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Karksilepis parva gen. et sp. nov. (Chondrichthyes) from the Burtnieki Regional Stage, Middle Devonian of Estonia

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Abstract. Dermal scales of a new chondrichthyan were discovered in four levels in sandstones of the Härma Beds (lower part of the Burtnieki Regional Stage, Middle Devonian) in the Karksi outcrop of South Estonia. The classification of *Karksilepis parva* gen. et sp. nov. Märss is still uncertain.

Key words: Chondrichthyes, Burtnieki Regional Stage, Middle Devonian, Estonia.

INTRODUCTION

Chondrichthyan scales are rare in Lower–Middle Palaeozoic rocks. Chondrichthyan-like scales, however, were described by Sansom et al. (1996) from the Ordovician of Colorado, USA, and by Young (1997) from central Australia. The earliest Elasmobranchii gen. nov. has been listed from the Early Llandovery (Early Silurian) of the Siberian Platform, Russia (Karatajūtė-Talimaa & Predtechenskyj 1995). *Niualepis* and *Elegestolepis conica* have been identified in the Middle Llandovery of South Yakutia and the Bratsk Region, Siberian Platform (Novitskaya & Karatajūtė-Talimaa 1986; Karatajūtė-Talimaa 1992). *Elegestolepis* sp. comes from the Upper Llandovery of Irkutsk Amphitheatre, Tuva, and North Mongolia (Vladimirskaya et al. 1986).

Scales of an elasmobranch (*Kannathalepis*) and possible chondrichthyans (*Frigorilepis* and *Wellingtonella*) originate from the Wenlock of the Canadian Arctic (Märss & Gagnier 2001; Märss et al. 2002, 2006). *Elegestolepis grossi* has been recognized in the Upper Silurian (Upper Ludlow–Přidoli) of Tuva (Karatajūtė-Talimaa 1973). Four chondrichthyan elasmobranch(?) genera, *Seretolepis*, *Altholepis*, *Knerialepis*, and *Ivanelepis*, established on the basis of scales, have been described from the Lochkovian of Podolia (Obruchev & Karatajūtė-Talimaa 1967; Karatajūtė-Talimaa 1968, 1977, 1997a; Hanke & Karatajūtė-Talimaa 2002). *Polymerolepis* Karatajūtė-Talimaa was first discovered in the Lochkovian of Podolia (Obruchev & Karatajūtė-Talimaa 1967). Later on it has also been identified in the coeval strata of Central Nevada (Turner & Murphy 1988) and on Ellesmere and Prince of Wales islands of the Canadian Arctic (Langenstrassen & Schultze 1996). The list of chondrichthyan and putative chondrichthyan taxa from the Lochkovian of the Mackenzie Mountains (MOTH locality), Canada, includes *Kathemacanthus*, *Altholepis*, *Seretolepis*, *Polymerolepis* species, and five unnamed taxa (Hanke & Wilson 1997, 1998; Wilson & Hanke 1998; Wilson et al. 2000). *Ellesmereia* are found in the Lochkovian of the Canadian Arctic (Vieth 1980). Scales of *Arauzia*, *Lunalepis*, and *Iberolepis* are known from the Lower Devonian, Lower Gedinnian (Lochkovian) of Spain (Mader 1986). *Pamyrolepis* nom. nud. Karatajūtė-Talimaa scales have been briefly described from the Emsian of the Eastern Pamyrs (Karatajūtė-Talimaa 1992; Leleshus et al. 2005).

Mongolepidids were first treated as belonging to Elasmobranchii, Chondrichthyes (e.g. Karatajūtė-Talimaa et al. 1990). Later on, Karatajūtė-Talimaa (1995) suggested that Mongolepidida is an independent group of lower vertebrates, still related to the Chondrichthyes. The group is rather widely known in the Silurian. *Mongolepis*, *Sodolepis*, and *Teslepis* have been described in the Upper Llandovery of West Mongolia (Karatajūtė-Talimaa et al. 1990; Karatajūtė-Talimaa 1992; Karatajūtė-Talimaa & Novitskaya 1992, 1997). Several taxa belonging to the mongolepidids come from the Upper Llandovery of different sites of China: *Xinjiangichthys* from Kalpin and Bachu counties, Xinjiang, *Shiqianolepis* and two taxa of uncertain affinity, *Rongolepis* and *Chenolepis*, from Shiqian county, Guizhou Province (Wang et al. 1998; Sansom et al. 2000). In the Wenlock (Lower Silurian) of the Siberian Platform Mongolepididae gen. nov. B has been identified together with *Elegestolepis*? sp. (Karatajūtė-Talimaa & Predtechenskyj 1995). The latest mongolepidids of the world were discovered in the probable Lochkovian

(Lower Devonian) strata of Eastern Mongolia (Wrona & Nyamsuren 1998) and in the Lower Emsian (Lower Devonian) of Gornyi Altai of Western Siberia, showing the wide stratigraphical range of the whole group (Rodina 2002).

Scales of chondrichthyans are rare in the East Baltic. *Lugalepis multispinata* comes from the Emsian(?) of Latvia (Karatajūtė-Talimaa 1997b), while the Eifelian (Middle Devonian) Narva Regional Stage (for short, RS) of Leningrad District, Russia, Belarus, and Lithuania contains a somewhat different form *Lugalepis* cf. *multispinata* (Karatajūtė-Talimaa 1992, 1997b). Rare chondrichthyan buccopharyngeal scales (= oral denticles) and teeth have been documented from the Givetian (Middle Devonian) of Estonia and from the Famennian (Upper Devonian) of Latvia (Ivanov & Lukševičs 1994; Mark-Kurik & Karatajūtė-Talimaa 2004).

In the course of lithological studies of Devonian sediments in Estonia, based upon outcrops and drill core material, a rich collection of vertebrate microfossils has been obtained. Notably abundant material has been collected from the Karksi outcrop in the Halliste old valley, near Karksi castle (Viljandi county) (Fig. 1). The sandstones here belong to the lower part of the Härma Beds of the Burtnieki RS and are famous for fish fossils. Vertebrates described in earlier studies include psammosteids (Obruchev & Mark-Kurik 1965; Mark-Kurik 1968, 1995), placoderms (Karatajūtė-Talimaa 1963), acanthodians (Valiukevičius 1998), and sarcopterygians (Vorobyeva 1977). Chondrichthyans have not been mentioned or described so far from these beds.

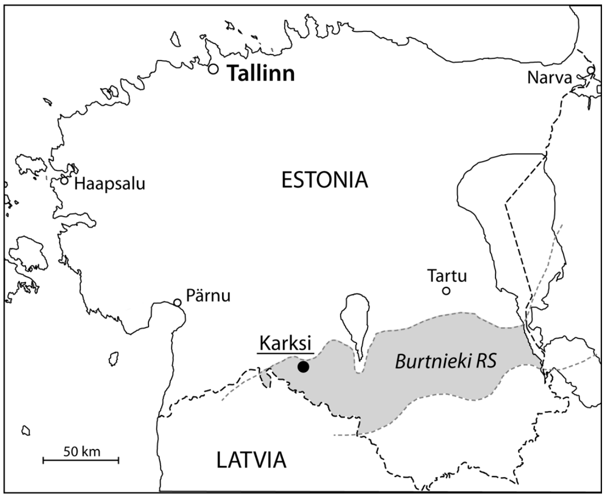


Fig. 1. Distribution of the Burtnieki Regional Stage and location of the Karksi outcrop.

