

The Middle Devonian acanthodian assemblage of the Karksi outcrop in Estonia

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Abstract. The taxonomic composition of the acanthodian assemblage of the Karksi outcrop, Estonia, is discussed. Two new species, *Rhadinacanthus deltosquamosus* n. sp. (Diplacanthiformes, Diplacanthidae) and *Ginkgolepis tenericostatus* n. sp. (Acanthodiformes, Cheiracanthidae), are described based on isolated scales. A re-description of *Nostolepis gaujensis* Valiukevičius (Climatiiformes, Climatiidae) scales from this locality is also given. Three diplacanthiform taxa, *Diplacanthus* sp. cf. *D. crassissimus* (Duff), *Diplacanthus* sp. cf. *D. tenuistriatus* Traquair and Diplacanthiformes indet., are described in open nomenclature.

Key words: Acanthodii, new species, Middle Devonian, Burtneiki Regional Stage, Estonia.

INTRODUCTION

The acanthodian assemblages of the Burtneiki Regional Stage (RS) (Fig. 1A) on the Main Devonian Field were reviewed by J. Valiukevičius (Valiukevičius 1988, 1998, 2000). He established a zonal biostratigraphical scheme for the Lower and Middle Devonian in the East Baltic and Belarus (Valiukevičius 1998), in which the *Diplacanthus gravis* interval Zone corresponds to both the Aruküla and Burtneiki RSs. The only species of the

zonal assemblage, which is known exclusively from the Burtneiki RS, is *Homacanthus talavicus* Lyarskaya, represented by isolated fin spines. Therefore, this stratigraphic interval remains an important level for acanthodian research in the East Baltic.

Valiukevičius studied acanthodian assemblages of the Burtneiki RS primarily from the core sections (Valiukevičius 1994, 1998). The only outcrop where he diagnosed the *Diplacanthus gravis* Zone is that in the Halliste old valley, near Karksi castle (Viljandi county)

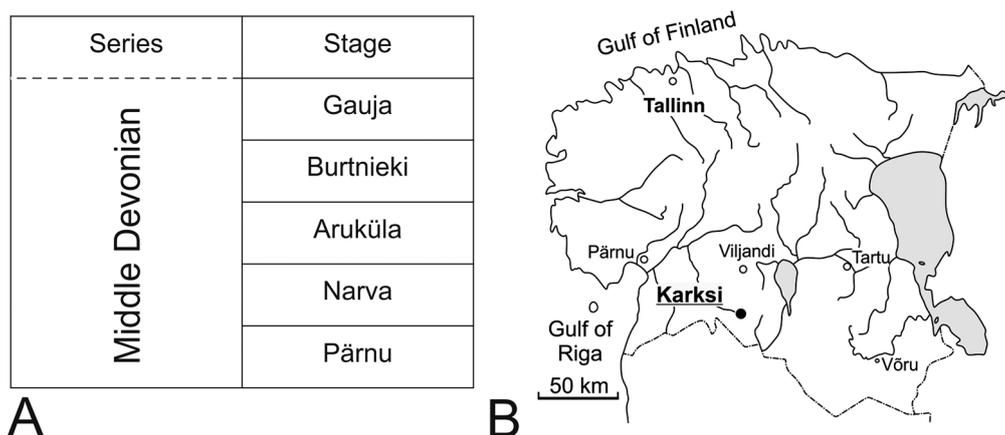


Fig. 1. A, fragment of the Middle Devonian stratigraphical chart of Estonia, showing the position of the Burtneiki Regional Stage. B, geographical location of the Karksi outcrop.

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(Valiukevičius 1998) (Fig. 1B). Overall, this outcrop is famous for an abundant association of vertebrate remains: psammosteids (Mark-Kurik 1968, 1995; Obruchev & Mark-Kurik 1965), placoderms (Karatajūtė-Talimaa 1963), sarcopterygians (Vorobyeva 1977), chondrichthyans (Märss et al. 2008; Ivanov et al. 2011; Ivanov & Märss 2014) and acanthodians (Valiukevičius 1998; Märss et al. 2008). It has been shown that the acanthodian assemblage of this locality is not only diverse and abundant, but also unique in including species new to science (Märss et al. 2008). For the first time the presence of *Nostolepis gaujensis* Valiukevičius scales in the Burtneiki RS was recorded in this locality (Märss et al. 2008).

The acanthodian material from the Karksi outcrop has not been illustrated yet and a description of the most interesting new acanthodian taxa from this locality has not been given. The main purpose of this article is to discuss the diversity of acanthodians of the Karksi outcrop and to give systematic description of previously unknown acanthodian taxa from this assemblage. A redescription of *N. gaujensis* scales from this locality is also provided.

MATERIAL AND METHODS

Ten sandstone samples (each 200–300 g) were collected from ten levels of the Karksi outcrop in 2015 (Fig. 2). The sandstones were weakly cemented and did not need acid preparation. Acanthodian microremains were hand-picked from the sand under a stereoscopic binocular microscope MBS-9. The best-preserved scales of each acanthodian taxon (both from the newly taken samples and from samples Karksi 90, 97, 02-1, 02-2, 02-3 and 02-4, examined previously by Märss et al. (2008), were coated with carbon and photographed under the scanning electron microscope Hitachi S-3400N in secondary electrons (SE) and back-scattered electrons (BSE) detection modes.

The thin sections of scales of *Nostolepis gaujensis* Valiukevičius, *Rhadinacanthus deltosquamosus* n. sp. and *Ginkgolepis tenericostatus* n. sp. were made using a polymethyl methacrylate thermoplastic Glass Fil (Print Product®) as a mounting medium and Mirka® Waterproof P1500 and P2500 finishing sandpapers. They were examined in a Leica DM4500 P polarization microscope using LAS V4.0 image capturing software. The collections of acanthodian remains, discussed in this article, are stored at the Department of Geology, Tallinn University of Technology (GIT), Estonia, and at St Petersburg State University and the Palaeontological Museum of St Petersburg State University (PM SPbSU).

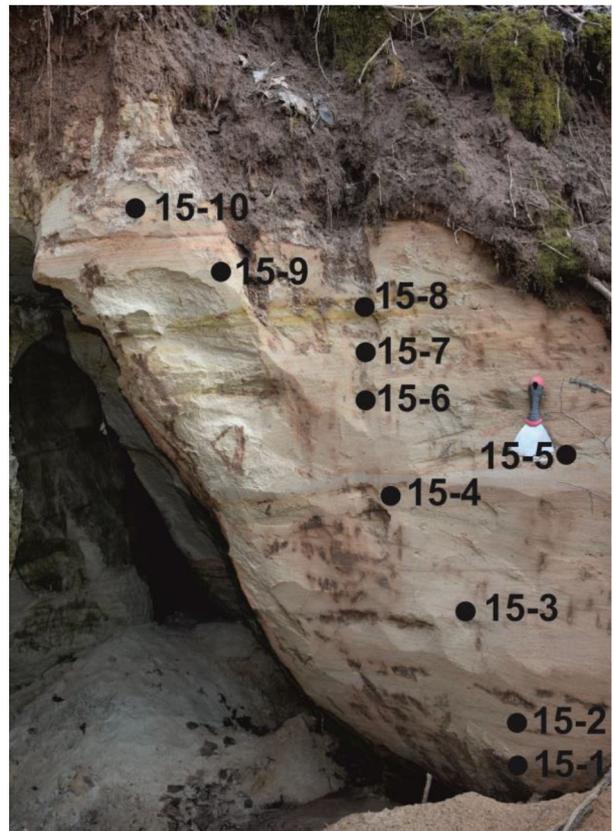


Fig. 2. Karksi outcrop. Levels of sampling.

THE ACANTHODIAN ASSEMBLAGE OF THE KARKSI OUTCROP

The samples studied previously (Märss et al. 2008), as well as those taken recently, contain abundant acanthodian microremains. However, the species composition of the assemblage, as well as relative abundance of the acanthodian taxa, is slightly different in these two groups of samples. The most significant differences are that *Nostolepis gaujensis* Valiukevičius scales (Fig. 3A–F) present in most of the previously studied samples (Märss et al. 2008) are absent in the recently taken ones, whereas *Ginkgolepis tenericostatus* n. sp. scales (Fig. 3G–P) are found in them for the first time (see Table 1).

