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PSAMMOSTEID MICROREMAINS FROM THE MIDDLE DEVONIAN (GIVETIAN) OF ESTONIA

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The Estonian locality of Essi in the Baltic Middle Devonian (Givetian) Abava Substage, called by Gross the "Übergangs-Stufe", has yielded numerous well preserved microremains of *Psammosteus* sp. They show a variety of structure and growth types: single elements that somewhat resemble thelodont and certain chondrichthyan scales on the one hand, and complex elements that are similar to tesserae of primitive heterostracans or to platelets ("tesserae") and scales of psammosteids on the other. Among the latter, specimens of both synchronomorial and cyclomorial growth types occur. These elements reveal the differences between *Psammosteus* and the other psammosteids and shed new light on the growth and relationships of heterostracans in general. The derivation of psammosteids from pteraspids and the secondary nature of psammosteid "tesserae" are equivocal issues.

Keywords: Psammosteids; Agnatha (Heterostraci); Devonian; Microremains; Growth; Relationships

INTRODUCTION

Modern biostratigraphy of Devonian fishes in the Baltic area began with the fundamental studies of Gross (1933, 1940, 1942, 1951) who described and/or revised the taxonomy of representatives of different groups, indicated their localities in Latvia and Estonia, and presented lists of fishes for local stratigraphical units with comments on the frequency of occurrence of fossils. Gross compared the Baltic fish faunas with those from Northwest Russia. He established biozones for the Middle and Upper Devonian; most of the Middle Devonian zones are still valid (Figure 1). It must be pointed

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Gross 1942+1951			Modern Baltic Subdivision	Fish Zones	
	Devononchus B. ornata-	h-Stufe h3 - h4	Ketleri Žagarė	B. ciecere	z
imosteus-St.	ketleriensis- Zonc Zone	h ₂ h ₁ c g-Stufe	Svété Můri Akmene Kursa	<u>B. ornata</u> Phyllolepis	FAMENNL
Post-Psan		ອ ສ ຍ c/f-Stufe	Eleja Amula Stipinai Bauska	curonica	DEVON
mmosteus-St.	B. curonica-Z. Psammosteus grossi-	Oper	Imula Pamūšis (Ogre) Snezha	Psammosteus falcatus - Bothriolepis maxima	UPPER
	Bothriolepis maxima- Zone	d-Stufe <u>c-Stufe</u> b ₂ -b ₄ -Stufe	Daugava Dubniki (Salaspils) Chudovo Plavinas, Pakov	Bothriolepis trautcholdi Bothriolenis	FRASP
Psa	Ps.mB.cellulosa-G.tubZ.	b ₁ Snetogor-Stufe	Sn. Gora	cellulosa	
8	Asterolepis radiata-Zone	a4 Podsnetogor-St.	Amata	B. prima, B. obrutschewi	L'
20	Asterolepis ornata-Zone	a ₃ Oredesch-Stufe	Gauja	Asterolepis ornata	ξz
	Coccosteus grandis-Leitfossil	Übergangs-Stufe	Burtnicki Abava*	Watsonosteus]5₹
	Pycnosteus tuberculatus-Zone	ob.	Salaca	Pycnosteus tuberculatus	Ξð
-Stufe	Pycnosteus palaeformis-	a ₂ Luga-Stufe unt.	Tarvastu Aruküla Kurcküla	Pycnosteus pauli	D 2
id.	Zone		Viljandi	Pycnosteus palaeformis	LB
Actinole	Pterichthys concatenatus- Schizosteus striatus- Zone	Narowa-Stufe a _i	Kernavê Na va Leivu Vadja	Coccosteus cuspidatus - Schizosteus striatus	MIDD
	Schizosteus heterolepis-Zone	Pernau-Stufe	Pärnu	Schizostens heterolepis	1

FIGURE 1 Key to the biostratigraphical and regional stratigraphical units of the Baltic Middle and Upper Devonian established and/or used by W. Gross, and their modern equivalents (from Mark-Kurik 1993a; modified according to Mark-Kurik 1997, and Ivanov and Lukševics 1996). The Abava Substage that has yielded the microremains described in the present paper is marked with an asterisk. *B* – *Bothriolepis; G. tub.* – *Grossilepis tuberculata Lacc.*-St. – *Laccognathus*-Stufe; *Ps.m.* – *Psammosteus maeandrinus.*

out that, while establishing zonal subdivisions based on different fishes (psammosteids, antiarchs, acanthodians), Gross preferred a mixed zonation including the most characteristic representatives of various groups when summing up the results.

