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Revision of *Psammosteus livonicus* Obruchev (Agnatha, Heterostraci) from the Devonian Amata Regional Stage of the NW of the East European Platform

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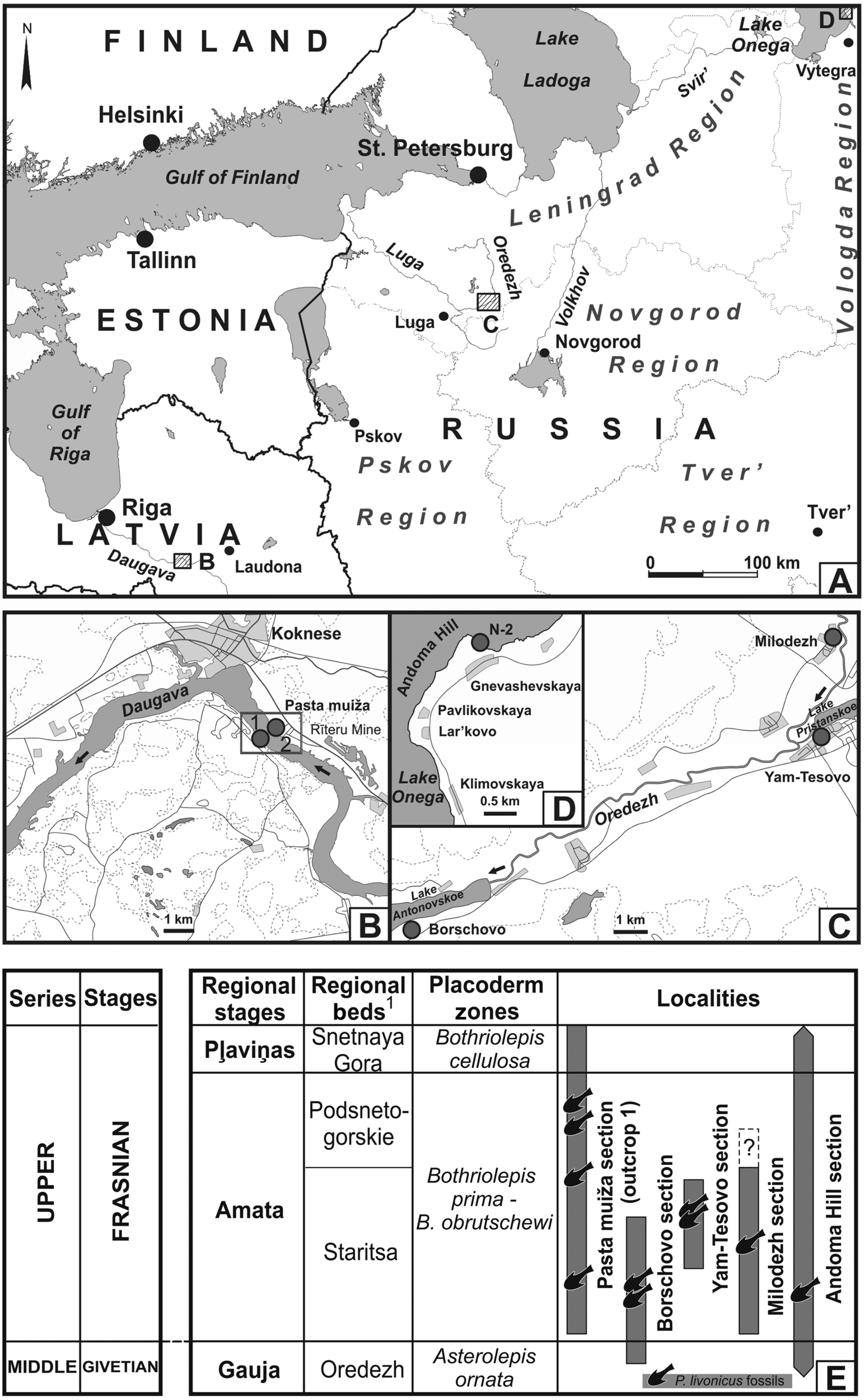
Abstract. The Devonian psammosteid agnathan *Psammosteus livonicus* Obruchev is revised using analysis of fossil material from collections in Russia, Latvia, Lithuania and Estonia that allowed the diagnosis and description of this species to be substantially extended. *Psammosteus livonicus* is similar to other species of *Psammosteus* in the characters of the dorsal plate, cyclomorial tesserae and stenobasal shape of the branchial plates. The study of the morphology of the branchial plates and tesserae (genus-level features) with consideration of species-level features of the ornamentation proves that the establishment of the genus *Oredezhosteus* Moloshnikov is baseless. The species *Psammolepis aerata* Obruchev in Halstead Tarlo 1965 and *Oredezhosteus kuleshovi* Moloshnikov 2009 are included as junior synonyms into the revised species based on the ornamentation features.

Key words: Agnatha, Heterostraci, Pteraspidiformes, Psammosteida, Late Devonian, Latvia, NW Russia.

INTRODUCTION

Two branchial plates and a ridge scale of a previously unknown psammosteid (Heterostraci, Pteraspidiformes) were discovered by D. Obruchev during field work at the Devonian vertebrate localities on the banks of the Daugava River upstream from Koknese, southern Latvia in 1959. The left bank exposure (outcrop 1, Fig. 1B) opposite to Pasta muiža became well-known as a result of the thorough study of the section and fauna by W. Gross (Gross 1942). Later, the new species *Psammosteus livonicus* Obruchev was established based on the Pasta muiža specimens, coming mostly from outcrop 1 (Obruchev & Mark-Kurik 1965, p. 238). V. Karatajūtė-Talimaa collected vertebrate fossils, including those belonging to *P. livonicus*, in this locality in 1959 and 1962 (Karatajūtė-Talimaa 1966). In 1963 she and E. Mark-Kurik joined L. Lyarskaya's excavations in Pasta muiža as that particular area of the Daugava River valley was threatened by flooding during the construction of the Pļaviņas Hydroelectric Power Plant. A dorsal plate and several branchial plates of *P. livonicus* were found during the field work (Mark-Kurik 1968). L. Lyarskaya, who continued to work in Pasta muiža in 1964, 1968 and 1969, collected additional branchial plates and ridge scales of *P. livonicus*. Today the Pasta muiža outcrop is submerged under of the Daugava River reservoir, which prevents the collection of topotype specimens. Still, there are detailed descriptions of this important, though vanished, Devonian vertebrate locality, given by Gross (1942) and particularly by L. Lyarskaya (Vorobyeva & Lyarskaya 1968; Lyarskaya 1972; see also L. Lyarskaya's stratigraphical data in Karatajūtė-Talimaa 1966).

The earliest known branchial plate fragment (PIN 220/527), recognized now as that of *Psammosteus livonicus*, was found by D. Obruchev in 1927 in the locality Milodezh, in the Leningrad Region, Russia, and was described in his DSc thesis (Obruchev 1943a) as a new species *Psammolepis*(?) *aerata*. He also assigned several other plates to this species: two fragments of a branchial plate (PIN 220/400, PIN 220/419) and a possible fragment of a scale (PIN 220/529) from the localities Milodezh and Goryni. Unfortunately, these specimens were not found later in the collections of the Borisiak Palaeontological Institute of the Russian Academy of Sciences (Moscow). For this reason they are not listed in the section 'Material' of this paper. Based on the examination of the photographs from the dissertation, it can be concluded that because of its transversely curved shape specimen PIN 220/529 may be a fragment of the *Psammosteus livonicus* ridge scale. Specimens PIN 220/400 and PIN 220/419 possess a different ornamentation, similar to that of *Psammolepis*.


FINLAND
Helsinki
St. Petersburg
Lake Ladoga
Lake Onega
Vytegra
Svir'
Gulf of Finland
Leningrad Region
Vologda Region
Tallinn
ESTONIA
Luga
Oredezh
Volkhov
Novgorod Region
Novgorod
Gulf of Riga
Pskov
RUSSIA
Pskov Region
Tver' Region
Tver'
Riga
LATVIA
Daugava
Laudona
0 100 km
A
B
C
D
Koknese
Pasta muiža
Rīteru Mine
1 km
Andoma Hill
N-2
Gnevashevskaya
Pavlikovskaya
Lar'kovo
Klimovskaya
0.5 km
Milodezh
Lake Pristanskoe
Yam-Tesovo
Lake Antonovskoe
Borschovo
Series
Stages
UPPER
FRASNIAN
MIDDLE
GIVETIAN
Regional stages
Regional beds[1]
Placoderm zones
Localities
Pļaviņas
Snetnaya Gora
Bothriolepis cellulosa
Amata
Podsnetogorskie
Staritsa
Bothriolepis prima - B. obrutschewi
Gauja
Oredezh
Asterolepis ornata
Pasta muiža section (outcrop 1)
Borschovo section
Yam-Tesovo section
Milodezh section
Andoma Hill section
?
P. livonicus fossils
E

Obruchev did not consider it reasonable to publish *Psammolepis*(?) *aerata* in the joint monograph Obruchev & Mark-Kurik (1965), probably due to poor fossil material and unclear systematic position. However, L. B. Halstead Tarlo, visiting Moscow in 1961 and studying the plate fragment from Milodezh, assigned it without doubt to the genus *Psammolepis*. Later Halstead Tarlo described it as the branchial plate of '*Psammolepis aerata* Obruchev, 1965 (in press)' and compared its ornamentation with that of *Karelosteus weberi* Obruchev, 1933 (Halstead Tarlo 1964, p. 108, 1965, p. 111).