Overall, the most abundant taxon in the assemblage is *Acanthodes?* sp. C (*sensu* Valiukevičius 1985) (Fig. 3Q), represented by the scales with a moderately large, rhombic, elongated crown with wide, rounded anterior and narrow, pointed posterior margins. The other abundant species are *Ptychodictyon sulcatum* Gross (which is the dominant species in the assemblages of the previously studied samples) (Fig. 3R), *Cheiracanthus brevicostatus* Gross (Fig. 3S) and *Diplacanthus crassisimus*

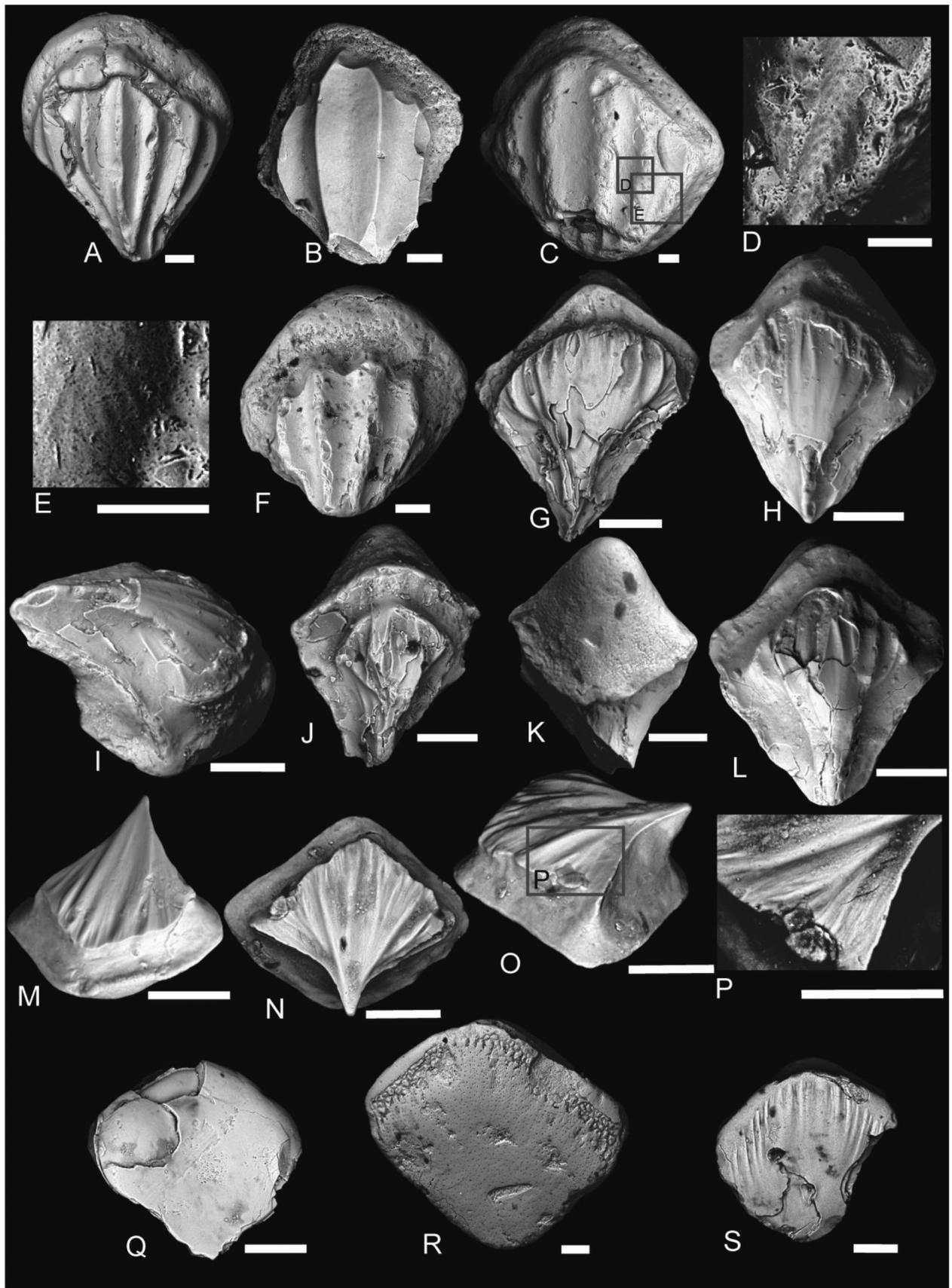


Table 1. The distribution of acanthodian microremains in samples from the Karksi outcrop, taken in 2015. Relative abundance of acanthodian scales: x, low; xx, medium; xxx, high; –, not found

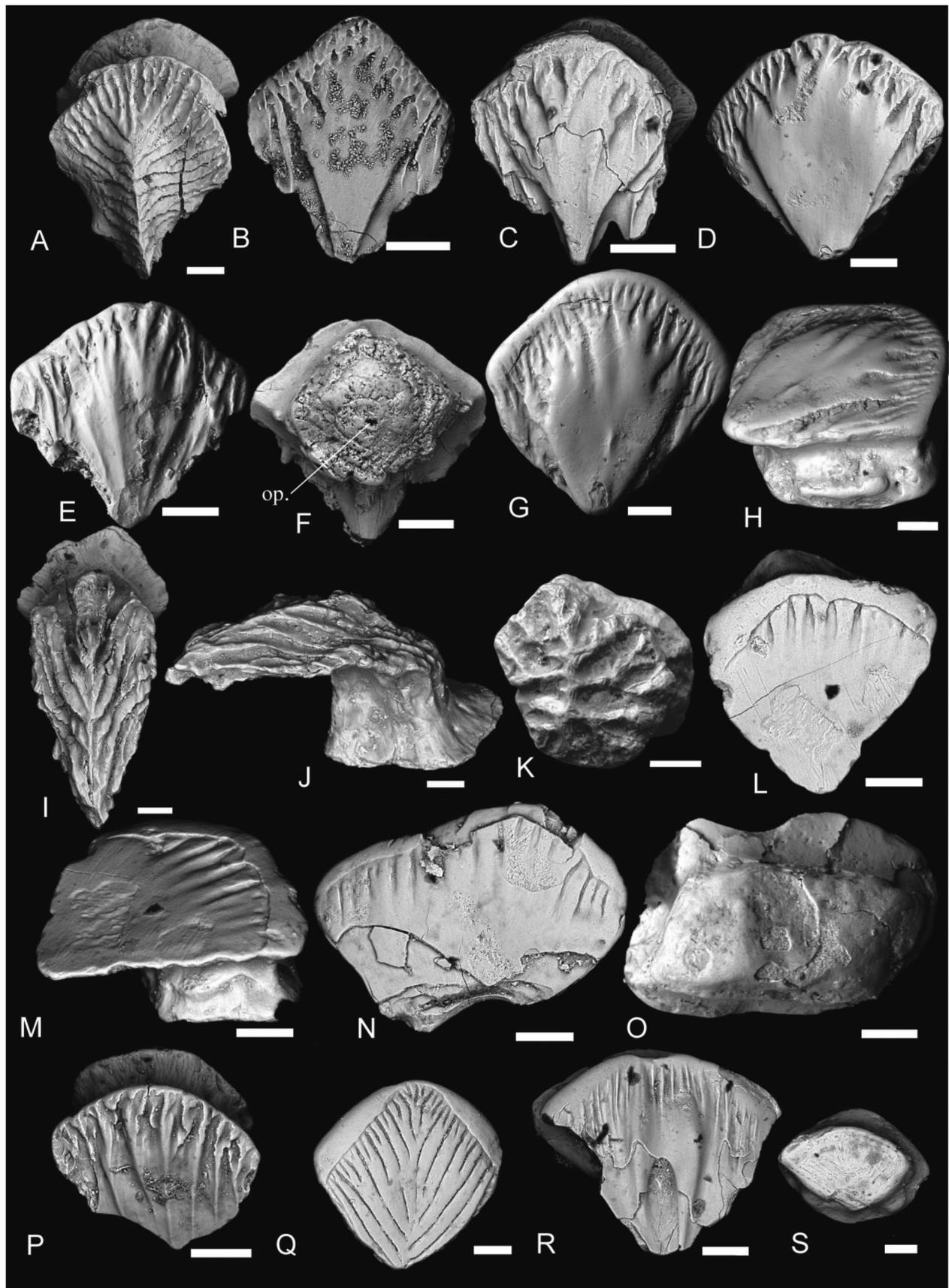
Acanthodian taxa	15-1	15-2	15-3	15-4	15-5	15-6	15-7	15-8	15-9	15-10
<i>Diplacanthus crassisimus</i>	x	–	xx	x	x	–	xx	x	x	xx
<i>Diplacanthus</i> sp. cf. <i>D. crassisimus</i>	–	–	x	–	x	x	x	x	–	x
<i>Diplacanthus</i> sp. cf. <i>D. tenuistriatus</i>	x	–	–	–	–	–	x	x	–	x
Diplacanthiformes indet.	–	x	–	–	–	–	x	–	x	–
<i>Rhadinacanthus longispinus</i>	x	x	x	x	x	–	x	x	–	xx
<i>Rhadinacanthus deltosquamosus</i> n. sp.	–	–	–	–	x	–	x	x	–	x
<i>Ptychodictyon rimosum</i>	–	x	–	x	x	x	x	x	–	xx
<i>Ptychodictyon sulcatum</i>	–	xxx	–	x	–	x	xxx	xx	–	xx
<i>Ginkgolepis tenericostatus</i> n. sp.	–	–	x	–	x	–	x	x	–	x
<i>Cheiracanthus brevicostatus</i>	x	x	–	x	xxx	xx	x	x	x	xx
<i>Cheiracanthus latus?</i>	–	–	–	–	–	–	x	–	–	xx
<i>Acanthodes?</i> sp. B	x	–	–	–	x	x	–	–	–	x
<i>Acanthodes?</i> sp. C	xx	xx	xxx	xxx	xx	xxx	xxx	xx	x	xxx
<i>Acanthodes?</i> sp. D	x	x	x	x	x	–	x	–	–	x