Being remarkably observant, Gross distinguished specific fish faunas of several strata which were later considered in the rank of regional stages, e.g. the subdivisions of the "Luga-Stufe" and the "Übergangs-Stufe". A review of the study and a short description of the latter unit, now called the Abava Substage are given in the present paper. The main aim is to describe a set of psammosteid microremains discovered in the Abava Substage in Estonia.

The psammosteids, known since Louis Agassiz's time and representing a very common fish group in the Baltic Devonian, have yielded large

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exoskeletal plates, their fragments and/or scales. These remains characterize the regional stratigraphical units, several psammosteid species being used as index fossils, especially in the Middle Devonian (Figure 1). Small skeletal elements of psammosteids have only been recorded from one unit and do not have the biostratigraphic value of the microremains of other fishes, such as acanthodians, but they give new information on the structure and growth of psammosteids.

The material described in this paper is housed in the collections of the Institute of Geology at Tallinn Technical University (with indices Pi).

STRATIGRAPHICAL BACKGROUND

Gross (1942, 1951) paid special attention to the Middle Devonian unit in the Baltic sequence that occupied a position intermediate between two higher rank biostratigraphic subdivisions, the "Actinolepis-Stufe" and "Laccognathus-Stufe" or, according to the present regional stratigraphic terminology, the Burtnieki and Gauja stages (Figure 1). This unit, called by Gross the "Übergangs-Stufe", had a mixed fish fauna but also contained species (Coccosteus grandis Gross, Osteolepis striata Gross) not occurring in over- and underlying strata. This fauna was recorded at two localities: Lenčupe (Lenzuppe), on the tributary of the Gauja (Livländische Aa) River (Figure 2), and Gibzde (Gibsde), south of Dundaga (Dondangen) in Latvia (the latter of these localities is no longer exposed). After the discovery of a new rich locality, Lejēji on the Abava River, western Latvia, Karatajūtė-Talimaa (1958) gave a geographic name to the unit: the Abava Beds. This name was published by Liepinš (1960) who changed the rank of the subdivision and used "formation" instead of "beds". Later on, the formation was only rarely recognized as an independent unit; in most cases, it was considered as the basal part of the Gauja Formation (e.g., Sorokin, 1981). When the fishes from two southern Estonian localities, Essi and Ratta müür on the Võhandu River (Figure 2) were found to be identical to those of the Abava Formation (particularly as a result of the excavations in 1963 and 1970), and new data were obtained on the structure and thickness of the formation in the Abava River basin (Kurik et al., 1989), it was decided to consider the unit as a regional stage (Mark-Kurik, 1993a); according to Sorokin (1996) it is an independent formation. In the recent stratigraphical scheme of the Devonian in Estonia the unit has been referred to a substage of the Burtnieki Regional Stage (Kleesment and Mark-Kurik, 1997). The Abava Substage appeared to be a good marker in the correlation of the



FIGURE 2 Location of the outcrop areas and fish localities of the Abava Substage (Middle Devonian, Givetian). (a) Main outcrop areas in Estonia and Latvia marked with squares; V.R., Võhandu River. (b) Localities on the middle course of the Võhandu, R., SE Estonia, indicated by open circles. (c) Section of the Essi locality; black bar shows the bed richest in fishes.

Middle Devonian sequences of the East Baltic and Scotland because of a number of characteristic genera (*Watsonosteus*, *Microbrachius*) discovered in both regions (Mark-Kurik, 1991; Dineley and Loeffler, 1993).

In western Latvia the Abava Substage is the most completely studied in the Abava River mouth region (Figure 2a) where several exposures including the stratotype at Lejēji are located, and additional information has been obtained from borehole cores (Kurik *et al.*, 1989). In this region the substage is predominantly composed of grey, light-brown, yellow and red finegrained sandstones and reddish-brown and grey siltstones. Conglomerate interbeds consisting of quartz and clastic rock pebbles occur at some levels. Fish remains can be found both in the conglomerates and cross-bedded sandstones. The thickness of the substage is about 65 m. In Estonia the Abava Substage can be examined in a section at Essi in the middle course of the Võhandu River, downstream from Leevi village (Figure 2b and c). Its lithological features are similar to those of the sequence in the Abava River mouth region (though bed-by-bed correlation of the Võhandu and Abava River outcrops is not possible). Fossil fishes occur at the top of the section; they are scarce in the uppermost red and violet clay, but abundant in the underlying white sandstone. An upstream outcrop, Ratta müür, and a more distant downstream exposure at Reo watermill have also yielded fish remains of the Abava Substage. The faunal list of the above three localities includes: *Ganosteus stellatus* Rohon, *Psammolepis abavica* Mark-Kurik, *Psammosteus* sp., *Watsonosteus* sp.n.?, *Asterolepis essica* Lyarskaya, *Microbrachius* cf. *M. dicki* Traquair, acanthodians, chondrichthyans, *Glyptolepis* sp., *Laccognathus* sp., a dipnoan and *Cheirolepis* sp.