In this paper we describe scales of a new chondrichthyan from the Karksi outcrop, Estonia. The authorship of the new taxon *Karksilepis parva* is attributed herein to Märss.

MATERIAL AND METHODS

Six samples (200–400 g) were collected from four levels of the Karksi outcrop (Fig. 2) and examined. All samples, those previously collected by A. Kleesment in 1990 and 1997 and the ones from two new levels

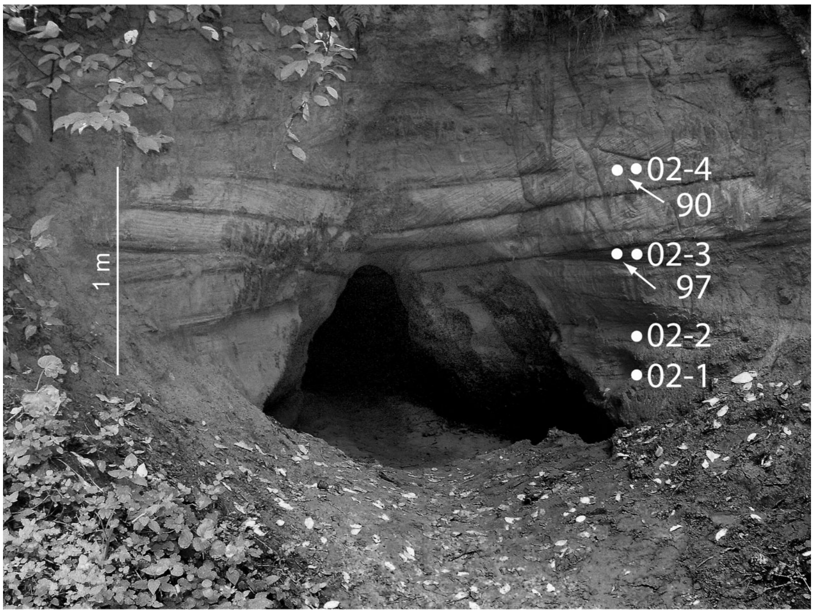


Fig. 2. Karksi outcrop. Levels of sampling.

(samples 02-1 and 02-2) contained abundant vertebrate microremains. Scales and tesserae or fragments of plates of heterostracans, placoderms, acanthodians, chondrichthyans, and osteichthyans (sarcopterygians and actinopterygians) were found (see Table 1). Psammosteids predominated, especially plate fragments and scales of *Tartuosteus maximus*, *Pycnosteus tuberculatus*, and *Ganosteus stellatus*. The diversity of acanthodians was high (16 taxa), and *Nostolepis gaujensis* scales were found for the first time in the Burtnieki RS (they were absent only in sample 02-3). Chondrichthyans were fairly rare but present in all six samples. In addition to the scales of the new taxon described herein, the samples contained teeth of an elasmobranch. As there was no indication that these teeth might belong to the taxon described below (except their co-occurrence in the samples from the same outcrop), they will be described elsewhere. Scales, plate fragments, and teeth of Sarcopterygii were found as well. Actinopterygians were represented by rare scales of *Cheirolepis* sp. (Kleesment et al. 2003; Märss et al. 2003).

The sandstones in the Karksi outcrop were very weakly cemented and did not need acid preparation. Samples were carefully washed to remove muddy (<0.01 mm) particles. Then the material was fractioned and sieved; the size ranges were 0.1–0.25 mm, 0.25–0.5 mm, 0.5–1 mm, 1–2 mm, and >2 mm. The two finest fractions were separated to heavy and light parts using bromoform (2.89 g/cm^3). The two heavy fractions obtained, and the two coarsest fractions were investigated using the binocular optical microscope. All microremains with well-preserved sculpture and shape were picked

Table 1. Distribution of vertebrate microremains in samples from the Karksi outcrop

Vertebrate taxa		Karksi 02-1	Karksi 02-2	Karksi 02-3	Karksi 97	Karksi 90	Karksi 02-4
Heterostraci	*Tartuosteus maximus*	xxx	x	x	x?	x	x
(Psammosteida)	*Pycnosteus tuberculatus*	xxx	xx	xx	xx	x	xx
	Ganosteus stellatus	x?	x?	–	x	–	x
	Psammosteus bergi	x?	–	–	x?	–	x?
	Psammosteidae gen. et sp. indet.	xx	xxx	xxx	xxx	xx	xxx
Placodermi		xx	xx	x	xx	–	xxx
Acanthodii	*Diplacanthus carinatus*	xx	x	–	x	x	x
	Diplacanthus sp.	xx	x	x	–	–	x
	Ptychodictyon rimosum	xx	x	xx	x	x	x
	Ptychodictyon sulcatum	xxx	xxx	xxx	xx	xx	xx
	Cheiracanthus longicostatus	x	x	x	x	x	–
	Cheiracanthus brevicostatus	xx	x	x	x	x	x
	Cheiracanthus sp.	x	–	x	x	–	x
	Cheiracanthus sp. nov. A	x	–	–	x	–	–
	Nostolepis gaujensis	x	xx	–	x	x	x
	Rhadinacanthus multisulcatus	–	x	–	–	x	–
	Rhadinacanthus sp.	–	–	x	–	–	x
	Acanthoides sp.	xx	–	–	–	–	–
	Acanthoides sp. A	–	–	–	–	x	–
	Acanthoides sp. B	–	–	–	x	x	x
	Acanthoides sp. D	–	–	–	xx	x	xx
	Acanthodii gen. et sp. indet.	x	xx	xx	–	–	–
Chondrichthyes	*Karksilepis parva* gen. et sp. nov.	x	x	x	x	x	x
	Elasmobranchii gen. et sp. (teeth)	x	–	–	–	–	x
Sarcopterygii		xxx	xx	xx	xxx	x	xxx
Actinopterygii	*Cheirolepis* sp.	–	x	–	x	–	–

Findings of vertebrate microremains: x, rare; xx, common; xxx, abundant; – not found.

out. The microstructure of chondrichthyan scales was examined in thin sections or by submerging elements into immersion liquids. A selection of scales was photographed using the scanning electron microscope JEOL-JSM-940-A. The described collection is housed in the Institute of Geology at Tallinn University of Technology under the collection numbers GIT 383 + specimen number.

