New data on psammosteid heterostracans (Pteraspidomorpha) and acanthodians (Acanthodii) from the Pärnu Regional Stage (Lower Eifelian, Middle Devonian) of Estonia

Vadim N. Glinskiy and Darya V. Pinakhina

Department of Sedimentary Geology, St Petersburg State University, 7/9 Universitetskaya nab., 199034 St Petersburg, Russia; vadim.glinskiy@gmail.com, darya.pinakhina@gmail.com

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Abstract. Vertebrate remains from the Lower Eifelian Pärnu Formation, Estonia, are described. New data on the topography of ornamentation and histology of psammosteids from the Pärnu Regional Stage are presented. The occurrence of the genus *Guerichosteus* Halstead Tarlo in the Lower Eifelian of the Main Devonian Field is established. Representatives of this taxon had previously been known from the Emsian (Lower Devonian) of the Holy Cross Mountains, Poland. The histological study of the exoskeleton of *Guerichosteus heterolepis* (Preobrazhensky) showed the presence of a thin layer of hypermineralized tissue (enameloid) on the surface of dentine tubercles. The taxonomic composition of the vertebrate assemblage from the Taali locality (Tori Parish, Pärnu County, southwestern Estonia) is described for the first time. Along with the taxa characteristic of the Pärnu Regional Stage, the acanthodian *Cheiracanthus* sp. cf. *C. splendens* is first recorded in this interval.

Key words: Agnatha, Psammosteida, Gnathostomata, Acanthodii, Middle Devonian, Main Devonian Field, histology.

INTRODUCTION

Remains of psammosteid heterostracans and acanthodians are very diverse and abundant in the Middle and Upper Devonian (Eifelian, Givetian and Frasnian stages) of the Baltic area, i.e. the Main Devonian Field (MDF). These remains characterize regional stratigraphic units, with several psammosteid and acanthodian species being used as index fossils (e.g. Gross 1942; Mark-Kurik 2000; Mark-Kurik & Põldvere 2012; Glinskiy 2013). Early Eifelian vertebrates are known from the Pärnu Regional Stage (RS) in the western part of the MDF (territory of Estonia and Latvia). They are still rather poorly studied due to the state of preservation of vertebrate remains, their relatively rare occurrence and small range of outcrops of the Pärnu Formation, confined only to Estonia (Sammet 1973; Kleesment & Mark-Kurik 1997).

Vertebrate assemblages of the Pärnu RS were described in detail by W. Gross in his works, dedicated to the biostratigraphy of the MDF (Gross 1933, p. 65, 1942). For the Pärnu RS, a psammosteid zone '*Schizosteus heterolepis* (Preobrazhensky, 1911)' was proposed by this author (Gross 1942). Later E. Mark-Kurik (Obruchev & Mark-Kurik 1965; Mark-Kurik 1968) described another psammosteid taxon – *Psammolepis toriensis* (Mark-Kurik, 1965) from this interval. The only author, who provided detailed descriptions of acanthodian assemblages of the Pärnu RS in the Baltic area, is J. Valiukevičius. According to him (Valiukevičius 1998), the *Laliacanthus singularis* acanthodian Zone corresponds to both the Rēzekne and Pärnu RSs. The zone has ten diagnostic species, but only four of them had been known from the Pärnu RS. Besides the index species, these are *Rhadinacanthus primaris* Valiukevičius, *Diplacanthus kleesmentae* Valiukevičius and *Watsonacanthus* cf. *oervigi* Valiukevičius. Valiukevičius mentioned that acanthodians are very poorly represented in the terrigenous deposits of the Pärnu RS. Thus, any new data on the acanthodian diversity of this interval is of particular interest.

The aim of this study is the description and analysis of material on psammosteids and acanthodians from the typical (Tori) and new (Taali) localities of the Pärnu RS in Estonia.

MATERIAL AND METHODS

All studied specimens are stored in the collections of the Palaeontological Museum of St Petersburg State University (PM SPU 86, 87), Russia; the Department of Geology, Tallinn University of Technology (GIT 116); the University of Tartu (TUG 1552), Estonia; the Institute of Geology and Geography (LIG 45), Vilnius, Lithuania and the Natural History Museum, University of Oslo

(PMO), Norway. Most of the acanthodian and some psammosteid remains were collected by the authors of the article in the Taali locality (Tori Parish, Pärnu County, southwestern Estonia) during the expedition in August 2016.

Psammosteid and acanthodian material was studied under the stereo zoom microscope Leica M205 C and under the scanning electron microscope (SEM) Hitachi S-3400N in secondary electrons (SE) and back-scattered electrons (BSE) detection modes. Thin sections were made using Technovit® EPOX Resin and Technovit® EPOX Hardener fast. The specimens enclosed in the epoxy resin were wet-ground on a glass slide to a needed level with the use of Mirka WPF finishing sandpaper P 800–1000. The sandpaper with a grade P 1200–2000 was used subsequently to polish a thin section. Thin sections of acanthodian scales were made using a polymethyl methacrylate thermoplastic Glass Fil (Print Product®) as a mounting medium and Mirka® Waterproof P1500 and P2500 finishing sandpapers. The photographs of thin sections were taken mainly with a polarization microscope Leica DM4500 P with the use of aniseed oil. Some of the psammosteid sections were photographed with the SEM in the BSE detection mode.

GEOLOGICAL BACKGROUND

In Estonia the Pärnu RS (Lower Eifelian, Middle Devonian) is represented by the Pärnu Formation, which is divided into the Tori (below) and Tamme (above) members (Mb.) (Mark-Kurik & Põldvere 2012). Most of the vertebrate material comes from the Tori Mb. It crops out mainly on the left bank of the Pärnu River (Tori Parish, Pärnu County) in southwestern Estonia (Fig. 1A, B). The Tori Mb. consists of light-yellow fine-grained cross-bedded sandstone with interlayers of grey clay (Kleesment & Mark-Kurik 1997) (Fig. 1C). It is overlain by yellow, greenish and purplish-grey horizontally-bedded sandstones and dolostones of the Tamme Mb. It is almost devoid of vertebrate remains (Kleesment & Mark-Kurik 1997).