Hence, the presence of *P. livonicus* in the eastern part of the Main Devonian Field (from the Andoma Hill locality) was mentioned much later (Ivanov et al. 2005). Afterwards Moloshnikov (2009) described a new genus and species *Oredezhosteus kuleshovi* based on fragments of branchial plates and a ridge scale from the locality of Yam-Tesovo, in the Leningrad Region. The specimens had an ornamentation characteristic of *P. livonicus*, but their preservation type differed from that of Pasta muiža specimens; this was probably the cause of the author's confusions. Moloshnikov also proposed to assign *Psammosteus livonicus* Obruchev to his new genus. Our investigation of the holotypes and originals of *Psammosteus livonicus* and *Oredezhosteus kuleshovi* permits us to assign both of these taxa to the former species and recognize the latter as its junior synonym. Moreover, the genus *Oredezhosteus* cannot be considered as valid due to the lack of reliable features to distinguish it from *Psammosteus*.

MATERIAL AND METHODS

The *Psammosteus livonicus* specimens under study are stored in the collections of the Borisiak Palaeontological Institute of the Russian Academy of Sciences (PIN 220 and 1737), Moscow, Russia; Natural History Museum of Latvia (G 43), Riga, Latvia; Laboratory of Bedrock Geology, Nature Research Centre (GTC 1690), Vilnius, Lithuania; Institute of Geology at Tallinn University of Technology (GIT 25 and 116), Tallinn, Estonia; Palaeontological Museum of St. Petersburg State University (PM SPU 71) and Museum of the Department of Vertebrate Zoology of St. Petersburg State University (thin sections collection A.3), St. Petersburg, Russia. The material described in this paper consists of 34 specimens: a dorsal plate, 22 branchial plates, 4 ridge scales, 5 tesserae, a fragment of an undeterminate plate and 1 microcell with an isolated tubercle. A thin section has also been studied. The presence of numerous distal fragments of branchial plates is due to their higher durability and selective preservation of skeletal elements in terrigenous deposits of the Main Devonian Field.

Psammosteid genera are predominantly determined on the basis of the characters of plates and general morphology of their ornamentation, consisting of dentine tubercles on their external surfaces. However, details of the tubercles (morphology and number of radial ribs, crenulations, ramifications, microtubercles and plumose wrinkles) are species-level characters. Ornamentation can change during ontogeny or healing of mechanical injuries. Slight wear of the crowns of tubercles, which can alter the original state of ornamentation, is especially misleading in species recognition (Novitskaya 1971). Therefore, a need arose to study details of the topographic variability of ornamentation and histology of psammosteid plates for determination of their original morphology. The ornamentation of the holotype and other specimens of *P. livonicus* was studied in detail under the trinocular microscopes Nikon AZ100 Multizoom and Leica M125. As a result the photographs, depicting topographic variations in the ornamentation in certain parts of the plates, were obtained. A tessera and several fragments with well-preserved ornamentation were also examined under the scanning electron microscope Hitachi TM 3000 and Hitachi S-3400N. Tomographic examination of specimen PM SPU 71-4 was made by SkyScan 1172 and software CTAn and CTVol.

The views on psammosteid systematics underwent some changes during the 20th century. At first psammosteids *sensu stricto* (from *Drepanaspis* to *Psammosteus*) in the group Heterostraci were proposed to form the families Drepanaspidae and Psammosteidae (Traquair 1900; Brotzen 1936; Berg 1940; Obruchev 1941) or only the family Drepanaspidae (Stensiö 1927), or only the family Psammosteidae (Woodward 1910; Gross 1937; Berg 1955). The families Drepanaspidae and Psammosteidae were united by several authors in the suborder Psammosteida (Kiaer 1932; Gross 1935; Halstead Tarlo 1965) and later they were assigned to the order Psammosteida (Obruchev 1964; Obruchev & Mark-

Fig. 1. A, map showing the localities of *Psammosteus livonicus* Obruchev. **B**, Pasta muiža, outcrop 1 on the left and outcrop 2 on the right bank of the Daugava River, Latvia. **C**, Milodezh, Yam-Tesovo and Borschovo, Russia. **D**, outcrop N-2 of Andoma Hill, Russia. **E**, the stratigraphical position of studied localities. [1], Regional Beds of the eastern part of the Main Devonian Field. Black psammosteid figures mark the approximate stratigraphic levels from which the specimens of *Psammosteus livonicus* were collected.

Kurik 1965). Psammosteids *sensu stricto* were also united with *Tesseraspis* in the order Drepanaspida (Stensiö 1958; Ørvig 1961) and also with the family Obrucheviidae in the suborder Psammosteida (Tarlo 1962) or the order Psammosteiformes (Halstead 1993). However, Gross (1963) showed that the juvenile stages of primitive psammosteids of the genus *Drepanaspis* demonstrated recapitulations of the ancestral features, drawing them closer to pteraspids. Still, the position of psammosteids in the order Pteraspidiformes is ambiguous. Currently psammosteids are often regarded as the family Psammosteidae (Janvier 1996; Pernègre & Elliott 2008). More rarely they are assigned to the suborder Psammosteida in the order Pteraspidiformes, which includes such families as Drepanaspididae, Guerichosteidae, Pycnosteidae, Psammolepididae, Psammosteidae and Obrucheviidae (Elliott et al. 2004). The latter classification is accepted in the present paper.

GEOLOGICAL BACKGROUND

The material comes largely from five localities of the Amata Regional Stage (RS) in Latvia and the NW region of Russia (Fig. 1). The Amata RS, usually 20–30 m thick (Kuršs et al. 1981), is subdivided into the Staritsa and Podsnetogorskie Regional Beds (RB) in the eastern part of the Main Devonian Field (Ivanov & Lebedev 2011). There were originally two outcrops near Pasta muiža (Fig. 1B), situated on the left bank (outcrop 1) and the right bank (outcrop 2) of the Daugava River, upstream from Koknese, Latvia. Practically all material, including the holotype, comes from outcrop 1 opposite to Pasta muiža, and only a single specimen was found by D. Obruchev at outcrop 2. Therefore, it is reasonable to refer to the main locality, i.e. outcrop 1, as Pasta muiža. The deposits in this locality were represented by fine-grained sandstones intercalating with clays of the Amata RS in the lower part and dolomites of the Pļaviņas RS in the upper part (Gross 1942; Vorobyeva & Lyarskaya 1968). The holotype of *Psammosteus livonicus* and some other specimens were found in the interval between the base of white sandstones of the Amata RS and 2–2.5 m below the lower boundary of the dolomite member of the Pļaviņas RS. Thus, in the type locality *P. livonicus* has been discovered both in the lower and upper parts of the Amata RS, where this taxon occurs together with the zonal antiarch species *Bothriolepis prima* Gross, 1942 and *B. obrutschewi* Gross, 1942 (Obruchev & Mark-Kurik 1965; Vorobyeva & Lyarskaya 1968).

The localities of Borschovo, Yam-Tesovo and Milodezh are situated in the Luga District of the Leningrad Region, NW Russia. The Borschovo locality (Fig. 1C) includes some outcrops on the left bank of Lake Antonovskoe, downstream of the Oredezh River. The remains of *P. livonicus* were discovered in the terminal eastern outcrop 3, situated to the right of the road from Borschovo village. The deposits in this outcrop are represented by pink, yellowish-grey, reddish-brown and light blue cross-bedded medium- and fine-grained sandstones, intercalating with purple and greenish clay. Psammosteid remains, including a branchial plate and separate tubercles of *P. livonicus*, were found at two levels in the middle part of the outcrop, in light blue and overlying yellowish-grey sandstones of the Staritsa RB (Ivanov & Lebedev 2011). The Yam-Tesovo locality encompasses a series of outcrops, situated close to each other on the left bank of Lake Pristanskoe. They are exposed in the upper part of the bank slope. The deposits of the section are represented by reddish-brown, more rarely light grey cross-bedded fine- and medium-grained sandstones with intercalations of purple and greenish clays and clay pebbles. Psammosteids, including *P. livonicus*, occur in reddish-brown sandstones of the upper part of the section, corresponding to the Staritsa RB (Hekker & Philippova 1935; Ivanov & Lebedev 2011).

