

A new psammosteid (Agnatha, Heterostraci) from the Amata Regional Stage of the Main Devonian Field and morpho-histological types of discrete micromeric elements in the family Psammosteidae

In memory of an outstanding palaeoichthyologist Elga Mark-Kurik

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Abstract. The range of diversity of psammosteids from the family Psammosteidae is still poorly known. Here a new species, *Psammosteus ramosus* sp. nov. Glinskiy, from the Amata Regional Stage of the Main Devonian Field is described. Its morphology, ornamentation, histology of exoskeletal plates, and micromeric elements are compared with those of other representatives of the family Psammosteidae. The comparison shows a close relationship of the new species with *Psammosteus falcatus* Obruchev, *P. kiaeri* Halstead Tarlo and *P. pectinatus* Obruchev, a group of species that is significantly different from other representatives of the genus *Psammosteus* and constitutes a separate evolutionary lineage. On the basis of morphological and histological features we here differentiate in the fields of tesserae of Psammosteidae the discrete micromeric elements of the ‘basic type’, known in *Psammosteus bergi* (Obruchev), *P. levis* Obruchev, *P. livonicus* Obruchev, *P. maeandrinus* Agassiz, *P. megalopteryx* (Trautschold), *P. praecursor* Obruchev and *Karelosteus weberi* Obruchev, and micromeric elements of the ‘progressive type’, known in *Psammosteus falcatus*, *P. cf. kiaeri* and *P. ramosus* sp. nov. Glinskiy.

Key words: Agnatha, Heterostraci, Psammosteida, Late Devonian, Main Devonian Field, new species.

INTRODUCTION

Psammosteids are a group of jawless vertebrates from the order Pteraspidoformes (suborder Psammosteida *sensu* Tarlo 1962). They are known from the Early–Late Devonian (from Pragian to Frasnian stages), primarily of Laurussia (Halstead Tarlo 1967a; Halstead 1987) and, to a lesser extent, of the peri-Gondwanan shelf, Armorica, Barentsian, Kara-Tajmyr and Siberian palaeocontinents (Bystrow 1959; Blicek et al. 2002; Delsate et al. 2004; Vařkaninová & Kraft 2016). The exoskeleton of psammosteids is composed of macromeric and mesomeric elements (plates of the cephalothorax, scales in the tail region) and micromeric elements (mostly tesserae). Discrete micromeric elements, situated between the main plates of the cephalothorax, form so-called ‘fields of tesserae’. Praepineal and paired lateral fields on the dorsal surface, and postoral and ventrolateral fields on the ventral surface of the cephalothorax can be distinguished (Obruchev & Mark-Kurik 1965, p. 40). In numerous articulated specimens of *Drepanaspis gemuendenensis* Schlüter, 1887 and in a single articulated cephalothorax of *Psammosteus megalopteryx*

(Trautschold, 1880), fields of tesserae may be found in their original articulation (Gross 1963; Halstead Tarlo 1965, pl. XVI, figs 1, 2), but in most cases their micromeric elements are found isolated (e.g. Mark-Kurik 1999; Blom et al. 2006). As a rule, these elements can be determined to the species level (Halstead Tarlo 1965; Obruchev & Mark-Kurik 1965; Glinskiy & Mark-Kurik 2016) on the basis of species-specific tubercles.

Discrete micromeric elements in the family Psammosteidae *sensu* Novitskaya (2004) are the most diverse morphologically. They possess a smaller base than other psammosteids. Rooted tesserae are also weakly connected with the cancellous aspidin of the plates (Gross 1933, p. 15, fig. 4; Obruchev 1947a, p. 197; Mark-Kurik 1999, p. 7). The small base size of discrete micromeric elements in representatives of Psammosteidae results in their higher concentration in the fields of tesserae and on the plates of the cephalothorax. Our study of micromeric elements of psammosteids from Frasnian deposits of the Main Devonian Field has shown that discrete elements of the representatives of the family Psammosteidae can generally be classified into two morpho-histological types: the ‘basal’ and

the ‘progressive’ ones. The aim of this research is the description of the earliest psammosteid species with a ‘progressive’ type of tesseræ, *Psammosteus ramosus* sp. nov. Glinskiy, and comparative description of morpho-histological types of discrete micromeric elements.

MATERIALS AND METHODS

The ornamentation of the specimens was cleaned mechanically by an instrument consisting of an air pump and a hypodermic needle (Selden 2003). The material was studied mainly under the stereo zoom microscope Leica M205 C, and also under the scanning electron microscope (SEM) Hitachi S-3400N in SE and BSE mode. The study of the inner structure of some micromeric specimens was undertaken with Bruker-microCT SkyScan 1172. Projection images were reconstructed with the software NRecon into cross section images rotated upright in the software DataViewer. The software CTAnalyzer was used to correct the visualization and interpretation of the reconstructed images. CTVox software was used for 3D volume rendering. The specimens were scanned by applying different parameters according to the sample type at a voltage of 40–100 kV and a current of 100–250 μ A, with a copper and aluminium filter for a half rotation of 180° at the highest camera resolution. Thin sections were made with the use of 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 120–1000. The sandpaper with a grade P 1200–2000 was used subsequently to polish a thin section. The photographs of thin section PM SPU 80-7 were taken with a polarization microscope Leica DM4500 P with the use of aniseed oil.

All specimens studied are stored in the collections of the Palaeontological Museum of St. Petersburg State University (the new taxon: PM SPU 80; material for comparison: PM SPU 71, 72, 75), St. Petersburg, Russia; Natural History Museum of Latvia (G 43), Riga, Latvia and Department of Geology, Tallinn University of Technology (GIT 680), Tallinn, Estonia.

GEOLOGICAL BACKGROUND

The material comes from two localities of the Amata Regional Stage (RS) in Northwest Russia and one locality in eastern Latvia (Fig. 1A). Most specimens (including the holotype) were found at the Andoma Hill locality on the southeastern bank of Lake Onega in the Vytegra District, Vologda Region, NW Russia (Fig. 1D).

The Andoma Hill locality is represented by a series of outcrops, stretching along the lake for a couple of kilometres. Remains of *Psammosteus ramosus* sp. nov. Glinskiy (Fig. 2A–F, Q, R; Fig. 3A–D, I, J; Fig. 4A–G; Fig. 5A; Fig. 6A–E, G, H) occur in layer AG 1-2, in the upper part of outcrop N-2 at Gnevashevskaya village (Ivanov et al. 2006). This layer is composed of red, fine and very fine, poorly cemented sandstones intercalated with thin layers of silty clay and siltstone. These deposits are assigned to the lower part of the Andoma Formation, which is correlated with the Amata–Pļaviņas interval (Lukševičs et al. 2012). Remains of the new species were found by A. Ivanov in 1984 in association with numerous isolated branchial plates, lateral scales and various micromeric elements of *Psammolepis undulata* (Agassiz, 1844), *Psammosteus livonicus* Obruchev, 1965 (see hereinafter in Obruchev & Mark-Kurik 1965), *P. praecursor* Obruchev, 1947a and *P. cf. cuneatus* Obruchev, 1965 (Glinskiy & Ivanov 2015).

The Borschovo locality is situated in the Luga District of the Leningrad Region, NW Russia. It is represented by a series of outcrops on the south bank of Lake Antonovskoe, in the Oredezh River basin (Fig. 1C). Remains of *P. ramosus* sp. nov. were found in the terminal eastern outcrop 3, situated to the east of the road from Borschovo village to the lake (Fig. 2N–P; Fig. 3K, L; Fig. 4H–O). The deposits in this outcrop are represented by variegated (pink, yellowish-grey, reddish-brown to light bluish-grey), cross-bedded, medium- and fine-grained sandstones, with intercalations of purple and greenish clay. Vertebrate remains, including those of the new species, were collected by a team of Russian–French–Latvian expedition in 2010 at the level (No. 12) of light bluish-grey sandstones of the Amata RS in the middle part of the outcrop. The only branchial plate of *P. ramosus* sp. nov. was found in association with numerous branchial plates, dorsal plates, ridge scales and rare micromeric elements of different psammosteids (Glinskiy 2013): *Psammolepis venyukovi* Obruchev, 1965, *Psammolepis undulata*, *Psammosteus livonicus*, *P. praecursor*. The presence of *P. cf. cuneatus* Obruchev at the same level needs further confirmation. One of the branchial plates of *P. praecursor* from this assemblage was previously misdiagnosed by V. Glinskiy as that of *P. levis* (Ivanov et al. 2011).