GEOLOGICAL BACKGROUND

The Middle Devonian Burtnieki RS is distributed in southeastern Estonia (Fig. 1). The total thickness of the stage is 60–95 m. The sequence is represented by light (white, yellowish, pinkish, and greyish-brown) fine-grained weakly cemented cross-bedded sandstones with siltstone and clay interlayers. The stage is divided into three successive cyclic sandstone complexes, the Härma, Koorküla, and Abava beds (Kleesment 1995; Kleesment & Mark-Kurik 1997). The lower unit, the Härma Beds, is 13–28 m thick. The beds cropping out in Karksi belong to the lower part of the Härma Beds. The cross-bedded sandstones of the Härma Beds with the stratotype section in Härma settlement at the Õhne River are usually well sorted and fine-grained, where the size fraction 0.1–0.25 mm clearly dominates (75–93%; Kleesment 1995). The sandstones in the Karksi outcrop and coeval sediments at the Ahja River and in the Tõrva area have the same composition as the Härma Beds. Sandstones of the Härma Beds possibly accumulated in regressive conditions of the Devonian basin in a fluvially dominated subaqueous delta plain environment, which was under influences of low-amplitude eustatic and tectonic movements, repeatedly interrupted by short subaerial periods (Kleesment 1997; Plink-Björklund & Björklund 1999).

The part of the Karksi outcrop that yielded fish microremains is a small sandstone scarp 3.5 m high and 6 m long. About 20 m upstream, in the upper part of the slope there is another, smaller fish-bearing locality. The levels with abundant fish microremains are represented by moderately sorted fine- to medium-grained sandstones which contain both particle types in equal amounts and up to 10% coarse and very coarse detrital material. In the coarse-grained (diameter 0.5–2 mm) detrital material, heterostracan, placoderm, and sarcopterygian plate fragments are fairly worn. Acanthodian and chondrichthyan scales are concentrated in beds with the grain size of 0.2–0.5 mm and are not worn, which gives evidence of more rapid accumulation of sediment. Probably the reworking and weathering of fish bones and plates took place in shore face environments, where under low-amplitude eustatic movements, sea level fluctuations caused repeated alternation of marine and non-marine conditions and intense redeposition and reworking of the detrital component. Interlayers with rich, well-preserved fish microremains possibly deposited in the nearshore realm during short periods of intense influx of detrital material. Such rapid burial in nearshore deltaic conditions resulted in the accumulation of well-preserved fish microremains. In these layers, besides moderate sorting of detrital material among fine-grained particles, subrounded to subangular quartz grains dominate (85–90%); in the coarse-grained fraction, rounded grains make up only 25–30%, referring to intense influx and rapid deposition. Such high concentrations of fish remains have been reported from nearshore marine (Davies et al. 2007), deltaic (Mancuso 2003), and lake deposits (Smith & Swart 2002).

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes

Order *et* Family *incertae sedis*

Karksilepis gen. nov. Märss

Derivation of name. From Karksi locality yielding scales of this taxon, and *lepis*, meaning scale, gender feminine.

Type species. *Karksilepis parva* gen. et sp. nov. Märss

Diagnosis. As for type species.

Karksilepis parva gen. et sp. nov. Märss

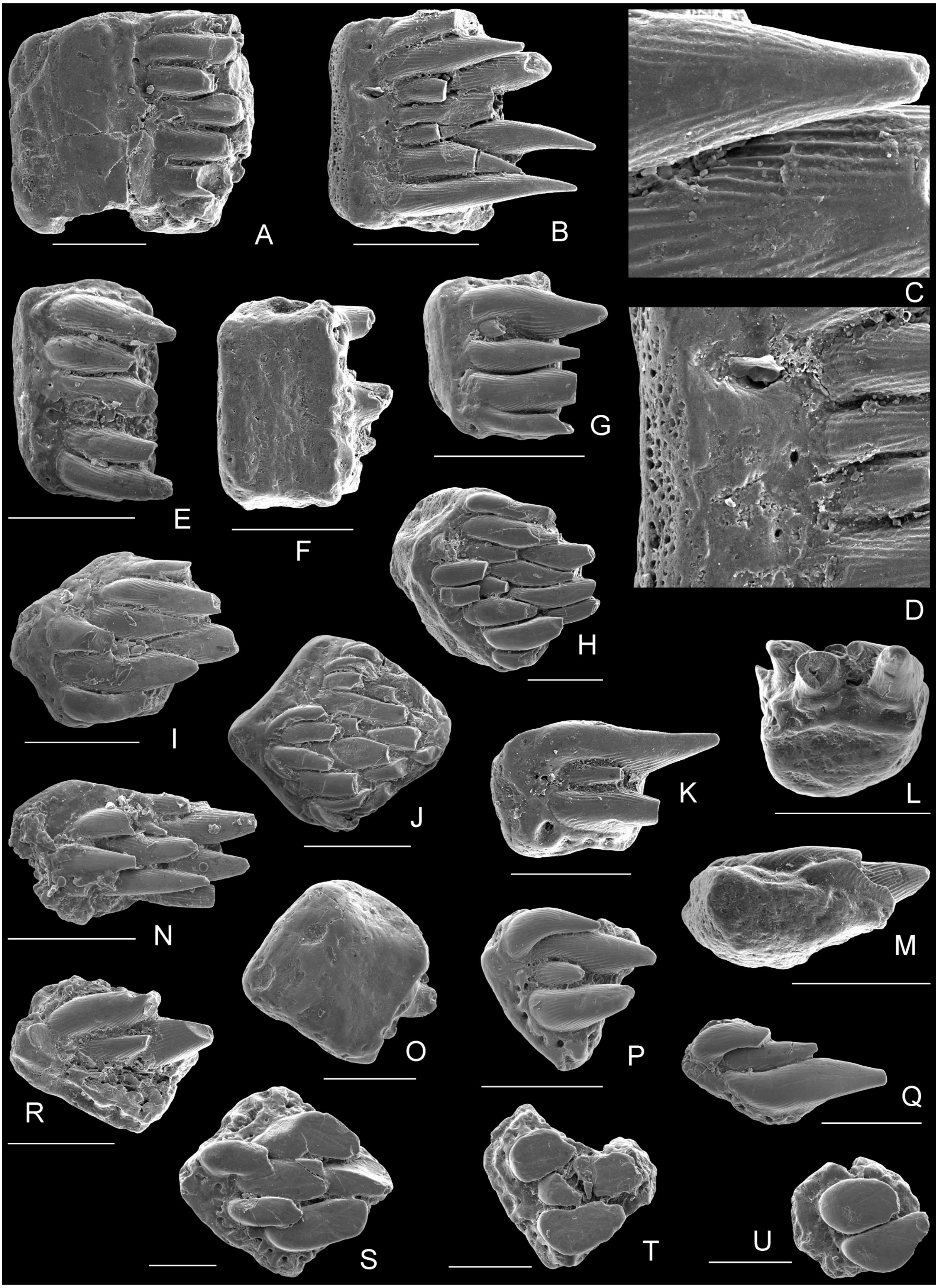
Figures 3–5

Chondrichthyes gen. et sp.: Märss 2006, figs 7A, B.

Derivation of name. Latin *parvus*, meaning small, an allusion to the size of the scales.

Holotype. GIT 383-4, scale in Fig. 3B, and its details in Fig. 3C, D.

