermediate cusp; lvc, large vascular canal opening; od., odontode; sc, sculptured field on the odontodes; str., striation on tooth; tbc, transverse basal vascular canal.


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Siverskij locality

The locality is situated on the right bank of the Oredezh River, in Siverskij village, near Siverskaya railway station, at the dam of a former hydroelectric power station (Fig. 1B). The outcrop is about 10 m high and 60 m long, one of a series of outcrops in the valley of the Oredezh River from Siverskaya to Belogorka villages (Ivanov et al. 2005). The deposits of the outcrops belong to the lower part of the Aruküla Regional Stage and are represented by striped yellow, brown and orange, fine- to medium-grained, poorly cemented to dense, micaceous-quartz sandstones with conglomerate intercalation. The sandstones contain clay balls, up to 8 cm in diameter, which form the interlayer in the upper part of the outcrop. Cross-stratifications dominate the section, while planar and wedge-shaped stratifications are rare. Three long lentiform conglomerate interlayers are exposed in the middle part of the section. They are variegated, with dominant yellowish and brownish colours, and contain siltstone balls and silty clay, quartz gravel and coarse sand. The interlayer boundaries are wavy and sharp. These conglomerate interlayers, as well as some levels of sandstones, contain the vertebrate remains in different states of preservation.

The vertebrates are mainly represented by isolated skeletal elements and their fragments, but well-preserved tiny remains are also common. The almost complete skeleton of the placoderm *Heterostius ingens* Asmuss is found at the same level in the Aruküla deposits near Belogorka village (Ivanov et al. 2005). The vertebrate assemblage of this locality belongs to the *Pycnosteus palaeformis* psammosteid Zone. It includes the psammosteid agnathans *Pycnosteus palaeformis* Preobrazhensky, *Schizosteus* cf. *S. asatkini* Obruchev, *S. striatus* (Gross), *Tartuosteus giganteus* (Gross) and *Psammolepis proia* Mark-Kurik; the placoderms *Actinolepis tuberculata* Agassiz, *Heterostius ingens* Asmuss, *Homostius latus* Asmuss, Coccosteidae, *Asterolepis* sp. and *Byssacanthus* sp.; the acanthodians *Haplacanthus* sp., *Cheiracanthus* cf. *C. brevicostatus* Gross, *Diplacanthus* sp., '*Acanthodes*' sp. and *Homacanthus* sp.; and the sarcopterygians *Glyptolepis* sp., *Dipterus radiatus* (Eichwald), *Gyroptychius pauli* Vorobyeva and *Thursius* sp. (Ivanov et al. 2005, 2012; Glinskiy 2012). Psammosteids, placoderms and sarcopterygians dominate in this vertebrate assemblage. The teeth of *Karksiodus mirus* Ivanov & Märss were found at two levels: one tooth in the sandstone layer between two conglomerate interlayers, the other in the sandstone layer above the upper conglomerate interlayer.

Zaitsevo locality

The Zaitsevo quarry is located 700 m east of Zaitsevo village, 1.2 km east of Stroganovo railway station, Gatchina District (Fig. 1B). The deposits of the Aruküla Regional Stage are represented here by brownish, pink-grey and yellow-grey, fine- to medium-grained, commonly weakly cemented to rarely dense, micaceous-quartz sandstones with interlayers and a lens of yellowish-grey clays and siltstones, with silty clay balls, up to 12 cm in diameter. Cross-stratifications are dominant through the section, while planar stratifications with concentration of oriented clay balls are rare. The densely cemented sandstones in the upper part of the section have a thin laminar structure and contain trace fossils.

The vertebrate remains are commonly represented by isolated skeletal elements and their fragments. The assemblage comprises the psammosteids *Pycnosteus palaeformis* Preobrazhensky, *Tartuosteus giganteus* (Gross) and *Psammolepis proia* Mark-Kurik (Glinskiy 2012); the placoderms *Actinolepis tuberculata* Agassiz, *Heterostius ingens* Asmuss, *Homostius latus* Asmuss, Coccosteidae, *Asterolepis* sp. and *Byssacanthus* sp.; the acanthodians *Haplacanthus* sp. and *Homacanthus* sp.; and the sarcopterygians *Glyptolepis* sp., Holoptychiidae and *Gyroptychius pauli* Vorobyeva. The psammosteids and placoderms dominate in this vertebrate assemblage of the *Pycnosteus palaeformis* psammosteid Zone of the Aruküla Regional Stage. The tooth of *Karksiodus mirus* Ivanov & Märss was found in brownish-grey, weakly cemented sandstone with clay balls.