The Ķūķu locality is situated on the right bank of the Gauja River, Raiskums parish, Pārgauja municipality, eastern Latvia (Fig. 1B). In 1965 fragments of branchial plates of the new species were gathered there by L. A. Lyarskaya (Fig. 2G–M; Fig. 3E–H; Fig. 5B–F). They were previously identified as the scales of Psammosteidae indet. These remains can be found in the upper part of the outcrop in white fine-grained sandstones (at the base of the Amata RS) together with

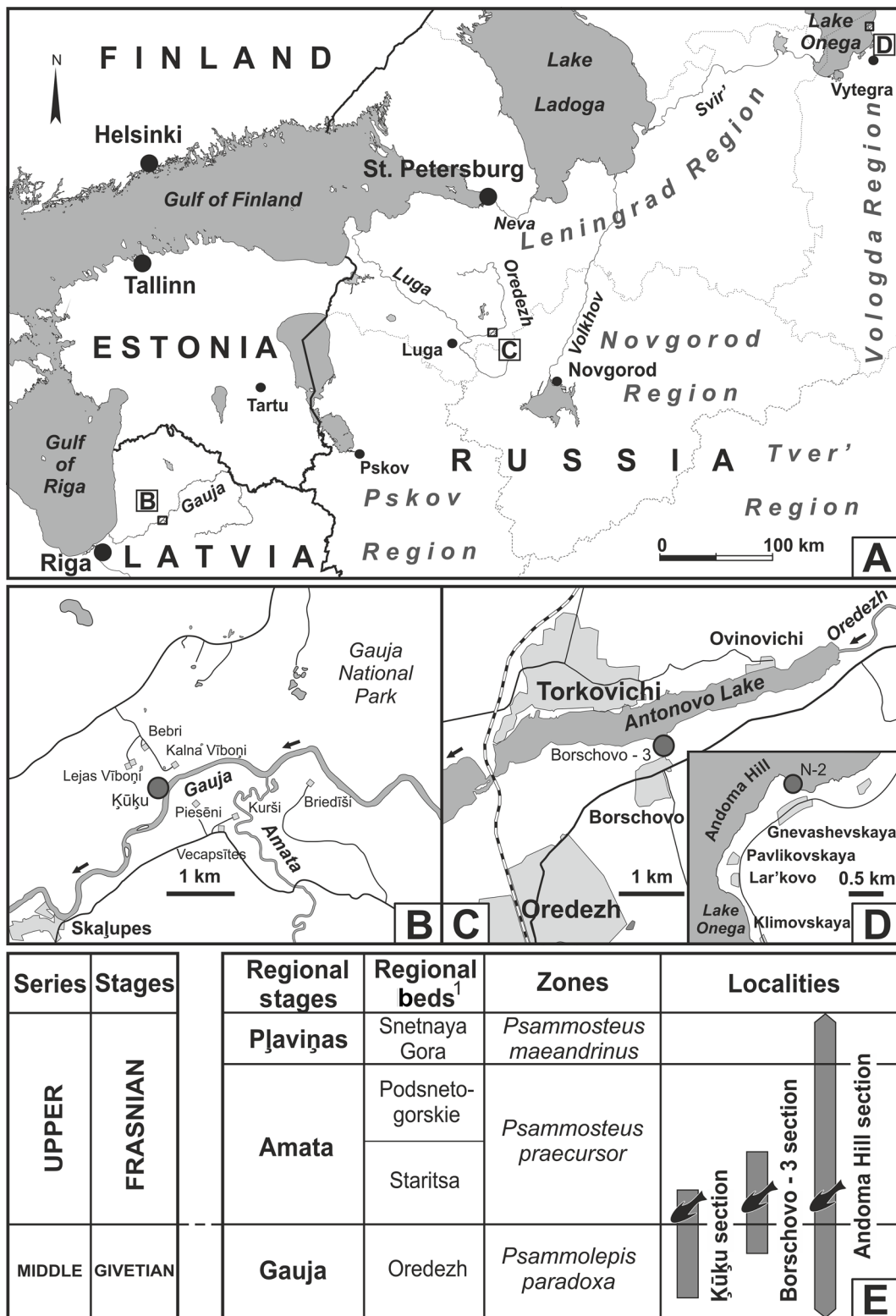
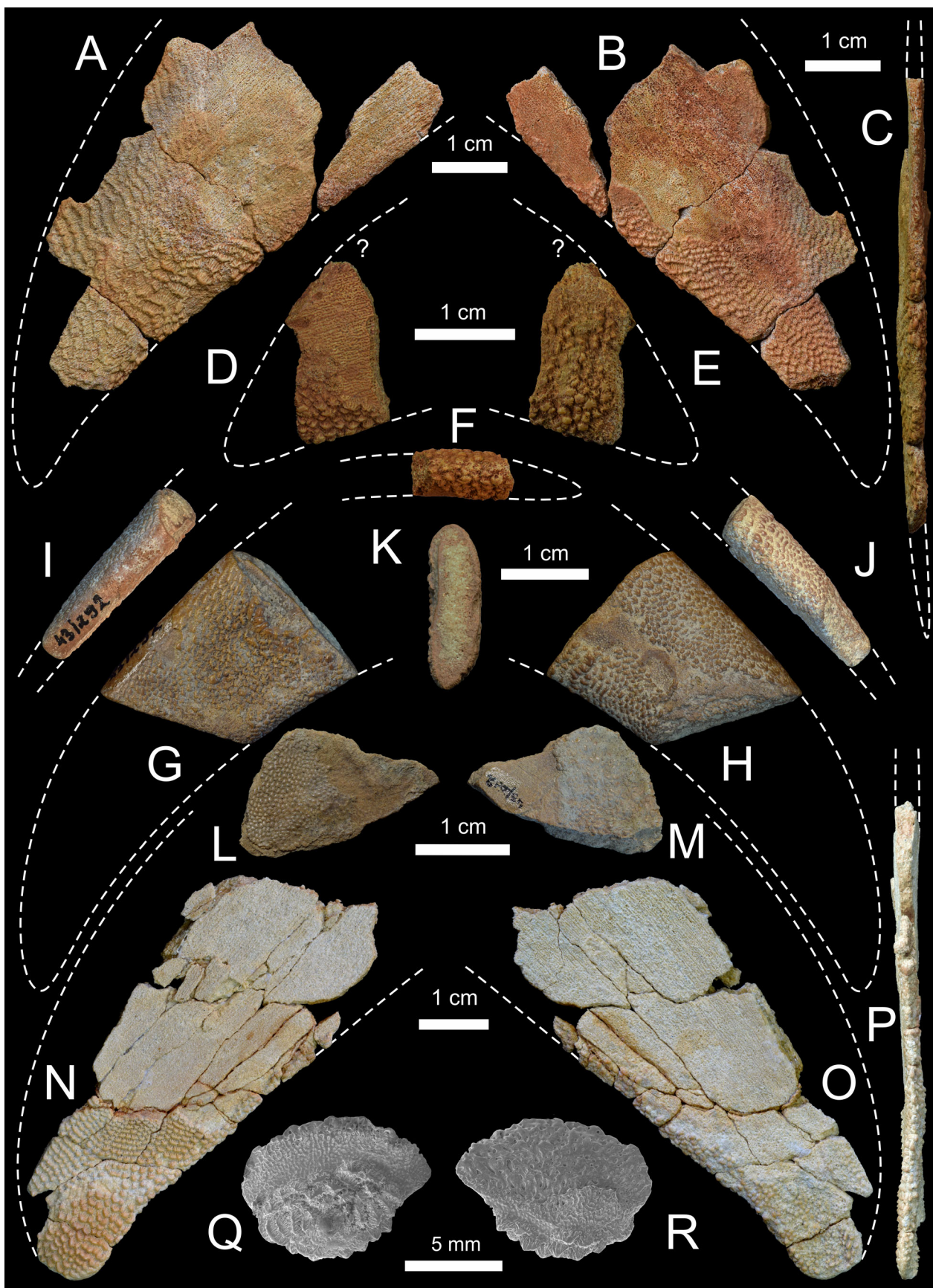


Fig. 1. A, a map showing the localities of *Psammosteus ramosus* sp. nov. Glinskiy from eastern Latvia and Northwest Russia. B, Kūķu locality on the right bank of the Gauja River, Latvia. C, outcrop 3 of the Borschovo locality, Russia. D, outcrop N-2 of the Andoma Hill locality, Russia. E, the stratigraphical position of the 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 the new taxon were collected.