The Milodezh locality (Fig. 1C) is a long cliff on the right bank of the Oredezh River near the village of the same name. This Staritsa RB outcrop is composed of reddish-brown cross-bedded fine- and medium-grained sandstones (Hekker & Philippova 1935); vertebrate fossils, presumably psammosteids, come from about the middle part of the section. The presence of the Podsnetogorskie RB here is not confirmed yet.

The locality on Andoma Hill is situated on the south-eastern bank of Lake Onega in the Vytegra District of the Vologda Region (Fig. 1D). This section is a cliff, a couple of kilometres long. Specimens of *P. livonicus* occur in the upper part of the outcrop N-2 at Gnevashevskaya village, in the layer AG 1-2. This layer is composed of variegated fine and very fine poorly cemented sandstones and sands, intercalating with thin layers of silty clay and siltstone. These deposits are assigned to the Andoma Formation, which is correlated with the Amata–Pļaviņas interval (Lukševičs et al. 2012; Glinskiy & Ivanov 2015).

The position of the boundary between the Middle and Upper Devonian in the Main Devonian Field is still ambiguous. Three boundary positions have been proposed: at the base of the Amata RS, in the Amata RS (at the base of the Podsnetogorskie RB) and at the base of the Snetnaya Gora RB of the Pļaviņas RS (Esin et al. 2000; Mark-Kurik & Põldvere 2012). The first position is accepted in the current research. Thus the Amata RS is assigned here to the Frasnian Stage.

SYSTEMATIC PALAEONTOLOGY

Subclass HETEROSTRACI Lankester, 1868
Order PTERASPIDIFORMES Berg, 1940
Suborder PSAMMOSTEIDA Kiaer, 1932
Family PSAMMOSTEIDAE Traquair, 1896
Genus *Psammosteus* Agassiz, 1844

1840 *Placosteus* Agassiz, p. 33 (nomen nudum) (pars).
1844 *Psammosteus* Agassiz, p. 103 (pars); 1947 Obruchev, pp. 517–518; 1964 Obruchev, p. 74; 1965 Halstead Tarlo, pp. 114–115; 1965 Obruchev & Mark-Kurik, pp. 215–219; 2004 Novitskaya, p. 189.
1844 *Ctenacanthus* Agassiz, p. 119 (pars).
1911 *Dyptychosteus* Preobrazhensky, p. 33.
1924 *Asterolepis*(?) Weber, p. 135.
1943 *Yoglinia* Obruchev, p. 41; 1965 Halstead Tarlo, pp. 93–95.
1965 *Psammolepis* Halstead Tarlo, p. 111 (pars).
1964 *Crenosteus* Halstead Tarlo, p. 117; 1965 Halstead Tarlo, p. 141.
2009 *Oredezhosteus* Moloshnikov, pp. 197, 199.

Type species. *Psammosteus maeandrinus* Agassiz, 1844.

Diagnosis. The dorsal plate is entirely covered with cyclomorial tesserae characterized by concentric type of growth. The ventral plate is elongated, without posterior notch and covered with tesserae. The branchial plates are stenobasal, transversely elongated, flattened. Their distal part bears ornamentation, the proximal part of the ventral side is covered with elongated tesserae, which are usually detached in fossils. Dentine tubercles are of various shapes, their structure can be complicated partly due to lengthening or branching of marginal crenulations. In some places tubercles fuse into ridges, especially on the branchial plates.

Species composition. *Psammosteus asper* Obruchev, 1965; *P. bergi* (Obruchev, 1943); *P. bystrowi* Obruchev, 1965; *P. cuneatus* Obruchev, 1965; *P. falcatus* Gross, 1942; *P. kiaeri* Halstead Tarlo, 1964; *P. levis* Obruchev, 1965; *P. livonicus* Obruchev, 1965; *P. maeandrinus* Agassiz, 1844; *P. megalopteryx* (Trautschold, 1880); *P. pectinatus* Obruchev, 1965; *P. praecursor* Obruchev, 1947; *P. tchernovi* Obruchev, 1965; *P. tenuis* Obruchev, 1965.

Remark. The genus *Oredezhosteus* Moloshnikov is included in the genus *Psammosteus* on the basis of stenobasal branchial plates and cyclomorial tesserae.

Psammosteus livonicus Obruchev, 1965
Figures 2–8

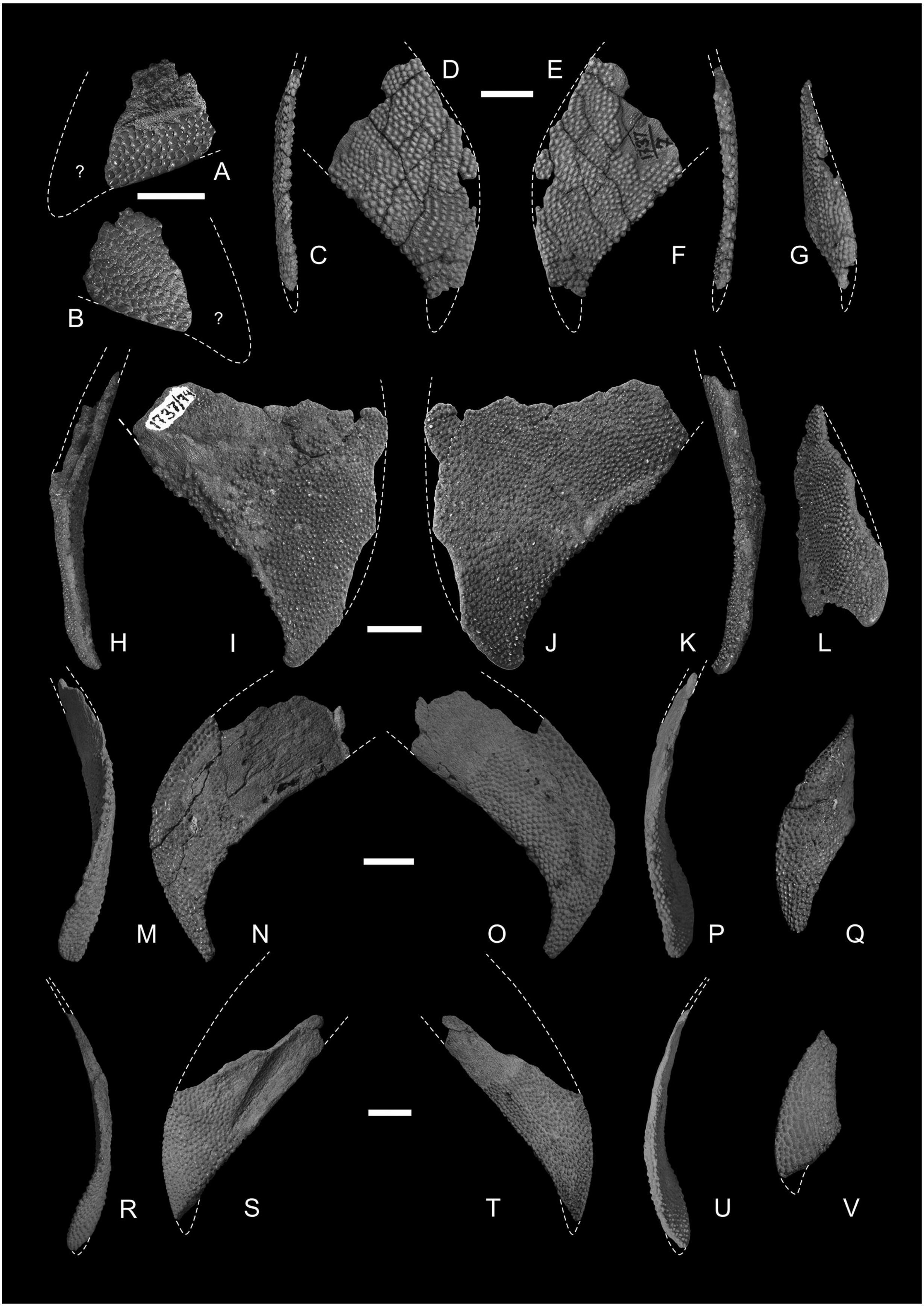
1965 *Psammosteus livonicus* Obruchev in Obruchev & Mark-Kurik, p. 238, pl. 94, figs 1, 2; 1965 Novitskaya, pp. 275–277, fig. 221; 1968 Mark-Kurik, pp. 420–421, fig. 11A; 1968 Obruchev & Mark-Kurik, p. 280, fig. 1, 3D; 2004 Novitskaya, p. 191; 2005 Elliott & Mark-Kurik, pp. 101, 103, fig. 4F.
1965 *Psammolepis aerata* Obruchev in Halstead Tarlo, p. 111, pl. 19, fig. 9.
2009 *Oredezhosteus livonicus* Moloshnikov, p. 199, fig. 1a.
2009 *Oredezhosteus kuleshovi* Moloshnikov, p. 200, fig. 1b, c; pl. 13, figs 1–5.