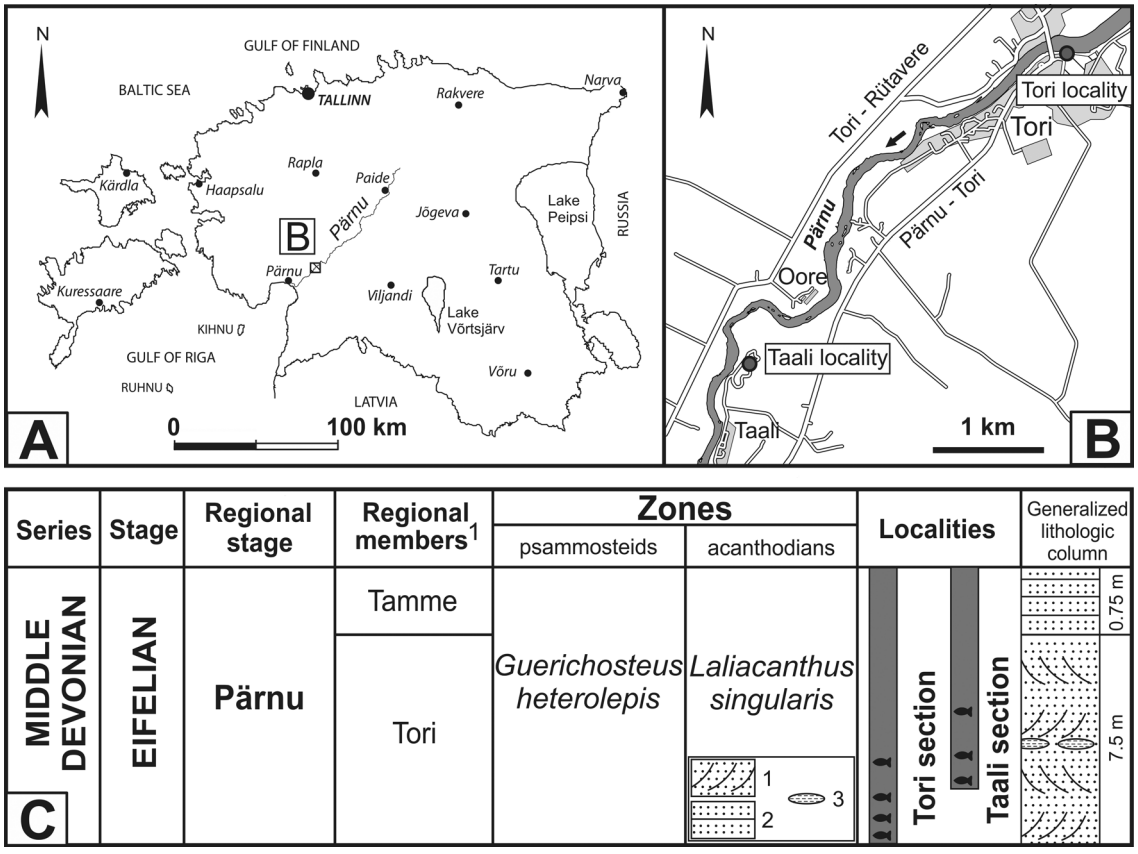


Fig. 1. A, map showing the position of localities along the Pärnu River in Estonia (adapted from Mark-Kurik & Põldvere 2012). **B**, Tori and Taali localities on the left bank of the Pärnu River. **C**, the stratigraphical position of the studied localities.[1], Regional stratigraphical units of Estonia. Black fish figures mark the approximate stratigraphic levels in which the vertebrates are found. Abbreviations for the generalized lithologic column: 1, cross-bedded sandstone; 2, dense parallel-bedded sandstone; 3, lenses of clay (up to 1 m in width).

The Tori (Tori Põrgu) locality is the stratotype of the Pärnu RS. It is represented by a cliff which stretches along the river for 1 km upstream of the bridge in the Tori settlement. The section of this locality is formed by the rocks of the Tori Mb. (7.5 m in thickness) and Tamme Mb. (0.75 m in thickness). Vertebrate remains occur there in the cross-bedded sandstone in the lower and middle parts of the Tori Mb. (Kleesment 1991). The following taxa are reliably identified here (Kleesment & Mark-Kurik 1997; Mark-Kurik 2000): psammosteids *Guerichosteus heterolepis* (Preobrazhensky) (Fig. 2A–V), *Psammolepis toriensis* (Mark-Kurik), *Tartuosteus*? sp.; placoderms *Actinolepis tuberculata* Agassiz, *Homostius* sp., *Byssacanthus dilatatus* (Eichwald); acanthodians *Archaeacanthus quadrisulcatus* Kade, *Diplacanthus kleesmentae* Valiukevičius, *Acanthodes*? sp. B Valiukevičius; sarcopterygians *Porolepis* sp., *Glyptolepis* spp., Osteolepididae indet., Dipnoi indet. Vertebrate remains of the Tori Mb. are represented primarily by isolated small fragments (a couple of centimetres in length). Larger fragments of psammosteid plates occur very rarely.

The Taali locality is situated downstream of the Tori locality. It is represented by a quarry, situated at the edge of the Tori settlement. The walls of the quarry (4.5 m in height) are formed by the rocks of the Tori (4.3 m thick) and Tamme Mbs (0.5 m thick). Vertebrate remains occur in the cross-bedded sandstone in the lower and middle parts of the Tori Mb. (about 0.5 and 1.8–2 m from the base of the quarry). The following taxa have been recorded here: *Guerichosteus heterolepis*, *Psammolepis toriensis*, *Actinolepis tuberculata*, *Byssacanthus dilatatus*, *Glyptolepis* sp., Osteolepididae indet., *Rhadinacanthus primaris* Valiukevičius (Fig. 3A, B, G, H), *Cheiracanthus gibbosus* Valiukevičius (Fig. 3C, I–L), *C.* sp. cf. *C. splendens* Gross (Fig. 3D, E), *Acanthodes*? sp. C Valiukevičius (Fig. 3F). To *Acanthodes*? sp. C are assigned acanthodiform scales with a smooth flat crown, high, well-defined neck and convex base similar to those described by Valiukevičius (1985). The fossils are represented by fragments of plates and complete micromeric elements (scales and tesserae of psammosteids) up to 2–3 cm in length, and scales of acanthodians. Large fragments (more than 10 cm) of psammosteid plates occur at the level 1.8–2 m.