(Duff) (Fig. 4A). The acanthodian assemblage of the Karksi outcrop is the best comparable with that of the sandy argillites in the uppermost part of the Novinka quarry (Leningrad Region, Russia), which also belongs to the Burtneki RS. The latter comprises the following species: *Diplacanthus gravis* Valiukevičius, *Diplacanthus crassisimus* (Duff), *Rhadinacanthus longispinus* (Agassiz), *Rhadinacanthus deltosquamosus* n. sp., *Ptychodictyon rimosum* Gross, *Ptychodictyon sulcatum* Gross, *Ginkgolepis tenericostatus* n. sp., *Cheiracanthus brevicostatus* Gross, *Cheiracanthus latus?* Egerton, *Acanthodes?* sp. C, *Acanthodes?* sp. B, *Acanthodes?* sp. D and *Acanthodes?* sp. Two of the species are found exclusively in these two localities: *R. deltosquamosus* n. sp. (Fig. 4B–H) and *G. tenericostatus* n. sp. (Fig. 3G–P). The assemblage from the Novinka quarry differs in the presence of *Diplacanthus gravis* Valiukevičius, the index species of the zone which corresponds to the Aruküla and Burtneki RSs (Valiukevičius 1998). At the same time the acanthodian assemblage of the Karksi outcrop is more diverse, comprising three possibly new diplacanthiform taxa (see Table 1): *Diplacanthus* sp. cf. *D. crassisimus* (Duff) (Fig. 4I, J), *Diplacanthus* sp. cf. *D. tenuistriatus* Traquair (Fig. 4K), *Diplacanthiformes* indet. (Fig. 4L–O); as well as *Nostolepis gaujensis* Valiukevičius. The presence of the last species in the

Burtneki RS was discovered in this locality for the first time by Märss et al. (2008). The nostolepid scales, which probably belong to this species, are also present in another Burtneki RS locality – the Kemka locality (Leningrad Region, Russia). A psammosteid *Pycnosteus tuberculatus* Zone, which corresponds to the Härma and Koorküla beds of the Burtneki RS, was established both in the Novinka and Kemka localities (Glinskiy 2013). Other acanthodian taxa, present in Karksi, are *C. latus?* (Fig. 4R), *R. longispinus* (Fig. 4P), *P. rimosum* (Fig. 3R) and *Acanthodes?* sp. B (Fig. 4S).

Below we describe six acanthodian taxa from the Karksi outcrop: *N. gaujensis* Valiukevičius, *R. deltosquamosus* n. sp., *G. tenericostatus* n. sp., *Diplacanthus* sp. cf. *D. crassisimus* (Duff), *Diplacanthus* sp. cf. *D. tenuistriatus* Traquair and *Diplacanthiformes* indet. The latter three diplacanthiform taxa can possibly be new species, but are extremely rare, and more material is needed to examine the microstructure and variability of their scales. It should also be noted that the scales from the Main Devonian Field, similar to the ones listed here as *Cheiracanthus latus?* Egerton (Fig. 4R), were previously assigned to *Cheiracanthus longicostatus* Gross. However, in their morphology they are more similar to *Cheiracanthus latus* Egerton. Further research with thorough comparison of these scales with

Fig. 3. Acanthodian scales from the Karksi and Novinka outcrops, Burtneki RS, Givetian, Middle Devonian. **A–F**, *Nostolepis gaujensis* Valiukevičius: A, GIT 730-22, sample Karksi 90-2; B, GIT 730-23, sample Karksi 02-2; C–E, GIT 730-24, sample Karksi 02-4; F, GIT 730-25, sample Karksi 97. **G–P**, *Ginkgolepis tenericostatus* n. sp.: G, GIT 730-37, sample Karksi 15-5; H, I, GIT 730-38, sample Karksi 15-8; J, K, GIT 730-39, sample Karksi 15-10; L, GIT 730-36, sample Karksi 15-8; M, PM SPbSU 86-56, sample Novinka; N–P, GIT 730-40, sample Karksi 15-10. **Q**, *Acanthodes?* sp., GIT 730-47, sample Karksi 15-7. **R**, *Ptychodictyon sulcatum* Gross, GIT 730-43, sample Karksi 02-2. **S**, *Cheiracanthus brevicostatus* Gross, GIT 730-45, sample Karksi 97. A–H, J, L, N, Q–S, top view; I, lateral view; K, bottom view; M, anterolateral view; O, P, lateral view of the crown and the neck surfaces. Scale bars = 100 µm.



the scales from the associated skeletons of different *Cheiracanthus* species is needed to verify this observation.

SYSTEMATIC PALAEOLOGY

Class ACANTHODII Owen, 1846
Order CLIMATIIFORMES Berg, 1940
Family CLIMATIIDAE Berg, 1940
Genus *Nostolepis* Pander, 1856

Type species. *Nostolepis striata* Pander, 1856

Nostolepis gaujensis Valiukevičius, 1998
Figures 3A–F, 5A–C

1998 *Nostolepis gaujensis* Valiukevičius in Valiukevičius, p. 34, pl. 8, figs 8, 9.

2009 *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius in Burrow et al., pp. 74, 78, fig. 3.

Holotype. Institute of Geology and Geography, Vilnius (GI) No. 25-1491, scale; Valiukevičius 1998, pl. 8, fig. 8a, b; Lithuania, Svėdasai-252 core, depth 76.4 m. Upper Devonian, Frasnian, Šventoji RS, Šventoji Formation.

Material. Over 20 well-preserved scales, including GIT 730-22, GIT 730-23, GIT 730-24, GIT 730-25, Karksi outcrop.

Occurrence. Middle and Upper Devonian; Givetian and Frasnian; the Burtneki RS of Estonia and Russia (Leningrad Region); the Šventoji Formation of Lithuania and its age analogues – the Gauja and Amata substages in Latvia.