Among the microremains from the white sandstone of the Essi locality are scales of a number of acanthodians (*Cheiracanthus* cf. *C. brevicostatus* Gross, *Cheiracanthus* sp., *Acanthodes*? sp.) together with scales of the palaeoniscoid *Cheirolepis* and chondrichthyan mucous membrane denticles. However, they are significantly less numerous than various psammosteid tubercles, small scales and tesserae-like exoskeletal elements. The silty, light-coloured, fine-grained sandstone has been extremely favourable for the preservation of the most delicate microremains described hereafter. In the dry state this rock is so friable that the fish microremains can be picked out with a fine brush and sand grains removed from their surface with two slightly wet brushes or a brush and a very sharp needle.

DESCRIPTION OF SMALL SKELETAL ELEMENTS OF PSAMMOSTEIDS

Isolated psammosteid tubercles are not uncommon among fish microremains in the Devonian rocks of the Baltic region. As a rule, they come from larger exoskeletal elements, medial and lateral plates, scales and platelets ("tesserae"), and are broken loose from a common spongy bone base. The elements described below are small independent ones, both single and complex (Figures 3, 4a-h, j, 5a-e, g, 6, 7). Some of them resemble turiniid thelodont scales, the others chondrichthyan scales. It is possible that similar microremains may occur in other horizons of the Baltic Devonian; however, in the white sandstone of the Essi locality, from where the material described here originated, these elements are dominant and perfectly preserved.



FIGURE 3 *Psammosteus* sp. (a)–(f), single elements of the exoskeleton. (a) Pi 703/1 in basal view. (b) Pi 703/2 in lateral view. (c) Pi 700/8 in lateral view. Pi 700/5 in anterolateral (d) and crown (e) view. (f) Pi 700/12 in lateral view. (g) Complex element in basal view (specimen lost). Drawings of (c)–(g) made after SEM photographs. bp – basal pore. Scale bars=0.1 mm. All specimens in Figs. 3–8 come from the Essi locality, Võhandu R., SE Estonia; Middle Devonian (Givetian), Abava Substage.

Systematic Attribution

Problems arise with how to determine the psammosteid to which the microremains under consideration belong to. The Essi locality has yielded macrofossils of two fairly different species, *Psammolepis abavica* Mark-Kurik and

an undescribed Psammosteus sp. (Ganosteus has not been found in this outcrop). In P. abavica the ornamentation consists of fan-shaped, polygonal and irregular closely-packed, comparatively flat tubercles with fine comblike crenulations more developed along their proximal edges (Obruchev and Mark-Kurik, 1965: pls. 38-40; Halstead Tarlo, 1965: 107-109; fig. 5f). There are typically 17-36 tubercles per 10 mm. The tubercles are so firmly attached to the exoskeletal plates that some strength is needed to break the aspidin trabeculae and pull the tubercles loose. This seems not to be the case with the independent elements which show a well formed compact base. Oak-leaf shape (Figures 5c, g, 6a-g, 7d-g) and elongated sharptopped crowns of the tubercles (Figures 4a, b, j, 6d, 8b) rather common in these elements do not fit at all in the range of variation seen in the tubercles of P. abavica. Some similarity occurs, however, in the serrated lateral ridges of the tubercles of P. abavica (Figure 4i) and the elements under consideration (Figures 4b, c, e, 6i). The scale-like "tesserae" of P. abavica known in the median plates or found isolated are of large size: 8-18 mm long and 6-20 mm wide (see Obruchev and Mark-Kurik, 1965: figs. 130-132), thus, much larger than the complex elements. The above data show that the independent microelements cannot be confined to P. abavica.