SYSTEMATIC PALAEONTOLOGY

Class PTERASPIDOMORPHI Goodrich, 1909
Suborder PSAMMOSTEIDA Kiaer, 1932
Family GUERICHOSTEIDAE Halstead Tarlo, 1964
Genus *Guerichosteus* Halstead Tarlo, 1964

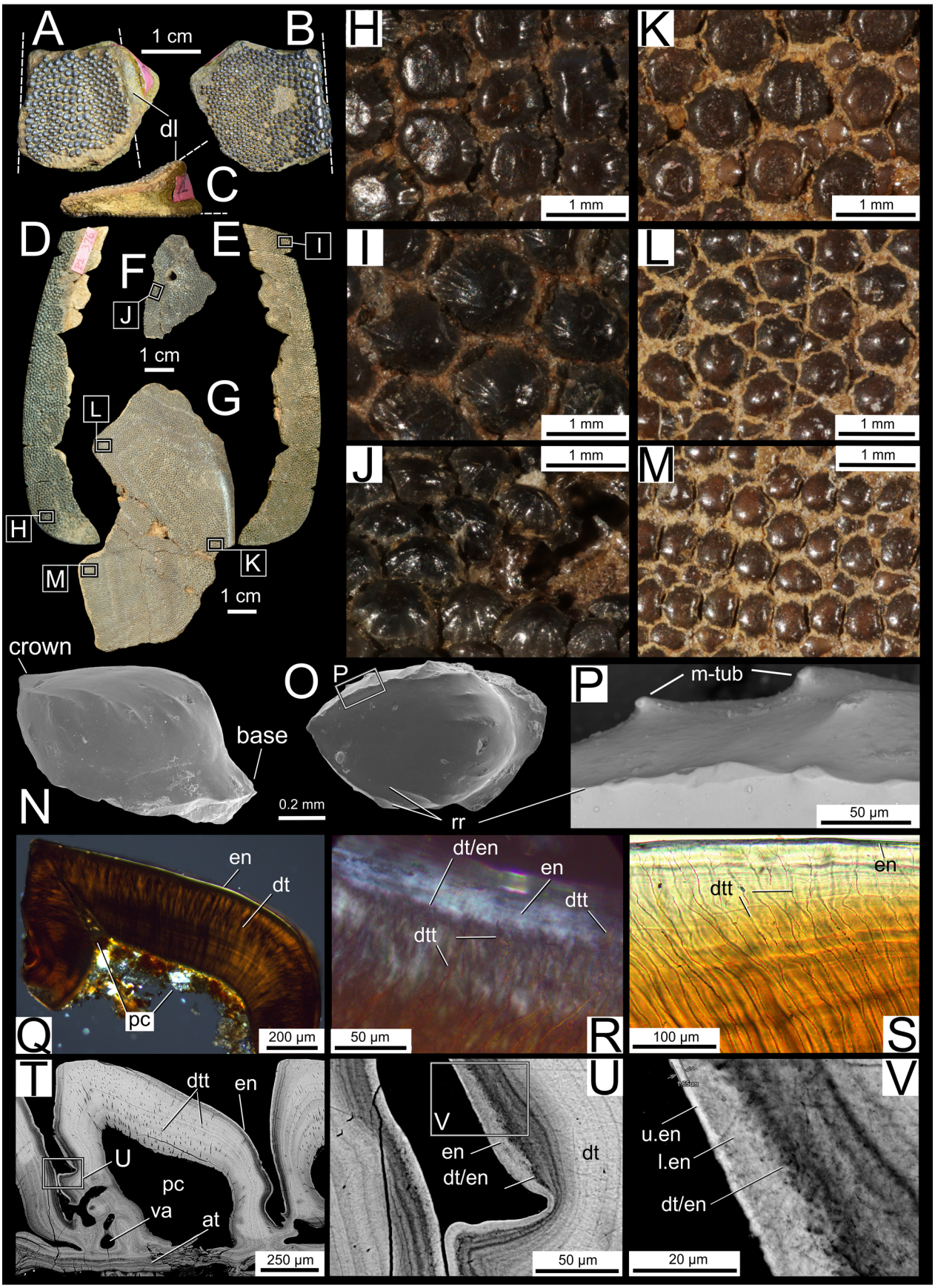
1911 *Psammosteus* Preobrazhensky, pp. 29–31, 35 (pars).
1930 *Pycnosteus*? Gross, p. 13.
1933 *Psammolepis* Gross, p. 12.
1940 *Schizosteus*? Obruchev, p. 766.
1957 Psammosteid (type A) Tarlo, p. 230.
1964 *Guerichosteus* Halstead Tarlo, pp. 28, 44, 59, 113; 1965 Halstead Tarlo, pp. 40–52.
1965 *Schizosteus* Obruchev & Mark-Kurik, pp. 80 (pars), 81 (pars), 82–84, 291 (pars), 292 (pars); 1965 Halstead Tarlo, pp. 55–56 (pars); 2004 Novitskaya, p. 171 (pars), 172.

Type species. *Guerichosteus kozlowskii* Halstead Tarlo, 1964.

Species composition. *Guerichosteus heterolepis* (Preobrazhensky, 1911), *G. kozlowskii* Halstead Tarlo 1964, *G. lefeldi* Halstead Tarlo 1964.