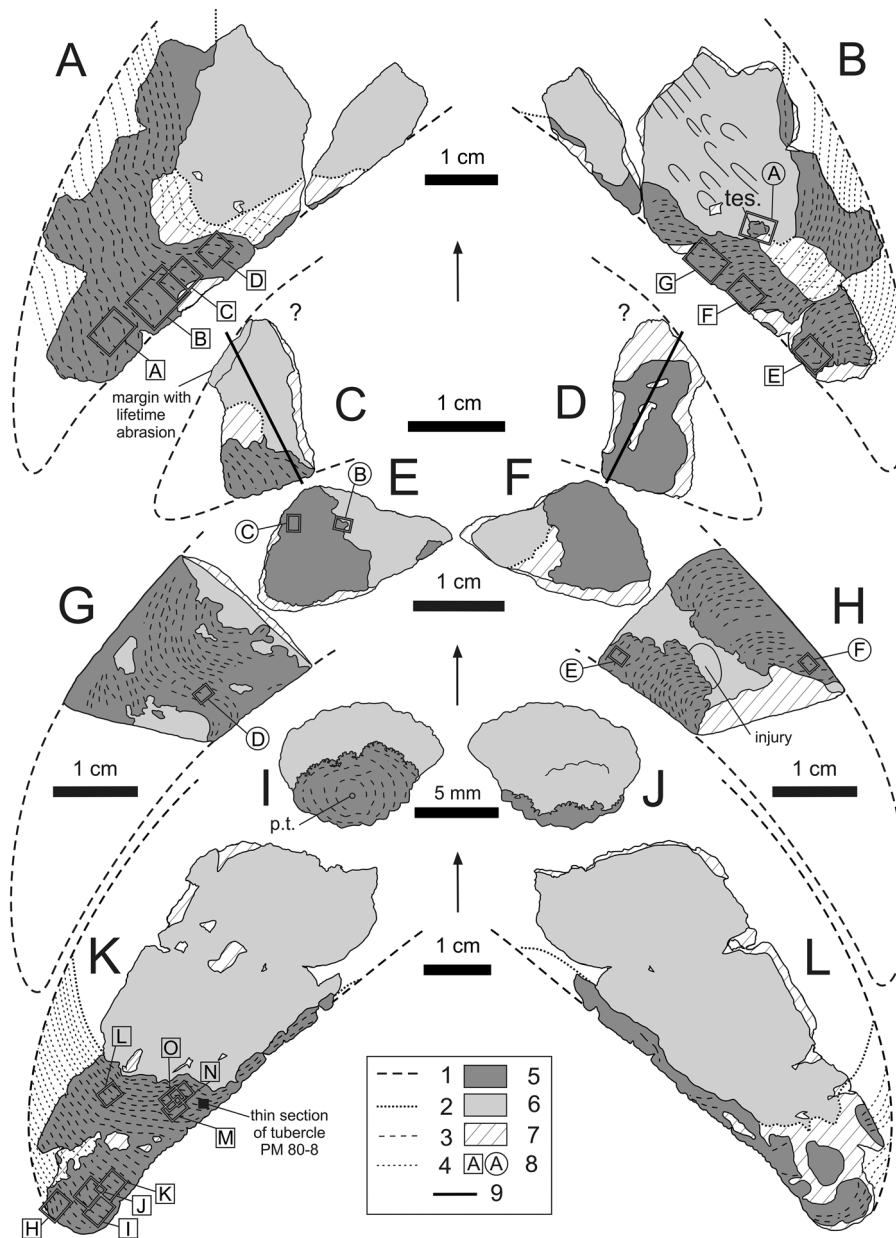


Fig. 3. *Psammosteus ramosus* sp. nov. Glinskiy, schematic drawings with positions of detail photographs in Figs 4, 5. **A, B**, PM SPU 80-2, holotype, fragment of left branchial plate. **C, D**, PM SPU 80-3, fragment of left branchial plate. **E, F, G** 43/292:1, fragment of branchial plate. **G, H**, G 43/292:2, fragment of left branchial plate. **I, J**, PM SPU 80-4, lateral scale. **K, L**, PM SPU 80-1, fragment of left branchial plate. Abbreviations: arrow indicates the anterior direction; p.t., primordial tubercle; tes, rooted tesserae; 1, supposed contour line of the plates; 2, supposed margin of the ornamented surface; 3, growth line; 4, supposed growth line; 5, ornamented surface; 6, unornamented surface; 7, destroyed parts of the plate; 8, letters inside a square indicate the photographs in Fig. 4, whereas those inside a circle indicate the photographs in Fig. 5; 9, the line in bold in the figures C, D is a line of the vertical thin section, which is shown in Fig. 7D.

Fig. 2. *Psammosteus ramosus* sp. nov. Glinskiy, branchial plates and a lateral scale from the Amata RS, Upper Devonian. **A–C**, PM SPU 80-2, holotype, fragment of left branchial plate, Andoma Hill, Russia; **A**, dorsal, **B**, ventral and **C**, posterior views. **D–F**, PM SPU 80-3, fragment of left branchial plate, Andoma Hill, Russia; **D**, dorsal, **E**, ventral and **F**, posterior views. **G–K**, G 43/292:2, fragment of left branchial plate, Ķūķu, Latvia; **G**, dorsal, **H**, ventral, **I**, anterolateral, **J**, posterior and **K**, across views. **L, M**, G 43/292:1, fragment of branchial plate, Ķūķu, Latvia; **L**, ventral? and **M**, dorsal? views. **N–P**, PM SPU 80-1, fragment of left branchial plate, Borschovo, Russia; **N**, dorsal, **O**, ventral and **P**, posterior views. **Q, R**, PM SPU 80-4, lateral scale, Andoma Hill, Russia; **Q**, external and **R**, visceral views. **Q, R**, SEM SE images.

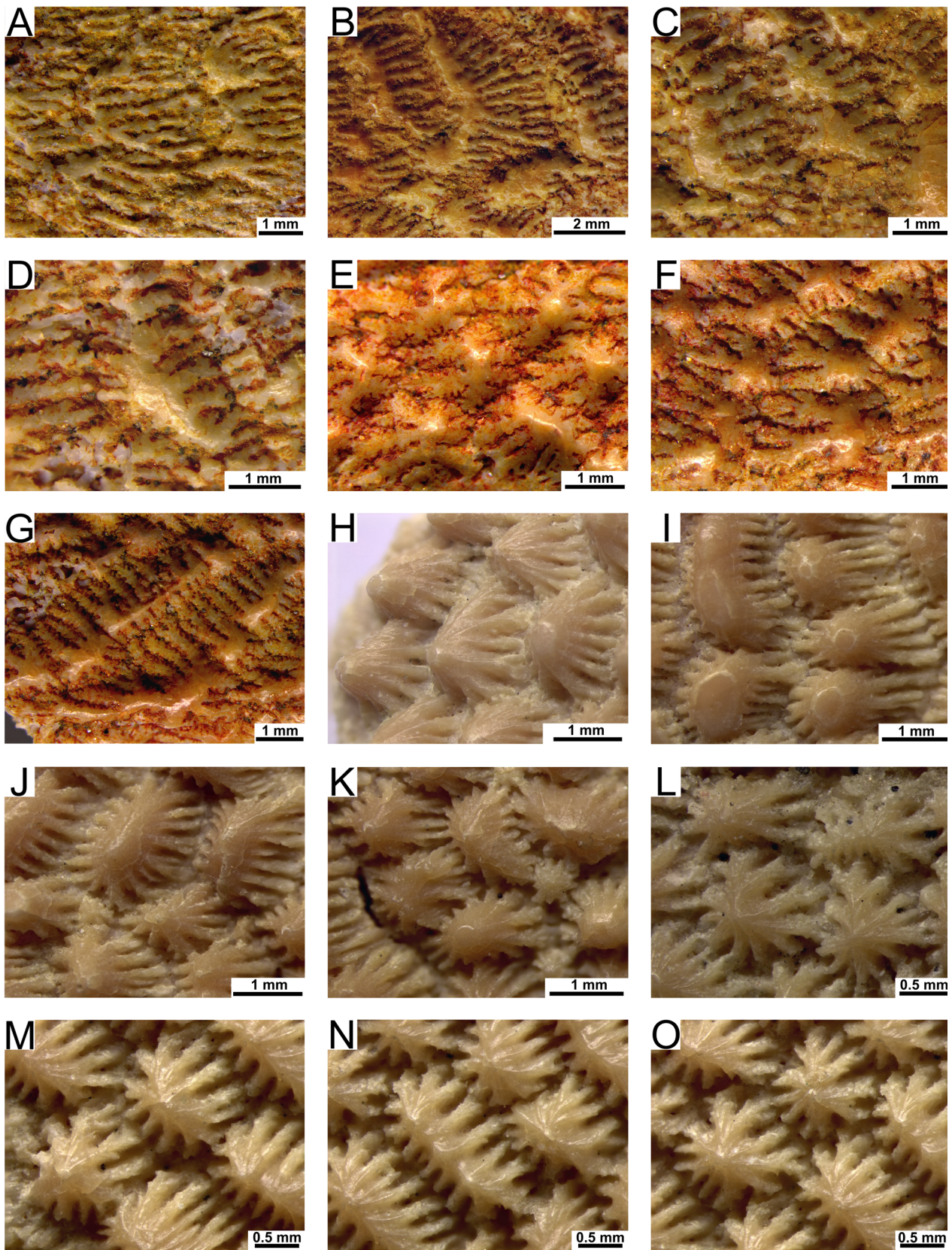


Fig. 4. *Psammosteus ramosus* sp. nov. Glinskiy, topographic variability of the ornament. Shots of ornamentation are shown in Fig. 3. **A–G**, PM SPU 80-2, holotype, fragment of left branchial plate, Andoma Hill, Russia. **H–O**, PM SPU 80-1, fragment of left branchial plate, Borschovo, Russia.

numerous branchial and median plates of *Psammolepis undulata* (Lyarskaya 1981).

Three positions of the boundary between the Middle and Upper Devonian in the Main Devonian Field have been proposed: at the base of the Amata RS, in the Amata RS at the base of the Podsnetogorskie Regional Beds (RB) and at the base of the Snetnaya Gora RB of the Pļaviņas RS (Ivanov & Lebedev 2011). The first position is accepted in the current research (Fig. 1E).

MORPHOLOGY AND TERMINOLOGY OF MICROMERIC ELEMENTS

The following morphological structures can be distinguished in the discrete and rooted micromeric elements of the family Psammosteidae *sensu* Novitskaya (2004): a crown, formed by one or several dentine tubercles and a base composed of cancellous aspidin (Figs 5A, G; 6A). Discrete micromeric elements are characterized also by the presence of a neck (a transitional part between a crown and a base) composed of cancellous aspidin and by a comparatively short base. Rooted tesseræ are usually recognized by a missing neck, and a large base area. Crown tubercles of all micromeric elements in the representatives of Psammosteidae vary substantially in shape (dome-shaped, cone- or peak-shaped) and orientation, which can be connected with their position on the body.