Fig. 3. Scales of *Karksilepis parva* gen. et sp. nov. Märss. **A**, GIT 383-3; **B**, GIT 383-4; **C**, close-up of B; **D**, close-up of B; **E**, GIT 383-30; **F**, GIT 383-2; **G**, GIT 383-29; **H**, GIT 383-18; **I**, GIT 383-26; **J**, GIT 383-17; **K**, GIT 383-1; **L**, GIT 383-23; **M**, GIT 383-5; **N**, GIT 383-28; **O**, GIT 383-27; **P**, GIT 383-25; **Q**, GIT 383-24; **R**, GIT 383-6; **S**, GIT 383-15; **T**, GIT 383-20; **U**, GIT 383-22. A, B, E, G–K, N, P–U, scales in crown view; F, O, scales in base view; L, a scale in posterior view; M, a scale in lateral view. A, F, H, K, L, Q–U, Karksi outcrop, sample 02-4; B = C = D, J, M, Karksi outcrop, sample 97; E, G, N, Karksi outcrop, sample 02-2; I, O, P, Karksi outcrop, sample 02-1. Scale bars 0.25 mm.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Type locality and horizon. Karksi outcrop (sample 97), South Estonia; Härma Beds, Burtnieki Regional Stage, Middle Devonian.

Material. 50 scales, fairly well preserved.

Occurrence. In four levels in Karksi outcrop (see Table 1 and Fig. 2).

Diagnosis. Scales very small to medium-sized, quadrangular (rectangular to rhomboidal), 0.25–0.8 mm long and 0.25–0.7 mm wide. Three to eighteen elongate, partly overlapping longitudinal odontodes on the scale surface; odontode width 0.05–0.1 mm and length 0.15–0.4 mm. Lower face of basal plate convex. Very fine dentine tubules in odontodes branch from wider dentine canals, and the latter in turn from pulp canal; vascular canals form network beneath odontodes in the basal plate; openings of vascular canals situated around odontodes. Flattened bone cell lacunae form lamellar structure of the basal plate. Sharpey fibres very fine.

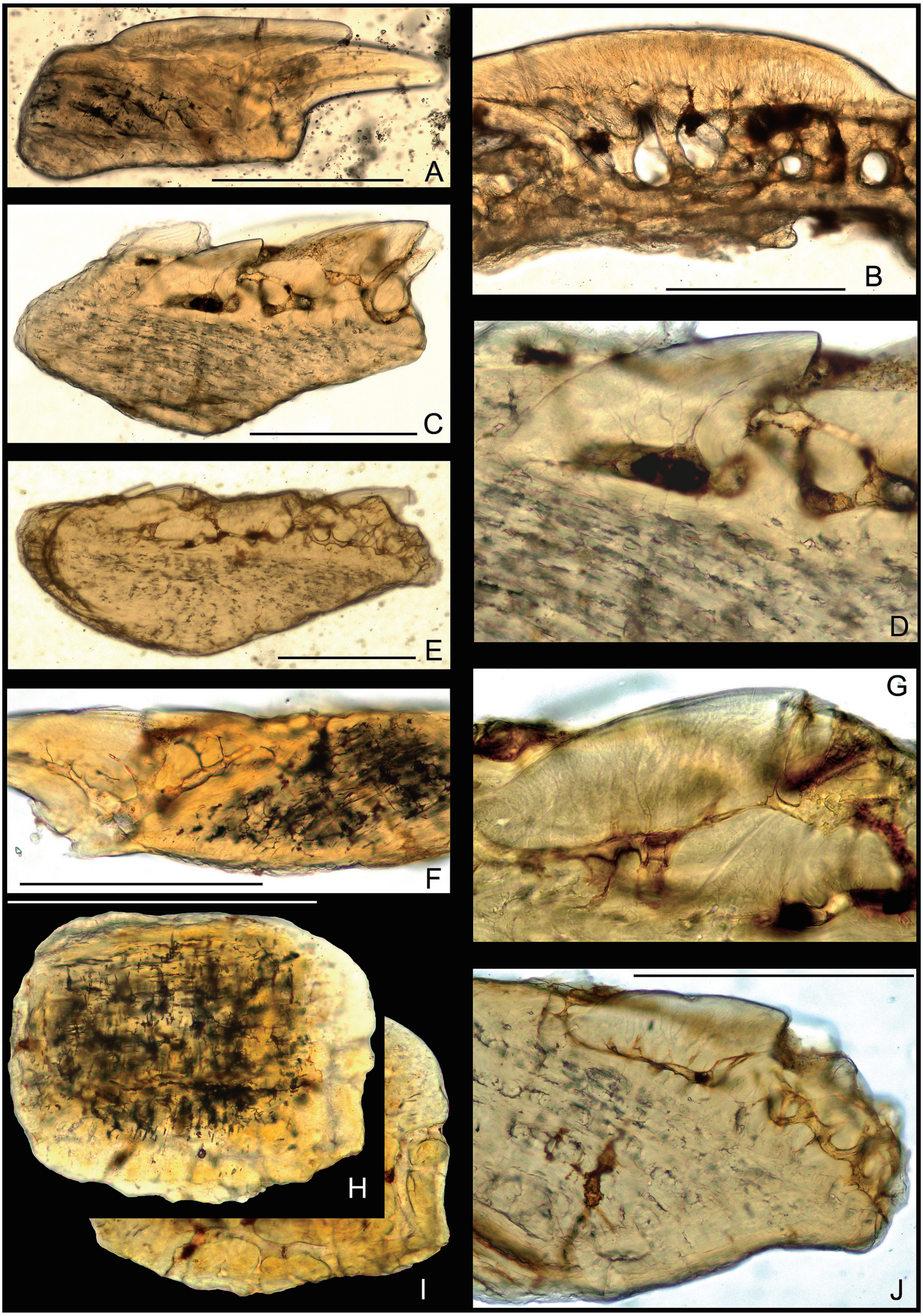
Description

Morphology. The scales are small to medium-sized, quadrangular, with the shape varying from high rectangle to relatively low rhomboid (Fig. 3A, B, E–K, N, P, Q). The length of the scales is 0.25–0.8 mm and width 0.25–0.7 mm. The height of the basal plate is about half the height of the scale (Fig. 3L). The scales are covered with odontodes forming polyodontodia. The number of odontodes varies from three (Fig. 3Q) to eighteen (Fig. 3J); their width is 0.05–0.1 mm and length 0.15–0.4 mm. The odontodes are attached to the basal plate of the scale. The rectangular high scales carry odontodes in one to two rows (Fig. 3A, B, E, G); the odontodes on rhomboidal scales are less regularly arranged in rows but still up to four rows can be counted (Fig. 3H, J, N), whereas more anterior odontodes partly cover the posterior ones. There is always lateral separation between adjacent odontodes (e.g. Fig. 3A, E, K). The odontodes can be directed horizontally (Fig. 3M) or rise to the posterior (Fig. 3K; see also Fig. 4). All odontodes are covered with fine ultrasculpture of longitudinal striation which starts at the conjunction of the odontode and basal plate and is directed upwards and posteriorwards, towards the peak of the odontode (Fig. 3A–E, G, I, K, M). The basal plate is larger than the area with odontodes. In some scales the basal plate strongly protrudes anteriorly (Fig. 3A). Relatively large deep pores open in the basal plate (Fig. 3G, K–M, P, Q) and make the surface of the plate uneven. The shape of the basal plate depends on the age of the scale. Vascular network canals open anteriorly of the odontodes in high rectangular scales (Fig. 3B, E, G) or around the odontodes in rhomboidal scales (Fig. 3K–M, P, Q). The lower surface of the basal plate can be either concave, smooth (Fig. 3F), or convex (Fig. 3L, M, O).