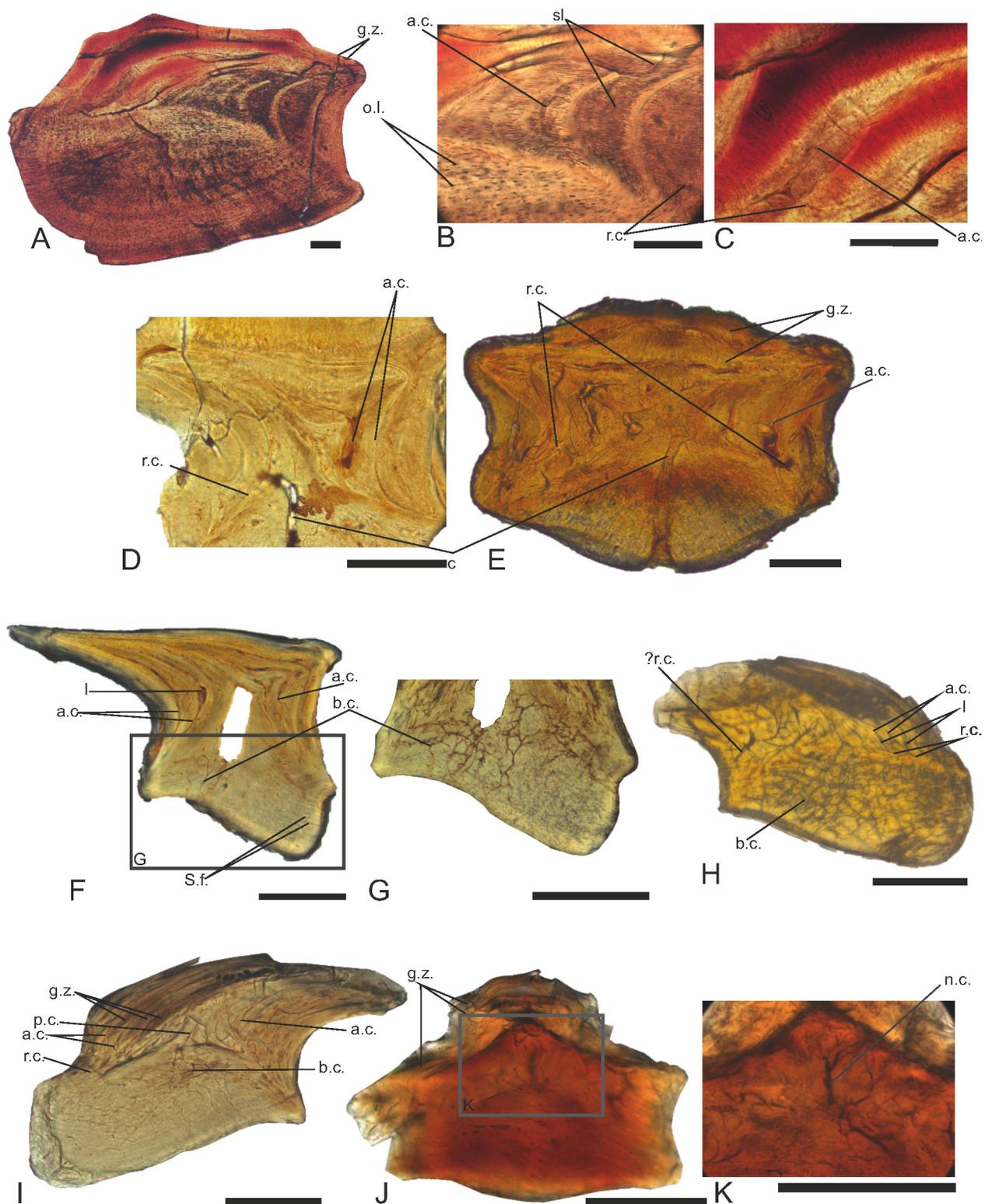
Description

Morphology of the scales. The scales are relatively large, up to 1.5 mm in length (Fig. 3A–F). The crown is horizontal in most scales and rhombic in outline; it can be more or less rounded. It bears 4–6 wide ridges, which are relatively sharp in better-preserved scales (Fig. 3B). Such scales also have a sharply defined anterior edge with the vertical ridges extending down the anterior face of the crown. In more abraded scales the ridges are relatively blunt, as is the anterior edge (Fig. 3A, C, F).

The ridges extend the length of the crown in the studied scales. Very rarely they converge and fuse near the posterior angle of the crown (Fig. 3A). In some scales the median ridges are joined by a rim along the anterior crown edge. A subrhombic base is rather convex and its tip is shifted anteriorly, so that the base protrudes in front of the crown. The neck is very low. A fine ultrasculpture occurs on the surface of better-preserved scales (Fig. 3D, E). It is represented by a honeycomb-like network of isometric depressions on the flatter parts of the crown (on the surface of the wide trough between the ridges) (Fig. 3D), which stretch and elongate on the sides of the ridges, forming fine striation there (Fig. 3E). There is also another morphotype of the scales of this species. They have an upright anteriorly notched crown which posteriorly becomes ridged (Fig. 3F). These scales are, probably, pinnal and come from the shoulder girdle region. Analogous morphotype of the scales, probably belonging to *N. costata* Goujet, 1976, has recently been described by Burrow & Murphy (2016).

Histology of the scales. There are six growth zones in the crown and in the neck of the examined scale (Fig. 5A). Stranggewebe (*sensu* Gross 1971) forms the posterior part of the crown and the neck, and the entire primordial scale (Fig. 5A, B). It is covered by a mantle of simple odontocytic mesodentine near the boundaries of growth zones (Fig. 5B). The other part of the crown is formed mostly by mesodentine, which is odontocytic in the basal parts of the growth zones and syncytial (*sensu* Valiukevičius & Burrow 2005) in the outer parts. The syncytial mesodentine becomes very similar to orthodentine close to the growth zone surfaces, with fine tubules oriented perpendicular to them (Fig. 5C). A thin layer of birefringent durodentine is developed in the uppermost parts of the growth zones in the central region of the crown. Relatively wide winding radial canals lie above the neck–base junction. Ascending canals branch upwards from them (Fig. 5B, C). Vascular canals are significantly wider in the posterior part of the studied scale. The base is composed of laminar bone tissue with numerous osteocyte cavities. The cavities are more abundant towards the apex of the base, where they also become more elongated and regularly oriented (Fig. 5B). In the primordial zone they are connected with numerous processes.

Fig. 4. **A**, *Diplacanthus crassisimus* (Duff), GIT 730-41, sample Karksi 97. **B–H**, *Rhadinacanthus deltosquamosus* n. sp.: **B**, PM SPbSU 86-38, sample Novinka; **C**, GIT 730-33, sample Karksi 02-4; **D**, GIT 730-36, sample Karksi 97; **E**, **F**, GIT 730-32, sample Karksi 15-10; **G**, **H**, GIT 730-34, sample Karksi 15-7. **I**, **J**, *Diplacanthus* sp. cf. *D. crassisimus* (Duff), sample Karksi 15-5, the scale was forfeited during thin sectioning. **K**, *Diplacanthus* sp. cf. *D. tenuistriatus* (Traquair), GIT 730-28, sample Karksi 15-7. **L–O**, *Diplacanthiformes* indet.: **L**, **M**, GIT 730-30, sample Karksi 15-9; **N**, **O**, GIT 730-31, sample Karksi 15-2. **P**, *Rhadinacanthus longispinus* (Agassiz), GIT 730-42, sample Karksi 15-10. **Q**, *Ptychodictyon sulcatum* Gross, GIT 730-44, sample Karksi 15-2. **R**, *Cheiracanthus latus?* Egerton, GIT 730-46, sample Karksi 97. **S**, *Acanthodes?* sp. **B**, GIT 730-48, sample Karksi 15-10. **A–E**, **G–I**, **K**, **L**, **N**, **P–S**, top view; **F**, **O**, bottom view; **J**, **M**, posterolateral view. Scale bars = 100 µm. Abbreviation: op., opening of a wide canal running through the base.