The situation is different for species of the genus Psammosteus. Loose attachment characterizes the platelets ("tesserae") and tubercles of the carapace plates, particularly the median plates of representatives of this genus (Halstead Tarlo, 1964; 1965; Obruchev and Mark-Kurik, 1965). The vertical section of the Late Devonian species Psammosteus megalopteryx (Trautschold) figured by Gross (1933: fig. 4B) shows that the fusion of the vascular canals in the upper part of the "spongiosa" enables the detachment of the "tesserae" from a median plate. The detachment of the "tesserae" is the reason why a fragment of the dorsal plate of Psammosteus sp. (Figure 8a), the only macromeric skeletal element of Psammosteus found from the Essi locality, is completely lacking ornamentation. It resembles the dorsal plates of Psammosteus bergi (Obruchev) from the underlying Salaca Substage of the Burtnieki Stage (Obruchev and Mark-Kurik, 1965: Figs. 185-189). The plate fragment is 165 mm long and 60 mm wide, rather flat and thin (1-2 mm). It might belong to a comparatively young individual. Along the edges several growth lines can be seen. There is a shallow step between two growth lines at the posterior end of the plate. Such steps are characteristic of the dorsal plates of P. bergi and P. megalopteryx (Obruchev and Mark-Kurik, 1965: pl. 79, fig. 2). The fragment shows an interrupted segment of a sensory line canal (Figure 8a, sc) and further



FIGURE 4 *Psammosteus* sp. (a)-(h), (j), single elements of the exoskeleton. (a) Pi 700/3; (b) 700/7; (c) Pi 700/9; (a)-(c) in lateral view. (d) Pi 700/11 in basal view. (e) Pi 700/10 in lateral view. (f) Pi 700/6 in lateral view, pulp cavity exposed. (g) Pi 700/15 in lateral view. (h) Pi 700/2 in posterolateral view. (j) Pi 700/16 in crown view. *Psammolepis abavica* Mark-Kurik. (i) Tubercle Pi 700/4 in lateral view. Scale bars = 0.1 mm.

anteriorly, a patch of shadowy, very small and shallow depressions left after the detachment of minute "tesserae" from the plate (Figure 8a, dp). Similar but much larger depressions forming a honeycomb pattern are known in *P. bergi* and *P. megalopteryx* (Obruchev and Mark-Kurik, 1965: pl. 44, fig. 2; pl. 79, fig. 2). The depressions in the plate of *Psammosteus* sp. coincide in size with the larger complex elements occurring among the specimens from Essi locality. It is clear that only a psammosteid, such as *Psammosteus*, which is characterized by loss of smaller exoskeletal elements owing to the specific microstructure of the median plates (see above note on the microstructure of *P. megalopteryx*), could yield the complex elements. If mechanically separated from larger plates, these micromeric elements could hardly preserve their individual complete structure. It must be pointed out that all possible transitional types between the complex and single elements occur and the whole set of microelements is considered to belong to *Psammosteus* sp.

Morphology

Being variable in shape and size, and revealing transitional types, the micromeric elements of Psammosteus sp. cannot be grouped easily. Of about 600 elements collected from the sandstone samples, two thirds are single elements that consist of a crown (odontode according to Ørvig, 1977) and a base. The rest of the specimens are complex elements. They comprise a number of crowns (odontodes) situated on a common base. Elements with twin crowns (Figure 5d) or three crowns (Figures 3g, 5c, 6a) predominate. Elements with 4 or 5 crowns are also rather common (Figure 6b-e). Those with a greater number of crowns (up to 26) are less frequent (Figures 5g, 6f-i, 7a-i). The comparative scarcity of these elements is, probably, caused by their structure. The base is often thin and spongy which would have made them more vulnerable. The same is true for such large, but thin psammosteid skeletal elements as the rostral, postorbital and cornual plates which also comprise superficial ornamentation of tubercles and spongy aspidin. These plates are very scarce in collections in comparison with the more massive branchial or ventral plates (see Obruchev and Mark-Kurik, 1965: table 1).

The single elements may be very small, 0.3-0.5 mm high, but they can also reach 1.0 mm in height. In the larger complex elements, forming tiny platelets ("tesserae") or scales, the size range varies from 1.0 to 2.1 mm in length and from 0.8 to 2.5 mm in width.

