A new elasmobranch *Karksiodus mirus* gen. et sp. nov. from the Burtnieki Regional Stage, Middle Devonian of Estonia

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Abstract. Teeth of a new elasmobranch *Karksiodus mirus* gen. et sp. nov. were discovered on two levels in the sandstones of the Karksi outcrop (South Estonia), corresponding to the Härma Beds, lower part of the Burtnieki Regional Stage (Givetian, Middle Devonian). These teeth differ from all known Palaeozoic elasmobranch teeth in the presence of a unique wide transversal tube-shaped basal canal, in very fine and dense striation of cusps and in an arched base without well-developed extensions. The order and family of this taxon are not specified.

Key words: *Karksiodus mirus* gen. et sp. nov., Chondrichthyes, Burtnieki Regional Stage, Givetian, Middle Devonian, Estonia.

INTRODUCTION

Chondrichthyan remains are rather sparse in the Devonian deposits of the Main Devonian Field (northwestern part of the East European Platform including Lithuania, Latvia, Estonia, and the Leningrad, Pskov and Novgorod regions). Their teeth, however, are found even more rarely. Ivanov & Lukševičs (1994) recorded teeth of *Protacrodus* sp. and *Protacrodus aequalis* Ivanov, respectively, from the Kursa and Mūri regional stages (Famennian, Upper Devonian of Latvia). Mark-Kurik & Karatajūtė-Talimaa (2004) documented a bicuspid tooth of an unidentified chondrichthyan from the Aruküla caves near Tartu, in the Viljandi Beds of the Aruküla Regional Stage (Givetian, Middle Devonian of Estonia). Recently, Märss et al. (2008) described chondrichthyan scales of *Karksilepis parva* Märss from the Karksi outcrop in South Estonia, from the Härma Beds of the Burtnieki Regional Stage (Givetian, Middle Devonian). The teeth of a new elasmobranch described below were collected from the same locality and stratigraphical level (Fig. 1A, B).

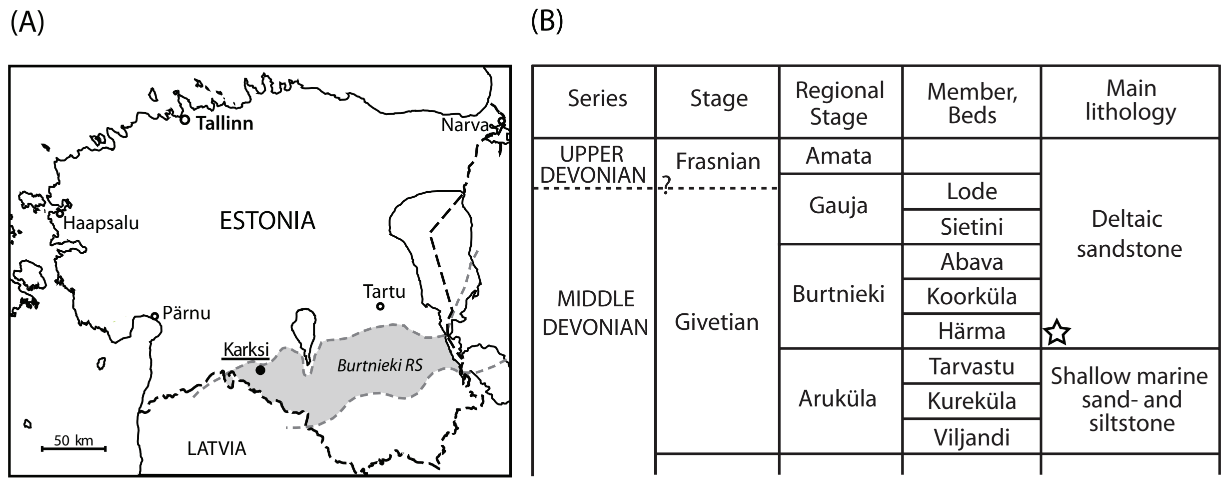


Fig. 1. Distribution of the Burtnieki Regional Stage (RS) and the location of the Karksi outcrop (A), and the stratigraphical level of collected specimens (shown by the asterisk in B).