Holotype. PIN 1737/7, right branchial plate (Obruchev & Mark-Kurik 1965, pl. 94, figs 1, 2), Latvia, left bank of the Daugava River, Pasta muiža, outcrop 1; Upper Devonian, Frasnian, Amata RS.

Material. Left branchial plates: GTC 1690-2, GTC 1690-3, GTC 1690-6, GIT 116-272, GIT 116-275, PIN 1737/8, Pasta muiža; PM SPU 71-1, Borschovo. Right branchial plates: GTC 1690-1, GTC 1690-4, GTC 1690-5, G 43-251, G 43-252, G 43-261, GIT 116-273, GIT 116-288, PIN 1737/7, Pasta muiža; PIN 1737/74, Yam-Tesovo. Small fragments of branchial plates: G 43-278, Pasta muiža; PIN 220/527, PM SPU 71-3, Milodezh; PIN 1737/75, Yam-Tesovo; PM SPU 71-6, Andoma Hill, outcrop N-2. Dorsal plate GIT 25-12, Pasta muiža. Ridge scales: G 43-285, G 43-304, PIN 1737/9, Pasta muiža; PIN 1737/76, Yam-Tesovo. Fragment of undetermined plate PM SPU 71-4, Yam-Tesovo. Tesserae: GIT 116-327, GIT 116-328, Pasta muiža, PM SPU 71-5, Yam-Tesovo, PM SPU 71-7, PM SPU 71-8 Andoma Hill, outcrop N-2. Isolated tubercle PM SPU 71-2, Borschovo. Thin section across of branchial plate: A.3-1, Pasta muiža. Remark: all Pasta muiža specimens come from outcrop 1, except ridge scale PIN 1737/9 which comes from outcrop 2.

Occurrence. Amata RS, Frasnian, Upper Devonian, *Bothriolepis prima–B. obrutschewi* Zone, Latvia, Russia.

Diagnosis. Ornamentation consists of large, dome-shaped, less often cone- and peak-shaped dentine tubercles (up to 2 mm in diameter, on average 0.7–1.5 mm), whose relative position is mostly regular. Rounded (including oval) tubercle bases are dominant, angular halberd- and fan-shaped bases are less common. Sharp radial ribs of tubercles start from the top of the crown, more rarely lower (in the case of high and abraded tubercles); some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ribs can diverge into several branches. At the bases of the tubercles ribs pass into marginal crenulations (usually 13–24). The crenulations vary in length and thickness; their tips are truncated. The tips can diverge into two, less often three or rarely four branches (ramifications). Radial ribs, crenulations and their ramifications bear microtubercles (usually 5–7). On the branchial plates two, more rarely three tubercles can fuse into short ridges, which are arranged either transversely or longitudinally (along the margins of branchial plates).

Description

1. *General morphology*. Dorsal plate GIT 25-12 is generally oval, with a truncated anterior margin and anteriorly concave lateral margins (Mark-Kurik 1968, fig. 11A). The plate is 26.5 cm long and 20 cm wide, 1–4 mm thick, and slightly convex (up to 2 cm) in its posterior part. The external surface has lost almost all ornamentation. Still, three tesserae have been preserved; they are 3–7 mm in diameter and show small groups of tubercles (Fig. 7: 44). The sensory canal system is exposed as narrow ridges of spongy aspidin; it consists of a couple of widely spaced medial dorsal canals and two pairs of transverse commissures (Elliott & Mark-Kurik 2005, fig. 4F, modified from Mark-Kurik 1968, fig. 11A).

   Branchial plates are stenobasal; a short base (proximal margin) is observed in juvenile individuals (Fig. 2N, O, S, T); the base increases in length in adults (Fig. 3A, B, E, F). As a rule, the plates are semicircularly expanded in width. The anterolateral margin is convex, the posterior margin is concave (Fig. 2D, E; Fig. 3E, F). Specimen PIN 1737/8 has an anterior proximal ledge (Fig. 3A, B; Fig. 4K, L). The distal end of the branchial plates, if not worn, is pointed and usually curved backwards (Fig. 2I, J, N, O). The distal angle varies from 30° to 65°. The shape of the proximal margin is unknown; it was probably rounded. The branchial plates are dorsally convex in width: 1.6 cm in GIT 116-273, 0.6 cm in GIT 116-272, 0.7 cm in GIT 116-275, 0.2 cm in PIN 1737/7, 0.4 cm in PIN 1737/8 and 0.5 cm in PIN 1737/74. Such curvature of the majority of plates was probably present in living individuals. Rare flattening of other branchial plates was the result of fossilization of skeletal tissues, plastic if wet (Obruchev & Mark-Kurik 1965). The distal part of the branchial plates is slightly dorsally convex in length. The ornamented surface is developed on the distal part of the branchial plates. As a rule, its area is smaller on the dorsal side than on the ventral one (Fig. 2I, J, N, O, S, T; Fig. 3A, B). The ornamentation on the ventral side sometimes occupies a large area, supposedly equal to or exceeding half of the width of the branchial plate (in PIN 1737/8, Fig. 3B). The boundary between the ornamented and unornamented surfaces of the branchial plates is either distally curved or almost straight. The ornamented surface can be substantially decreased, for example in branchial plate GIT 116-273 (Fig. 3E, F); specimen GIT 116-273 has many secondary tesserae predominantly on the ventral side, represented by tubercles in the area of detached primary tesserae, weakly attached by the aspidine of the large plate (Fig. 3E, F; Fig. 4M, N). The incomplete length of the branchial plates varies from 1.8 cm (GIT 116-275) to 11.9 cm (PIN 1737/8). Incomplete width of the most completely preserved branchial plate is from 5.6 cm (GIT 116-272) to 17.0 cm (PIN 1737/8). The thickness of the plates (from proximal to distal part) is 0.1–0.3 cm in GIT 116-272 and 0.4–0.5 cm in PIN 1737/8.

   Ridge scales are elongated, with convex proximal and pointed distal ends (Fig. 3I–O; Fig. 4O–R). According to their position on the body, the ridge scales are externally convex in width. The ornamentation covers almost the entire external surface; only a narrow band at the proximal margin stays unornamented. On the visceral side the ornamented surface occurs in the distal part, occupying roughly 1/3 of the total surface. Incomplete length of the ridge scales varies from 3.0 cm (PIN 1737/76) to 6.75 cm (PIN 1737/9), the width is from 1.7 cm (PIN 1737/76) to 2.20 cm (PIN 1737/9). The maximal thickness of the plates is 0.35 cm (PIN 1737/76) and 0.33 cm (PIN 1737/9). The plates are dorsally curved to the width of 0.25 cm (PIN 1737/9) and 0.30 cm (PIN 1737/76). Based on the state of preservation of the ornamentation it can be proposed that specimens PIN 1737/9 and PIN 1737/76 resided on the ventral side of the body.

Fig. 2. *Psammosteus livonicus* Obruchev, branchial plates of adult and juvenile individuals from the Amata RS, Upper Devonian. **A**, **B**, PIN 220/527, fragment of left branchial plate, Milodezh, Russia; A, dorsal and B, ventral views. **C**–**G**, PIN 1737/7, holotype, right branchial plate, Pasta muiža, Latvia; C, anterolateral, D, dorsal, E, ventral, F, posterior and G, distal views. **H**–**L**, PIN 1737/74, right branchial plate, Yam-Tesovo, Russia; H, anterolateral, I, dorsal, J, ventral, K, posterior and L, distal views. **M**–**Q**, GIT 116-272, left branchial plate, Pasta muiža, Latvia; M, anterolateral, N, dorsal, O, ventral, P, posterior and Q, distal views. **R**–**V**, GIT 116-275, left branchial plate, Pasta muiža, Latvia; R, anterolateral, S, dorsal, T, ventral, U, posterior and V, distal views. Scale bars = 1 cm.