A few rhomboidal to roundish scales have their basal plates covered with several (two to seven) odontodes with a flat and smooth surface. The length of these scales is 0.45–0.75 mm and width 0.3–0.7 mm (Figs 3S–U; 5D). The width of the odontodes is 0.1–0.2 mm and length 0.2–0.4 mm. The odontodes are oval (Fig. 3T, U) to oblong (Fig. 3S), more than twice as long as their width. The odontodes lie close to each other (Fig. 3T, U), some space may be between the anterior odontodes and the neighbouring ones (Fig. 3S). Anterior odontodes partly cover the odontodes situated behind them; their posterior apices are usually broken (Fig. 3S). On the sides of odontodes the surface is finely striated. The basal plate is convex, slightly larger than the crown (Fig. 3S–U). The pores occur in the facets of the basal plate and on the plate around the odontodes, making the surface of the plate uneven.

Histology. Vertical longitudinal (Fig. 4A–G, J), horizontal (Figs 4H, I; 5A, B), and vertical cross-sections (Fig. 5C) were made from both juvenile (Figs 4B; 5A, B) and mature (Figs 4A, C–J; 5C, D) scales. Very fine branching dentine tubules occur in the odontodes (Fig. 4B, D, G, J). They branch from wider dentine canals (Figs 4B–G, J; 5B), and pulp canals, which in turn are connected with the vascular canal network beneath the odontodes (Figs 4C, E, F, I, J; 5B, C). At least one dentine canal extends into each odontode. Vascular canals open on the surface of the basal plate around the odontodes. The basal plate contains tightly packed flattened osteocyte lacunae (Fig. 3C–F, H, J), which give the basal plate structure lamellar appearance. Very fine Sharpey fibre tubules occur in the basal plate (Fig. 5A). One sectioned scale with flat and smooth odontodes (Fig. 5D) has microstructure identical to that of other scales.

Fig. 4. Microstructure of the scales of *Karksilepis parva* gen. et sp. nov. Märss. **A**, scale GIT 383-38 in vertical longitudinal section; **B**, medial part of the scale GIT 383-31 in vertical longitudinal section; **C**, scale GIT 383-35 in vertical longitudinal section; **D**, close-up of C; **E**, scale GIT 383-33 in vertical longitudinal section; **F**, posterior part of the scale GIT 383-37 in vertical longitudinal section; **G**, close-up of E; **H**, **I**, scale GIT 383-39 in horizontal section; photos focused on different levels to show bone cell lacunae in the middle part of the basal plate (H) and vascular canals on the upper part of the basal plate (I); **J**, posterior part of the scale GIT 383-34 in vertical longitudinal section. A, F, Karksi outcrop, sample 02-1; B–D, Karksi outcrop, sample 02-4; E, J, Karksi outcrop, sample 90; H = I, Karksi outcrop, sample 97. Scale bars 0.25 mm.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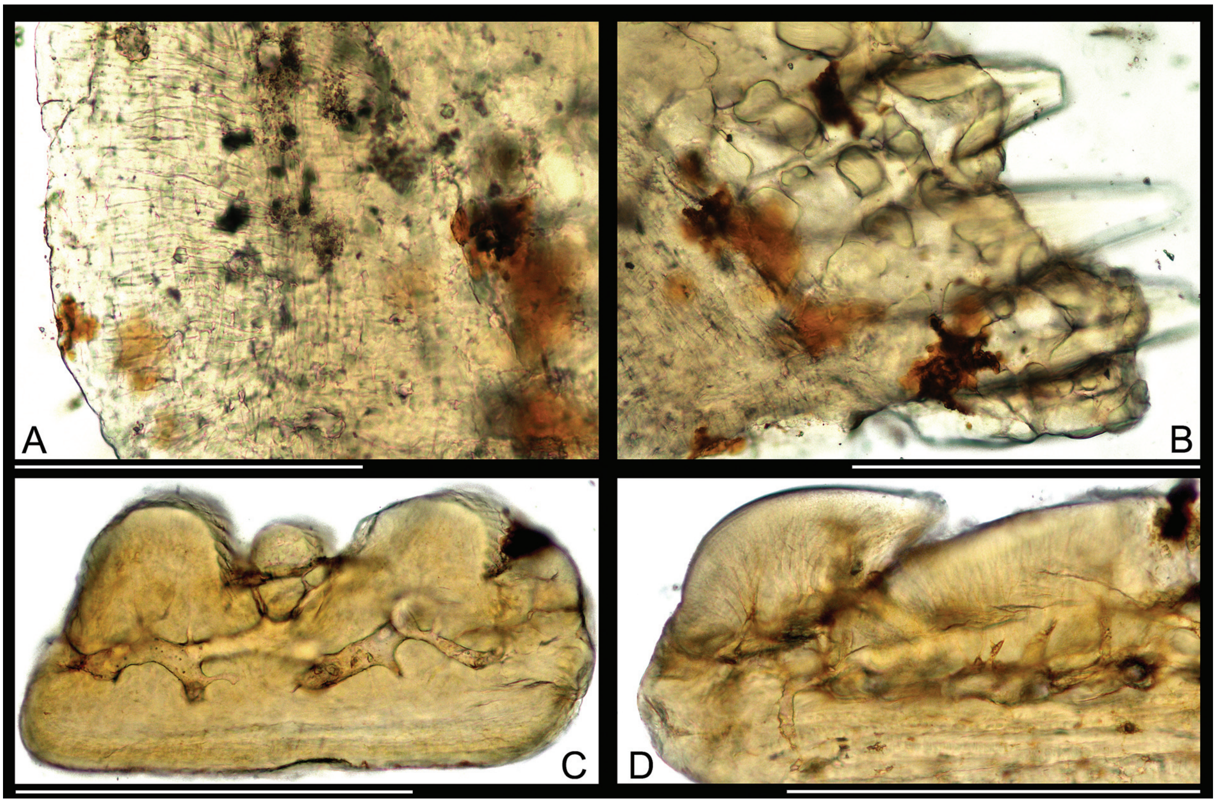

Fig. 5. Microstructure of the scales of *Karksilepis parva* gen. et sp. nov. Märss. **A**, **B**, horizontal section of the scale GIT 383-40; A, the section shows the anterior part of the scale with Sharpey fibre tubules, B, the section shows the vascular canal network beneath the spines in the basal plate; **C**, vertical cross section of the scale GIT 383-41; **D**, vertical longitudinal section of the scale GIT 383-36. A–C, Karksi outcrop, sample 02-1; D, Karksi outcrop, sample 02-4. Scale bars 0.25 mm.