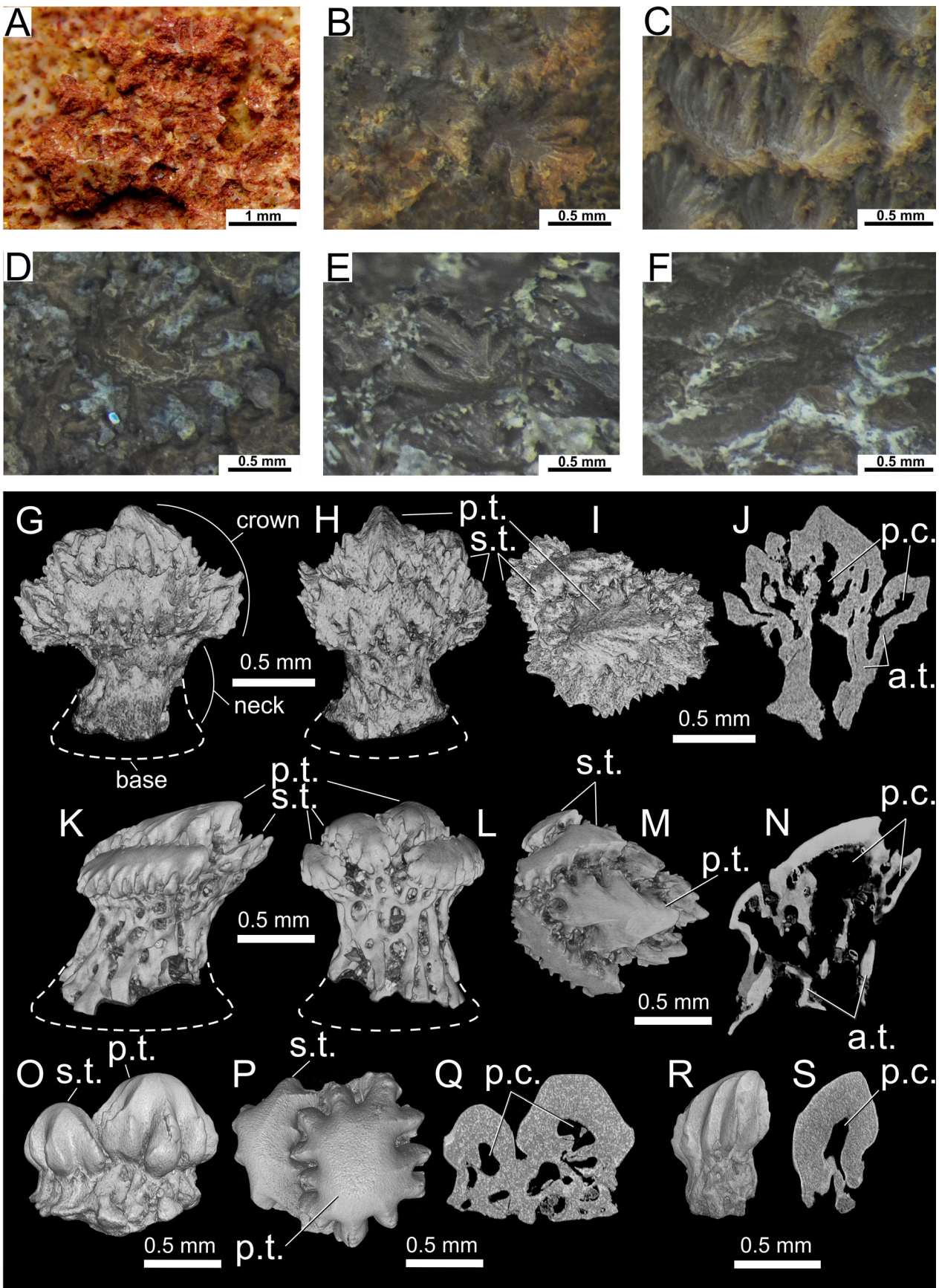
Various exoskeletal elements, including micromeric elements of psammosteids, can be formed by *cyclomorial* or *synchronomorial* (also *synchronomorial*) growth (Ørvig 1951; Halstead Tarlo 1964, p. 44). *Cyclomorial elements* possess a centre of growth or primordium. There is usually a primordial dentine tubercle in the superficial layer, which was formed prior to the other tubercles and around which the subsequent growth of an element took place. Main plates, scales and cyclomorial tesseræ of psammosteids are characterized by cyclomorial growth. This type of growth usually manifests itself in areal (concentric) zones of growth of tubercles in the superficial layer. Cancellous and lamellar aspidin layers may also have areal zones of growth, visible on the visceral side of macromeric elements. Sometimes these zones are weakly developed, but the primordial tubercle, which gives evidence of cyclomorial growth type, can be distinguished. *Synchronomorial elements* are characterized by the absence of a centre of growth. Growth of the whole element is contemporaneous. The synchronomorial type of growth is characteristic of mesomeric unnamed plates, positioned on the periphery of dorsal and ventral plates and often rooted (fused) with them (Halstead Tarlo 1964, p. 44), and of some micromeric elements, such as

synchronomorial tesseræ and simpler complex elements (Mark-Kurik 1999, p. 16).

Discrete cyclomorial tesseræ are dominant in the fields of tesseræ in *Drepanaspis* and can also be rooted with larger median plates (Halstead Tarlo 1964, p. 44). In *Schizosteus striatus* (Gross, 1933), *Schizosteus splendens* (Eichwald, 1844) (family Guerichosteidae) and *Psammolepis venyukovi* Obruchev, 1965 (family Psammolepididae), the tesseræ, rooted with rostral and postorbital plates are also cyclomorial and belong to praepineal and lateral fields (Obruchev & Mark-Kurik 1965). Psammosteids from the family Drepanaspidae (e.g. *Drepanaspis*) and Guerichosteidae (e.g. *Schizosteus*) possessed rooted unnamed plates and tesseræ showing a synchronomorial type of growth in the vicinity and on the margins of dorsal and ventral plates (Halstead Tarlo 1964, p. 44). In the representatives of the families Psammolepididae and Psammosteidae, rooted tesseræ (Obruchev & Mark-Kurik 1965, p. 49) of synchronomorial and/or cyclomorial types of growth partially or completely cover the dorsal and ventral plates. This evolutionary tendency in the psammosteid lineage is called ‘advanced tesserization’ (Obruchev & Mark-Kurik 1965, p. 64). Thus, in the representatives of *Psammosteus* it is expressed in full substitution of median plates by cyclomorial tesseræ and in coverage of the most part of the ventral side of branchial plates by them.

The following morphological terms were proposed to distinguish various isolated micromeric elements of *Psammosteus* sp. from Givetian deposits (Burtnieki RS) of the Essi locality, Estonia: single elements, complex elements and ‘tesseræ’ (Mark-Kurik 1999). A single element is a solitary primordial odontode (Ørvig 1977), mounted on an aspidin base (Mark-Kurik 1999, p. 9). A complex element has a crown that consists of two or more primordial odontodes (Mark-Kurik 1999). In the case of simpler (basic) complex elements, the bases are fused to form one common base and developed synchronomorially (*Ibid.*, p. 18). Mark-Kurik (1999) distinguishes one more type of complex elements. Such elements are developed cyclomorially; they have a narrow overlap area and the primordial tubercle, which is situated at their posterior margin (*Ibid.*, pp. 16, 17). A cyclomorial platelet or ‘tessera’ is a polygonal element with a primordial tubercle (it can be situated concentrically or eccentrically in relation to a geometric centre of a tessera), concentrically surrounded by much smaller and simpler tubercles (*Ibid.*, pp. 15, 16).

The terms proposed by Mark-Kurik (1999) for describing micromeric elements are used in this article. It should be noted that the term ‘complex element’ is used by that author to refer to several types of micromeric elements in *Psammosteus*, namely: (1) basic complex elements with the synchronomorial type of growth and



(2) scales and scale-like elements with the cyclomorior type of growth, which probably come from the tail and the caudal part of the cephalothorax. The description of these elements is the same as that of the lateral scales of *Psammosteus* sp. from Givetian deposits (Burtnieki RS) of the Joosu quarry locality, Estonia (Mark-Kurik 1993). In the text below, we use the term ‘complex element’ to refer to the elements of the first type mentioned above.

The term ‘tessera of concentric or eccentric structure’ was earlier used for the description of cyclomorior tesseræ (Obruchev 1947b, p. 517, 1964, p. 73; Obruchev & Mark-Kurik 1965). In Obruchev’s opinion, ‘concentric tesseræ’ possess a primordial tubercle, situated concentrically (centrally) and concentric zones of satellite tubercles (Obruchev 1947a, p. 197; Obruchev & Mark-Kurik 1965, pp. 211, 215). According to him, such tesseræ are characteristic only of *Psammosteus* (e.g. Obruchev 1947b). He applied the term ‘eccentric tesseræ’ in two meanings: to refer to tesseræ with an offset centre of growth and to refer to those devoid of concentric lines of growth. He reckoned that they are characteristic of *Psammolepis* (Obruchev 1947b, 1964, p. 73; Obruchev & Mark-Kurik 1965, pp. 86, 211). However, cyclomorior tesseræ with an eccentric position of a tubercle as well as concentric lines of growth are known in *Psammosteus* (Obruchev & Mark-Kurik 1965, p. 234; Mark-Kurik 1999, p. 16). Thus, in order to characterize cyclomorior tesseræ more thoroughly, the following features must be noted: the position of the primordial tubercle (concentric, eccentric) and the presence or absence of concentric zones of growth of satellite tubercles.