Revised diagnosis. Animals are of medium sizes. Branchial plates narrow euribasal (length:width ratio 1.9–2); free anterolateral ledge and distal tip; dorsal lamella is present; branchial opening is situated medially at the posterior margin. Cornual plates are rectangular. Ventral plate has deep V-shaped posterior notch. Ornamentation is represented by rounded, oval or

Fig. 2. *Guerichosteus heterolepis* (Preobrazhensky, 1911), branchial, orbital, postorbital plates and tubercle from the body scale (A–P), vertical thin section (Q, R) from the Tori locality and vertical thin sections (S–V) from the Taali locality, Pärnu RS, Middle Devonian of Estonia. **A–C**, TUG 1552-2, lectotype, fragment of the left branchial plate; A, dorsal, B, ventral, C, transverse views. **D, E**, GIT 116-1, fragment of the left branchial plate; D, dorsal, E, ventral views. **F**, GIT 116-2, orbital plate, lateral and ventral sides. **G**, GIT 116-3, postorbital plate, dorsal view. **H**, **I**, details of ornamentation from GIT 116-1. **J**, detail of ornamentation from the lateral side of GIT 116-2. **K–M**, details of ornamentation from GIT 116-3. **N–P**, PM SPU 87-2, tubercle from body scale GIT 116-8; N, lateral view; O, top view; P, detail of its microsculpture. **Q–R**, PM SPU 87-2, thin section of the tubercle; Q, R, in polarized light using crossed Nicols. **S**, PM SPU 87-3, thin section of tubercle from median plate PM SPU 87-1 in ordinary transmitted light. **T–V**, PM SPU 87-4, thin section of median plate PM SPU 87-1; T, tubercle; U, V, details of its microstructure. SEM SE images – N–O; SEM BSE images – P, T–V, J–O. Abbreviations: at, aspidin trabeculae; dl, dorsal lamella of the branchial plate; dt, dentine; dtt, dentine tubules; dt/en – junction of tissues; en, enameloid; l.en, lower layer of enameloid; pc, pulp cavity; m-tub, microtubercles of the crown; rr, radial ribs on the crown; u.en, upper layer of enameloid; va, vascular canals of aspidones.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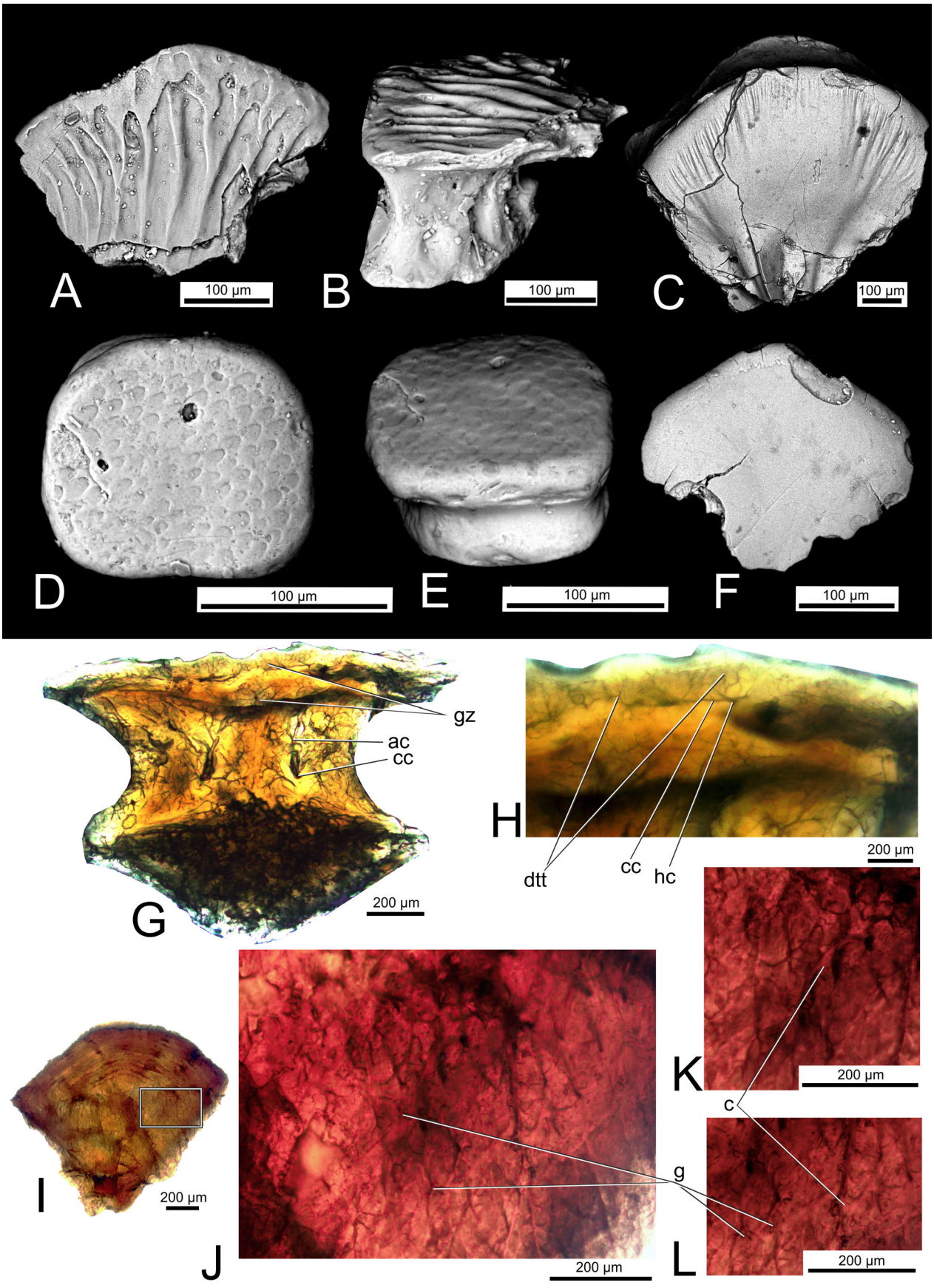
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angular dome-shaped tubercles (1–2 mm) with prominent radial ribs which extend to the sharply pointed summits of the tubercles; tubercles' bases are smooth or complicated by elongated radial ribs (marginal serrations); smaller tubercles (occasionally arranged in concentric rows) are situated between large ones; short ridgelets are rare.