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Single Elements

The simplest single elements are rounded or elongated and almost lack a base (Figure 3a and b). In these elements the surface of the crown is smooth and slightly convex; the crown sides are ridged. There is an elongated basal pore (Figure 3a: bp) surrounded by a shallow thickening. The latter may bear some swellings (Figure 3b) situated irregularly around a slit-like basal opening.

Rather common are specimens in which both crown and base are well developed. The crown may be flat (Figures 3f and 4g), blunt (Figure 4c, e, f) or sharp-topped to a variable degree (Figures 3c-e, 4a, b, h); and in extreme cases being very long and tapering to a posterior point (Figure 4j). The crowns bear well developed ridges which may be serrated and/or show some spinelets on the posterior face (Figures 3c and 4h). The posterior face of the crown may carry ridges that slightly radiate from the neck (Figure 5b and e). The crown usually rises steeply from the base being somewhat reclined, or it can sweep down (Figure 5b and e).

The neck, if developed, is narrow and may be furrowed. In the latter case, a zigzag furrow distinctly separates the crown from the base (Figures 3c, f, 4a, e, 5e).

As a rule, the crown is dependent than the base, but in the flat-topped specimens they may be almost equal in depth (Figures 3f and 4g). In some rare tiny elements the base consists of a thin stellate platelet. In several specimens (Figure 3c) the base is narrower than the crown. However, frequently it is wider than the crown, conical, and is stellated at the perimeter (Figures 3d, e, 4a, b, g, h, 5b, e). The bottom of the base is slightly concave (Figure 5b), flat (Figures 3c, 4b, f) or convex (Figure 4a and c). The surface of the base may be comparatively smooth or knobby, particularly on the bottom of the base (Figures 4d and 5a). The spongy aspidin base shows several openings which may be rather large and oval (Figures 3d and 4e), or elongate and forming subparallel slits (Figure 3c). The larger basal pores may be connected with the single pulp cavity (Figure 4f).

Histological structure Fourteen single elements were sectioned to study their microstructure. All of them show characters typical for the psammo-steid dentine tubercles (see Gross, 1933; Halstead Tarlo, 1964; Novitskaya, 1965; Figure 8b and c). The roughly parallel dentine tubules (dt) radiate from a spacious pulp cavity (Figures 4f, 8b, c: p). At the surface of the crown the dentine tubules re-branch into finer tubules. In instances where the base is deeper, vascular spaces of aspidones can be seen in cross section (Figure 8c: vs).



FIGURE 5 *Psammosteus* sp. (a) Single element Pi 700/11 in laterobasal view (the same specimen as in Fig. 4(d). (b) Single element Pi 700/14 in posterior view. (c) Complex element in crown view (specimen lost). (d) Complex element Pi 701/2 in laterobasal view. (e) Single element Pi 700/13 in posterior view. (g) Complex element Pi 701/1 in crown view. *Psammolepis abavica* Mark-Kurik. (f) Tubercle Pi 700/1 in crown view. Scale bars = 0.1 mm.

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Complex Elements

As already mentioned, the complex elements comprise two or more crowns joined together by an underlying aspidin base. There are specimens with twin crowns that still exhibit their individual components: namely two single elements with crowns of equal size and two basal pores. Often, however, the fusion of the elements is more complete (Figure 5d). In these twin elements one of the crowns is usually larger and more sharp-topped. In the elements with three crowns (Figures 3g, 5c, 6a) the discreteness of the single elements is even less apparent. An oak-leaf-shaped crown (Figures 5c, g, 6a-g, 7d-g) occurs in which the single elements cannot be clearly distinguished. The rather gently sloping crowns of the oak-leaf shape are perfectly interlocked with one another. Such crowns are frequently constricted in the middle (Figures 6c, 7d-f), and the margins of the "leaves" are finely serrated. One crown is often considerably larger, erect or reclined, and situated at the posterior edge of the element (Figures 5g, 6c, d, 7e).

The spongy base of the complex elements has the same structure as that of the single elements but is, as a rule, shallower. However, variable-shaped openings, including the oval slit-like ones observed in the base of several single elements (Figures 3c, d, 4b), are also visible in the complex elements (Figure 6d and e). The bottom of the base, showing a labyrinth of several openings, is straight (Figure 3g), but may also be slightly concave or convex (Figure 6i). The area occupied by the crowns may be as wide as the base or smaller, leaving a free margin of variable width anteriorly (Figures 5c, 6b, c, h, 7d, e, g-i) or anterolaterally (Figures 6a, e, g, 7a). The complex elements are generally irregular (circular, oval, rhombic or polygonal) thus resembling in shape the psammosteid "tesserae". The elements with a well developed free anterior margin (Figures 6e, g, 7d, h) are rather similar to the small body scales of psammosteids (cf. Mark-Kurik, 1993b, fig. 3).