Comparison. The differences between *Nostolepis gaujensis* and *N. kernavensis* Valiukevičius, 1985 are very weak. The ridges on the scales of *N. gaujensis* are slightly lower and a bit blunter, the troughs between them are wider and shallower. In some scales of *N. kernavensis* the medial ridges are significantly more prominent than the others. Valiukevičius (1998) mentioned that *N. gaujensis*, contrary to *N. kernavensis*, does not have ridges meeting in pairs and the medial groove does not differ from the lateral ones in width and depth. However, we consider that these features are variable intraspecifically. Some of the scales of the described species from the Karksi outcrop have converging and fusing ridges (Fig. 3A), and some of them have a significantly wider medial groove (Fig. 3B). At the same time, some *N. kernavensis* scales have parallel ridges and the central groove completely equal to the lateral ones. The two species are very close in their histological features; they both even show perpendicularly oriented dentine tubules in the upper parts of the growth zones in the anterior crown and very long lacunae in the stranggewebe, enveloped by odontocytic mesodentine (Valiukevičius 1985). However, at least in the studied scale of *N. gaujensis* the stranggewebe is much more extensive, forming the whole of the posterior part of the crown and the neck, as well as the entire primordial scales and several first growth zones. In *N. kernavensis* the stranggewebe is mostly confined to the posterior part of the crown, very rarely penetrating into the primordial scale (Valiukevičius 1985).

Remarks. Morphologically similar scales, assigned to *Nostolepis* cf. *N. gaujensis* have been described from the ?Frasnian siltstones of the Chuche Formation, Colombia (Burrow et al. 2003). The comparison of their histological structure with that of the species described herein is not possible because its outer layers are preserved only in the Colombian scales. Other scales with the morphology conformable to *N. gaujensis* are described as *Nostolepis* cf. *N. gaujensis* and come from ?Frasnian deposits near Chahriseh (Gholamalien et al. 2000; Turner et al. 2002, figs 9, 10) and Bidu 1 (Chanaruh; Frasnian) north of Kerman, Iran (Janvier 1974, 1977). Hairapetian et al. (2006) described the scales of *Nostolepis* sp. cf. *N. gaujensis* from the Chariseh section, noting that these scales are comparable with those of *N. gaujensis* in most details, the only morphological

differences being fewer (four) ridges and a lower neck in the latter species. They also mention that these differences might be putative because *N. gaujensis* description was based on only five scales, hardly encompassing the total scale diversity range in this taxon (Hairapetian et al. 2006). Indeed, it seems that the number of the ridges on the scales, which we assign here to *N. gaujensis*, varies from four to six like in *Nostolepis* cf. *N. gaujensis* from Iran and some of the scales have just a pronounced neck. Therefore these features may vary intraspecifically. The difference in histological structure is that in the Iranian scales of *Nostolepis* cf. *N. gaujensis* stranggewebe in the posterior crown is observed only in the lower neck area and stranglakunae are short, whereas in *N. gaujensis* scales from Karksi the stranggewebe extends onto the whole of the posterior crown and primordium, and stranglakunae are long. However, only one scale of the latter species was examined and these features might also vary within the species.

The scales from the Aztec siltstone (?late Givetian) of Antarctica (Mount Crean, Lashly Mountains), defined by Burrow et al. (2009) as *Nostolepis* sp. cf. *N. gaujensis*, are very similar to the scales from Karksi. It was mentioned that the main distinguishing features of these scales are the sharpness of the ridges and crown edges and the ‘honeycomb’ ultrasculpture. The latter is also present on the scales from Karksi, as described above. The edges of the crown and the ridges of the best-preserved scales are sharp too (Fig. 3B). It should be noted that the histological structure of the type material of *N. gaujensis* still needs to be examined.

Order DIPLACANTHIFORMES Berg, 1940
Family DIPLACANTHIDAE Woodward, 1891
Genus *Diplacanthus* Agassiz, 1844

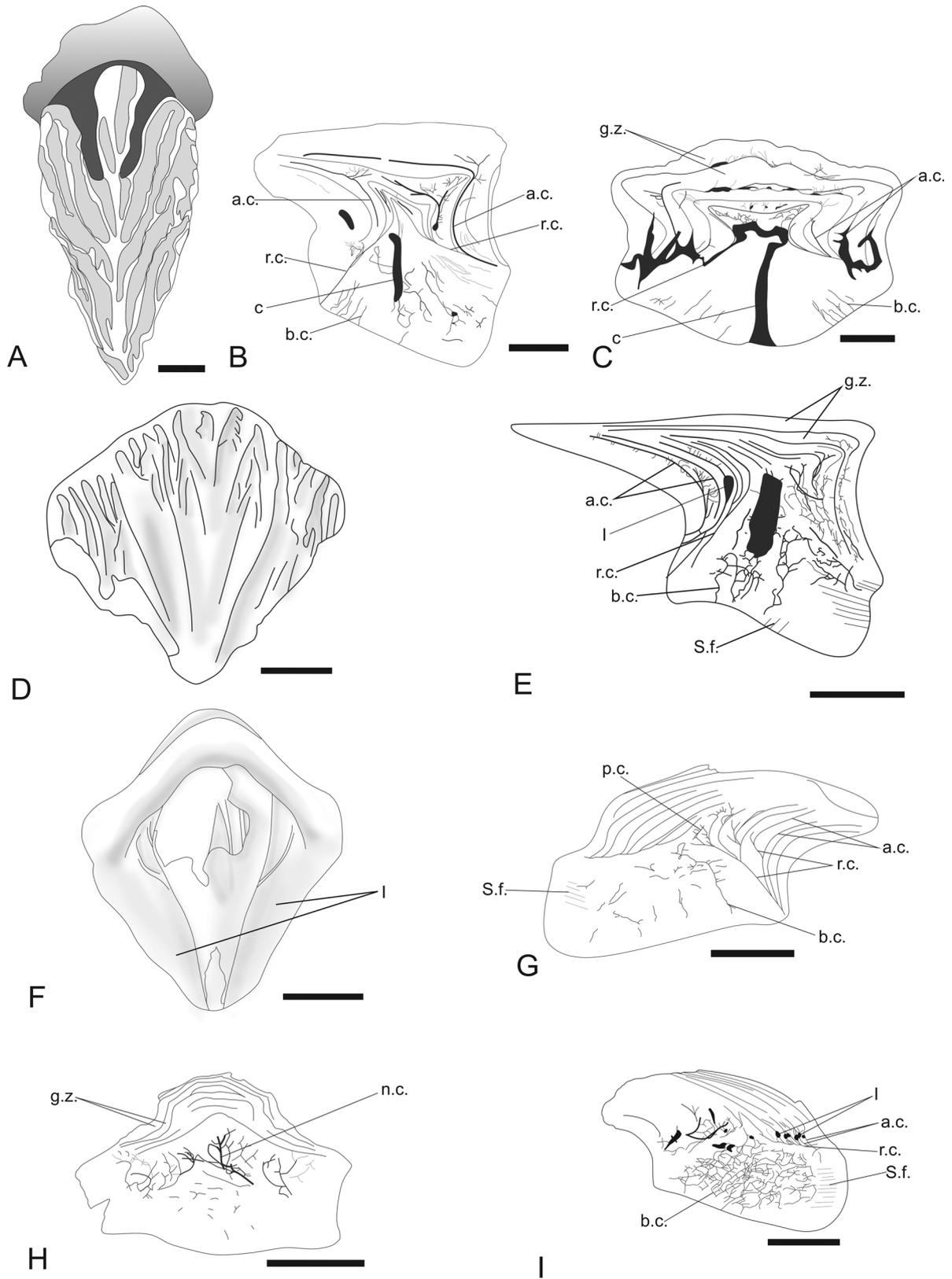
Type species. *Diplacanthus crassissimus* Duff, 1842

Diplacanthus sp. cf. *D. crassissimus* (Duff, 1842)
Figures 4I, J, 6A

Material. Two well-preserved scales: GIT 730-26, GIT 730-27 and one scale, which was lost during thin sectioning, the outcrop of Karksi.

Occurrence. Middle Devonian; Givetian; Burtneiki RS of Estonia.