Remarks. *Guerichosteus heterolepis* is attributed to the genus on the basis of similarities in the morphology of the branchial plates, postorbital plates and in the ornamentation characters (size and morphology of tubercles) and their topography. The ornamentation of *Guerichosteus* is very similar to that of '*Hariosteus*'. Apparently they belong to one genus, because these taxa differ only in the density of tubercules. The topography of the ornamentation of *Guerichosteus heterolepis* shows that the sizes, shape of bases and density of tubercles may change on different plates of one species. Thus *G. kotanskii* Halstead Tarlo 1964 and *G. kulczyckii* Halstead Tarlo 1964 are apparently the junior synonyms of *G. kozlowskii*, because these taxa have identical tubercles and details of the ornamentation (including short ridgelets, accessory small tubercles), whereas the difference in sizes are primarily the result of the topographical mutability of their plate fragments. Areal zones of tubercles are visible on the parts of plates with loosely packed tubercles of '*Hariosteus*'. This type of ornamentation is characteristic of e.g. *Drepanaspis*, *Guerichosteus*, however, '*Hariosteus*', one species of *Ganosteus*, scales of '*Psammolepis*' *undulata* Agassiz, 1844, tesserae of *Drepanaspis* and Psammosteidae *sensu stricto* also have the areal zones with graduated sizes of tubercles (Gross 1963, p. 146; Halstead Tarlo 1964, pp. 38–39, 1965, p. 50, text-figs 8B, 9B; Glinskiy & Nilov 2017). Areal zones demonstrate the stage of ontogenetic development – widening of the aspidin layers of the plate. If the psammosteids have the similar morphology of plates and tubercles, the areal zones or growth zones (bands) with graduated sizes of tubercles should be considered as the population variability or as the diagnostic character for the species. *Guerichosteus* can be distinguished from *Schizosteus* by the presence of the dorsal lamella on the branchial plates and the absence of tubercles' marginal crenulations.

Guerichosteus heterolepis (Preobrazhensky, 1911)
Figure 2A–V

1911 *Psammosteus heterolepis* n. sp. Preobrazhensky, pp. 29–31, 35, pl. 1, fig. 7, pl. 2, figs 8, 9.
1930 *Pycnosteus*? Gross, p. 13.
1933 *Psammolepis heterolepis* Gross, p. 12, pl. 2, fig. 16.
1940 *Schizosteus*? *heterolepis* Obruchev, p. 766.
1964 *Schizosteus heterolepis* (Preobrazhensky) Halstead Tarlo, p. 99, pl. 3, fig. 6; 1965 Obruchev & Mark-Kurik, pp. 81–84, 292, pl. 5, figs 1–8, pl. 6, figs 1–8, text-figs 20–23; 1965 Halstead Tarlo, pp. 57–59, pl. 14, fig. 4, text-fig. 12B–E; 2004 Novitskaya, p. 172, fig. 92.

Lectotype. TUG 1552-2, fragment of the branchial plate, Tori, Pärnu River, Estonia, Middle Devonian, Eifelian, Pärnu RS, Tori Mb; Preobrazhensky 1911, pl. 1, fig. 7 (lectotype designated by Obruchev & Mark-Kurik 1965).

Material. Left branchial plates: TUG 1552-2 (Pi 372), GIT 116-1, GIT 116-13, PMO A28130a-d, Tori. Orbital plate: GIT 116-2, Tori. Postorbital plate: GIT 116-3, Tori. Tesserae: GIT 116-4, GIT 116-5, Tori. Body scales: GIT 116-6, GIT 116-7, GIT 116-8, GIT 116-14, Tori. Ridge scales: GIT 116-9, Oore mill; GIT 116-10, GIT 116-11, TUG 1552-5, Tori. Fragments of the median plate: TUG 1554-2, Tori; PM SPU 87-1, Taali; PMO A28131d, Tori. Fragments of undetermined plates: TUG 1552-3, TUG 1552-4, Tori. Thin section across tubercle from the body scale: PM SPU 87-2, Tori. Thin sections across the median (PM SPU 87-1) plate PM SPU 87-3, PM SPU 87-4, Taali.

Occurrence. Middle Devonian; Eifelian; Pärnu RS of the Baltic States; Adrov RS of Belarus.

Revised diagnosis. Tubercles are usually large (up to 1–2 mm), dome- or blister-shaped; short radial ribs with rare microtubercles; tubercles' bases are smooth or complicated by marginal serrations and very diverse in shape: rounded, oval, polygonal or irregular; tubercles are densely packed, but sometimes can be loosely packed or also arranged in tight rows; small, round or angular tubercles are situated around large ones.

Fig. 3. Morphology of acanthodian scales (A–F) and microstructure of acanthodian scales (G–L) from the Taali locality, Pärnu RS, Middle Devonian of Estonia. **A**, **B**, PM SPU 86-25, *Rhadinacanthus primaris* Valiukevičius, 1986. **C**, PM SPU 86-61, *Cheiracanthus gibbosus* Valiukevičius, 1986. **D**, **E**, PM SPU 86-75, *Cheiracanthus* sp. cf. *C. splendens* Gross, 1973. **F**, PM SPU 86-80, *Acanthodes*? sp. C Valiukevičius, 1985. A, C, D, F crown view; B, E posterolateral view. **G**, **H**, PM SPU 86-25, *Rhadinacanthus primaris* Valiukevičius, 1986, vertical transverse section; G, general view, H, magnified area of the crown region. **I**–**L**, PM SPU 86-61, *Cheiracanthus gibbosus* Valiukevičius, 1986, subhorizontal section through the lower part of the crown (above the first growth lamella); I, general view, J–L, enlagred fragments of the section. SEM BSE images – A–F. Abbreviations: gz, growth zones; ac, ascending canal; c, 'cavities' formed by widening and fusing of canals; cc, circular canal; dtt, dentine tubules; hc, horizontal canal; g, 'glomes' of tubules.