Several specimens, including two or more crowns of equal size and shape, seem to indicate that the growth of these complex elements might be synchronomorial (Figures 5d, 6a, b, f, i, 7a, f). The complex elements, with one larger crown and several closely packed smaller crowns situated semicircularly or irregularly in front and at the sides of the larger one, show that the growth of the elements was cyclomorial (Figures 5c, 6c-e, g, 7b, d, e, g). In a number of elements (Figures 3g, 7c, h, i) the growth type is not quite clear (it might be synchronomorial). The large crowns, forming primordia in the elements with the cyclomorial growth type, may be considered the equivalents of the common more or less sharp-topped single



FIGURE 6 *Psammosteus* sp. complex elements of the exoskeleton. (a) Pi 696/1; (b) Pi 696/2; (c) Pi 696/3; (a)–(c) in crown view. (d) Pi 696/4 in laterocrown view. (e) Pi 696/5; (f) Pi 697/1; (g) Pi 697/2; (h) Pi 697/3; (e)–(h) in crown view. (i) Pi 697/4 in lateral view. Scale bars = 0.5 mm.



FIGURE 7 *Psammosteus* sp. complex elements of the exoskeleton in crown view. (a) Pi 698/1; (b) Pi 698/2; (c) Pi 698/3; (d) Pi 698/4; (e) Pi 698/5; (f) Pi 699/1; (g) Pi 699/2; (h) Pi 699/3; (i) Pi 699/4. Scale bars = 0.5 mm.



FIGURE 8 *Psammosteus* sp. (a) fragmentary dorsal plate, Pi 704. (b), (c) vertical longitudinal sections of single elements; (b) Pi 702/2; (c) Pi 702/1. Scale bars: for (a) = 10 mm; for (b) and (c) = 0.1 mm. dt – dentine tubules; dp – depressions left after detachment of complex elements or "tesserae"; p – pulp cavity; sc – sensory canal; vs – vascar space.

elements. The single elements with a swept-down crown (Figure 5b and e) can also be recognized in the complex elements showing similar crowns of tubercles (e.g. Figure 6i).

DISCUSSION

Psammosteid skeletal elements, that are comparable to the complex elements in *Psammosteus* sp. from the Middle Devonian of Estonia, are known in the Late Devonian species, *Psammosteus falcatus* Gross (Obruchev and Mark-Kurik, 1965: pl. 89, figs. 1–3; Halstead Tarlo, 1965, fig. 44C and D). These elements, usually described as isolated "tesserae", consist of a very large, high-crowned and complicated tubercle surrounded by much smaller and simpler tubercles. The "tesserae" exceed in size the complex elements, being 4 mm high and 3.5–4.5 mm in diameter. Still, the main difference between the "tesserae" and complex elements lies in

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their structure rather than in their measurements. The "tesserae" of P. falcatus show the typical cyclomorial growth that started around the central tubercle. The same type of growth is well known in "tesserae" of the Late Devonian Psammosteus cf. P. maeandrinus Agassiz (Obruchev and Mark-Kurik, 1965: pl. 70, fig. 1) and P. megalopteryx (Halstead Tarlo, 1964: pl. 1, figs. 2 and 5). In both species the central round tubercles are of the same size, or slightly larger than the surrounding concentrically placed oval or kidney-shaped tubercles. A larger primordial, sharp-topped tubercle occurs frequently in the complex elements of Psammosteus sp. It is, however, not situated in the centre of the element or somewhat eccentrically (e.g. as in *P. megalopteryx*), but at its posterior margin. Thus, the complex elements of *Psammosteus* sp. described here differ in their growth type from the "tessera" of the other species of the genus. Moreover, its simpler complex elements underwent synchronomorial growth. In the single elements the base might become deeper during growth. The micromeric elements of Psammosteus, particularly the single ones, occupied the external surface of the meso- and macromeric plates, being slightly connected with them. In addition these elements might have also developed in the skin between larger plates and/or in the posterior part of the body and tail.