MATERIAL AND METHODS

Six vertebrate samples were collected for this study from four levels in the Karksi outcrop (Fig. 2). All samples contained remains of various vertebrates, including psammosteid heterostracans, placoderms, numerous acanthodians, sarcopterygians and actinopterygians (Märss et al. 2008, table 1), but also fairly well preserved scales of the chondrichthyan *Karksilepis parva* Märss. Two samples (02-1 and 02-4) yielded altogether four elasmobranch teeth. As there was no indication that these teeth might belong to *K. parva* (except for their co-occurrence in the samples from the same outcrop), they were neither thoroughly studied nor described.

The sandstones in the Karksi outcrop are very weakly cemented and do not need acid preparation. The preparation methods used in this study are the same as those described in Märss et al. (2008). A tooth fragment was first used for the SEM study, afterwards thin-sectioned and its microstructure was examined. This tooth fragment was partly pyritized.

The described collection is housed in the Institute of Geology at Tallinn University of Technology under the collection number GIT 383 with specimen numbers 42-45.

GEOLOGICAL BACKGROUND

The Devonian Baltic Basin was situated in equatorial latitudes on the margin of the Laurussian supercontinent. The basin was characterized by siliciclastic deposition, with an influx of clastic material from the Baltic Shield (Kuršs 1992; Kleesment 1997; Plink-Björklund & Björklund 1999). The Burtnieki Regional Stage of Givetian age occurs in southeastern Estonia (Fig. 1A) between the Aruküla Regional Stage below and the Gauja Regional Stage above (Fig. 1B). The Burtnieki Regional Stage is 60–95 m thick and is represented by light fine-grained weakly cemented cross-bedded sandstones. It is divided into the Härma, Koorküla and Abava beds (Kleesment 1995; Kleesment & Mark-Kurik 1997). The beds exposed in the Karksi outcrop belong to the lower part of the Härma Beds (Märss et al. 2008). Sandstones of the Härma Beds possibly accumulated in regressive conditions of the Devonian basin in a fluvial-dominated subaqueous delta plain environment, which was affected by low-amplitude eustatic and tectonic movements and interrupted by recurrent short subaerial periods (Kleesment 1997, 2009; Plink-Björklund & Björklund 1999).

Abundant fish microremains are found in four levels of moderately sorted fine- to medium-grained sandstones in the lower part of the Karksi outcrop (Märss et al. 2008). The character and spatial distribution of the fish remains suggest that the accumulation took place in deltaic shoreface environments during short periods of intense influx of detrital material, where under low-amplitude eustatic movements, sea level fluctuations caused repeated alternation of marine and non-marine conditions. Similar concentrations of fish remains have

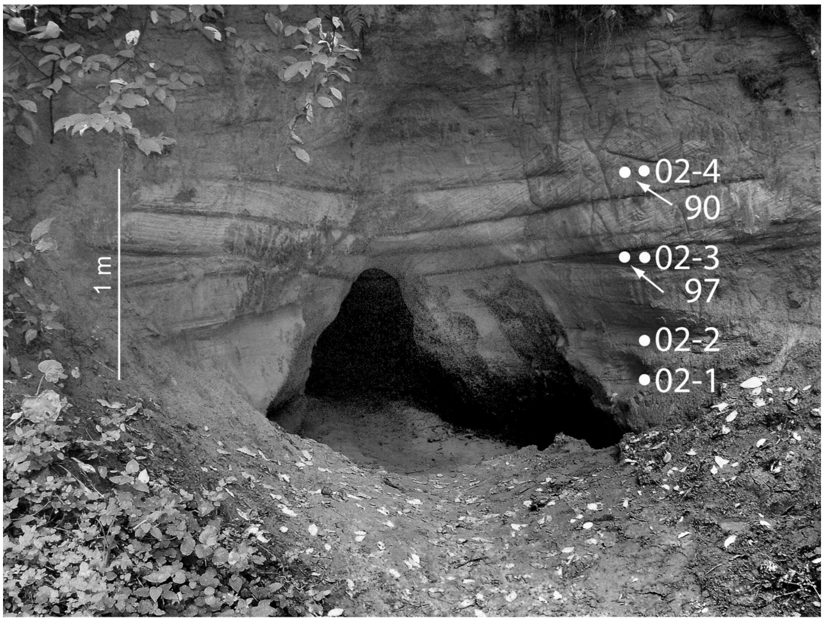


Fig. 2. Karksi outcrop. Levels of six samples that contained remains of various vertebrates; four elasmobranch teeth were found in samples 02-1 and 02-4.

been reported from the Ordovician nearshore marine deposits of Bolivia (Davies et al. 2007), the Triassic deltaic deposits of Argentina (Mancuso 2003) and the Mid-Triassic lake deposits of Namibia (Smith & Swart 2002).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order *et* Family *incertae sedis*
Genus *Karksiodus* Ivanov & Märss gen. nov.