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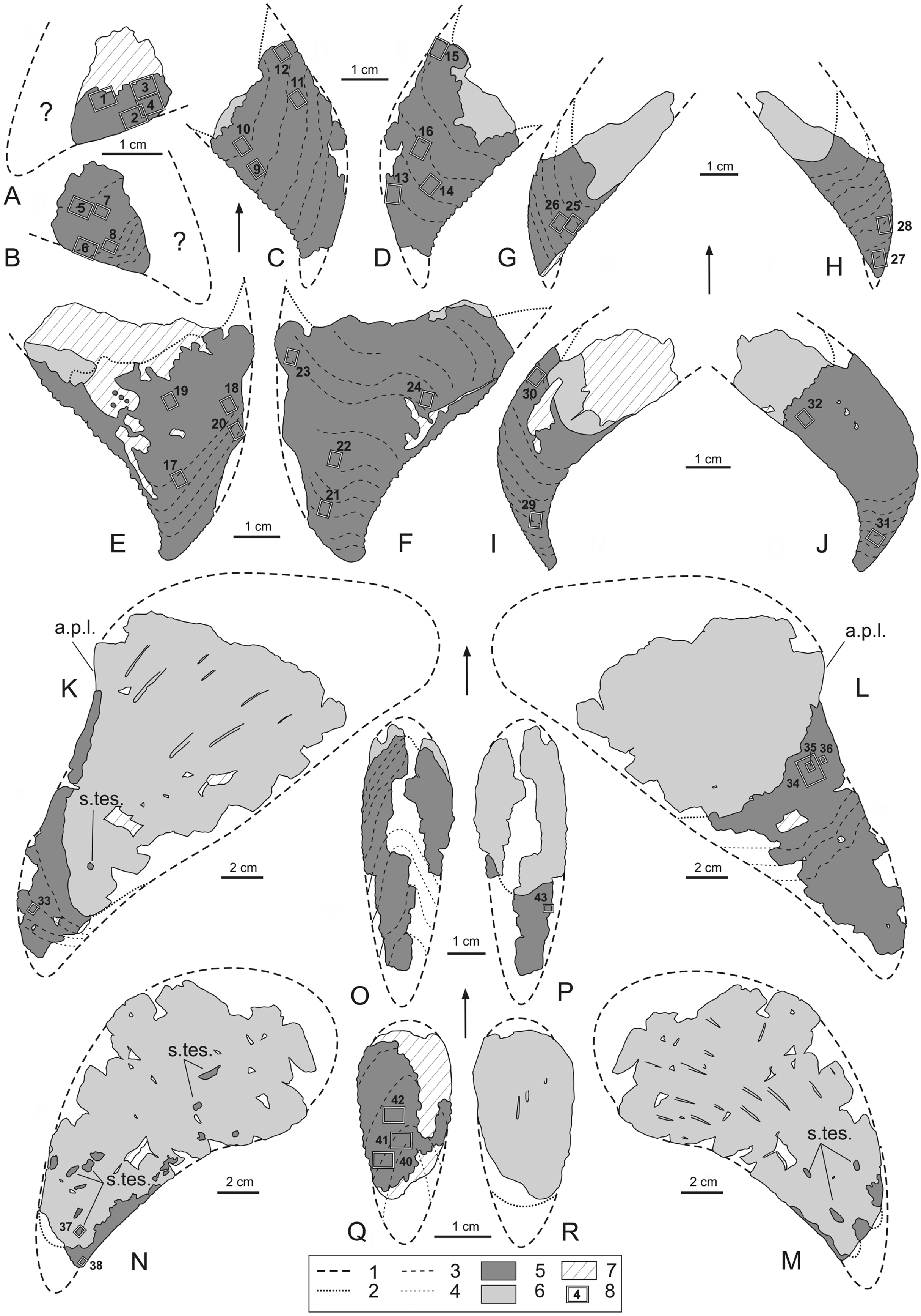
The tesserae (GIT 116-327, GIT 116-328) from the ventral side of branchial plate GIT 116-272 have rhombic shape, and a high cone-shaped central tubercle, surrounded by circles of smaller ones (Fig. 7C, D). Incomplete length of GIT 116-327 is 3.1 mm, the width is 2.2 mm. Specimen PM SPU 71-5 has a crown of dentine tubercles, neck and base of aspidin (Fig. 7E).

2. *Ornamentation*. The ornamentation is represented by tubercles, which vary in the shape of their bases. The ornamented surface has one dominant round morphotype of tubercle bases. Single tubercles can fuse into ridges (Glinskiy 2013). The ornament of the branchial plates consists of dome-, cone- or peak-shaped dentine tubercles (Fig. 6: 9, 10, 21, 27; Fig. 7: 31). The height of the cone- and peak-shaped tubercles reaches 1.3 mm. Their crowns are vertical (the angle with the base of the tubercle is 90°). More rarely they are slanted (with an angle less than 90°); in the latter cases the bases of tubercles can be round, oval, angular, fan- or halberd-shaped (Fig. 6: 1, 3, 11, 12, 15, 20). Bases of polygonal, leaf-like and other shapes are rarer (Fig. 6: 2, 4, 7, 12). The tubercle base with crenulations is up to 2 mm in length. Their average size is 0.7–1.5 mm. Sharp radial ribs of tubercles commonly start from the top of the crowns (Fig. 6: 7, 10, 12, 16; Fig. 7: 29–32, 39) (of dome- or peak-shaped tubercles), but sometimes (because of their large sizes, characteristics of growth and life-time abrasion) they do not reach the top (of cone- and dome-shaped tubercles). Some ribs diverge into several branches (Fig. 6: 2, 10, 12, 16, 17, 27; Fig. 7A, C). Ribs and their branches pass into marginal crenulations. The length of crenulations of individual tubercles varies from 0.2 to 0.8 mm. Crenulations are usually wide, but sometimes substantially more narrow ones can be found between them (Fig. 6: 9, 15, 23). Their ends are truncated (Fig. 6: 5, 8, 9–12). The tubercle length can extend in the case of long marginal crenulations (PM SPU 71-3). The number of crenulations varies from 13 to 27. As a rule, individual tubercles have 13–24 crenulations. Tips of the crenulations can branch into two or three, more rarely four ramifications (Fig. 6: 1, 3, 5, 10, 15; Fig. 7A). In a number of cases radial ribs and corresponding marginal crenulations are very densely located and branch frequently (Fig. 6: 1–4, 25, 26). Radial ribs, crenulations and sometimes their ramifications bear microtubercles numbering up to 11, usually 5–7 (Fig. 7A,C, E). Small tubercles of later generations (with the diameter of the base 0.2–0.4 mm) are usually rounded, more rarely elongated; they bear 7–12 marginal crenulations (Fig. 6: 6–8, 19, 22, 23; Fig. 7A, B, 32). On the branchial plates and ridge scales two, more rarely three or four tubercles fuse into short ridges with a length up to 2–3 mm (Fig. 6: 2, 4, 6, 18, 25, 26; Fig. 7: 33, 40). The number of crenulations of fused tubercles varies from 20 to 40 (Fig. 6: 2, 4, 25, 26).

The ornamentation of the ridge scales is characterized by tubercles with an oval base, while circular bases appear more rarely; there are short ridges (Fig. 7: 40–42). The crowns of tubercles are slanted (on average 60°) and directed backwards. Tubercles on the external side have normal size, but the visceral side of specimen PIN 1737/9 consists of very fine tubercles with the diameter at the base of 0.2–0.3 mm (Fig. 7: 43). The length of small ridges is 0.4–0.6 mm. The tessera bears one central conical tubercle with the base length of 1 mm and small pointed tubercles 0.5 mm in diameter, which surround the central one forming a circle.

3. *Ornamentation topography*. The tubercles are located predominantly regularly, and only in exceptional cases – irregularly (Fig. 6: 5, 6). Marginal crenulations of neighbouring tubercles on the ornamented surface often overlap each other. The ornamented surface on branchial plates can be divided into three zones (Fig. 5). Tubercles are mostly high, cone- and peak-shaped in the distal zone A. The relative position of tubercles in this part of the branchial plates is mostly regular due to insignificant variation in the length of crenulations and bases (round, more rarely oval) of tubercles (Fig. 6: 13, 20, 21, 27; Fig. 7: 29, 31). Tubercles are located in the nodes of a square (Fig. 6: 21, 27; Fig. 7: 31) or, more rarely, rhombic network (Fig. 7: 29). In the median zone B low, predominantely dome-shaped tubercles of identical sizes and with constant length of crenulations are present along with high cone- and peak-shaped tubercles with varied shapes of bases (Fig. 6: 9, 11, 14, 16–18, 22, 25, 26). These tubercles are collocated regularly (less often irregularly), essentially in the nodes of a rhombic network (Fig. 6: 9, 17; Fig. 7: 30,

Fig. 3. *Psammosteus livonicus* Obruchev, specimens from the Amata RS, Upper Devonian. **A–H**, branchial plates of adult individuals, **I–Q**, ridge scales of adult individuals. **A–D**, PIN 1737/8, left branchial plate, Pasta muiža, Latvia; A, dorsal, B, ventral, C, distal and D, anterolateral views. **E–H**, GIT 116-273, right branchial plate, Pasta muiža, Latvia; E, dorsal, F, ventral, G, posterior and H, distal views. **I–K**, PIN 1737/9, ventral ridge scale, Pasta muiža, Latvia; I, external, J, visceral and K, lateral views. **L–O**, PIN 1737/76, ventral ridge scale, Yam-Tesovo, Russia; L, external, M, visceral, N, lateral and O, proximal views. Scale bars: A–H = 2 cm, I–O = 1 cm.