Description. Obruchev & Mark-Kurik (1965), and also Halstead Tarlo (1965) have described the general morphology and, partially, the ornamentation of the species. The branchial plate is extremely narrow euribasal with a free anterolaterally projecting margin (= anterolateral ledge; 1.5 cm in width) and distal tip (Fig. 2D, E). The dorsal lamella is located medially (Fig. 2A, C). It fuses with the ventral lamella at an angle of 10° in the zone of the anterolateral ledge (thickness of the plate is from 0.4 cm) and orients at an angle of 30° in the median zone (maximal thickness is 1 cm) (Fig. 2C). The ornamented surface on the dorsal side of the plate is thin (width about 2 cm). Its border is oriented towards the anterolateral margin at an acute angle (~11°) (Fig. 2A).

Ornamentation and topography. The tubercles are fairly large (from 0.4 to 1.7–2 mm, usually approximately 1 mm). The crowns of the tubercles are dome- or blister-shaped. They are oriented vertically or can be slightly slanted towards the surface of the plate (Fig. 2H–J, N, O). Radial ribs (12–17) are robust and can ramify (Fig. 2I, J). Ribs bear rare microtubercles (up to 5) (Fig. 2O, P) and can reach the base of the tubercle, forming marginal serrations. However, in most cases (branchial plates, body scales) radial ribs are short and the base of the tubercle is smooth (Fig. 2N, O). Tubercles usually have rounded and oval (more rarely irregular and polygonal) bases. Rarely two tubercles fuse, forming short ridgelets (Fig. 2H). Small, mostly angular, tubercles, filling the spaces between the larger tubercles are occasionally located concentrically around large ones (Fig. 2K, L, M). They are usually closely-packed on the orbital, branchial, dorsal plates, scales and loosely packed on the post-orbital plate. On the postorbital plate they can form very tight longitudinal rows (Fig. 2M). On the dorsal side of the branchial plates (TUG 1552-2, GIT 116-13) there are growth zones with different sizes of tubercles. Tubercle surfaces do not bear cell imprints.

Histology. The superficial layer of the plates consists of orthodentine tubercles covered by a thin layer (from 8 to approximately 20 µm) of enameloid (Fig. 2Q–V). The latter covers the whole tubercle down to its base (Fig. 2T). It reaches the maximum thickness in the upper part of the tubercle. Upper and lower layers can be distinguished in the enameloid (Fig. 2U, V). The upper one (up to 1.65 µm in thickness) is the most hypermineralized. The thicker (approximately 10 µm) lower layer is less mineralized. It is penetrated by dentine tubules (Fig. 2R, S) as in durodentine tissue. Orthodentine comprises dentine tubules, which start to branch intensively near the enameloid–dentine boundary. Their ramifications are short in other regions of dentine (Fig. 2S). Each tubercle has a large and simple pulp cavity. The thickness of the L1 layer is 0.2 mm. The aspidin trabeculae of the L2 layer form large cavities (up to 0.4 mm).

Comparison. The branchial plates of *Guerichosteus heterolepis* have a free anterolateral ledge with the distal corner and dorsal lamella, as can be seen on the adult specimens of *G. kozlowskii* (Halstead Tarlo 1965, pl. 9, figs 2, 3, 6). Halstead Tarlo (1964, p. 99) mentioned that the ornamentation of *G. heterolepis* is similar to that of *G. kozlowskii*. *Guerichosteus heterolepis* is also similar to *G. kozlowskii* (Halstead Tarlo 1965, text-fig. 8B, pl. 10, fig. 3, pl. 12, fig. 7) in the presence of small tubercles between larger ones (it is not the specific character) and to other specimens (Ibid., pl. 7, figs 3, 4) in the presence of small (about 0.5 mm) tubercles. The species differs from *G. lefeldi* Halstead Tarlo, 1964 in the size of ornamentation, which is larger. *Guerichosteus heterolepis* probably differs from the other species of *Guerichosteus* in higher topographic mutability (shape of tubercle bases, density of ornamentation).

Remarks. Previous reconstructions of the dorsal side of the branchial plate of *Guerichosteus heterolepis* (Obruchev & Mark-Kurik 1965; Novitskaya 2004, text-fig. 92a) were made on the basis on two different specimens (TUG 1552-2 and GIT 116-1) without taking into account the tubercles that have dropped off from the medial region. The dorsal side of the branchial plates of *Guerichosteus* is oriented at a larger angle towards the ventral side, not like in *Schizosteus* (Halstead Tarlo 1964, p. 28; Glinskiy 2014). It should also be noted that the orbitale of *G. heterolepis* bears several radial lateral line canals (Obruchev & Mark-Kurik 1965), and not one, as suggested by Halstead Tarlo (1965). The pattern of the growth lines on the postorbital plate of this species is identical to that of *Guerichosteus* (Halstead Tarlo 1965, pp. 58–59). The ornamention of the postorbital plate of *G. heterolepis* is close to that of '*Hariosteus*' *kielanae* Halstead Tarlo, 1964 and '*H*'. *lobanowskii* Halstead Tarlo, 1964. *Guerichosteus heterolepis* differs from them in the dominance of angular-shaped small tubercles and a generally relatively denser arrangement of tubercles. The species '*H*'. *kielanae* and '*H*'. *lobanowskii* are described based on fragmentary material. They are distinguished by the characters of ornamentation topography. However, the material of *G. heterolepis* shows that the ornamentation, similar to either *G. kozlowskii*, '*H*'. *kielanae* (Halstead Tarlo 1965, text-fig. 9) or '*H*'. *lobanowskii* (straight rows of closely-packed tubercles) can be present on certain regions of different plates of the same species (Fig. 2H, K–M). The topographical study of the ornamentation of the more complete material of *Guerichosteus* and '*Hariosteus*' is needed.