Derivation of name. From the Karksi locality, where the teeth of this taxon were found, and Greek word *odus*, meaning tooth, gender masculine.

Type species. *Karksiodus mirus* gen. et sp. nov.

Diagnosis. As for type species.

Karksiodus mirus Ivanov & Märss sp. nov.
Figures 3, 4

Chondrichthyan tooth: Mark-Kurik & Karatajūte-Talimaa 2004, fig. 3A, p. 770.

Derivation of name. From Latin *mirus*, meaning astonishing, extraordinary.

Holotype. GIT 383-45, tooth with well-preserved lateral cusp and base (Fig. 3A–C).

Type locality and horizon. Sample 02-1, Karksi outcrop, South Estonia; Härma Beds, Burtnieki Regional Stage, Givetian, Middle Devonian.

Material. Four variously preserved teeth, including holotype (GIT 383-42 to 383-45): two abraded teeth with broken cusps and the wall of the basal canal, and an incomplete tooth with a well-preserved lateral cusp, which was used for thin sectioning.

Occurrence. Two levels with two samples (02-1 and 02-4) in the Karksi outcrop (see Fig. 2).

Diagnosis. Teeth with diplodont tricuspid crown directed lingually; long, sigmoidally curved lateral cusps with inner lateral carina; all cusp sides finely striated by numerous cristae; small central cusp displaced labially; arched base insignificantly extended lingually and labio-basally, turned up lingually, bearing prominent tube of transversal basal canal; teeth with orthodont crown and strongly vascularized base.