DISCUSSION

Karksilepis gen. nov. is similar to osteostracans by having bone cell cavities in its exoskeleton. Osteostracans have distinct radial structure of peripheral sections of the base of tesserae, which are absent on the basal plate of *Karksilepis* gen. nov. In *Karksilepis* gen. nov. the upper layer is comprised of orthodentine, in osteostracans (if present) the equivalent layer consists of mesodentine. *Karksilepis* gen. nov. differs from osteostracans in having a specific vascular canal network in the basal plate below the odontodes. The ultrasculpture of striation is present in thelodonts, heterostracans, osteostracans, and in *Karksilepis parva* gen. et sp. nov. The convex basal plate of the scales of *Karksilepis* gen. nov. is superficially similar to the scale base of acanthodians but their crown sculpture and growth of the scale are different.

The greatest similarities can be found between *Karksilepis* gen. nov. and some chondrichthyan taxa. Chondrichthyans constitute a very diverse group, with the representatives having very different features. In the elasmobranch chondrichthyan taxa *Elegestolepis* Karatajūtė-Talimaa, *Kannathalepis* Märss & Gagnier, and *Ellesmereia* Vieth monodontodia are simple, the crown has one pulp cavity, one neck, and one basal canal, while *Karksilepis* gen. nov. Märss has complex polyodontodia. A possible elasmobranch *Seretolepis* Karatajūtė-Talimaa has peculiar lamelliform odontodes on the crown, the base built from aspidine, and basal and neck openings. *Knerialepis* Hanke & Karatajūtė-Talimaa has the scales whose odontodes consist of mesodentine and the basal plate of aspidine. Vascular canals are developed between the basal plate and the crown, making *Knerialepis* similar to *Karksilepis*, but the sculpture in the former consists of posteriorly fusing wedge-shaped flat odontodes. In *Altholepis* Karatajūtė-Talimaa the crown is formed of a great number of narrow anchor-shaped odontodes pointed posteriorly; the scale crown is built from orthodentine and the base – from aspidine. *Ivanelepis* Karatajūtė-Talimaa has scales with a few oblong odontodes and neck and basal openings. *Arauzia* Mader is defined as a possible hybodontiform taxon with rather high scales with upwards directed odontodes of cyclomorial growth and vascular canal openings in the neck and base (Mader 1986). The cladoselachid taxa *Iberolepis* Mader and *Lunalepis* Mader have the scale crown and microstructure somewhat resembling those of acanthodians (ibid.). The possible chondrichthyans *Frigorilepis* Märss et al. and *Wellingtonella* Märss et al. have monodontode scales without neck canals. In chondrichthyan scales, the neck canals can be present or absent in the same fish, for example, the fin scales of *Polymerolepis* Karatajūtė-Talimaa lack neck canals (G. Hanke, pers. comm. 2008) while the scales of other parts of the body have them (see also Karatajūtė-Talimaa 1998).

Karatajūtė-Talimaa (1997b) erected the elasmobranch order Lugalepidida based on the characteristics of pectoral and pelvic fins, complex scales in which the odontodes (polyodontodia) of the crown are formed of orthodentine, and the non-growing base of acellular bone tissue; there is no horizontal canal system on the boundary between the crown and the basal plate. According to Karatajūtė-Talimaa (ibid.), this order differs from Mongolepidida, whose representatives have scales with a growing base and odontodes of lamelline forming longitudinal odontocomplexes of the crown. *Karksilepis parva* gen. et sp. nov. is externally rather similar to *Lugalepis multispinata*, which comes from the Emsian(?) and Eifelian of Lithuania, Latvia, Belarus, and Kaliningrad District, Russia (Karatajūtė-Talimaa 1997b). Both taxa have scales whose crowns consist of numerous spiniform odontodes. Karatajūtė-Talimaa (1997b) defined such scales in *L. multispinata* as polyodontodia of synchronomorial type. Nevertheless, these taxa differ in that the upper surface of odontodes of *L. multispinata* has a longitudinal groove in the medial part, while *K. parva* gen. et sp. nov. possesses spines with round cross section. Only *K. parva* gen. et sp. nov. has ultrasculpture of fine striation. The basal plate of the scales of *L. multispinata* consists of a spongy acellular bone tissue and thin basal lamina, but our new taxon has flattened bone cell lacunae forming the lamellar structure of basal plates.

The scales of Cladodontida also are formed of orthodentine and the basal plate of scales is either of cellular bone tissue (in *Cladolepis*) or acellular (in *Ohiolepis* and *Protacrodus*) (Gross 1973). Karatajūtė-Talimaa (1997b) noted that some Mongolepidida (*Mongolepis*, *Sodolepis*) have an acellular bone developed in the base of scales and some (*Teslepis*) have a cellular bone with fusiform bone cells; the horizontal system of canals is present in both Mongolepidida and Cladodontida. It would be most appropriate to accommodate *Karksilepis* gen. nov., having orthodentine in the complex odontodes, horizontal canal network beneath the odontodes in the basal plate, and a cellular bone in the base, within the Cladodontida. Difficulties rise when considering the growth of the crown. In Cladodontida odontodes of approximately the same size were added areally, forming rather regular ring-like zones (Karatajūtė-Talimaa 1992), while in *Karksilepis* gen. nov. they occur in irregular rows. As a conclusion, at present we prefer to leave the family and order for *Karksilepis parva* gen. et sp. nov. Märss open.

RESULTS

Based on the features of scale sculpture, the vascular canal network, and the placement of the canal openings beneath the odontodes in the basal plate, a new chondrichthyan of uncertain order and family, *Karksilepis parva* gen. et sp. nov. Märss, is established with specimens from the Härma Beds, Burtnieki Regional Stage, Karksi outcrop, Estonia. This is the first time that chondrichthyan dermal scales were discovered in Estonia. Previously only chondrichthyan buccopharyngeal denticles have been documented from the region (Mark-Kurik & Karatajūtė-Talimaa 2004). The teeth of an elasmobranch from the same outcrop will be discussed in another study.

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REFERENCES

Davies, N. S., Sansom, I. J., Albanesi, G. L. & Cespedes, R. 2007. Ichnology, palaeoecology and taphonomy of a Gondwanan early vertebrate habitat: insights from the Ordovician Anzaldo Formation, Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **249**, 18–35.

Gross, W. 1973. Kleinschuppen, Flossenstacheln und Zähne von Fischen aus Europäischen und Nordamerikanischen Bonebeds des Devons. *Palaeontographica Abt. A*, **142**, 51–155.

Hanke, G. & Karatajūtė-Talimaa, V. 2002. *Knerialepis*, a new generic name to replace *Kneria* Karatajūtė-Talimaa 1997. *Journal of Vertebrate Paleontology*, **22**, 703.