Kemka locality

A series of Middle Devonian outcrops are exposed on both banks of the canyon-like valley of the Kemka River (right tributary of the Luga River), 9 km upstream from the river mouth, in the middle course and between the mouths of Domanov and Lobovoj creeks (Fig. 1B). The tooth of *Karksiodus mirus* Ivanov & Märss was collected in one of these outcrops, on the right bank of the river. The outcrop is about 7 m high and 40 m long. The deposits belonging to the lower part of the Burtnieki Regional Stage comprise pinky-yellow or brownish, fine- to coarse-grained, cross-bedded sandstones containing clay balls with interlayers of bluish-grey or yellow siltstones, mudstones and clays. The sandstones are normally weakly cemented but some dense interlayers with carbonate cement are also found.

The vertebrates are represented by their isolated skeletal elements and fragments but parts of the skeleton are rarely recorded from there. The ichthyoassemblage

belongs to the *Pycnosteus tuberculatus* psammosteid Zone and the *Asterolepis delli* placoderm Zone, and includes the psammosteids *Pycnosteus tuberculatus* (Rohon), *Ganosteus stellatus* Rohon (Glinskiy 2012); the placoderms *Actinolepis* sp., *Homostius latus* Asmuss, *Holonema* sp., *Dickosteus* sp., *Asterolepis* cf. *A. delli* Gross; the acanthodians *Haplacanthus* sp., *Ptychodictyon* sp., '*Acanthodes*' sp.; the sarcopterygians *Glyptolepis* sp., Porolepiformes, Dipteridae, Osteolepididae; and the actinopterygian *Cheirolepis* sp. The placoderm remains are abundant in the assemblage. The *Karksiodus* tooth was found within a carbonate-cemented, dense sandstone interlayer.

Novinka locality

The Novinka quarry is located 1.1 km south of Novinka village (railway station), Gatchina District (Fig. 1B). The deposits of the Burtnieki Regional Stage include yellow-grey, fine- to medium-grained, commonly weakly cemented, micaceous-quartz sandstones with interlayers of yellowish-grey and bluish-grey clays and siltstones (Ivanov et al. 2012).

Vertebrate remains have been collected from pinkish-grey and red medium-grained trough-cross-stratified sandstones. The vertebrates are represented mainly by isolated skeletal elements and fragments of bones, plates, fin spines, scales and teeth. The diverse agnathan and fish remains include the psammosteids *Pycnosteus tuberculatus* (Rohon), *Pycnosteus* sp., *Ganosteus stellatus* Rohon, *Tartuosteus maximus* Mark-Kurik, *Psammolepis abavica* Mark-Kurik and *Psammosteus bergi* (Obruchev); the placoderms *Rhynchodus* sp., *Actinolepis magna* Mark-Kurik, *Homostius* cf. *latus* Asmuss, *Heterostius* sp., *Dickosteus* sp. and *Asterolepis delli* Gross; the acanthodians *Homacanthus* sp., '*Acanthodes*' sp. and *Nostolepis* sp.; and the sarcopterygians *Glyptolepis* sp., Porolepiformes indet., *Conchodus* sp., Dipnoi indet. and Osteolepididae indet. (Ivanov & Glinskiy 2011). Psammosteid and large arthrodiran remains are dominant in this assemblage. This assemblage belongs to the *Pycnosteus tuberculatus* and *Asterolepis delli* zones. The teeth of *Karksiodus mirus* Ivanov & Märss were found in the upper layer of yellowish-grey siltstones.