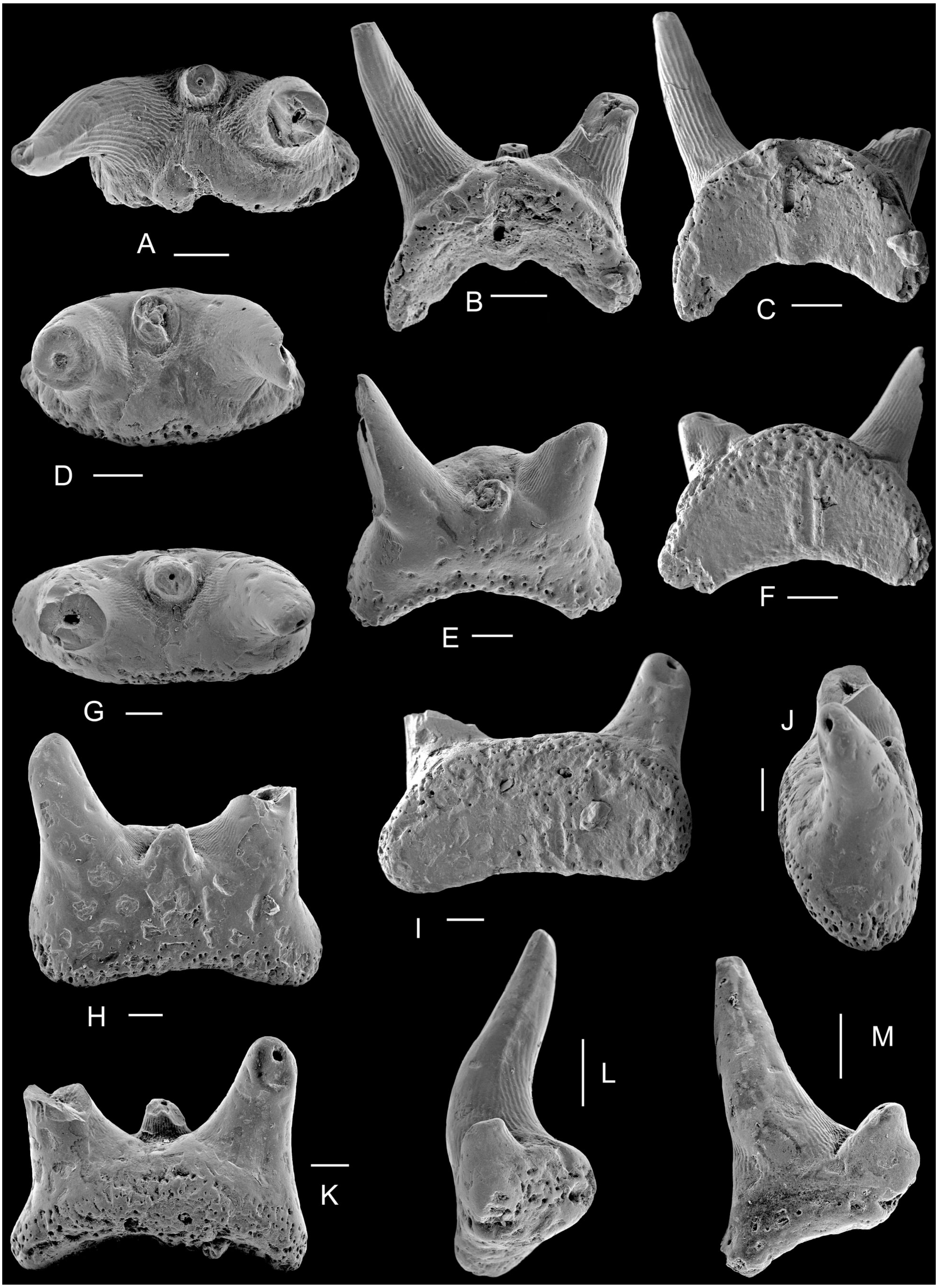
Description

External morphology. The teeth possess a symmetrical diplodont, tricuspid crown and an arched base (Fig. 3A–I, K). The crown is lingually directed and not consolidated (Fig. 3A): the cusps are separated from each other by a small space (Fig. 3B, E, H, K). The cusps in the crown are rounded in cross section (Fig. 3A, D, G). Both long lateral cusps are sigmoidally curved, divergent mesio-distally and bear distinct lateral cutting edges (carina) on the inner cusp side (Fig. 3A, L). The angle between the lateral cusps is about 50°. The small central cusp is displaced more labially than the lateral ones (Fig. 3A, D, G). All cusp surfaces are covered by numerous, almost parallel, distinct and fine cristae (Fig. 3A–C, L, F), which are gently sinuous near the base but straight in the upper part of the cusp (Fig. 3A, left side, M). Part of the cristae are converged at the lateral cutting edges (Fig. 3A, L). No differences are observed between the sculptures of the labial and lingual faces of the cusps.

The base is oval in occlusal view, slightly extended lingually and labio-basally, wider than the crown (Fig. 3A, D, G, J). The base has a moderate convex occlusal and a strongly concave basal surface (Fig. 3B, K), and is devoid of any articulation elements such as the occlusal (apical) button, labio-basal projection or tubercle. The elongate lateral parts of the base form the bifurcated labial margins (Fig. 3E). The labial side of the base displays a shallow longitudinal groove, which is perforated by numerous foramina of tiny vascular canals (Fig. 3E, M). The basal surface of the central depressed part bears a transversal prominence, which is a wall of the basal vascular canal and is visible on the well-preserved tooth base (Fig. 3B, C). The external wall may be worn or broken in some specimens (Fig. 3F, I).

Internal structure (only one thin section is available for description). The crown of the tooth is built of orthodentine and covered by a thin external layer of probably enameloid (Fig. 4A, en). The thin-sectioned tooth fragment is partly pyritized, that is why the external layer of the cusp looks dark; it differs from the internal unpyritized orthodentine layer. The orthodentine in the tooth crown has fine branched dentine tubules, which spring from the pulp canal (Fig. 4A, B, dt). In the