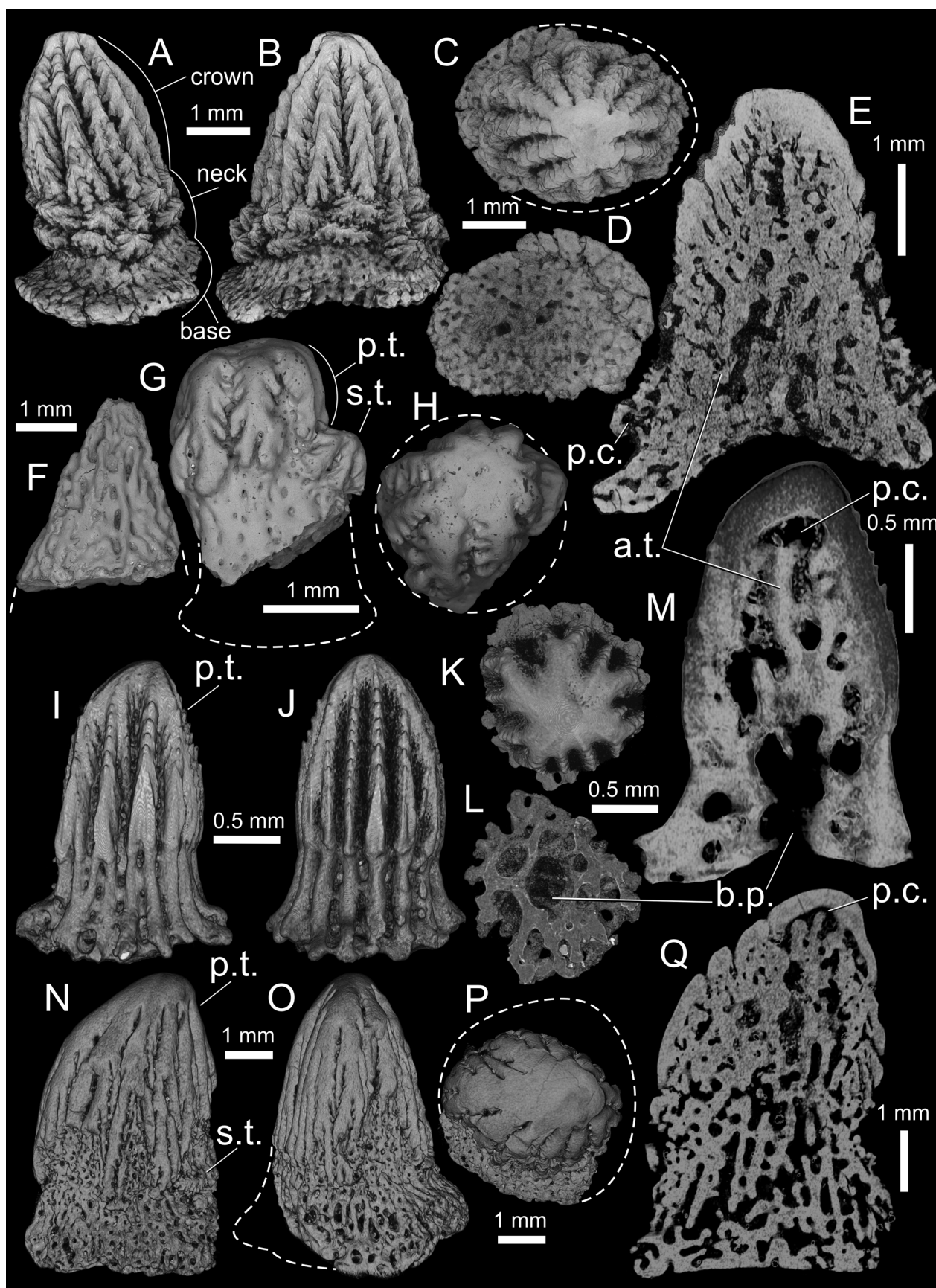
On the basis of morphological and histological differences it is proposed to differentiate two types of discrete micromeric elements in the fields of tesseræ in representatives of Psammosteidae *sensu* Novitskaya (2004): the ‘basic type’ and the ‘progressive type’. In micromeric elements belonging to the ‘basic type’, tubercles are similar both in general shape and in inner structure. In the discrete tesseræ of the ‘basic type’, the crown is formed by a primordial tubercle and satellite

tubercles (Fig. 5A–C, E–G, I, J). The primordial tubercle is as a rule larger than satellite tubercles or has a comparable size. Pulp cavities of the tubercles are identical, usually hollow; rarely trabeculae of cancellous aspidin can penetrate into them (Fig. 5J, Q). Micromeric elements belonging to the ‘basic type’ are known in early representatives of the genus, such as *Psammosteus* sp. from the Early Devonian (Givetian) of Estonia (Mark-Kurik 1999, fig. 8). We assign these micromeric elements, defined by Mark-Kurik (1999) as those of *Psammosteus* sp., to *Psammosteus bergi* (Obruchev, 1943) (Fig. 5R, S). The same micromeric elements are also present in *Psammosteus levis* Obruchev 1965, *P. livonicus* Obruchev, 1965, *P. maeandrinus* Agassiz, 1844, *P. megalopteryx* (Trautschold, 1880), *P. praecursor* Obruchev, 1947b (Fig. 5G–Q) and also *Karelosteus weberi* Obruchev, 1933 (q.v. Glinskiy 2014, p. 23, fig. 1:3).

In micromeric elements belonging to the ‘progressive type’, the crown is formed by a large primordial tubercle (Fig. 6A–C, G, H, I–K, N, O). It is situated centrally on the top of a conical aspidin mound (neck) and covers the upper half of the neck by its long and complicated marginal crenulations (Fig. 6E, M, Q). A primordial tubercle can have one or several pulp cavities, usually filled in by aspidin trabeculae. Satellite tubercles in the tesseræ belonging to the ‘progressive type’ can retain simple inner structure, characteristic of the ‘basic type’. Discrete tesseræ of ‘progressive type’ differ from discrete single elements by the presence of satellite tubercles, arranged in concentric zones on the neck (Fig. 6A, B, G). Often in the fossil record, elements of ‘progressive type’ that are devoid of dentine are found, with the remaining aspidin part represented by a conical aspidin mound (neck) and a base (Fig. 6F).

The first morphological description of discrete micromeric elements of ‘progressive type’ was based on the material of *Psammosteus falcatus* Obruchev in Gross, 1942 (Obruchev 1964, pl. 6, fig. 5; Obruchev & Mark-Kurik 1965, pp. 219, 254; Halstead Tarlo 1965, pp. 135, 137, fig. 4: C, D). The unusual shape and large

Fig. 5. *Psammosteus ramosus* sp. nov. Glinskiy, rooted tessera and topographic variability of the ornament (A–F). Shots of ornamentation are shown in Fig. 3; micromeric elements of the ‘basic type’ in some species of *Psammosteus* and their microstructure (G–S). **A**, PM SPU 80-2, holotype, rooted tessera, fragment of left branchial plate, Andoma Hill, Russia. **B**, **C**, G 43/292:1, fragment of branchial plate. **D–F**, G 43/292:2, fragment of left branchial plate. **G–J**, PM SPU 75-12, *Psammosteus maeandrinus* Agassiz, 1844, discrete tessera, Andoma Hill (outcrop OK-3, layer 5), Russia (Upper Devonian, Frasnian, Pļaviņas RS); **G**, lateral, **H**, anterior and **I**, top views, **J**, vertical section. **K–N**, PM SPU 75-13, *Psammosteus megalopteryx* (Trautschold, 1880), discrete tessera, Lake Il’men’ (outcrop 11/56, sample B4), Russia (Upper Devonian, Frasnian, Daugava RS); **K**, lateral, **L**, anterior and **M**, top views, **N**, the vertical section. **O–Q**, PM SPU 71-5, *Psammosteus livonicus* Obruchev, 1965, discrete tessera, Yam-Tesovo, Russia (Upper Devonian, Frasnian, Amata RS); **O**, lateral and **P**, top views, **Q**, vertical section. **R**, **S**, GIT 680-380, *Psammosteus bergi* (Obruchev, 1943), discrete single element, Essi (Essi müür), Estonia (Middle Devonian, Givetian, Burtnieki RS); **R**, lateral view, **S**, vertical section. G–S, MicroCT images. Abbreviations: a.t., aspidin trabeculae; p.c., pulp cavity; p.t., primordial tubercle; s.t., satellite tubercle.



sizes of these elements were noted (the height of the tesseræ of *P. falcatus*, specimen PM SPU 75-9, can attain 7–8 mm). Micromeric elements of ‘progressive type’ belonging to *Psammosteus falcatus*, *P. cf. kiaeri* Halstead Tarlo, 1964, *P. ramosus* sp. nov. are known. Single elements and tesseræ similar to them are dominant in the fields of tesseræ in this psammosteid lineage.

SYSTEMATIC PALAEONTOLOGY

Class PTERASPIDOMORPHI Goodrich, 1909
Subclass HETEROSTRACI Lankester, 1868
Order PTERASPIDIFORMES Berg, 1937
Suborder PSAMMOSTEIDA Kiaer, 1932
Family PSAMMOSTEIDAE Traquair, 1896
Genus *Psammosteus* Agassiz, 1844

Psammosteus ramosus sp. nov. Glinskiy
Figures 2–4; 5A–F; 6A–E, G, H; 7

2015 *Psammosteus* sp. nov. 2, Glinskiy & Ivanov, p. 57.