Hanke, G. F. & Wilson, M. V. H. 1997. Examination of shark-like scales from the Mackenzie Mountains, Northwest Territories, Canada. In *Circum-Arctic Palaeozoic Vertebrates: Biological and Geological Significance* (Wilson, M. V. H., ed.), *Ichthyolith Issues Special Publication*, **2**, 15.

Hanke, G. F. & Wilson, M. V. H. 1998. Structure and variation of acanthodian and chondrichthyan scales from the Lower Devonian of the Mackenzie Mountains, Canada. In *Circum-Arctic Palaeozoic Faunas and Facies* (Ginter, M. & Wilson, M. V. H., eds), *Ichthyolith Issues Special Publication*, **4**, 18–19.

Ivanov, A. & Lukševičs, E. 1994. Famennian chondrichthyans from the Main and Central Devonian Fields. *Daba un muzejs*, **5**, 24–29.

Karatajūtė-Talimaa, V. N. 1963. Genus *Asterolepis* from the Devonian deposits of the Russian platform. In *Voprosy geologii Litvy* [*Problems of Lithuanian geology*] (Grigelis, A. & Karatajūtė-Talimaa, V. N., eds), pp. 65–223. Institut geologii i geografii AN Litovskoj SSR, Vilnius [in Russian].

Karatajūtė-Talimaa, V. N. 1968. New Thelodonti, Heterostraci and Arthrodina from the Chortkov Stage of Podolia. In *Ocherki po filogenii i sistematike iskopaemykh ryb i beschelyustnykh* [*Essays on the phylogeny and systematics of fossil fishes and agnathans*] (Obruchev, D. V., ed.), pp. 33–42. Nauka, Moscow [in Russian].

Karatajūtė-Talimaa, V. N. 1973. *Elegestolepis grossi* gen. et sp. nov. ein neuer Typ der Placoidschuppe aus dem oberen Silur der Tuwa. *Palaeontographica Abt. A.*, **143**, 35–50.

Karatajūtė-Talimaa, V. N. 1977. Structure and systematic position of the scales of *Polymerolepis whitei* Kar.-Tal. In *Ocherki po filogenii i sistematike iskopaemykh ryb i beschelyustnykh* [*Essays on the phylogeny and systematics of fossil fishes and agnathans*] (Menner, V. V., ed.), pp. 46–60. Nauka, Moscow [in Russian].

Karatajūtė-Talimaa, V. 1992. The early stages of the dermal skeleton formation of chondrichthyans. In *Fossil Fishes as Living Animals* (Mark-Kurik, E., ed.), pp. 223–231. *Academia*, **1**, Tallinn.

Karatajūtė-Talimaa, V. 1995. The Mongolepidida: scales structure and systematic position. *Geobios, Mémoire spécial*, **19**, 35–37.

Karatajūtė-Talimaa, V. 1997a. Chondrichthyan scales from Lochkovian (Lower Devonian) of Podolia (Ukraine). *Geologija*, **22**, 5–17.

Karatajūtė-Talimaa, V. 1997b. *Lugalepis* – a new genus of Elasmobranchs from Devonian of the western part of the Main Devonian Field. *Geologija*, **21**, 24–31.

Karatajūtė-Talimaa, V. 1998. Determination methods of the exoskeletal remains of Early Vertebrates. *Mitteilungen aus dem Museum für Naturkunde in Berlin Geowissenschaftliche Reihe*, **1**, 21–52.

Karatajūtė-Talimaa, V. N. & Novitskaya, L. I. 1992. *Teslepis* – a new representative of mongolepid elasmobranchs from the Lower Silurian of Mongolia. *Paleontologicheskij Zhurnal*, **4**, 36–46 [in Russian].

Karatajūtė-Talimaa, V. N. & Novitskaya, L. I. 1997. *Sodolepis* – a new representative of mongolepidids (Chondrichthyes ?) from the Lower Silurian of Mongolia. *Paleontologicheskij Zhurnal*, **5**, 96–103 [in Russian].

Karatajūtė-Talimaa, V. & Predtechenskyj, N. 1995. The distribution of the vertebrates in the Late Ordovician and Early Silurian palaeobasins of the Siberian Platform. In *Etudes sur les Vertebres inferieurs*. *VII^e Symp. Intern., Parc de Miguasha, Quebec, 1991* (Arsenault, M., Lelievre, H. & Janvier, P., eds), *Bulletin du Museum National d'Histoire Naturelle (Paris), Série 4*, **17**, 39–56.

Karatajūtė-Talimaa, V. N., Novitskaya, L. I., Rozman, K. S. & Sodov, J. 1990. *Mongolepis* – a new Lower Silurian genus of elasmobranchs from Mongolia. *Paleontologicheskij Zhurnal*, **1**, 76–86 [in Russian].

Kleesment, A. 1995. Lithological characteristics of the uppermost terrigenous Devonian complex in Estonia. *Proceedings of the Estonian Academy of Sciences, Geology*, **44**, 221–233.

Kleesment, A. 1997. Devonian sedimentation basin. In *Geology and Mineral Resources of Estonia* (Raukas, A. & Teedumäe, A., eds), pp. 205–208. Estonian Academy Publishers, Tallinn.

Kleesment, A. & Mark-Kurik, E. 1997. Devonian. Lower Devonian. Middle Devonian. In *Geology and Mineral Resources of Estonia* (Raukas, A. & Teedumäe, A., eds), pp. 107–121. Estonian Academy Publishers, Tallinn.

Kleesment, A., Märss, T. & Niit, M. 2003. The Devonian of Estonia and the study of its vertebrate microfossils at the beginning of the new century. In *The Fourth World Meeting of Estonian Geologists. Estonian Geology in the Beginning of the New Century. Conference Materials and Excursion Guide* (Plado, J. & Puura, I., eds), pp. 31–33. The Geological Society of Estonia and Institute of Geology, Tallinn, and University of Tartu, Tartu [in Estonian].

Langenstrassen, F. & Schultze, H.-P. 1996. Unterdevonische Fischfunde aus Sedimenten des Flachmeerbereiches der kanadischen Arktis. *Neues Jahrbuch für Geologie und Paläontologie Abhandlung*, **201**, 33–93.

Leleshus, V., Mark-Kurik, E. & Karatajūtė-Talimaa, V. 2005. Devonian fishes from Tajikistan. In *Middle Palaeozoic Vertebrates of Laurussia: Relationships with Siberia, Kazakhstan, Asia and Gondwana* (Ivanov, A. & Young, G., eds), *Ichthyolith Issues*, **9**, 22–26.

Mader, H. 1986. Schuppen und Zähne von Acanthodiern und Elasmobranchiern aus dem Unter-Devon Spaniens (Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie*, **28**, 1–59.

Mancuso, A. C. 2003. Continental fish taphonomy: a case study in the Triassic of Argentina. *Journal of South American Earth Sciences*, **16**, 275–286.

Mark-Kurik, E. 1968. New finds of psammosteids (Heterostraci) in the Devonian of Estonia and Latvia. *Eesti NSV Teaduste Akadeemia Toimetised, Keemia, Geoloogia*, **17**, 409–424.