Fig. 3. Teeth of *Karksiodus mirus* gen. et sp. nov. **A–C**, holotype GIT 383-45; A, occlusal, B, lingual and C, oblique basal views. **D–F**, GIT 383-44; D, occlusal, E, oblique labial and F, oblique basal views. **G–K**, GIT 383-43; G, occlusal, H, labial, I, oblique basal, J, lateral and K, lingual views. **L**, **M**, GIT 383-42; L, lateral and M, labial views. A–C, G–M, sample 02-1; D–F, sample 02-4, Karksi outcrop, South Estonia; Härma Beds, Burtnieki Regional Stage, Givetian, Middle Devonian. Scale bars 0.25 mm.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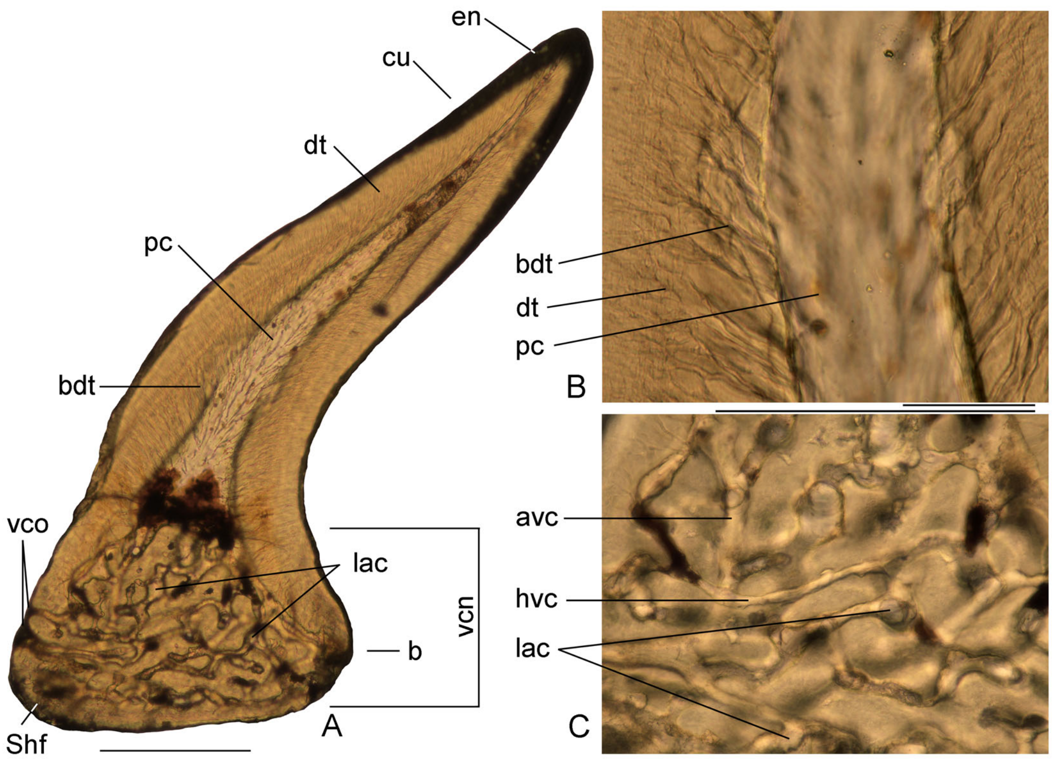

Fig. 4. *Karksiodus mirus* gen. et sp. nov., microstructure of tooth GIT 383-42. Karksi outcrop, sample 02-1. (**A**) Transversal section from the lateral cusp along the pulp canal. (**B**) Detail of cusp microstructure. (**C**) Detail of base microstructure. Scale bar for A and C equals 0.25 mm, for B, 50 µm. Abbreviations: avc, ascending vascular canal; b, base; bdt, bunches of dentine tubules; cu, cusp; dt, dentine tubules; en, enameloid; hvc, (sub)horizontal vascular canal; lac, lacuna; pc, pulp canal; Shf, Sharpey fibre tubules; vcn, vascular canal network; vco, vascular canal opening in the labial part of the tooth.

lower part of the cusps the tubules are arranged in groups or bunches (Fig. 4A, B, bdt), but become more evenly distributed upwards. The trabecular dentine compounds the tooth base and runs up to the crown, into the basal part of lateral cusps (Fig. 4A).