Etymology. From Latin ‘ramus’ (branch) and ‘ramosus’ (full of branches), referring to the shape of marginal crenulations on dentine tubercles.

Holotype. PM SPU 80-2, fragment of the left branchial plate, Andoma Hill, southeastern bank of Lake Onega, outcrop N-2, layer AG 1-2 (Andoma Formation, Upper Devonian, Frasnian, Amata RS).

Material. Fragments of the left branchial plate: PM SPU 80-1, Borschovo, outcrop 3; PM SPU 80-2, PM SPU 80-3, Andoma Hill, outcrop N-2; G 43/292:2, Қўқў outcrop. Fragment of branchial plate G 43/292:1, Қўқў outcrop. Lateral (body) scale: PM SPU 80-4, Andoma Hill, outcrop N-2. Discrete tesseræ: PM SPU 80-5, PM SPU 80-6, PM SPU 80-7, Andoma Hill, outcrop N-2. Thin sections: thin section of discrete tessera PM SPU 80-7, Andoma Hill, outcrop N-2; thin section of isolated tubercle PM SPU 80-8 from branchial plate PM SPU 80-1; thin section across branchial plate PM SPU 80-3.

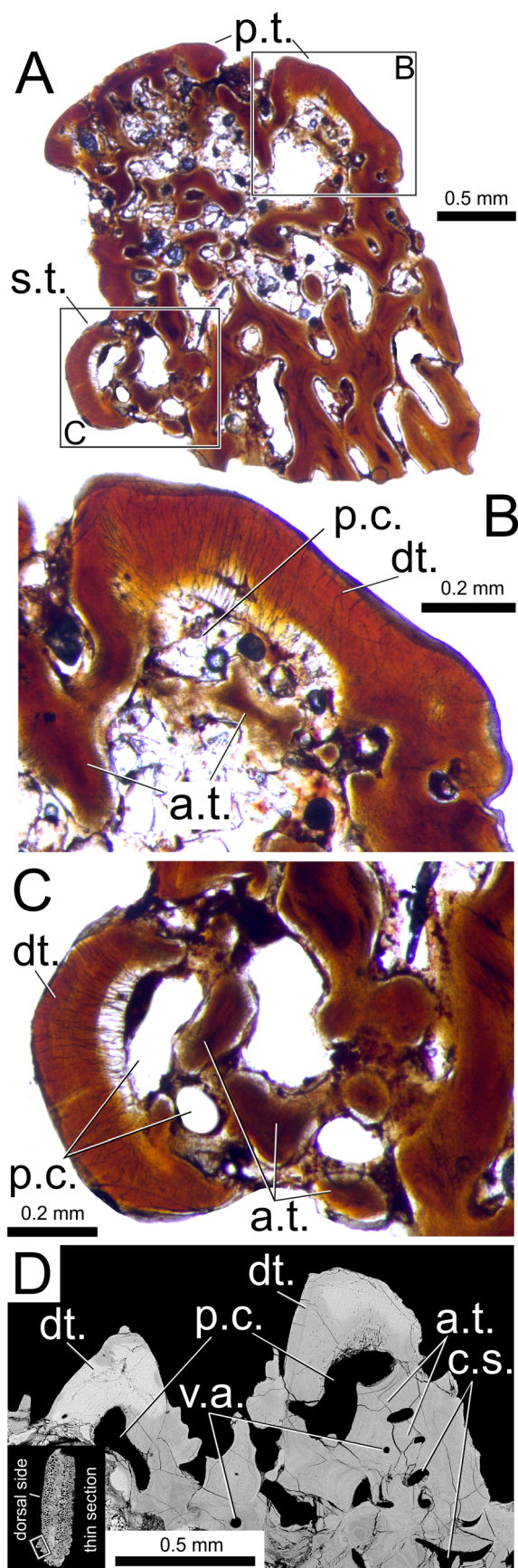
Occurrence. Amata RS, Frasnian, Upper Devonian, *Psammolepis praecursor* Zone (Glinskiy 2013), Leningrad and Vologda Regions of Northwest Russia, eastern Latvia.

Diagnosis. Moderate-sized branchial plates, discrete tesseræ belong to ‘progressive type’. Dentine tubercles large (up to 2.6 mm in total), conical and dome-shaped; their bases mostly rounded; marginal crenulations (6–19) massive, penetrate deeply into crown and their tips may branch; flanks of crenulations along their whole length covered by large, massive ramifications; tips of crenulations and ramifications truncated; ramifications of large tubercles bear indentations on their flanks; radial ribs pass from crowns of tubercles onto their crenulations, ramifications and indentations, where they form plumose wrinkles; large microtubercles (up to 12) situated on the upper side of marginal crenulations. Ridges of tubercles better developed on the dorsal side of branchial plates.

Description

1. *General morphology.* Branchial plates are very short and wide or extremely stenobasal (the term first mentioned in Obruchev & Mark-Kurik 1965, pp. 134, 219). They are semicircularly expanded in width and flattened (Fig. 2A, B, G, H, N, O). The anterolateral margin is partly represented in specimen G 43/292:2 (Fig. 2G, H); it is generally convex. Straight anterolateral margin of PM SPU 80-3 is a result of lifetime abrasion (Fig. 2D, E; Fig. 3C, D). The posterior margin is concave. The distal tip of the plates is curved backwards or medially (Fig. 2A, B, N, O). Branchial plates without deformation are insignificantly dorsally convex in width (0.5 mm) (Fig. 2C, F). The distal part of the branchial plates (PM SPU 80-2) is slightly dorsally convex in length (1.4 mm from the proximal side, less than 1 mm from the distal side). The ornamented surface is developed on the distal part of the branchial plates. The area of the ornamented surface on the dorsal side is more or less equal to that on the ventral side of the plates (Fig. 3A, B, E–H, K, L) or slightly smaller (Fig. 3C, D).

Fig. 6. Discrete micromeric elements of the ‘progressive type’ in some species of *Psammosteus* and their microstructure. A–E, PM SPU 80-5, *Psammosteus ramosus* sp. nov. Glinskiy, discrete tessera, Andoma Hill, Russia; A, lateral, B, posterior, C, top and D, visceral views, E, vertical section. F, PM SPU 80-9, *Psammosteus cf. ramosus* sp. nov. Glinskiy, fragment of discrete tessera – aspidin mound without surmounted dentine tissue, lateral view, Andoma Hill (outcrop N-2, layer AG 1-2), Russia. G, H, PM SPU 80-7, *Psammosteus ramosus* sp. nov. Glinskiy, fragment of discrete tessera, Andoma Hill, Russia; G, lateral and H, top views. I–M, PM SPU 75-11, *Psammosteus cf. kiaeri* Halstead Tarlo, 1964, discrete single element, Andoma Hill (outcrop OK-3, layer 5), Russia (Upper Devonian, Frasnian, Пјавињас RS); I, lateral, J, anterior, K, top and L, visceral views, M, vertical section. N–Q, PM SPU 75-10, *Psammosteus falcatus* Obruchev in Gross, 1942, fragment of discrete tessera, Lovat’ River (outcrop 140, layer 6), Russia (Upper Devonian, Frasnian, Snezhna RS); N, lateral, O, anterior and P, top views, Q, vertical section. F–H, SEM BSE images; A–E, I–Q, MicroCT images. Abbreviations: a.t., aspidin trabeculae; b.p., basal pore; p.c., pulp cavity; p.t., primordial tubercle; s.t., satellite tubercle.



The boundary between the ornamented and unornamented surfaces of the branchial plates is usually distally convex. Branchial plates are of moderate sizes. The measurements of the fragments are given in Table 1.

Lateral scales have rounded margins; they are short, wide and flattened. In specimen PM SPU 80-4 the right margin is concave (Fig. 2Q, R). Ornamentation is developed in the posterior part on both sides of scales (Fig. 3I, J). On the external side the area of the ornamented surface slightly exceeds half of the total area of this side of the plate (shortened ornamented zone). The area of the anterior unornamented surface is large. On the visceral side the ornamented surface covers approximately a quarter of the total area. The length of scale PM SPU 80-4 is 6.8 mm; the width is 8.9 mm. The thickness of the plate in the unornamented part is 0.8 mm; it is 2.5 mm in the zone with ornamentation.

The micromeric elements belonging to the species are discrete tesserae (Fig. 6A–H) and rooted tessera (Fig. 5A), preserved on the ventral side of branchial plate PM SPU 80-2. Discrete tesserae of ‘progressive type’ have a high crown, formed by a large single primordial tubercle, a high neck and a rounded small base (Fig. 6A–D, G, H). The crown is subvertically oriented (Fig. 6A, B, G) or slanted (PM SPU 80-6). Satellite tubercles sit on the neck, forming up to two areal zones (Fig. 6A, B, G). The area of the base is equal to or slightly exceeds that of the crown. Its visceral side has a medial depression (Fig. 6D, E). The most complete specimen PM SPU 80-5 is 4.5 mm in height and 4 mm in length of the base. The rooted tesserae on the ventral side of the branchial plates are low and small (3 mm in length). Tubercles are situated concentrically; the primordial tubercle does not differ from them either in shape or in size.