Fig. 5. Microstructure of acanthodian scales. **A–C**, *Nostolepis gaujensis* Valiukevičius, GIT 730-24, sample Karksi 02-4. **D, E**, *Rhadinacanthus deltosquamosus* n. sp.: **D**, GIT 730-49, sample Karksi 97; **E**, GIT 730-34, sample Karksi 15-7. **F, G**, Diplacanthiformes indet., GIT 730-30, sample Karksi 15-9. **H–K**, *Ginkgolepis tenericostatus* n. sp.: **H**, GIT 730-40, sample Karksi 15-10; **I**, GIT 730-37, sample Karksi 15-5; **J, K**, GIT 730-38, sample Karksi 15-8. **A–D**, **F–I**, longitudinal vertical sections; **E, J**, transverse vertical sections. Scale bars = 100 µm. Abbreviations: a.c., ascending canal; b.c., vascular? canals of the base; c, wide canal, running through the base; g.z., growth zones; l, lacuna; n.c., vascular canals in the neck; o.l., osteocyte lacuna; r.c., radial canal; sl, stranglakuna; S.f., Sharpeys’s fibre traces.



Description

Morphology of the scales. The scales are moderately large, the length of the crown is up to 0.7 mm, the width – up to 0.3 mm. The crown of the scales is rhombic in outline with an elongated posterior part and a rounded anterior corner. It is much longer than wide.

Posterolateral edges of the crown are slightly denticulated (Fig. 4I, J). The sculpture consists of high sharp ridges, running from the sides of the crown towards the medial part, where they fuse with a medial ridge at a very sharp angle. Some of the opposite ridges fuse with the medial ridge at one point, others – at different levels. The ridges are inclined posteriorly; they are sharp and slightly serrated. Several smooth trough-like grooves run from the neck onto the anterior part of the crown across its anterolateral edges. In one of the scales two of these grooves are comparatively broader and deeper. They divide the anterior part of the scale into three zones (Fig. 6A). The neck is high, and rhomboidal or rounded in horizontal cross section; it is widening towards the base. Several pores are visible slightly above the sharp neck–base junction. The base is slightly convex or almost flat. It is situated under the anterior part of the crown.

Histology of the scales was not studied because of scanty material.

Comparison. The scales studied resemble in their morphology those of *D. crassisimus* (Duff 1842). Ours differ from the scales of that species in the shape of the crown, which is elongated, whereas in *D. crassisimus* it is isometric or widened. In *D. crassisimus* the ribs cross over the central ridge without interruption, contrary to *Diplacanthus* sp. cf. *D. crassisimus*, in which many of the opposite ridges meet with the central ridge at different points. The most outstanding morphological difference is grooves running from the neck onto the anterior part of the crown without interruption in *Diplacanthus* sp. cf. *D. crassisimus*; these are absent in *D. crassisimus*.

Diplacanthus sp. cf. *D. tenuistriatus* (Traquair, 1894)
Figure 4K

Material. Two moderately preserved scales: GIT 730-28, GIT 730-29, the outcrop of Karksi.

Occurrence. Middle Devonian; Givetian; Burtneki RS of Estonia.

Description

Morphology of the scales. The scales are of medium size (the length and the width are approximately 0.4 mm). The crown is isometric in shape and polygonal (Fig. 4K). It is sculptured with robust ridges. There is a central ridge, running across the whole crown length. The other ridges run from the sides of the crown towards the central ridge and fuse with it. The transverse ridges do not differ from the central one in size. The opposite ridges in the anterior crown make a V-shaped pattern. In the central part of the crown they are oriented perpendicularly to the central ridge. They turn posteriorly in the posterior part of the crown. Some of the opposite ridges fuse with the median one in one point, others – at different levels. Transverse ridges often ramify dichotomically near the edges of the crown; the ramifications do not differ in size and in robustness from them. They also give off multiple small and short side branches, which lie in the deep grooves between the ridges. The neck is high. The base is almost flat.

Histology of the scales was not studied because of scanty material.

Comparison. In the sculpture of the crown these scales slightly resemble those of *D. tenuistriatus* (Traquair, 1894). The side ridges on the scales of this species also tend to bifurcate towards the lateral corners. However, they are much more delicate, serrated and inclined posteriorly in *D. tenuistriatus* (Traquair, 1894). In the scales described herein the ridges are robust and blunt (however, the latter character might be connected with the state of preservation of scales); the grooves between the ridges are much wider, the transverse ridges on these scales not only bifurcate, but they also give off small short side branches.

Genus *Rhadinacanthus* Traquair, 1888

Type species. *Rhadinacanthus longispinus* (Agassiz, 1844)

Rhadinacanthus deltasquamosus n. sp.
Figures 4B–H, 5D, E, 6B–D

Etymology. After *delta* (Lat.), meaning delta and *squamosus* (Lat.), meaning squamous, name referring to the scale crown sculpture.

Fig. 6. Line drawings of scale crown morphology and microstructure. **A**, *Diplacanthus* sp. cf. *D. crassisimus* (Duff), sample Karksi 15-5. **B–D**, *Rhadinacanthus deltasquamosus* n. sp.: **B**, GIT 730-49, sample Karksi 97; **C**, GIT 730-34, sample Karksi 15-7; **D**, GIT 730-32, sample Karksi 15-10. **E**, *Diplacanthiformes* indet., GIT 730-30, sample Karksi 15-9. **F–I**, *Ginkgolepis tenericostatus* n. sp.: **F**, GIT 730-36, sample Karksi 15-8; **G**, GIT 730-37, sample Karksi 15-5; **H**, GIT 730-38, sample Karksi 15-8; **I**, GIT 730-40, sample Karksi 15-10. **A**, **D**, **F** – top view of the scale crowns; **B**, **E**, **G**, **I**, vertical longitudinal sections; **C**, **H**, vertical transverse sections. Scale bars = 100 µm. Abbreviations: a.c., ascending canals; b.c. vascular? canals of the base; c., wide canal, running through the base; g.z., growth zones; l, lacuna; n.c., vascular canals of the neck; p.c., canal in the scales' primordium; r.c., radial canals; S.f., Sharpey's fibre traces; l, ledges.

Holotype. GIT 730-32, scale, Fig. 4E, F. Estonia, Karksi outcrop, Middle Devonian, Givetian, Burtneki RS, Härma Beds.

Material. Ten well-preserved scales, including GIT 730-32, GIT 730-33, GIT 730-34, GIT 730-35, Karksi outcrop; PM SPbSU 86-38, Novinka quarry.

Occurrence. Middle Devonian; Givetian; Burtneki RS of Estonia and Leningrad Region of Russia.

Diagnosis. A diplacanthid with the scale crown sculpture represented by a prominence having a V-shaped outline, which divides into numerous branching ridges in the middle and anterior parts of the crown. Posteriorly converging ridges are developed on this prominence on some of the scales. A large canal runs through the base into the first growth lamella, where it twists horizontally and fuses with radial canals, some of which are very complex, winding and widened. The opening of the canal is situated slightly posterior to the tip of the base.

Description

Morphology of the scales. Scales are of moderate size, with the length of the crown 0.4–0.6 mm in general. The crown is rhombic in shape; its anterior margin is rounded in most scales. Posterolateral edges of the scales sometimes bear rounded denticulations (Fig. 4B, C, E, F). The length of the crown is usually almost equal to its width, but the scales with elongated and slightly shortened crowns are also present. There is a large prominence on the surface of the scales, which has a V-shaped outline (Fig. 4A–D, E, G, H). It is delimited by two deep grooves in the posterior part of the crown. The grooves are straight or very slightly curved. They converge at a sharp (usually 40°–60°) angle at the posterior tip of the crown. The prominence height gently increases posteriorly. In the middle, or, more often, in the anterior part of the crown it is divided into numerous (9–15 in the scales studied) ridges. These, in turn, branch multiple times to form anteroposteriorly oriented smaller and thinner ridges. Very rare are the scales, with posteriorly converging ridges developed on the whole surface of the medial prominence (Fig. 4E). However, its V-shaped outline is still discernible. An ultrasculpture, represented by very delicate longitudinal striation, is visible on the surface of the best-preserved scales. The neck is well defined and of moderate height. Often two rounded elongated prominences are found on the posterolateral sides of the neck (Fig. 4H). The base is rhombic in outline. Its width is slightly smaller than that of the crown. It is moderately convex and its tip is slightly shifted anteriorly. A very small opening occurs posterior to it in the medial part of the base (Fig. 4F).

Histology of the scales. The studied thin sections revealed four to five growth zones (Figs 5E, 6B, C).