Karksi locality

Apart from the four teeth of *Karksiodus mirus* Ivanov & Märss described earlier (Ivanov et al. 2011), three additional incomplete teeth have been found in the Härma Beds, Burtnieki Regional Stage of the Karksi outcrop in South Estonia (Fig. 1A). The teeth were collected in the samples from two levels, 02-1 and 90 (= 02-4) of this outcrop (Märss et al. 2008). Besides the teeth of the elasmobranch *Karksiodus* and the scales of the putative chondrichthyan *Karksilepis parva* Märss, the vertebrate assemblage from the Karksi locality also contains the scales of typical chondrichthyans. One scale from sample 02-4 (Fig. 3C, D) possesses a rhomboid crown with a slightly acuminated posterior part. The crown is shallowly inclined anteriorly and projected over the scale base. The anterior part of the external crown surface bears 11 narrow and long ridges. These are separated by deep depressions anteriorly, are smooth in the middle part and do not reach the smooth crown posteriorly. The ridges are of different length and some of them are branched posteriorly. The anterior edge of the crown is uneven and sinuous. The scale neck is not well developed anteriorly but is deeply constricted posteriorly. The base is low and smaller than the crown, with its upper surface rising towards the crown and having a flat basal surface. The second scale, from sample 97 (Fig. 3E) is incompletely preserved. It has a small, slightly inclined crown, narrow neck and large oval base. The crown surface is flat, with an uneven anterior edge. The base has a pyramidal upper surface and a slightly concave basal surface.

DENTAL MORPHOLOGY

External morphology

Compared with the already described specimens, the new collection of *Karksiodus* teeth provides additional and systematically valuable characters, such as a variable dental morphology. The range of tooth sizes is substantial: the width of the base varies from 0.5 mm (Fig. 2C, D) to 2.3 mm (Fig. 2J, K), mostly measuring 1.2–1.6 mm.

The tooth crown includes two to four cusps. The bicuspid tooth (Mark-Kurik & Karatajūtė-Talimaa 2004, fig. 3A) bears two large lateral cusps on the crown. The more common tricuspid teeth possess two main lateral cusps with a small central cusp displaced more labially than the lateral ones. The crowns of the four-cusped teeth have an additional intermediate cusp (cusplet) placed either between the central and lateral ones or in line with the central cusp (Fig. 2J, K), or placed more medially in line with both lateral cusps (Fig. 3A, B). The intermediate cusp, as observed in one broken tooth, is either narrower than the central cusp or of the same width. Cusp striations among the known teeth of *Karksiodus* vary from very fine and dense to coarse and sparse. The cusps are usually rounded in cross section but sometimes oval and flattened labio-lingually. The