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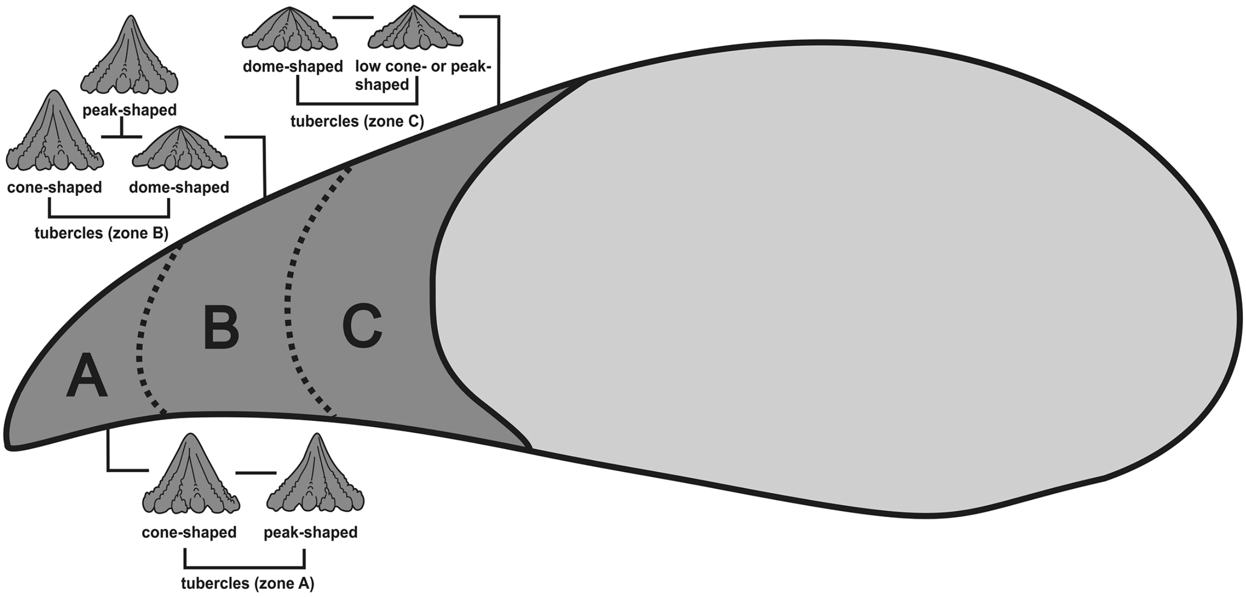


Fig. 5. Location of topographical zones of tubercles on branchial plate of *P. livonicus*: A, distal; B, median; C, proximal.

32, 36, 39). The median zone of the ornamented surface is characterized by fused tubercles forming ridges, but there are rare exceptions, when ridges are located in other zones (PM SPU 71-1). Closer to the anterolateral and proximal margins of the branchial plate the ridges are aligned subparallel to the margins (Fig. 6: 18; Fig. 7: 33) of the plate, but further from the margins of the plate they become to form transverse rows (Fig. 6: 14, 28; Fig. 7: 29). In the proximal zone C only low cone-, peak- and dome-shaped tubercles are present (Fig. 6: 10, 12, 15, 19; Fig. 7: 30, 32, 36). Generally they have a round base and are located regularly in the nodes of a rhombic network. In the distal and median zones the length of the base of the tubercles reaches 0.7–2 mm, in the proximal zone their size is 0.3–2 mm. Small tubercles of later generations can be present between large ones (Fig. 6: 6, 19, 22–24).

4. *Internal structure*. According to Novitskaya (1965, 2004), the superficial layer of the plates of psammosteids (without some Obrucheviidae) is formed by orthodentine tubercles which lack enameloid (Keating et al. 2015) (see Fig. 8). The inner dentine is replete with a larger quantity of dentinal tubules and external dense dentine is clearly observed inside the tubercle. Both types of skeletal tissues are developed evenly. The tubercles are separated from each other by grooves with open pores, leading into internal cavities (ampullae according to Johanson et al. 2013), the bottom and partly the walls of which consist of aspidin. The median spongy layer is composed of small-celled reticular and large-celled cancellous aspidin. As shown by previous studies (Novitskaya 1965) and our new data, the reticular layer of the branchial plates is weakly developed in *Psammosteus livonicus*. Aspidin of the median layer is composed of very massive differently directed trabeculae, separated by small cavities (Fig. 8). The basal lamellar layer in the dorsal plate and on the dorsal side of branchial plates of *P. livonicus* is formed by thin aspidin lamellae, overlapping each other and penetrated by a loose network of vascular canals (Halstead 1969). Tomographic examination of specimen PM SPU 71-4 has shown the complicated radial structure of the pulp cavities inside the dentine tubercles (Fig. 7D). The main pulp cavity and the

Fig. 4. *Psammosteus livonicus* Obruchev, positions of detail photographs on the branchial plates and ridge scales in Figs 6 and 7. **A**, **B**, PIN 220/527, left branchial plate; **C**, **D**, PIN 1737/7, holotype, right branchial plate; **E**, **F**, PIN 1737/74, right branchial plate; **G**, **H**, GIT 116-275, left branchial plate; **I**, **J**, GIT 116-272, left branchial plate; **K**, **L**, PIN 1737/8, left branchial plate; **M**, **N**, GIT 116-273, right branchial plate; **O**, **P**, PIN 1737/9, ventral ridge scale; **Q**, **R**, PIN 1737/76, dorsal ridge scale. Abbreviations: arrow indicates the anterior direction; a.p.l., anterior proximal ledge; s.tes, secondary tesserae; 1, contour line of the plate; 2, margin of ornamented surface; 3, growth line; 4, supposed growth line; 5, ornamented surface; 6, unornamented surface; 7, destroyed parts of the plate; 8, photograph of ornament.

canals (radial pulp canals) radiating from it can be distinguished. The latter correspond in their direction to the radial ridges and marginal crenulations. There are inner cavities (microtubercular chambers) in the higher portions of the canals, which are located inside the microtubercles.

Comparison. The dorsal plate of *Psammosteus livonicus* resembles largely the plate of *P. praecursor* Obruchev in its shape and the pattern of the lateral line sensory system canals (Elliott & Mark-Kurik 2005). The shape of the branchial plates of adult individuals of *P. livonicus* is close to that of *P. praecursor*, which also has an elongated proximal margin. *Psammosteus livonicus* can be distinguished from other species of the genus *Psammosteus* primarily by the size and morphology of tubercles. The common tubercles of *P. asper* Obruchev resemble mostly those of *P. livonicus*, although their marginal crenulations are less numerous (7–12). *Psammosteus livonicus* differs from *P. bystrowi*, whose ornamentation comprises rare and large rounded tubercles, but they have slightly tapering and less frequent crenulations (8–15). In comparison with the species described here, tubercles of *P. cuneatus* Obruchev have smaller average size, domination of fan-like and halberd-like shapes and simple, shorter, tapering ends of crenulations (9–18); the tubercles of *P. cuneatus* are regularly and densely located. In massiveness of aspidin *Psammosteus livonicus* is different from *P. maeandrinus* and similar to *P. praecursor.*

Remarks. There are two other genera of psammosteids with ornamentation resembling that of *Psammosteus livonicus. Psammosteus livonicus* differs from *Karelosteus weberi* Obruchev, 1933 in smaller tubercles (the average tubercle size of *Karelosteus* is 1.5–4 mm), primarily rounded shape of their bases, mostly vertical orientation of tubercle crowns and robustness of marginal crenulations; their ends are truncated. *Psammosteus livonicus* can be distinguished from *P. venyukovi* Obruchev, 1965 by a less regular shape of tubercles and their larger average size, the absence of pyramid-shaped forms among them and variation in the length of crenulations of individual tubercles.