The zones are superpositional and relatively wide. The surface of the older growth zones in the medial part of the crown is flatter than that of the younger zones (Figs 5E, 6C). It seems that the medial prominence on the crown surface became more pronounced as the scale grew. The enameloid is not clearly developed. A very wide canal runs from the point just behind the tip of the base into the first growth lamella where it twists horizontally (Figs 5D, E, 6B, C). It is connected with radial canals which pass into the region of the neck–base junction (Figs 5E, 6C); they open on the sides of the neck just above the margin between the neck and the base. Some of these canals are very complex and sinuous. Such canals are highly variable in diameter along their length, being very widened in some parts and constricted in others. Other radial canals are simple, straight and comparatively narrow. Ascending canals branch off upwards from the radial canals. The ascending canals which are connected with complex radial canals are often widened in the lower region of the neck. Ascending canals turn horizontally at the crown–neck junction. Numerous intensively ramifying dentine tubules branch off from the horizontal canals. Many Williamson canals are seen in the base of the studied scales, but their abundance probably depends on the age of the scales (Burrow & Murphy 2016). Bone cell lacunae are absent.

Comparison. The species described herein most closely resembles *R. longispinus* (Agassiz 1844). The major differences from this species are the presence of a V-shaped prominence in the medial part of the scale crown and a wide canal running through the base into the first growth lamella where it twists horizontally and fuses with complex widened radial canals. The canal opens up on the surface of the base slightly behind its tip.

Diplacanthiformes indet.
Figures 4L–O, 5F, G, 6E

Material. Six well-preserved scales, including GIT 730-30, GIT 730-31, Karksi outcrop.

Occurrence. Middle Devonian; Givetian; Burtneki RS of Estonia.

Description

Morphology of the scales. The scales are of moderate size: the average crown length and width are 0.4 mm. The crown of the scales is triangular in outline, with a rounded anterior edge (Fig. 4L, M). It is sculptured with 9–17 wide flat-topped ridges. There is a comparatively wide unsculptured rim along the anterior edge of the scale, which is separated by a thin groove from the rest of the crown surface. The crown is flat and the ridges are almost parallel. They fade out in the anterior part of the crown. The neck is well defined and comparatively

high. The base is smaller than the crown and a little convex, with a tip slightly shifted anteriorly. Some of the scales are fused in pairs (Fig. 4N, O). The crown, neck and the base of the scales are fused in such complex elements by their antero- and posterolateral sides. The margin between the scales in such elements is marked by a dent between the posterior angles of the scale crowns and by a depression between their fused bases. The surfaces of some of the scales display an ultrasculpture represented by fine longitudinal striation.

Histology of the scales. Only one longitudinal vertical thin section was made due to scarcity of the material. It shows that the scales probably belong to a *Diplacanthus* type (*sensu* Valiukevičius 1995). Six growth zones of moderate width can be counted. The vascular canals are relatively wide. Radial canals run along the neck–base junction. The ascending canals branch upwards from the radial canals in each growth zone. Some ascending canals are not connected with the radial canals but open to the exterior in the lower portion of the neck (Figs 5F, 6E). Some of such canals have widenings. The canals in the posterior part of the neck are generally parallel to its concave sides, whereas they are more winding and complex in the anterior part. Numerous winding and branching dentine tubules radiate from the ascending canals and interconnect them. The ascending canals turn horizontally when they reach the crown plate and run in the basal parts of the growth lamellae, giving off numerous very fine dentine tubules. An utterly thin layer of enameloid is probably present in the uppermost parts of inner growth lamellae. No bone cell lacunae are visible in the base. The base is penetrated by numerous complex branching canals. Sharpey's fibres radiate from the apex of the base. There is a large cavity in the zone of primordium and adjacent part of the base. However, it could be an artefact and formed after the death of an animal.

Remarks. The scales described herein differ from *Rhadinacanthus* scales in their crown sculpture, which is formed by flat-topped ridges and almost slit-like grooves, whereas the ridges on *Rhadinacanthus* scales are sharper and do not have a wide unsculptured rim along the anterior edge of the crown, separated by a groove from the rest of the crown surface. None of the scales described herein has denticulated posterolateral crown margins, but they are often serrated in *Rhadinacanthus* scales. However, the scales of at least some *Rhadinacanthus* species (Burrow et al. 2016) have fine longitudinal striations on the crown reminiscent of those on the scales described. Growth zones are much thinner in the scales described than in previously known *Rhadinacanthus*. The sculpture on the crown formed by wide flat-topped ridges is present on the body scales of *Gladiobranchus*

probaton Bernacsek & Dineley, 1977 from the Lower Devonian of the Delorme Formation, District of Mackenzie. The general shape of the crown of *G. probaton* is also similar to that of the species described by Hanke & Davis (2008). However, there is no wide unsculptured rim along the anterior edge of the scales of *G. probaton*.

Although the scales of this species belong to a *Diplacanthus* type, they lack basal vascular canals and have few (up to four) thick growth zones, while in the scales described herein canals of the base are well developed and growth zones are thinner and more numerous. The sculpture on the crown of *Milesacanthus* Young & Burrow, 2004 scales also consists of the ridges with flattened crests and slit-like grooves between them. However, they have a complicated system of canals, opening out as numerous pores on the neck and in the grooves of the anteriormost crown (Young & Burrow 2004; Hairapetian et al. 2006), which is lacking in the scales described here. Analogous sculpture, consisting of sub-parallel grooves, is described on the scales of *Diplacanthus poltnigi* Valiukevičius, 2003. However, they extend over the entire length of the scales or converge at the extreme posterior area, but fade rather close to the anterolateral edges of the scales described here (Valiukevičius 2003). They are also very different histologically, for example, no multibranching radial canals characteristic of *D. poltnigi* can be observed in the scales described.

Order ACANTHODIFORMES Berg, 1940
Family CHEIRACANTHIDAE Berg, 1940
Genus *Ginkgolepis* n. gen.

Etymology. After *Ginkgo*, because the outlines of the crowns of scales are reminiscent of the contour of *Ginkgo biloba* leaves.

Type species. *Ginkgolepis tenericostatus* n. sp.; Middle Devonian; Givetian; Burtneki RS of Estonia and Russia.

Diagnosis. Small to very small scales. The crown is fan-shaped or rhombic in outline. The anterior margin is rounded or rounded-angular; the posterior margin is pointed, with sharp posterior angle. Posterolateral edges of the crown are concave. Its sculpture is represented by posteriorly converging ridges. Larger scales possess two sharp ridges, which run upwards from the neck–base junction at the lateral corners of the scales and turn horizontally when they reach the crown surface, forming lower ledges along posterolateral edges of the crown. The neck is low. The base is strongly convex, with anteriorly shifted tip. The scales belong to an *Acanthodes* histological type (*sensu* Valiukevičius 1985). Vascular canals are notably very thin (comparable in thickness with dentine tubules in small scales). The crown is formed by durodentine.

Species composition. Besides the type species, *Cheiracanthus talimae* Valiukevičius, 1985 from the Narva and ?Aruküla RSs (Upper Eifelian–?Lower Givetian) of the Main Devonian Field should also be assigned to this genus. At least some scales from the Upper Devonian (Famennian) of the Orel region (Russia), defined previously as ‘*Devononchus*’ *kellerensis* (Lebedev & Lukševičs 2017), probably, belong to *Ginkgolepis* too.

Comparison. The scales of this genus differ from all other representatives of cheiracanthids in having a base with a tip, which is strongly shifted ahead of the anterior margin of the crown and a low, often weakly defined neck. Most of the scales have characteristic ridges, running upwards from the neck–base junction and forming lower ledges along posterolateral edges of the crown.

Occurrence. Middle Devonian; Eifelian and Givetian; Narva and Burtņieki RSs of Estonia and Russia and, probably, Upper Devonian; Famennian of Russia.

Remarks. The scales, described by Valiukevičius (1985) as *Cheiracanthus talimae* are closer to other cheiracanthids in their crown sculpture and histology than the type species. They retain a thicker, wider medial ridge. The ridges on the crown are strongly defined and cover the whole surface of the crown and the lateral ledges. The ascending and radial canals are wider and the primordial canal is more complex.