2. Ornamentation. Ornamentation is represented by large tubercles with the area of the base up to 1–1.5 mm in diameter. The mean length of marginal crenulations is 0.8–1 mm, ranging in number (without their branch tips) from 6 to 19, 13–16 on average. The general size of the tubercles including the length of marginal crenulations can attain 2.6 mm in total (Fig. 4B, I). The crowns of the tubercles have a conical and dome-like, rarely

Fig. 7. Vertical thin section of discrete tessera (A–C) and branchial plate (D) of *Psammosteus ramosus* sp. nov. Gliniskiy. A–C, PM SPU 80-7, discrete tessera, Andoma Hill, Russia: A, general view; B, part of primordial tubercle, C, satellite tubercle. D, PM SPU 80-3, branchial plate, Andoma Hill, Russia. Abbreviations: a.t., aspidin trabeculae; c.s., cancellous aspidin spaces; dt., dentine; p.c., pulp cavity; p.t., primordial tubercle; s.t., satellite tubercle; v.a., vascular canals of aspidones. D, SEM BSE image.

Table 1. Measurements of fragments of branchial plates (in mm)

	PM SPU 80-1	PM SPU 80-2	PM SPU 80-3	G 43/292:1	G 43/292:2
Length of the fragment	30	31	17	13	20
Width of the fragment	70	63	12	20.2	22.9
Maximal thickness in the distal part	3	2.9	5	5	6.7
Maximal thickness in the proximal part	2.4	2.6	–	3.3	5.5

peaked shape. They are oriented vertically or can be slightly slanted towards the surface of the plate (Fig. 4H). The mean height of the tubercles is 1 mm. Tubercles with round or oval bases are dominant (Fig. 4E, F, J, O) and those with angular, fan- or poleaxe-shaped bases are more rare (Fig. 4I–K). As a rule, thin radial ribs diverge from the top of the crown, which can be observed on low-crowned unabraded tubercles (Fig. 4L–O). Ribs branch on the marginal crenulations and ramifications (second-order marginal crenulations) forming fine plumose wrinkles (Fig. 4H, M–O; Fig. 5B, C, E). Marginal crenulations are massive and complicated, but not tapered. Finer and simpler crenulations may be present between them (Fig. 4B, C, I). The crenulations on the proximal side of branchial plates tubercles attain substantial length (up to 2.2 mm) and are more complicated (Fig. 4A, B, F, I), in comparison with those on the distal side of these tubercles. The tips of marginal crenulations often ramify into two or three long branches (Fig. 4A, B, F, I, L, O). Massive ramifications occur on the flanks of marginal crenulations. They can attain substantial length and can bear indentations on their margins in large tubercles (Fig. 4A, B). Ramifications are usually densely distributed along the whole length of marginal crenulations (Fig. 4C–G, I–O; Fig. 5B, C, D, F; Fig. 6A, B, F, G). Large microtubercles are situated along the whole length of marginal crenulations (up to 12 in discrete tesserae); small, scarcely discernible microtubercles are also observed on the ramifications (Fig. 6A, B).

Tubercles on the branchial plates often fuse into long ridges. The length of the ridges is up to 1 cm (Fig. 2A; Fig. 4B, C, G, I, N). The number of crenulations of fused tubercles exceeds 17. The tubercles of the lateral scale have predominantly round or oval bases; the crowns are oriented vertically; short ridges are present. Discrete tesserae bear a large primordial tubercle with very long marginal crenulations, covering the conical aspidin mound almost totally. Small tubercles of later generations on the branchial plates and tesserae are usually rounded, more rarely elongated; they bear 6–11 marginal crenulations, which are usually short, simple and unbranched (Fig. 4B,

J, K; Fig. 6A, B, F). Some small tubercles on the ventral side of branchial plate PM SPU 80-2 (holotype) have a low (Fig. 4E–H) count of marginal crenulations, which intensely ramify towards their tips (Fig. 4E, F). The diameter of the bases of these small tubercles of later generations is 0.3–0.5 mm. There are also blisters with simple marginal crenulations, covering injuries on the plates (Fig. 2E, G, H; Fig. 3D, G, H).

3. Ornamentation topography. On the plates and micromeric elements of the new species known to date tubercles are arranged predominantly in regular concentric rows. The tubercles are not situated densely relative to each other (Fig. 4F, K, O). Rows of tubercles are oriented generally subperpendicular to the long axis (=to anterolateral and posterior margins) of branchial plates (Fig. 2A, G). The tubercles in rows are larger and have more massive and pronounced ridges on the dorsal side of the plates. The rows of the branchial plates can also have a slight proximal curvature (Fig. 3A, B, G, H). Small tubercles of later generations are situated between the large ones on the branchial plates. The ornamented surface on the branchial plates can generally be divided into two zones, the distal and the proximal one. In the distal zone the tubercles have a predominantly conical and peak-like shape; the crowns are usually slanted distally, the ridges in the rows are large and long, and the rows stand far from each other due to proximally developed marginal crenulations. In the proximal zone the tubercles have predominantly a simpler structure. They are dome-shaped and low cone-shaped with a vertically oriented crown. They possess short marginal crenulations, weakly growing longer in the proximal direction. The shapes of the bases are various in both zones and their topography is unique for every specimen. Small tubercles of late generations are situated in the proximal zone. The shape and orientation of the tubercles' crowns on the lateral scales is the same as in the proximal zones of the ornamented parts of the branchial plates. On the external surface of the lateral scale, the tubercles with conical and dome-shaped crowns are arranged in concentric rows around the large primordial tubercle (Figs 2Q, 3I).

4. *Internal structure.* The superficial layer of the plates consists of orthodontine tubercles, covered by a thin layer (up to 1.5 μm) of hypermineralized tissue (PM SPU 80-8). The pulp cavities of dentine tubercles can be either hollow (Fig. 7D) or filled with aspidin trabeculae (Fig. 6E; Fig. 7B, C). Pulp cavities are connected with radial pulp canals, which run under marginal crenulations. Large dentine tubercles on the branchial plates, lateral scales and the primordial tubercle of micromeric elements are situated on cancellous aspidin mounds (Fig. 6E; Fig. 7A, D). The mounds on the branchial plates can also fuse into aspidin ridges (Fig. 2A, B). Satellite tubercles of discrete tesseræ and small tubercles on the branchial plates generally have hollow pulp cavities. Cancellous aspidin has large spaces and vascular canals of aspidones; the reticular layer of the branchial plates is weakly developed (Fig. 7D).

Comparison. The branchial plates of the new species are more stenobasal than those of typical representatives of the genus *Psammosteus*. *Psammosteus ramosus* sp. nov. Glinskiy resembles *P. falcatus* Obruchev in Gross, 1942, *P. kiaeri* Halstead Tarlo, 1964, *P. pectinatus* Obruchev, 1965 and, to a lesser extent, *P. tenuis* Obruchev, 1965 in the extremely stenobasal shape of the branchial plates, details of ornamentation and its topography (Kiaer 1915, pl. 5, fig. 5; Halstead Tarlo 1964, pl. 2, fig. 2; Obruchev & Mark-Kurik 1965, pls 87–89, 91, 93). The rows of tubercles on branchial plates of *P. ramosus* sp. nov. can have a slight proximal curvature, as opposed to what can be seen in *P. kiaeri* and *P. pectinatus*. In the new species the tubercles in the rows on the branchial plates fuse into rather long ridges, just like in *P. falcatus*, *P. kiaeri* and *P. pectinatus*. However, in the new species these ridges are shorter than in *P. kiaeri* and they are very weakly developed on the proximal side of the plates, which differentiates it from *P. pectinatus* and places it somewhat closer to *P. falcatus*. The new species also differs from *P. pectinatus* in the size of the branchial plates, in the latter species they are small (Obruchev & Mark-Kurik 1965, pl. 93, fig. 2; Glinskiy & Ivanov 2015, fig. 1: 6). Lateral scales, both in size and in shape, most closely resemble those of *Psammosteus bergi* (Obruchev, 1943) and *P. megalopteryx* (Trautschold, 1880). The concentric arrangement of tubercles around the primordial tubercle (like on the tesseræ) and their position at the posterior end of scales is seen in some scales of *Psammosteus* sp. (Mark-Kurik 1993, fig. 3B) and also in isolated scales of *P. bergi* (Mark-Kurik 1999, fig. 7D, E, G–I). Lateral scales of *P. ramosus* sp. nov. are also similar to those of *P. bergi* (Mark-Kurik 1999, fig. 7D) in a greater reduction of the external ornamented surface. The new species comes close to *P. cf. kiaeri* and *P. falcatus* (Fig. 6 A–Q) in

terms of morphology and inner structure of discrete elements, and is substantially different from other species of *Psammosteus*. High and complicated tubercles of exoskeletal elements in *P. ramosus* sp. nov. are situated on cancellous aspidin mounds or ridges, like in *P. falcatus* (Novitskaya 1965, fig. 227), *P. cf. kiaeri* and *P. pectinatus*.