DISCUSSION

Genus-level systematics of psammosteids is based on morphological features of dorsal, ventral and branchial plates, types of tesserae and variations in their spatial distribution. The general morphology of the ornament, for example, size of tubercles (in the case of *Pycnosteus*, *Ganosteus* and *Karelosteus*), can also be considered as a genus-level feature. On the contrary, in the species-level psammosteid systematics differences in the ornamentation become important (Obruchev & Mark-Kurik 1965). *Psammosteus livonicus* has cyclomorial tesserae and stenobasal branchial plates, characteristic of the genus *Psammosteus*. In spite of the well-grounded inclusion of *P. livonicus* into the genus *Psammosteus* by the previous authors (Obruchev & Mark-Kurik 1965; Mark-Kurik 1968; Elliott & Mark-Kurik 2005), Moloshnikov (2009) proposed the assignment of *P. livonicus* to a new genus *Oredezhosteus.* According to his view, the following general features are distinctive for the new genus: width of the branchial plates with a long base (proximal margin), tubercles occupying more than half of the width of the branchial plate and high large dome-shaped symmetrical tubercles. When describing branchial plate PIN 1737/74, which became the holotype of *Oredezhosteus kuleshovi*, the length of the plate base was erroneously estimated, as its proximal part was missing. As the other specimens show (Fig. 3), the branchial plates of adult individuals of *P. livonicus* are stenobasal and the extension of their proximal margin is associated with the larger size of these plates. Such ontogenetic tendency towards elongation of the bases of branchial plates is visible in other members of the genus *Psammosteus: P. bergi* (Obruchev, 1943), *P. praecursor* Obruchev, 1947 and *P. megalopteryx* (Trautschold, 1880) with abundant fossil material (Obruchev & Mark-Kurik 1965). The anterior proximal ledge (Fig. 3A, B; Fig. 4K, L) in specimen PIN 1737/8 is not typical for branchial plates of adult individuals of *Psammosteus.* It is probably connected with a developmental defect caused by an injury, e.g. a bite (Fig. 7: 34). The only exception is the *Psammosteus megalopteryx* branchial plate (Obruchev & Mark-Kurik 1965, fig. 196).

As redescription has shown, the ornamentation can occupy different areas on the dorsal and ventral sides of the branchial plates. Therefore, this character should not be regarded as stable even within a species. Thus, in order to assess the side to which a branchial plate belongs, first of all the relative size of the ornamentation on its dorsal and ventral sides must be taken into account, as well as the marks of life-time abrasion of the tubercles' tops on the ventral side by the seafloor. Furthermore, the unornamented surface of the dorsal side of branchial plates of *Psammosteus* has linear grooves for muscle attachment and the ventral side bears imprints of detached tesserae. The curvature of the plate, which could have been changed during fossilization, should also be noted. Small tubercles between large ones are present in the majority of psammosteids: this feature occurs in the early species *Schizosteus heterolepis* (Preobrazhensky, 1911), as well as in the later forms, for example in *Karelosteus weberi*. Therefore, this feature cannot be regarded as distinctive for a genus.

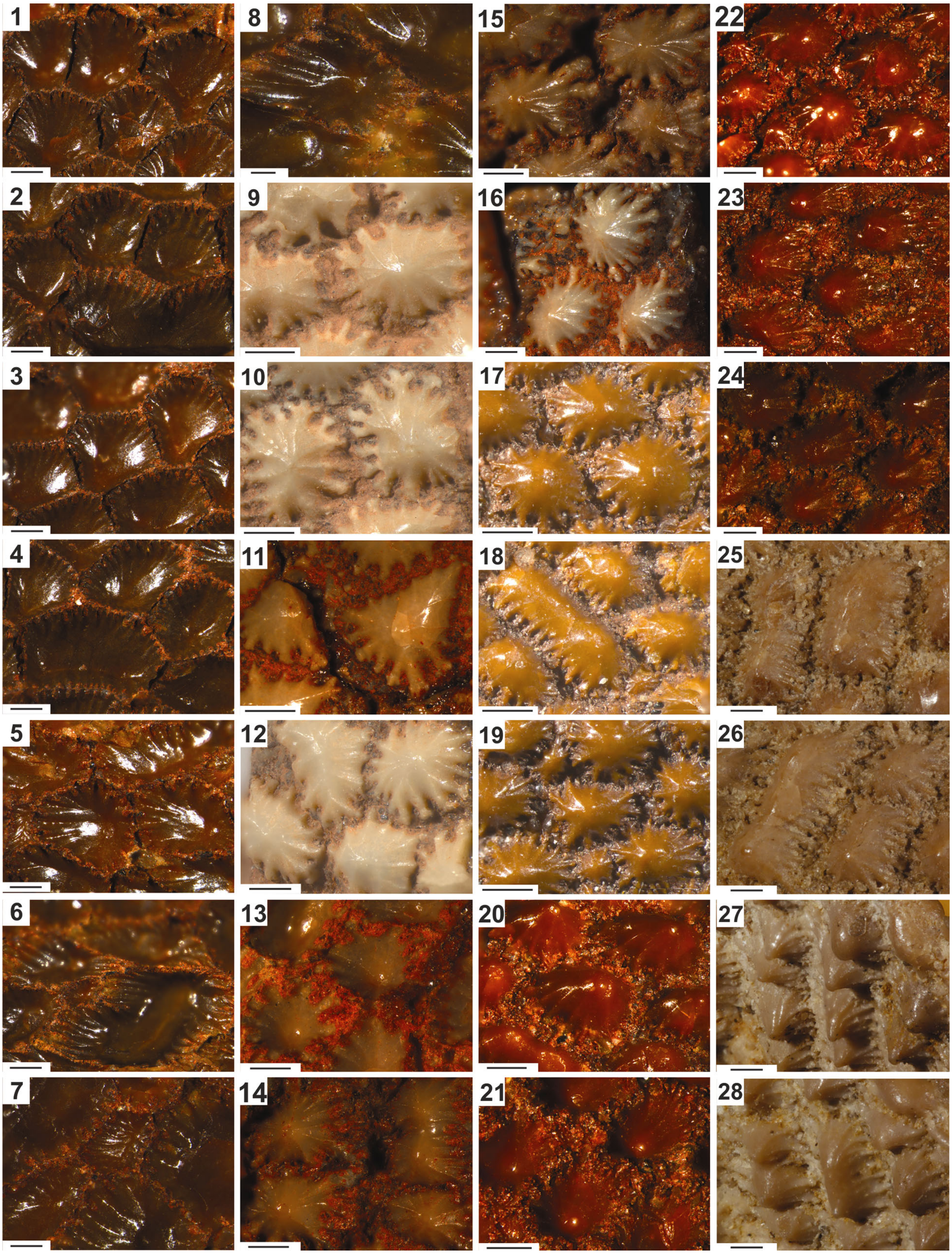
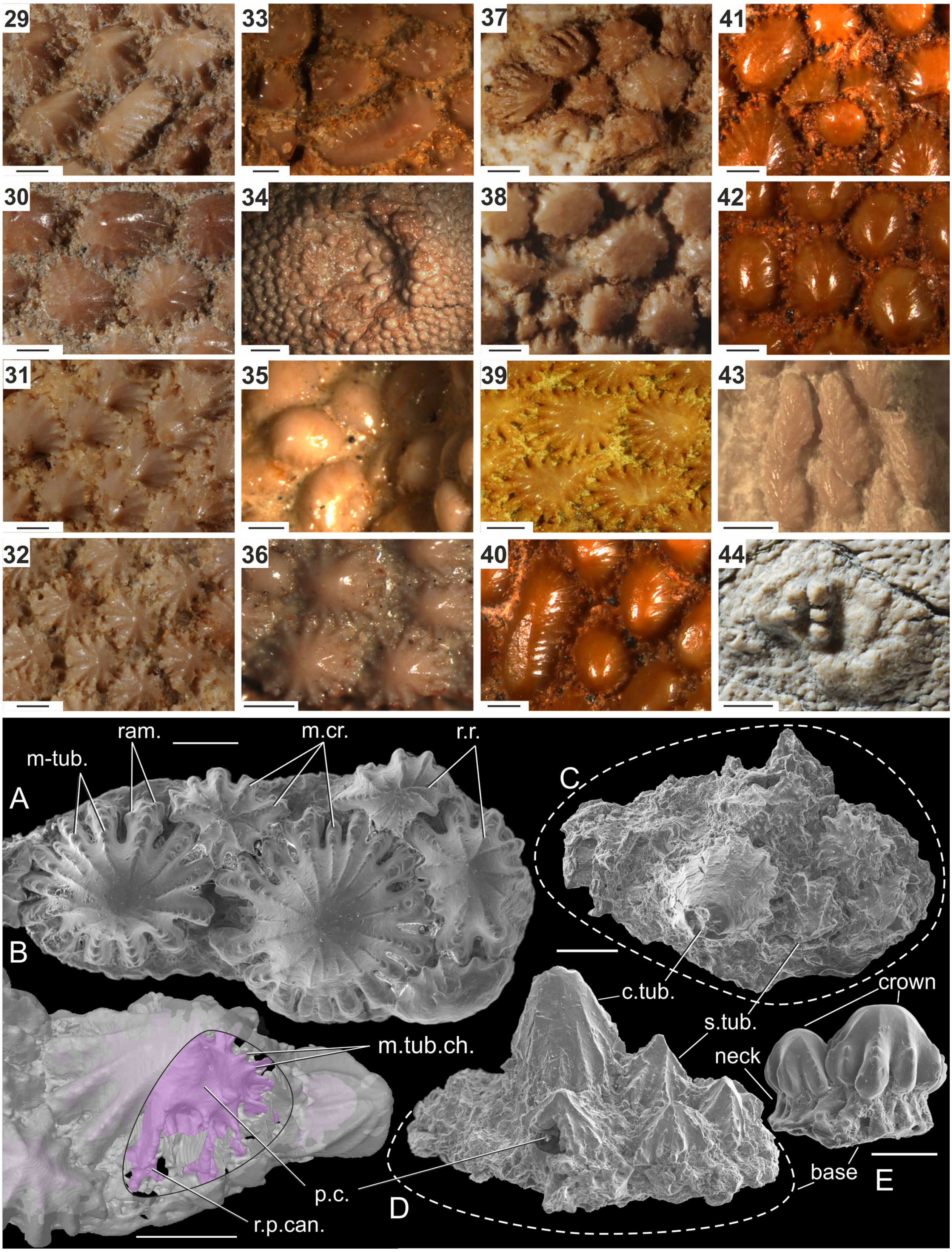