Ginkgolepis tenericostatus n. sp.

Figures 3G–P, 5H–K, 6F–I

Etymology. After *tener* (Latin) – soft, delicate and *costa* (Latin) – rib, vein, referring to the delicate roundish ridges with very fine anterior branching of ridges on the crowns of the scales.

Holotype. GIT 730-36, scale, Fig. 3L. Estonia, Karksi outcrop, Middle Devonian, Givetian, Burtņieki RS, Hārma Beds.

Material. Six well-preserved scales; GIT 730-36, GIT 730-37, GIT 730-38, GIT 730-39, GIT 730-40, Karksi outcrop; PM SPbSU 86-56, Novinka quarry.

Occurrence. Middle Devonian; Givetian; Burtņieki RS of Estonia and Russia.

Diagnosis. Scales with two scale morphotypes. One of them has very narrow lateral ledges along posterolateral edges of the crown or is devoid of them. The other morphotype has wide ledges. The sculpture on the scale crown consists of up to ten low thin ridges with roundish crests and with delicate branching finer ridges, well pronounced on the small scales of the first morphotype. The ridges are shorter in the medial part of the crown

and longer on the sides. The longer side ridges tend to converge towards the posterior angle of the crown. A slightly more pronounced groove-like concavity can often be present in the anteromedial part of the crown. A network of thin winding and branching canals is often present in the base.

Description

Morphology of the scales. The scales have two morphotypes. The scales of the first morphotype are slightly larger (the length of the crown is 0.3–0.4 mm, the width 0.2–0.3 mm) (Figs 3G–L, 6F). The posterior part of the crown is elongated and many of the scales have a rounded anterior margin. The posterolateral edges of the main crown surface have concave outline and meet posteriorly at a very sharp angle. The crown sculpture is fan-like in shape. It is formed by low and thin roundish-roofed ridges, which fade out in the anterior or middle parts of the crown. The lateral ridges usually ramify close to the lateral corners of the crown. The ridges on each side of the scales are laterally curved. The medial ones are separated by a depression, which can be low, relatively wide and groove-like, or narrow, but they always have slightly convex lateral margins. Wide sharp ridges rise up from the neck–base junction and turn horizontally when they reach the crown level to form wide, lower ledges along posterolateral edges of the crown. There is a distinctive margin between the ledges and the main crown, which corresponds to the most lateral ridges of the crown plate. However, it is not sharp: some ramifications of the lateral ridges even pass onto the ledges. The neck is low in the anterior part and high in the posterior part of the scale. The posterior part of the scale overhangs the base. The base is very convex and its tip protrudes ahead of the anterior margin of the crown (Fig. 3K).

The scales of the second morphotype are small (the length of the crown is up to 0.2 mm, the width – up to 0.3 mm) (Fig. 3M–P). Their crown is rhombic in outline; its width equals or slightly exceeds its length. The posterolateral edges are concave and meet posteriorly at a sharp angle. The sculpture on the crown consists of up to ten small thin round-topped ridges, situated radially. They ramify towards the anterior edge of the crown, forming numerous very fine, delicate branches (Fig. 3P). The ridges laterally on the crown tend to meet on its posterior part. These two groups of ridges are separated medially by a shallow groove-like depression. The neck is very low and weakly defined in the anterior part of the scale and moderate in height in its posterior part. Sometimes there are very narrow sharp ridges, running up from the neck–base junction at the lateral corners of the scale. They turn horizontally at the crown level, forming ledges, which fuse with posterolateral

edges of the crown. Notably there is no distinctive margin between the ledges and the main crown plate in the scales of this morphotype. The base is always larger than the crown and moderately convex; its tip is shifted towards the anterior part of the scale.

Histology of the scales. Four to ten growth zones are distinguishable in the crown (Figs 5H–K, 6G–I). The upper part of each growth zone is formed by enameloid. A system of very thin canals can be observed in the anterior part of the crown. The canals are almost as thin as dentine tubules, but in the largest scales they are substantially wider than tubules (Figs 5I, 6G). Curved radial canals run there in the region of the neck–base junction. Ascending canals rise up from the radial ones in each growth zone. In some scales each of them has a lacunal widening in the midsection of the neck (Figs 5H, 6I). These widenings possibly mark the point where the ascending canals fuse with circular canals. Some tubules radiate from these widenings in all directions. The ascending canals turn horizontally at the anterior edge of the crown and run in the basal portions of the growth lamellae. The canals are situated much less regularly in the posterior part of the smaller scales. They can form a random network without relation to growth zones (Figs 5H, 6I). In the larger scales some radial canals (which are often wider than in the anterior part) above the neck–base junction with a few ascending canals run up from them. In the largest scales there are two levels of radial canals in the posterior part: right along the neck–base junction and above it in the lower portion of the neck (Figs 5I, 6G). The ascending canals pass in each growth zone from these radial canals. The margins of the posterior growth zones themselves are visible only in the larger scales. The primordial scale has a canal which is comparable in thickness with the other ascending canals, but has short canals radiating from it in every direction (Figs 5I, 6G). This canal is connected with the neighbouring ones by the longest of these tubules. Numerous short winding canals form a network in the base of the scale. This network can occupy the whole base in some smaller scales or be mostly confined to the apical region of the base near the primordial scale. No bone cell lacunae are visible in the base. Thin Sharpey's fibre bundles are packed in layers in the base.

Comparison. The scales of *G. tenericostatus* differ from those of *G. talimae* in details of the crown sculpture: the ridges are much more delicate and a medial depression can be distinguished, while *G. talimae* has a high robust medial ridge. The surfaces of the ledges are strongly ridged in *G. talimae*, but mostly unsculptured in *G. tenericostatus*. The primordial canal is simpler in *G. tenericostatus* than in *G. talimae*.

RESULTS

The Karksi outcrop yielded one of the most abundant and diverse acanthodian assemblages of the Burtneiki RS on the Main Devonian Field known to date: it comprises 15 acanthodian taxa (see Table 1 and Märss et al. 2008). Two new species, *Rhadinacanthus deltosquamosus* n. sp. and *Ginkgolepis tenericostatus* n. sp., are described in this article based on isolated scales. Three more acanthodian taxa, *Diplacanthus* sp. cf. *D. crassisimus* (Duff), *Diplacanthus* sp. cf. *D. tenuistriatus* Traquair and *Diplacanthiformes* indet. are of interest, but, as they are extremely rare, more material is needed to define their taxonomic status more precisely.

Only one species specific to the Burtneiki RS, *Homacanthus talavicus* Lyarskaya, was known before. The new data show that the acanthodian assemblages of the Burtneiki RS can also be distinguished by the first appearance of *Nostolepis gaujensis* Valiukevičius and by the presence of *Rhadinacanthus deltosquamosus* n. sp. and *Ginkgolepis tenericostatus* n. sp., which are known exclusively from this stratigraphic unit. These species have relatively wide distribution within the Main Devonian Field, as they are present not only in the Karksi outcrop, but also in the Novinka quarry (Leningrad Region). The new data on the acanthodian diversity of the mentioned localities show that the acanthodian assemblage of the Burtneiki RS is substantially different from that of the Aruküla RS both in the eastern and western parts of the Main Devonian Field.

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Akantoodide kooslus Karksi paljandis Eestis (Givet' lade, Kesk-Devon)

Darya V. Pinakhina ja Tiiu Märss

On arutletud akantoodide koosluse taksonoomilise koosseisu üle Karksi paljandis Eestis. Kaks uut liiki, *Rhadinacanthus deltasquamosus* n. sp. (Diplacanthiformes, Diplacanthidae) ja *Ginkgolepis tenericostatus* n. sp. (Acanthodiformes, Cheiracanthidae), on kirjeldatud isoleeritud soomuste põhjal. *Nostolepis gaujensis* Valiukevičius (Climatiiformes, Climatiidae) on taaskirjeldatud samast leiukohast. Kolm diplakantiidset taksonit, *Diplacanthus* sp. cf. *D. crassissimus* (Duff), *Diplacanthus* sp. cf. *D. tenuistriatus* Traquair ja Diplacanthiformes indet., on käsitletud avatud nomenklatuuris.