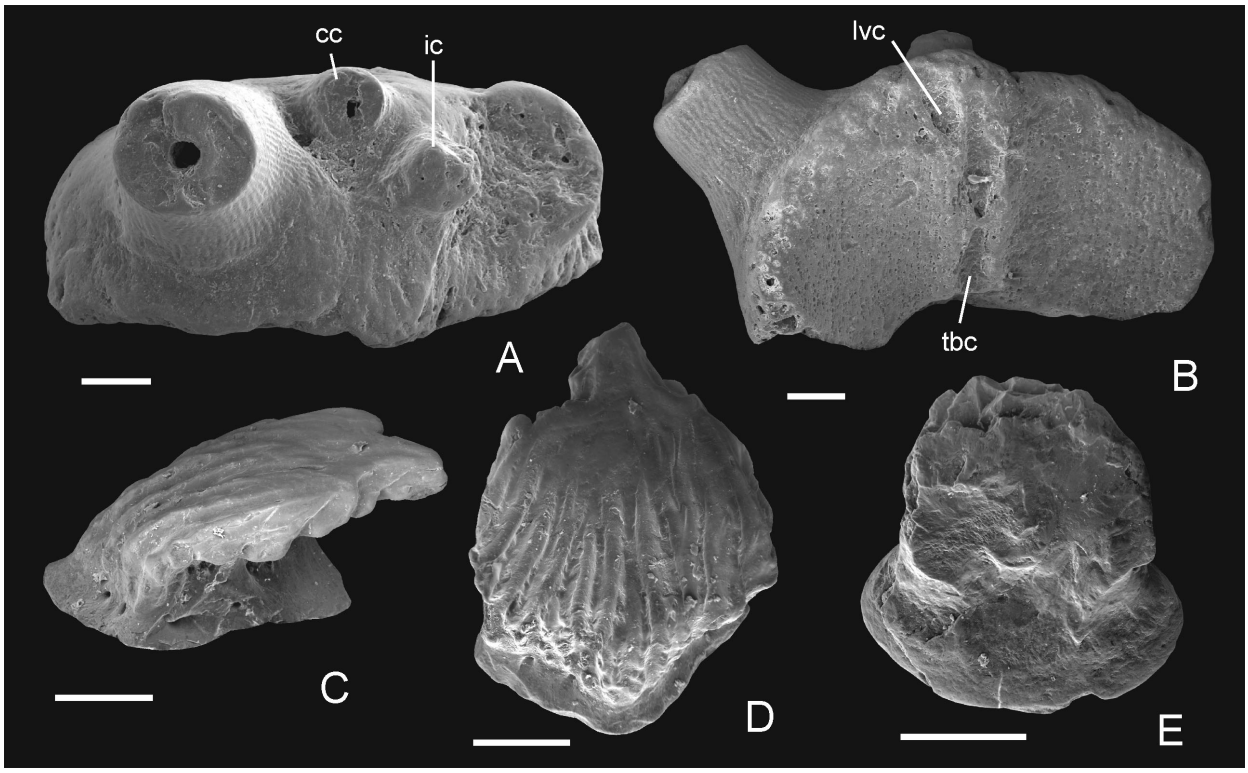

Fig. 3. Chondrichthyan remains from the Burtnieki Regional Stage of the Karksi outcrop, Estonia. **A**, **B**, tooth of *Karksiodus mirus* Ivanov & Märss, 2011; GIT 383-49, sample 02-1, A, occlusal and B, oblique basal views. **C**–**E**, chondrichthyan scales; **C**, **D**, GIT 383-48, sample 02-4; C, lateral and D, crown views; **E**, GIT 383-47, sample 97, crown view. Scale bars equal 200 µm. Abbreviations: cc, central cusp; ic, intermediate cusp; lvc, large vascular canal opening; tbc, transverse basal vascular canal.

angles between the lateral cusps range from 40° to 60°, the largest angle occurring in the bicuspid and multicuspid teeth; the lateral cusps of tricuspid crowns diverge at an angle of about 50°.

The structure of the base of all known teeth of *Karksiodus* varies largely. The tooth base shows various degrees of curvature, from slightly curve (Fig. 2A–D, J, K; Mark-Kurik & Karatajūtė-Talimaa 2004, fig. 3A) to strongly arcuated (Fig. 2E, G; Ivanov et al. 2011, fig. 3A–C). The bicuspid, multicuspid and some small tricuspid teeth have the flattest bases. The length of the lateral prominent parts (projections) of the tooth base can vary from short (Fig. 2K) to considerably long (Fig. 2E). These projections are well developed in the large teeth with strongly arched bases. The prominence of the transverse basal vascular canal wall on the basal surface of the tooth varies from not being salient to strongly salient. In the former case the external wall of the canal is contained within the smooth basal surface. The tricuspid teeth with strongly arched bases and extended lateral projections possess the most prominent transverse basal canal wall. In the bicuspid, multicuspid (Fig. 2J, K) and small tricuspid teeth (Fig. 2C, D) this canal is only slightly protruded. The transverse basal canals commonly run along the entire midline of the base, but they can have an asymmetrical position, disposed from the midline either mesially or distally (Fig. 2G; Ivanov et al. 2011, fig. 3F, I).

Internal structure

A longitudinal thin section of a tooth (Fig. 4A) and fragmented teeth from the new collection add some new features of the internal structure of the *Karksiodus* teeth. Orthodentine tubules make up the lateral cusps from the base to the cusp apex (Fig. 4D), but they are more densely concentrated and wider at the cusp/base boundary (Fig. 4C). The boundary between the orthodentine of the cusps and the trabecular dentine of the base is distinct. Some of the cusps of the new specimens have well-preserved external surfaces but no enameloid layer was detected in any of the teeth, even during the SEM study of the cross section of the tooth cusp polished and acid-etched. Probably the external layer of the cusp forming the striation consists of hypermineralized superficial orthodentine.