The presence of a hypermineralized layer – enameloid, covering tubercles, is known (but not shown in photographs) in other psammosteids: *Drepanaspis* sp., '*Psammolepis*' *proia* Mark-Kurik 1965 (in Obruchev & Mark-Kurik 1965) (*non Pl. paradoxa*), *Traquairosteus*? *ramosus* (Glinskiy, 2017) and *Psammosteus* sp. = *P. bergi* (Obruchev, 1943) (Gross 1935; Bystrow 1955, 1959; Märss 2006; Glinskiy & Nilov 2017). The study of the photographs of thin sections presented in literature (Kiaer 1915, pl. 3, figs 4–6; Halstead Tarlo 1964, pl. 13, figs 3, 4; Glinskiy & Mark-Kurik 2016) suggests that enameloid is certainly present in such psammosteids as *Drepanaspis gemuendenensis* Schlüter, 1887, *Guerichosteus kozlowskii*, *Psammolepis arctica* (Kiaer, 1915) and *Psammosteus livonicus* Obruchev 1965 (in Obruchev & Mark-Kurik 1965). It should be noted that enameloid is very thin in psammosteids (~20 μm).

Class ACANTHODII Owen, 1846
Order DIPLACANTHIFORMES Berg, 1940
Family DIPLACANTHIDAE Woodward, 1891
Genus *Rhadinacanthus* Traquair, 1888

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

Rhadinacanthus primaris Valiukevičius, 1986
Figure 3A, B, G, H

1986 *Rhadinacanthus primaris* Valiukevičius sp. nov.; Valiukevičius & Karatajūtė-Talimaa, pp. 116, 117, pl. II, figs 1–4; fig. 1.4,6; fig. 2.6,7.
2015 *Rhadinacanthus primaris* Valiukevičius; Plax, pl. IV, fig. 1.

Holotype. LIG 45-1295, scale (Valiukevičius & Karatajūtė-Talimaa 1986, pl. II, fig. 1). Belarus, Kupcheli-325 borehole, depth 274 m. Middle Devonian, Upper Emsian(?)–Eifelian, Vitebsk RS.

Material. Three well-preserved scales: PM SPU 86-25, PM SPU 86-120 (Taali quarry) and the holotype.

Occurrence. Lower(?) and Middle Devonian; Emsian(?) and Eifelian; Rēzekne and Pärnu RSs of the Baltic States; Vitebsk RS of Belarus.

Description

Morphology of the scales. Small scales with the length of the crown about 0.3–0.4 mm. The crown is flat and subhorizontally oriented. The sculpture on its surface is represented by very thin ridges, which run parallel to each other in the posterior part of the crown and diverge in a fan-like manner in its anterior part (Fig. 3A). Most of the ridges in the medial part of the crown dichotomize towards its anterior margin, giving off numerous finer ridges. The ridges gradually fade posteriorly. An unornamented rim can be developed along the anterior margin of the crown. The neck is well defined and high, with vertical grooves running in its lower part (Fig. 3B). Small rounded prominences can be present on the posterolateral walls of the neck. The base is convex, its tip is well defined and subcentrally situated.

Histology of the scales. Due to scarcity of the material only one transverse vertical section was studied. It shows at least two relatively wide growth zones in the crown. The crown is composed of mesodentine. Horizontal canals of the crown are very narrow, almost as narrow as dentine tubules. They give off numerous intensively branching winding dentine tubules. Neighbouring horizontal canals are connected with very thin circular canals (they are almost as thin as dentine tubules). The tubules do not form distinct 'Scheitelung' (*sensu* Gross 1973) under the ridges (Fig. 3G, H). The most outstanding feature of the vascular canal system of the neck is a wide circular canal, situated in its lower part above the base (Fig. 3G). Wide ascending canals branch upwards from it. They ramify, giving off branches in different directions. These canals are not oriented strictly in relation to growth lamellae: some of them cross these zones diagonally (though the growth lines are not distinct in the neck). A very dense network of relatively wide winding canals is developed in the base.

Comparison. *Rhadinacanthus primaris* most closely resembles *R. longispinus* (Agassiz, 1844). These scales are very similar in morphology, though *R. primaris* scales have a more delicate ornamentation, with distinct fan-like divergence of ridges near the anterior margin of the crown. As suggested by Burrow et al. (2016), there is no distinct 'Scheitelung' (*sensu* Gross 1973) under the ridges of *R. primaris* scales, which is well developed in the scales of *R. longispinus* (Burrow et al. 2016). Each growth zone in *R. longispinus* scales has its own vascular and dentinal canal system, whereas in the studied scales of *R. primaris* many of the vascular canals seem to cross growth zone margins.

Order ACANTHODIFORMES Berg, 1940
Family CHEIRACANTHIDAE Berg, 1940
Genus *Cheiracanthus* Agassiz, 1835

Type species. *Cheiracanthus murchisoni* Agassiz, 1835.

Cheiracanthus gibbosus Valiukevičius, 1986
Figure 3C, I–L

1986 *Cheiracanthus gibbosus* Valiukevičius sp. nov.; Valiukevičius & Karatajūtė-Talimaa, pp. 118, 119, pl. III, figs 2–4; pl. IV, figs 3, 5; fig. 4.1–3.

Holotype. LIG, 45-1022, scale (Valiukevičius & Karatajūtė-Talimaa 1986, pl. IV, fig. 3). Latvia, Ludza-15 borehole, depth 431.3 m. Lower(?)–Middle Devonian, Upper Emsian(?)–Eifelian, Rēzekne RS.

Material. Four well-preserved scales: PM SPU 86-61, PM SPU 86-121 (Taali quarry), the holotype and specimen LIG 45-1292 (Belarus, Cherikov-I borehole, depth 411.8–418.4).

Occurrence. Middle Devonian; Emsian(?) and Eifelian; Rēzekne and Pärnu RSs of Latvia and Estonia; Vitebsk and Adrov RSs of Belarus.

Description

Morphology of the scales. The scales are large and robust; the length of the crown is about 0.6 mm. It is thick, rhomboidal in outline, with a rounded anterior margin. The crown sculpture is represented by two broad low medial ridges, which are separated by a short narrow U-shaped or slit-like groove near the posterior angle of the crown and fuse anteriorly to form a wide flat prominence, which covers almost the entire crown area (Fig. 3C). These ridges gradually increase in height posteriorly. Short fine ridges are developed near the anterior margin of the crown. They are oriented sub-perpendicular to it and cover both the lateral regions of the crown and the anterior part of the fused medial ridges. The neck is well defined and considerably high; the base is convex; its tip is slightly shifted anteriorly.