Fig. 6. *Psammosteus livonicus* Obruchev, topographic variability of the ornament. Details of ornamentation are shown in Fig. 4. **1–8**, PIN 220/527, left branchial plate; **9–16**, PIN 1737/7, holotype, right branchial plate; **17–24**, PIN 1737/74, right branchial plate; **25–28**, GIT 116-275, left branchial plate. Scale bars: 1–6, 9–28 = 0.5 mm; 7, 8 = 0.2 mm.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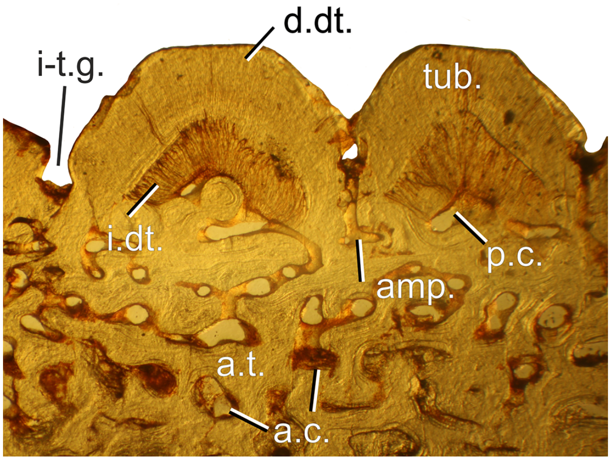

Fig. 8. Vertical thin section of branchial plate A.3-1, Pasta muiža, Latvia. Abbreviations: a.c., aspidin cavity; amp., ampullae; a.t., aspidin trabeculae; i.dt., inner dentine; i-t.g, intertubercular grooves; d.dt., dense dentine; p.c., pulp cavity; tub., dentine tubercles.

The significant distinctive features of the genus *Oredezhosteus* proposed by Moloshnikov (2009) are the large size of tubercles and the characters of tubercles' shape. The general morphology of the ornament can indeed help to distinguish a genus. However, a new genus cannot be based on the general morphology of the ornament only. In contrast to *Karelosteus*, which is not known fully enough and is provisorily retained, *P. livonicus* is known on the basis of complete branchial plates, a dorsal plate and a cyclomorial tesserae. The morphology of plates and cyclomorial type of tesserae indicate that the genus *Oredezhosteus* is not valid. The features based only on the ornament are not sufficient to distinguish a new genus. If such were the case, each species of *Psammosteus* should be described as a new genus on the basis of uniqueness of its ornamentation. Researchers would also have to deal with the problem of a poor basis for the systematics of psammosteids at the species level. It is recommended that a new genus should not be based only on its ornamentation before necessary data at the genus level of psammosteid systematics are available.

Some plate specimens of *P. livonicus* show the signs either of weak (Fig. 6: 1–4, 9, 11–13, 17–21) or strong abrasion of the ornamentation (Fig. 7: 38). High tubercles are liable to abrasion, whereas smaller and lower tubercles situated between the higher ones preserve initially pointed tips with ridges converging at them (Fig. 7A, E). It is the abrasion, which, being incorrectly interpreted by Moloshnikov (2009), led this author to the unreasonable establishment of the species '*Oredezhosteus kuleshovi*'. '*Psammolepis aerata*' should also be assigned to *P. livonicus* because of the overall character of the ornamentation, which is especially comparable on the ventral side of the branchial plate. Abrasion, dense position and shortness of crenulations on the dorsal side of the plate initially complicated the identification of specimen PIN 220/527. However, the count of radial ribs and marginal ramifications passing into them allowed us to become firmly convinced that the specimen belongs to *P. livonicus.*

The specimens of *P. livonicus* show some injuries to the surficial layer. Various healing mechanisms can be observed. For example, there is a bite mark, presumably left by a sarcopterygian, on the ventral side of branchial plate PIN 1737/8 (Fig. 3B; Fig. 7: 34). The mark is covered with a new generation of bubble-shaped tubercles, so-called blisters (Fig. 7: 35). L. Halstead Tarlo (Halstead 1969) suggested that such regeneration was the result of reaction to some kind of aggravation because any signs of mechanical damages of the former sculpture were not discovered in association with them. Our example shows that the origin of blisters is connected with the reaction to a mechanical injury. The growth of tubercles of a new generation occurs at the place of mechanical damage of the surficial layer on ridge scale PIN 1737/76. Overgrowth of large, broken off tubercles with smaller tubercles shows that the damage was healed (Fig. 7: 41). This phenomenon was previously known in *Ganosteus stellatus* (Obruchev & Mark-Kurik 1965).

Fig. 7. *Psammosteus livonicus* Obruchev, topographic variability of the ornament (**29–44**); SEM photographs (**A**, **C–E**); 3D model of pulp canals based on microtomographic data (**B**). Serial arrangement of photographs is shown in Fig. 4. **29–32**, GIT 116-272, left branchial plate; **33–36**, PIN 1737/8, left branchial plate; **37**, **38**, GIT 116-273, right branchial plate, Pasta muiža, Latvia; **39**, PM SPU 71-6, fragment of branchial plate, Andoma Hill, Russia; **40–42**, PIN 1737/76, ridge scale; **43**, PIN 1737/9, ridge scale; **44**, GIT 25-12, dorsal plate; **A**, PM SPU 71-4, tubercles with varying degrees of abrasion, top view, Yam-Tesovo, Russia; **B**, 3D reconstruction of histological structure of specimen PM SPU 71-4; **C**, **D**, GIT 116-327, cyclomorial tessera from the ventral side of the branchial plate, Pasta muiža, Latvia; top (C) and lateral (D) view; **E**, PM SPU 71-5, tessera, lateral view, Yam-Tesovo, Russia. Note: Pasta muiža, Yam-Tesovo and member AG-1-2 in the outcrop N-2 at the Andoma Hill are the Upper Devonian, Amata RS localities. Scale bars: 29–33, 35–42, A–D = 0.5 mm; 34 = 2 cm; 43 = 0.2 mm; 44 = 2 mm. Abbreviations: c.tub., central tubercle; m.cr., marginal crenulations; m-tub., microtubercles; m-tub.ch., microtubercular chambers; p.c., pulp cavity; ram., ramification of marginal crenulations; r.p.can., radial pulp canals; r.r., radial ribs; s.tub., tubercles satellites.

RESULTS

Analysis of the morphology of the branchial plates with consideration of species-level features of their ornamentation proves that the establishment of the genus *Oredezhosteus* Moloshnikov is baseless. The species *Psammolepis aerata* Obruchev in Halstead Tarlo 1965 and *Oredezhosteus kuleshovi* Moloshnikov, 2009 are included in the revised species – *Psammosteus livonicus* Obruchev, 1965 as its junior synonyms on the basis of the ornamentation analysis.

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Ida-Euroopa platvormi loodeosa Devoni Amata lademe lõuatu kala *Psammosteus livonicus* Obruchev (Heterostraci) taksonoomiline revisjon

Vadim N. Glinskiy ja Elga Mark-Kurik

Devoni psammosteiidi *Psammosteus livonicus*'e kollektsioonid Venemaal, Lätis, Leedus ja Eestis võimaldasid selle liigi diagnoosi ning kirjeldust märkimisväärselt täiendada. *Psammosteus livonicus* sarnaneb seljakilbi kuju, stenobasaalsete branhiaalplaatide ja tesseeride ringja ornamendi (perekonna tunnuste) poolest perekond *Psammosteus*'e teiste liikidega. Branhiaalplaatide, eriti liigi taseme aspektist olulise luude ornamendi detailne uurimine näitas, et S. Mološnikovi (2009) püstitatud perekond *Oredezhosteus* pole piisavalt põhjendatud. Lähtudes ornamendist on nii ekslikult kirjeldatud liik *Psammolepis aerata* Obruchev (vt Halstead Tarlo 1965) kui ka S. Mološnikovi uus takson *Oredezhosteus kuleshovi* tegelikult *P. livonicus*'e nooremad sünonüümid.