The internal vascularization system is composed of three types of canals. (1) The large transversal basal canal in the lower part of the base (Fig. 3B, C, F) occurs as a wide prominent tube close to the basal surface, where it runs all along the midline of the base. The wall of that tube consists of compact tissue. (2) The network of vascular canals within the entire base (Fig. 4A, C, vcn) rises up into the basal part of the lateral cusp (Fig. 4A). These vascular canals are rather thin if compared with basal and pulp canals, but with almost equal cross section; intersections of the canals form lacunae-like widenings (Fig. 4A, C, lac), which makes their appearance somewhat tortuous. Most of the canals run subparallel to the lower base surface (Fig. 4A, hvc) and open on the labial surface of the base, in the longitudinal groove, as well as on the lingual torus of the base. In the upper part of this network the canals are subvertically arranged (Fig. 4A, C, avc). (3) The pulp canal in the lateral cusps is wide in the basal part of the cusp but becomes narrower higher up and almost reaches the cusp tip (Fig. 4A, pc). Unfortunately, the transition from the canal network to the pulp canal is pyritized. Sharpey fibre tubules (Fig. 4A, Shf) are weakly developed.

Remarks. An incomplete tooth from the Aruküla Formation (Givetian, Middle Devonian) of the Aruküla cave (Tartu, Estonia) was illustrated by Mark-Kurik & Karatajūte-Talimaa (2004, fig. 3A). This tooth is rather similar to those described herein in the base structure but has a bicuspid crown. It is assigned to our new taxon.

The scales of the chondrichthyan *Karksilepis parva* Märss described from the same beds of the Karksi locality have the same type of ultrasculpture on the elongate odontodes of scales (Märss 2006; Märss et al. 2008). The upper layer of the scales in *Karksilepis parva* is composed of orthodentine resembling the teeth described herein and of many other elasmobranchs. *Karksilepis* has a specific horizontal vascular canal network in the basal plate beneath the odontodes, while *Karksiodus* gen. nov. has such a network in the basal part of the teeth. The horizontal vascular canal system in the base of scales is also known in Mongolepidida and some chondrichthyans (Karatajūtė-Talimaa 1997). Flattened bone cell lacunae form a lamellar structure of basal plates in *Karksilepis*, while the tooth of *Karksiodus* gen. nov. does not show any osteocyte lacunae. The ultrasculptural striation of bony units can occur simultaneously in the dermal scales and buccopharyngeal denticles of a taxon, while both units are built from dentine (e.g., in the thelodont *Phlebolepis elegans* Pander; Märss & Wilson 2008). Teleosts (*Denticeps clupeoides*, Clupeomorpha) as well show close structural agreement between teeth and odontodes, whereas the oral teeth are similar in shape, size and structure to odontodes (Sire et al. 1998).

The teeth of *Karksiodus mirus* gen. et sp. nov. are specific and distinctive from all other shark teeth known so far; they have no analogues among the fossil sharks with or without preserved squamation. The question is, how we should treat the elements of *Karksiodus* and *Karksilepis*, as belonging to one genus or to two genera, if there is no close analogue in body morphology and the collections have scattered scales and teeth? We can exploit taphonomic data, historical approach in taxonomical studies and the features of elements.

Chondrichthyan remains are very rare in the Devonian deposits of the East European Platform, especially in sandstones. Other groups of vertebrates, such as psammosteids, placoderms, acanthodians and porolepiforms, predominate in those assemblages while the chondrichthyans are occasional accessory elements. Sometimes the Devonian localities contain a few teeth of one shark taxon found in the same levels with the scales or denticles of some other taxon (e.g. Ivanov & Lukševičs 1994; Ivanov 1999). Fifty scales of *Karksilepis parva* Märss were discovered in four levels in sandstones of the Karksi outcrop. *Karksiodus mirus* gen. et sp. nov. is represented by only four teeth in two levels of that site. One tooth of *Karksiodus mirus* occurs in the Aruküla locality in the Viljandi Beds, Aruküla Regional Stage, where the *Karksilepis parva* scales have not been found so far. The taphonomic reasons in our case cannot serve as an argument for uniting the scales and teeth in one taxon, or to separate them.

A few taxa among the numerous Palaeozoic elasmobranchs are only known and described on the basis of articulated specimens with well-preserved squamation. In the Devonian the skeletons of two sharks, a few specimens of *Antarctilamna* and one specimen of *Protacrodus* have been found with teeth and scales (Gross 1938; Young 1982). The same applies to a few xenacanthid, ctenacanthid and euselachian sharks in the Carboniferous and Permian. The squamation of chondrichthyans is considered as the least diagnostic after endoskeleton, teeth and fin spines.

The scales of representatives of some orders, for example symmoriids, coronodontids, squatinactids and ‘omalodontids’, are not known at all. Therefore two parallel taxonomic approaches have widely been in use: one employs scale features and the other tooth characteristics.