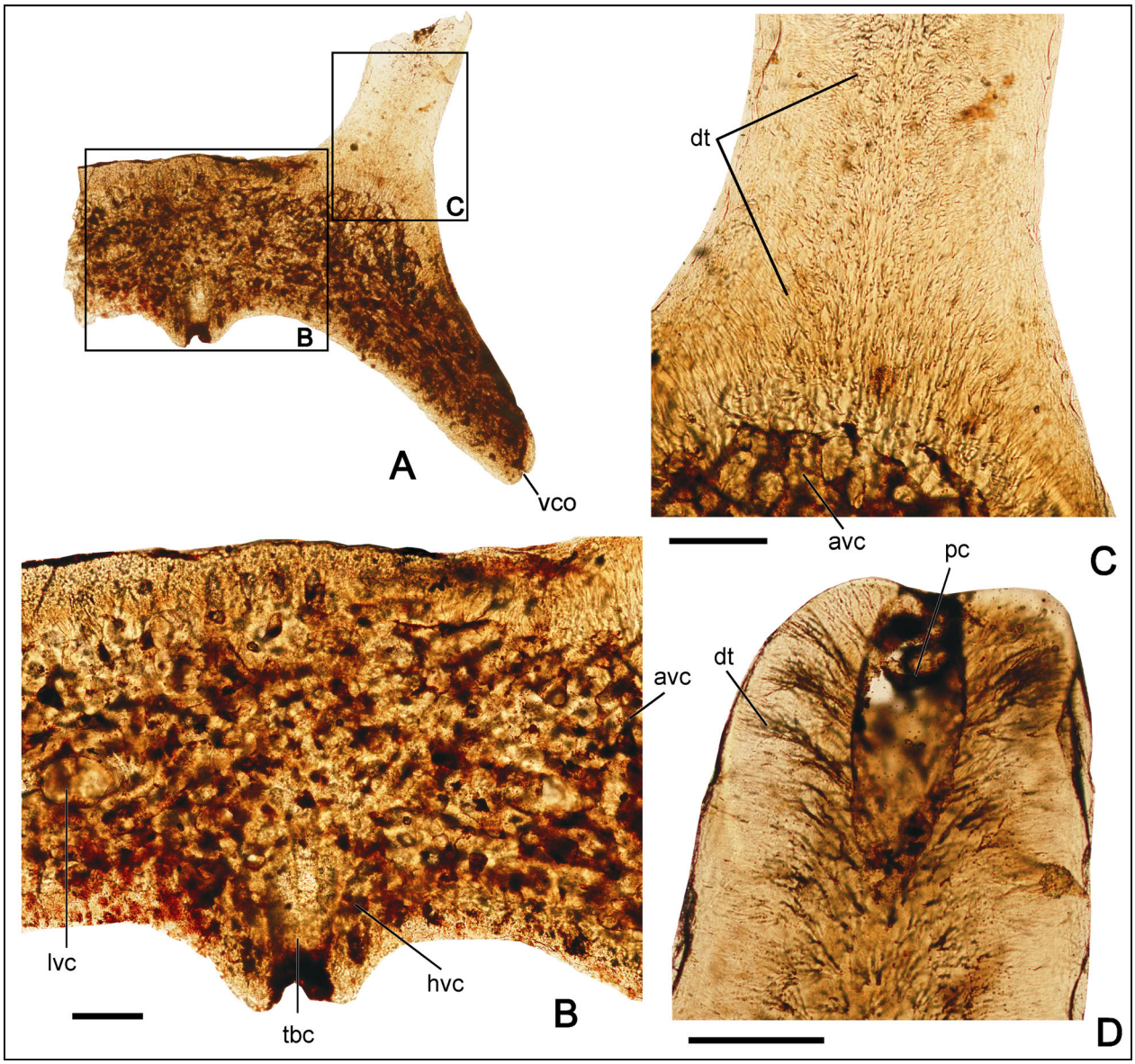

Fig. 4. *Karksiodus mirus* Ivanov & Märss, 2011, microstructure of tooth PM SPU 70-3, Kemka locality; Burtnieki Regional Stage. **A**, longitudinal section from the base and the lateral cusp (details in **B** and **C** shown by frames); **B**, detail of base microstructure; **C**, detail of the microstructure on the cusp/base boundary; **D**, detail of the microstructure of the cusp. Scale bars equal 100 µm.

Abbreviations: avc, ascending vascular canal; dt, dentine tubules; hvc, (sub)horizontal vascular canal; lvc, large vascular canal opening; pc, pulp canal; tbc, transverse basal vascular canal; vco, vascular canal opening.