Histology of the scales. Due to scarcity of the material only a horizontal section of the lower part of the crown was studied. It shows a very complex dense network of ascending, circular and horizontal canals characteristic of the species (Fig. 3I–L). Many of the canals are wide and form extensive cavities (Fig. 3K, L). Horizontal canals branch intensively, giving off numerous very fine canals.

Comparison. In their morphology the scales are rather similar to those of *C. latus*? Egerton. The scales of the described species are much more robust, have a thicker crown and more extensive medial ridges. They differ histologically in the structure of mesodentine of the lower part of the crown, which has a characteristic dense complex network of widened canals.

Remarks. The scales of *C. latus*? Egerton, mentioned above, were defined as *C. longicostatus* Gross in Valiukevičius (1985), but in their morphology they seem to be similar to those of *C. latus* Egerton. More research is needed on this subject. This taxon is one of the most common cheiracanthids in the Middle Devonian of the Main Devonian Field.

Cheiracanthus sp. cf. *C. splendens* Gross, 1973
Figure 3D, E

Material. One scale, PM SPU 86-75, the Taali quarry.

Occurrence. Middle Devonian; Eifelian; Pärnu RS of Estonia.

Description

Morphology of the scale. The scale is very small, the length of the crown is about 0.2 mm. The crown has isometric, square, rounded outline, however, it was affected by abrasion. It is flat, horizontally oriented and devoid of sculpture. The crown surface has an ultrasculpture, represented by a network of tongue-shaped depressions. Their length varies from 8 to 15 μm, the width – from 6 to 10 μm. The 'tongues' gradually deepen anteriorly. They are arranged in longitudinal rows. The neck is well defined and of medium height. The base is convex and of the same height as the neck.

Comparison. In its morphology the scale is very close to the scales of *C. splendens* Gross, 1973 from the erratic boulders of the Narva RS in Estonia. The only difference is that in the latter the 'tongues' are convex and partially overlap each other, whereas in the described scale they represent depressions. The 'tongues' on the scales of *C. splendens* are more elongated, reaching 25 μm in length (Märss 2006).

DISCUSSION

The diversification of psammosteids had taken place before the Givetian (Obruchev & Mark-Kurik 1968). *Guerichosteus heterolepis* (Preobrazhensky, 1911), a representative of an old evolutionary line of psammosteids (Guerichosteidae), *Psammolepis toriensis* Mark-Kurik, 1965, a basal representative of a progressive psammosteid group (Psammolepididae) and *Tartuosteus*? sp., a typical representative of the *Schizosteus*-lineage, are present in the sandstones of the Pärnu RS. Thus, along with last archaic psammosteids, two major lineages of more derived psammosteids are present in the Pärnu deposits. The latter became widespread from the end of the Eifelian till the Frasnian in the Baltic area and beyond it (Lukševičs et al. 2010). It may be concluded that the radiation of psammosteids with the appearance of major groups had ended by the early Eifelian (Pärnu Age). The genus *Guerichosteus*, which had previously been known from the Emsian of Poland and perhaps of the Baltic States (*Rhinopteraspis cornubica* Zone), is also found in the Eifelian of the East Baltic area (Estonia). Two of the acanthodian species diagnostic of the *Laliacanthus singularis* Zone are found in the Taali locality – *Rhadinacanthus primaris* Valiukevičius and *Cheiracanthus gibbosus* Valiukevičius. The first one has already been known from this interval, whereas *C. gibbosus* is recorded for the first time in the Pärnu RS. Another taxon, which had not been known before from this interval, is *Cheiracanthus* sp. cf. *C. splendens* Gross.

It is very close to *C. splendens* Gross, which was described from erratic boulders of the Narva RS in Estonia (Gross 1973).

CONCLUSIONS

The genus *Guerichosteus*, which had previously been known from the Emsian of Poland (Holy Cross Mountains, placoderm sandstone, *Rhinopteraspis cornubica* Zone), is also found in the Lower Eifelian of Estonia. The presence of a hypermineralized capping layer (enameloid) in the exoskeleton of *Guerichosteus heterolepis* (Preobrazhensky, 1911) is shown. The acanthodians *Cheiracanthus gibbosus* Valiukevičius and *Cheiracanthus* sp. cf. *C. splendens* Gross are described from the Pärnu RS for the first time. The latter taxon has an ultrasculpture, formed by the network of tongue-like depressions. Such ultrasculpture has not been described in acanthodians before. It most closely resembles that of *C. splendens* from the Narva RS, but the 'tongues' are convex in the latter.

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Uusi andmeid psammosteiidsete lõuatute (Pteraspidomorpha) ja kalade (Acanthodii) kohta Kesk-Devoni (Alam-Eifeli) Pärnu lademest Eestis

Vadim N. Glinskiy ja Darya V. Pinakhina

On kirjeldatud Pärnu lademes leiduvate psammosteiidide histoloogiat ja ornamentatsiooni topograafiat. Esmakordselt on nn Peadevonivälja alalt kindlaks tehtud perekonna *Guerichosteus* Halstead Tarlo levik Alam-Eifelis (Kesk-Devoni algus), senised leiud olid teada pisut vanematest kihtidest (Emsist, Alam-Devon) Poola Świętokrzyskie mägedest. *Guerichosteus heterolepis*'e (Preobrazhensky) välisskeleti histoloogiline uuring näitas, et tuberkulid on kaetud õhukese emailikihiga. Taali paljandis (Tori vallas Pärnu maakonnas Eesti edelaosas) kirjeldati esmakordselt vertebraatide kooslust, milles tavaliste Pärnu lademe vormide kõrval leiti uudisena sellelt tasemelt akantood *Cheiracanthus* sp. cf. *C. splendens*.