Chondrichthyans are a very diverse group in terms of their squamation pattern, which depends on shark ecology (e.g. Reif 1978, 1982). The body of a shark can be covered with morphologically variable scale types (e.g. Reif 1974), or, vice versa, some sharks from different, non-related groups possess very similar squamations (but dissimilar dentition).

Apart from some similarities between *Karksiodus mirus* gen. et sp. nov. and *Karksilepis parva*, both having surface striation of elements and orthodentine in the tooth cusps and scale odontodes, there also are several specific features. *Karksilepis* has osteocyte lacunae in the base as well as a strong vascular canal system in a thin layer of the base beneath the odontodes, consisting of wide canals as seen in crown view (Märss et al. 2008, fig. 5B) and large holes as seen in side view (Märss et al. 2008, fig. 4B). They are not the same type of canals as in the tooth base of *Karksiodus*, which are round in cross section and of the same size. Osteocyte lacunae are absent in the tooth base of *Karksiodus* and the transversal basal canal occurs as a prominent tube close to the basal surface.

All features together support our treatment of the scales and teeth as different taxa. Findings of articulated specimens will affirm or refute it. At present we prefer to leave *Karksiodus mirus* gen. et sp. nov. as a separate taxon and its family and order open.

DISCUSSION

Comparison of teeth

The teeth of *Karksiodus* gen. nov. differ from those of all known Palaeozoic elasmobranchs in the presence of a unique tube-shaped prominent transversal basal canal close to the basal surface, in very fine and dense striation of cusps and in the turned up lingually, arched base which is without well-developed extension. Such striation of cusps more resembles that on teeth of struniiform sarcopterygians.

The teeth of many Palaeozoic elasmobranchs, such as Antarctilamniformes, Phoebodontiformes, Cladoselachiformes, Xenacanthimorpha, Symmoriiformes, Ctenacanthiformes and several Euselachii, except omalodontid-like sharks, have a lingual extension of the tooth base (e.g. Ginter et al. 2010). The dentition in omalodontid-like chondrichthyan genera *Anareodus*, *Aztecodus*, *Doliodus*, *Manberodus*, *Omalodus*, *Portalodus* and *Siberiodus* contains the teeth, which are devoid of the lingual base extension but possess the base extended labially or labio-basally, or have an almost symmetrical base without developed lingual and labial parts (Ivanov & Rodina 2004; Hairapetian et al. 2008). Some authors merged the mentioned genera into the order Omalodontiformes (e.g. Ginter et al. 2008, 2010), but their teeth show different external morphology and internal structure (Ivanov & Rodina 2004). Such integration of all elasmobranch taxa, which have teeth with a labially extended base, can be compared with assembling all Palaeozoic sharks with a lingually extended base into one order. The different base structures, both the omalodontid-like and the lingually extended type, have appeared in different groups of chondrichthyans independently. The base structure in teeth of *Karksiodus* gen. nov. slightly resembles that of some omalodontid-like sharks like *Aztecodus* and *Manberodus* (Ginter et al. 2010), which have an arched base without considerable extensions and any articulation elements, but whose teeth possess different crown structure and vascularization type.

Apart from *Karksiodus* gen. nov., several chondrichthyans have a diplodont crown of teeth: the Early Devonian problematic taxon *Leonodus*, elasmobranchs of the *Antarctilamna–Wellerodus* group, most Middle and Late Devonian omalodontid-like elasmobranchs and the Late Palaeozoic–Triassic xenacanthimorph sharks. However, the teeth of all mentioned chondrichthyans differ largely from those of *Karksiodus* gen. nov. The teeth of *Leonodus* have usually a bicuspid crown and a lingually elongated base with a labio-basal tubercle (Wang 1993; Botella et al. 2009). The teeth crowns of most of the omalodontid-like elasmobranchs, besides *Omalodus*, are of asymmetric diplodont type, sometimes with irregular intermediate cusplets (Ivanov & Rodina 2004). The sharks of the *Antarctilamna–Wellerodus* group had teeth with a lingually extended base, bearing the occlusal button and labio-basal projection. The crown structure, described by Burrow et al. (2009) in tricuspid teeth of *Antarctilamna–Wellerodus*, most resembles *Karksiodus* gen. nov. in the cusp type, their arrangement and in the cusp histology but differs in the sculpture of the cusps.