Mark-Kurik, E. 1995. Muistsed kalad ja nende kivistised Eestis [Ancient fishes and their fossils in Estonia]. *Eesti Loodus*, 8, 226–228 [in Estonian].

Mark-Kurik, E. & Karatajūtė-Talimaa, V. 2004. Chondrichthyan remains from the Middle and Late Devonian of the Baltic area. *Archiv für Geschiebekunde*, **3**, 767–772.

Märss, T. 2006. Exoskeletal ultrasculpture of Early Vertebrates. *Journal of Vertebrate Paleontology*, **26**, 235–252.

Märss, T. & Gagnier, P.-Y. 2001. A new chondrichthyan from the Wenlock, Lower Silurian, of Baillie-Hamilton Island, the Canadian Arctic. *Journal of Vertebrate Paleontology*, **21**, 693–701.

Märss, T., Wilson, M. V. H. & Thorsteinsson, R. 2002. New thelodont (Agnatha) and possible chondrichthyan (Gnathostomata) taxa established in the Silurian and Lower Devonian of the Canadian Arctic Archipelago. *Proceedings of the Estonian Academy of Sciences, Geology*, **51**, 88–120.

Märss, T., Niit, M. & Kleesment, A. 2003. New findings of fish microremains in sections of the Burtnieki Regional Stage. In *The Gross Symposium 2. Advances in Palaeoichthyology*. *Riga, Latvia, September 8–14, 2003* (Schultze, H.-P., Lukševičs, E. & Unwin, D., eds), *Ichthyolith Issues Special Publication*, **7**, 42–43.

Märss, T., Wilson, M. V. H. & Thorsteinsson, R. 2006. Silurian and Lower Devonian thelodonts and putative chondrichthyans from the Canadian Arctic Archipelago. *Special Papers in Palaeontology*, **75**, 1–140.

Novitskaya, L. I. & Karatajūtė-Talimaa, V. N. 1986. Remarks about the cladistic analysis in connection with myopterygian hypothesis and the problem of the origin of gnathostomes. In *Morfologiya i evolyutsiya zhivotnykh* [*Morphology and evolution of animals*] (Vorobyeva, E. & Lebedkina, N., eds), pp. 102–125. Nauka, Moscow [in Russian].

Obruchev, D. V. & Karatajūtė-Talimaa, V. N. 1967. Vertebrate faunas and correlation of the Ludlovian – Lower Devonian in eastern Europe. *Journal of the Linnean Society (Zoology)*, **47**, 5–14.

Obruchev, D. V. & Mark-Kurik, E. 1965. *Psammosteidy (Agnatha, Psammosteidae) devona SSSR* [*Devonian psammosteids (Agnatha, Psammosteidae) of the USSR*]. ENSV TA Geoloogia Instituut, Tallinn, 304 pp. [in Russian, with English summary].

Plink-Björklund, P. & Björklund, L. 1999. Sedimentary response in the Baltic Devonian Basin to postcollisional events in the Scandinavian Caledonides. *GFF*, **121**, 79–80.

Rodina, O. A. 2002. Early Devonian mongolepid vertebrates of western Siberia. In *Geology of the Devonian System. Proceedings of the International Symposium. Syktyvkar,* *Komi Republic, July 9–12, 2002* (Yushkin, N. P., Tsyganko, V. S. & Männik, P., eds), pp. 106–108. Geoprint, Syktyvkar.

Sansom, I. J., Smith, M. M. & Smith, M. P. 1996. Scales of thelodont and shark-like fishes from the Ordovician of Colorado. *Nature*, **379**, 628–630.

Sansom, I. J., Aldridge, R. J & Smith, M. M. 2000. A microvertebrate fauna from the Llandovery of South China. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **90**, 255–272.

Smith, R. M. H. & Swart, R. 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid-Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of Central Namibia. *Palaios*, **17**, 249–267.

Turner, S. & Murphy, M. A. 1988. Early Devonian vertebrate microfossils from the Simpson Park Range, Eureka County, Nevada. *Journal of Paleontology*, **62**, 959–964.

Valiukevičius, J. 1998. Acanthodians and zonal stratigraphy of Lower and Middle Devonian in East Baltic and Byelorussia. *Palaeontographica Abt. A*, **248**, 1–53.

Vieth, J. 1980. Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie*, **23**, 1–69.

Vladimirskaya, E. V., Eltysheva, E. V., Krivobodrova, A. V., Karatajūtė-Talimaa, V. N. & Chekhovich, V. D. 1986. Problems of the Silurian paleobiography and stratigraphy of Tuva in connection with new data on brachiopods of Chergak series. *Zapiski Leningradskogo gornogo instituta*, **107**, 26–35 [in Russian].

Vorobyeva, E. 1977. *Morfologija i osobennosti evoljutsii kisteperykh ryb* [*Morphology and peculiarities of the evolution of lobe-finned fishes*]. Nauka, Moscow, 239 pp. [in Russian].

Wang, N. Z., Zhang, S. B., Wang, J. Q. & Zhu, M. 1998. Early Silurian Chondrichthyan microfossils from Bachu county, Xinjiang, China. *Vertebrata PalAsiatica*, **10**, 257–267.

Wilson, M. V. H. & Hanke, F. G. 1998. Body form and fin spines in species with scales of chondrichthyan growth pattern from the Lower Devonian of the Mackenzie Mountains, Canada. In *Circum-Arctic Palaeozoic Faunas and Facies* (Ginter, M. & Wilson, M. V. H., eds), *Ichthyolith Issues Special Publication*, **4**, 57–58.

Wilson, M. V. H., Hanke, G. F. & Soehn, K. L. 2000. Diversity and age of the Devonian vertebrate assemblage at MOTH, Mackenzie Mountains, Northwest Territories, Canada. In *Pan-Arctic Palaeozoic Tectonics, Evolution of Basins and Faunas* (Antoshkina, A., Malysheva, E. & Wilson, M. V. H., eds), *Ichthyolith Issues Special Publication*, **6**, 137–141.

Wrona, R. & Nyamsuren, G. 1998. New Early Devonian chondrichthyan scales (Chondrichthyes) from Eastern Mongolia. *Mongolian Geoscientist*, **10**, 79.

Young, G. C. 1997. Ordovician microvertebrate remains from the Amadeus Basin, central Australia. *Journal of Vertebrate Paleontology*, **17**, 1–25.

Karksilepis parva gen. et sp. nov. (Chondrichthyes) Kesk-Devoni Burtnieki lademest Eestis

Tiiu Märss, Anne Kleesment ja Moonika Niit

On kirjeldatud kõhrkala soomuseid, mis avastati Lõuna-Eestist Karksi paljandi liivakividest neljal tasemel. Liivakivid kuuluvad Kesk-Devoni Burtnieki lademe Härma kihtidesse. Uue taksoni *Karksilepis parva* gen. et sp. nov. Märss sugukonda ja seltsi ei ole hetkel võimalik täpsemalt määratleda.