The species in the genus *Psammosteus* differ from each other primarily in details of ornamentation on branchial plates (Halstead Tarlo 1964, p. 39). General details of ornamentation, its topography and histological characteristics of branchial plates of *Psammosteus ramosus* sp. nov. are close to those of *P. falcatus* Obruchev in Gross, 1942, *P. kiaeri* Halstead Tarlo, 1964 and *P. pectinatus* Obruchev, 1965. In the details of tubercle morphology the new species also resembles *P. asper* Obruchev, 1965, *P. bystrowi* Obruchev, 1965, *P. livonicus* Obruchev, 1965 and *P. tenuis*, and is different from other species of the genus *Psammosteus*. It resembles *P. asper*, *P. livonicus* and *P. tenuis* in the massiveness of its crenulations and ramifications. As in *P. asper*, *P. falcatus*, *P. kiaeri* and *P. pectinatus*, marginal crenulations go deep into the crowns of the tubercles in the species described herein. The new species is similar to *P. asper* in its indented and rugose marginal crenulations. In the latter species such morphology of marginal crenulations is formed by microtubercles, not ramifications. The new species differs from *P. bystrowi* in a more complex form of marginal crenulations and the presence of ramifications. In the new species, ramifications are situated along the whole length of marginal crenulations as opposed to *P. livonicus*, in which they are confined to the tips of marginal crenulations (Glinskiy & Mark-Kurik 2016, fig. 6: 9, 10, fig. 7A). The new species is most closely similar to *P. falcatus*, *P. kiaeri* and *P. pectinatus* in the presence of ramifications along the whole length of the marginal crenulations. The main species-specific difference of the new species is that ramifications are large, massive, and densely and evenly distributed along the whole length of the flanks of marginal crenulations. *Psammosteus ramosus* sp. nov. differs from *P. kiaeri* (Kiaer 1915, pl. 5, fig. 5; Halstead Tarlo 1964, pl. 2, fig. 2) in larger structural elements: each crenulation is thicker and more massive; these crenulations do not fork at the very crown base and bear larger ramifications and microtubercles. The new species is closest to *P. pectinatus* in details of tubercle structure. It generally differs from the latter in short branching tips of the marginal crenulations and longer ramifications (Fig. 6A, B). In their general morphology the tubercles of the new species resemble those of *P. falcatus* (and *P. tenuis*), but they differ in bearing microtubercles, in larger, short, massive ramifications without fine branching and in having more simple plumose wrinkles.

Remarks. The exoskeletal elements of *P. ramosus* sp. nov. include discrete micromeric elements, tesseræ of ‘progressive type’, which are also known in *P. falcatus* and *P. cf. kiaeri* and, probably, will be discovered in *P. pectinatus*. This group is substantially different from the main evolutionary lineage of species in the genus *Psammosteus* and also *Karelosteus* (q.v. Glinskiy 2014) in all these characters, and especially in possessing the discrete micromeric elements of ‘progressive type’ instead of those of ‘basic type’. Specimen PM SPU 80-9 is defined as *P. cf. ramosus* sp. nov., because it possesses a naked aspidin mound without dentine tubercles.

The extension of cancellous aspidin trabeculae into the pulp cavity of large dentine tubercles is well known in *Ganosteus stellatus* Rohon, 1901 (Novitskaya 1965, figs 206, 208). The microstructure of large tubercles and micromeric elements of ‘progressive type’ in the described *Psammosteus* lineage and in the plates of *Traquairosteus pustulatus* (Traquair, 1897) is similar, because in both cases the undergrowth of cancellous aspidin and development of a cancellous aspidin mound are seen under growing dentine tubercles (Tarlo 1961, fig. 3C). However, dentine tubercles in *T. pustulatus* are simple, reduced in size (Halstead Tarlo 1965, p. 150). A similar model of skeletal development is also seen in a heterostracan *Lepidaspis serrata* Dineley & Loeffler, 1976: it possesses dentine ridges on the aspidin ridges, filled with aspidin trabeculae (Keating et al. 2015, fig. 2A–D).

DISCUSSION

The evolution of the exoskeleton in the representatives of the family Psammosteidae *sensu* Novitskaya (2004) resulted in the reduction of exoskeletal structures in comparison with other psammosteids, which made it possible to lighten the skeleton and improve locomotion capabilities. A number of evolutionary transformations are observed in major plates of the exoskeleton (progressive development of stenobasal branchial plates, elongation of median plates), which are connected with contraction in width of the cephalothorax (Obruchev & Mark-Kurik 1965, pp. 54, 55). The extremely stenobasal shape of branchial plates, characteristic of the juvenile stage of development in many *Psammosteus* species (Obruchev & Mark-Kurik 2016), is retained in some species of *Psammosteus* in the adult stage (paedomorphism). This phenomenon is manifested independently in different evolutionary lineages of *Psammosteus*. All representatives of *Psammosteus*, as opposed to other groups of psammosteids, are also characterized by the reduction in size of mesomeric exoskeletal elements, the lateral scales. According to Obruchev, this is connected

with an increase in the mobility of the tail (Obruchev 1945, p. 263; Obruchev & Mark-Kurik 1965, p. 217). *Psammosteus* is characterized by a general constriction of the base of rooted micromeric elements – tesseræ. At the same time they occupy most of the surface of cephalothoracic plates (advanced tesserization). Morphotypes of micromeric exoskeletal elements in Psammosteidae are probably more varied than in other psammosteids (as they are known only in Psammosteidae to date). In discrete micromeric elements of the cephalothorax an increase in height is observed. The height of such elements corresponds to the usual thickness of a dorsal median plate in representatives of the family Psammosteidae, suggesting that discrete exoskeletal elements could be situated in the skin at approximately the same level as the plate.

Thus, discrete tesseræ of ‘progressive type’, characteristic of one of the lineages in the genus *Psammosteus*, stand out by their height, which is attained by the enlargement of an aspidin mound (neck) and its overgrowth by the dentine of the primordial tubercle. The development of discrete tesseræ of ‘progressive type’ in the lineage *P. ramosus* sp. nov.–*P. falcatus* was by successive accretion of satellite tubercles to the neck of single elements. Tesseræ of this type, formally circular tesseræ (Halstead Tarlo 1967b; Karatajūtė-Talimaa 1998), are a result of multifunctional adaptation through paedomorphism, because the reduction in the count of tubercles in the crown provides the lightening and improvement of locomotion while preserving the protective function. Single elements represent the first ontogenetic stage of development of micromeric elements in psammosteids.

According to Obruchev (Obruchev & Mark-Kurik 1965, p. 43), the presence of lateral dorsal canals of the lateral line sensory system on the dorsal plate of *Psammosteus* points at the general constriction of the cephalothorax. Thus, lateral fields of tesseræ were much narrower in *Psammosteus* than in other psammosteids, in which lateral dorsal canals were situated in wide fields of tesseræ. The increase in the mobility of Psammosteidae in comparison with other psammosteids is also indicated by a progressive complication of the pattern of the lateral line system on the dorsal plate. Thus, in a late representative of the group, *cf. Psammosteus* from the Frasnian of Arctic Canada, sensory canal grooves have a very elaborate pattern (Elliott & Mark-Kurik 2005).

Psammosteid heterostracans underwent the stages of assimilative (e.g. Drepanaspididae, Obrucheviidae) and regressive (Psammosteidae) phases of exoskeletal development during their evolution. The phase of exoskeletal regression usually coincided with the increase in the mobility of the animals. Thus the ecological specialization changed from demersal *Drepanaspis*

(Blieck 2016) with armoured body type to the most active demersal forms like *Psammosteus*.

RESULTS

At least two evolutionary lineages within Psammosteidae *sensu* Novitskaya (2004) can be distinguished now based on the differences in the morphology and histological details of the exoskeleton. The species *Psammosteus ramosus* sp. nov. Glinskiy is the oldest known representative of the psammosteid lineage with discrete cyclomerial tesserae of ‘progressive type’ and a peculiar histological structure of the other plates. The new species comes close to *P. falcatus* Obruchev in Gross, 1942, *P. kiaeri* Halstead Tarlo, 1964 and *P. pectinatus* Obruchev, 1965, but is strongly different from other known representatives of the genera *Psammosteus* and *Karelosteus weberi* Obruchev, 1933. Obruchev did not exclude the possibility that the genus *Psammosteus* may be divided into several genera in the future (Obruchev & Mark-Kurik 1965, p. 219).

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Uus psammosteiid (Agnatha, Heterostraci) Amata regionaalsest lademest Peadevoniväljal ja diskreetsete mikromeerseid elementide tüübid sugukonnas Psammosteidae

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Sugukonda Psammosteidae Novitskaya (2004) kuuluvate psammosteiidide mitmekesisus on siiani puudulikult teada. Artiklis kirjeldame uut liiki *Psammosteus ramosus* sp. nov. Glinskiy Amata regionaalsest lademest Peadevoniväljal ja võrdleme selle väliskeleti plaatide morfoloogiat, ornamente ning histoloogiat, aga ka nende mikromeerseid elemente selle sugukonna teiste esindajate omadega. Võrdlus näitab lähedast seost uue liigi ja *Psammosteus falcatus* Obruchev (vt Gross, 1942), *P. kiaeri* Halstead Tarlo, 1964 ning *P. pectinatus* Obruchev, 1965 vahel. Viimased kuuluvad liikide rühma, mis oluliselt erineb perekonna *Psammosteus* teistest esindajatest ja moodustab eraldiseisva evolutsioonilise liini. Morfoloogiliste ja histoloogiliste tunnuste alusel eristame sugukonnas Psammosteidae diskreetseid primaarseid tüüpi (*basic type*) ning progressiivset tüüpi (*progressive type*) mikromeerseid elemente.