The teeth of xenacanthimorph sharks diverge from the teeth of *Karksiodus* gen. nov. in the presence of the occlusal button and basal tubercle on the lingually extended base, and in the cusps which are not sigmoidally curved and not covered by such a striation as described herein. The sigmoidally curved cusps are charasteristic of phoebodontid teeth (Ginter & Ivanov 1992; Ginter et al. 2010).

Diversity of chondrichthyans in the Middle Devonian

The Middle Devonian chondrichthyan taxa *Antarctilamna* and *Gladbachus* were described on the basis of the endoskeleton but the dentition is known only in *Antarctilamna* (Young 1982; Heidtke & Krätschmer 2001; Ginter et al. 2010). Many Early and Middle Devonian chondrichthyan taxa, such as *Aztecodus*, *Celtiberina*, *Leonodus*, *Mcmurdodus*, *Omalodus*, *Phoebodus*, *Portalodus*, *Protodus* and *Wellerodus*, have been established on the basis of isolated teeth (Ginter et al. 2010). The Givetian elasmobranchs already possessed all variations in the tooth morphology and the crown and base features, which developed more widely in Late Palaeozoic groups. The diplodont, cladodont, phoebodont and protacrodont crown types appear in the elasmobranch dentitions in the Givetian. Various structures of the tooth base are known from that time: a base extended lingually or labio-basally, a base without developed lingual and labial parts. The elasmobranch teeth from the beginning of the Carboniferous showed no such wide variation in the tooth base; the base structure of omalodontid-like teeth disappeared in the post-Devonian stage of the evolution of elasmobranch dentition.

The chondrichthyans were more diverse in the Middle Devonian than in the Early Devonian, especially in the Givetian. The representatives of such genera as *Aztecodus*, *Mcmurdodus*, *Omalodus*, *Phoebodus*, *Portalodus*, *Antarctilamna* and *Wellerodus* occur in the Givetian of various regions and palaeogeographic provinces. Recently teeth of the oldest protacrodontid and cladodont (possibly symmoriid) chondrichthyans were discovered in the Late Givetian of the Kuznetsk Basin, western Siberia, Russia (Ivanov & Rodina 2007). The Givetian so-called *Omalodus* chondrichthyan assemblage (Ivanov & Derycke 1999) is widely distributed in the world. It occurs in Siberia of Russia (Ginter & Ivanov 1992), Poland (Ginter 1995), Spain (Ginter et al. 2008), Morocco (Hampe et al. 2004), Mauritania (Derycke et al. 1998; Ivanov & Derycke 1999) and New York State of the USA (Wells 1944; Turner 1997), which indicates that the Givetian was the beginning of the Palaeozoic radiation of elasmobranch fishes. Although very rare in the deposits of the Main Devonian Field, the findings of teeth of a new taxon show a wider geographical distribution of Givetian sharks even in the facies of the Old Red Sandstone.

RESULTS

Teeth of a new elasmobranch *Karksiodus mirus* gen. et sp. nov. were discovered in the Middle Devonian Härma Beds of the Burtnieki Regional Stage, in the Karksi outcrop of Estonia. They differ from all known chondrichthyan teeth in several features of dental morphology: in the presence of a unique transversal basal canal occurring as a prominent tube close to the basal surface, in very fine and dense striation of cusps and in an arched base without well-developed extension and articulation elements. The *Karksiodus* teeth demonstrate some similarities with those of the *Antarctilamna–Wellerodus* shark group in the crown structure and with those of *Aztecodus* and *Manberodus* in the base structure.

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Uus kõhrkala *Karksiodus mirus* gen. et sp. nov. Kesk-Devoni Burtnieki lademest Eestis

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On kirjeldatud uue kõhrkala *Karksiodus mirus* gen. et sp. nov. hambad, mis avastati Lõuna-Eestist Karksi paljandi liivakividest kahel tasemel. Liivakivid kuuluvad Kesk-Devoni Burtnieki lademe Härma kihtidesse. Leitud hambad erinevad kõigist teistest Paleosoikumi kõhrkalade hammastest ainulaadse põigitise, basaalse pinna lähedal asuva laia torukujulise kanali esinemise, hamba tippude väga peene triibutuse ja selle tiheduse ning kaarja, laienduseta aluse poolest.