The vascularization system of the *Karksiodus* teeth includes four types of vascular canals: transverse basal canals (Fig. 4B, tbc), thin and small canals forming the network within the base (ascending and horizontal, Fig. 4B, avc and hvc), rare large canals (Fig. 4B, lvc) and pulp canals within the lateral cusps (Fig. 4D, pc). The external wall of the tube-like transverse canal consists of compact tissue as mentioned by Ivanov et al. (2011) and is not perforated by small canals. The inner surface is penetrated by several foramina of horizontal and ascending small vascular canals connecting the transverse canal with its network. One large vascular canal opens on the lingual rim of the tooth base, alongside the foramen of the transversal canal (Figs 2E, G; 3B, lvc). The large canal is subdivided within the base into two branches and runs sub-parallel with the basal surface (Fig. 4B, lvc). This canal is connected with thin canals. The thin ascending vascular canals are graded to

the broadened pulp canal of the lateral cusp (Fig. 2I). The teeth of *Karksiodus* exhibit a compound vascularization system.

RESULTS

To summarize the already known and new data, *Karksiodus mirus* Ivanov & Märss occurs in the Givetian, Middle Devonian of South Estonia: the Aruküla Regional Stage of the Aruküla cave, Tartu (Mark-Kurik & Karatajūtė-Talimaa 2004), and the Burtnieki Regional Stage of the Karksi outcrop (Ivanov et al. 2011), and in the Leningrad Region, Northwest Russia: the Aruküla Regional Stage of the Lemovzha, Siverskij and Zaitsevo localities, and the Burtnieki Regional Stage of the Kemka and Novinka localities.

In *Karksiodus*, variations in tooth morphology, such as the curvature of the base, length of lateral parts, prominence of the transverse basal canal and details of cusp external sculpture (striations) are possibly related to different stages of tooth growth as observed in the tricuspid teeth of various sizes. However, the variability in the crown structure (number of cusps and angles between the lateral cusps), as well as some variability in the base (position of the basal canal and possibly base curvature), suggest that *Karksiodus* dentition displayed weakly developed heterodonty in which the bicuspid, tricuspid and multicuspid teeth were located in different positions on the jaws.

With the new tooth material, the arrangement of the tooth rows can be tentatively reconstructed. The teeth would not extensively overlap each other but rather the lingual rim of each tooth would be in contact with the shallow longitudinal groove on the labial side of the tooth in front; the basal surface of adjacent teeth in the same row would abut on each other forming an arch-like structure.

Nevertheless, the new material has not provided enough evidence to clarify the interrelationships of *Karksiodus* with other chondrichthyans. The variations in the crown structure, especially the changeable number of intermediate (including central) cusplets, resemble the tooth structure of the *Doliodus* and the *Antarctilamna–Wellerodus* group. The latter differs from *Karksiodus* in having a lingual extension of the base and elements for tooth-to-tooth articulation, including the apical button and labio-basal projection (Ginter et al. 2010). On the other hand, *Doliodus* dentition includes commonly the tooth row with fused bases but the isolated teeth possess labio-basal extensions of the base (Turner 2004; Maisey et al. 2014). None of these groups display the same histological characters presented by *Karksiodus*, namely, the complex vascularization system made up of four distinct canal types, which is so far unique to *Karksiodus* among either extinct or extant chondrichthyans.

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Uusi andmeid *Karksiodus*'e (Chondrichthyes) kohta Peadevoniväljalt

Alexander Ivanov ja Tiiu Märss

Karksiodus mirus Ivanov & Märss, 2011, hambaid on peale juba kirjeldatud Karksi leiukoha Lõuna-Eestis leitud veel viiest uuest leiukohast, mis asuvad Loode-Venemaal Leningradi oblastis (nn Peadevoniväljal). Materjal pärineb Lemovža, Siverski ja Zaitsevo paljandist, Aruküla lademest ja Kemka ning Novinka leiukohast, Burtnieki lademest ja Givet' ladejärgust Kesk-Devonis. *Karksiodus mirus*'e hammaste eripäraks on varieeruvus tippude arvus, külgmiste tippude vahelises nurgas, hambaaluse kaare kujus ja aluse ristkanali seina eenduva osa paksuses.