The shape and structure of the single elements resemble the scales of turiniid thelodonts (see Karatajūtė-Talimaa, 1978; Turner and Dring, 1981; Turner *et al.*, 1981; Turner, 1991; Turner and Young, 1992). They also show some similarity in shape to scales of the chondrichthyans (Ørvig, 1966; Zangerl, 1981; Mader, 1986; Turner, 1993). This resemblance seems to indicate that psammosteid elements may have served the function of scales. However, the microstructure of the elements is different from that of the scales of thelodonts and chondrichthyans and excludes the attribution of them to the representatives of these groups.

The genus *Psammosteus* is characterized by loss of its "tesserae" that probably took place prior to burial. As a result, a honeycomb pattern was left on the external surface of the spongy aspidin plates. According to Halstead Tarlo (1964), the growth and remodelling of the psammosteid plates occurred above and in the more superficial part of the middle layer, immediately below the dentine tubercles. It seems that in *Psammosteus* the resorption and regrowth proceeded in a rather different way to that in other psammosteids, e.g. *Psammolepis*. In the latter the tubercles are very firmly attached to the meso- and macromeric plates, though, undoubtedly, remodelling also took place in their rather thick exoskeletal elements.

The difference in the structure of the exoskeleton seems to contradict a close relationship between *Psammolepis* and *Psammosteus* as proposed

by Halstead Tarlo (1964). This controversy is mentioned by Mark-Kurik (1993b) who took into consideration the differences in the squamation of these psammosteids. The micromeric elements of *Psammosteus* sp. that vary in growth types permit the assumption that they were primary rather than secondary. The latter possibility was expressed by Blieck (1984; Blieck *et al.*, 1991). However, even in very young psammosteid individuals, e.g. *Drepanaspis* (Gross, 1963), it is posible the skin between the larger exoskeletal plates could produce micromeric elements. Based on the similarity of the plate pattern of pteraspids to juvenile psammosteids lacking "tesserae" and the secondary nature of psammosteid "tesserae" it has been suggested that psammosteids were derived from pteraspids (Janvier and Blieck, 1993; Janvier, 1996). However this proposal seems to be open to question.

Janvier and Blieck (1993) defined a tessera as a small, free bony element without any area of overlap, and considered the interstitial "tesserae" or platelets of the psammosteids as quite different skeletal elements. In the present paper a neutral terminology for various microremains of *Psammosteus* sp. has intentionally been used as they cannot be easily classified. Single elements resembling thelodont and chondrichthyan microremains ought to be called scales; basic complex elements with or without a narrow overlap area seem to coincide in their structure with the real tesserae of primitive heterostracans (Dineley and Loeffler, 1976; Elliott and Loeffler, 1989; Elliott *et al.*, 1991: fig. 3A), while larger and more complicated elements could represent a special kind of psammosteid "tesserae" or platelets and scales. Actually, all these elements belong to the same set of skin derivatives of *Psammosteus* sp.

Evidence for the potential of psammosteid skin to produce both single and complex elements is seen in the secondary tubercles or "blisters" formed under pathological conditions. The "blisters" comprise both isolated tubercles and groups containing smaller or larger numbers of tubercles (Heintz, 1957: pl. 19, figs. 2–6; Obruchev and Mark-Kurik, 1965: pl. 51, fig. 1; Mark-Kurik, 1966: pl. 1, figs. 2 and 3; Ørvig, 1976: figs. 14–16; Ørvig, 1977, fig. 2A).

Thus, several problems concerning growth, relationships and terminology of psammosteids require further discussion.

CONCLUSION

(1) Psammosteids, particularly, the representatives of the genus *Psammosteus* have micromeric skeletal elements, resembling in several cases the lodont or chondrichthyan scales.

- (2) Samples are dominated by single elements; complex elements are less numerous owing to their more delicate structure. Single elements consist of a crown (odontode) and a base. Complex elements show 2-3 crowns (odontodes), with less frequently 4 5 or more crowns situated on a common basal plate.
- (3) The growth of the complex elements was probably both synchronomorial and cyclomorial. Several tensely interlocked crowns of almost uniform size and shape situated on a basal plate provide evidence of synchronomorial growth. In the case of cyclomorial growth the elements exhibit a crown at the posterior edge of the element up to double the normal size, and a number of smaller crowns either arranged in a fan-shaped manner or without a definite pattern in front of and beside the large one.
- (4) In the genus *Psammosteus*, the structure, growth and remodelling of the exoskeletal elements differ from those in all other psammosteids in that its representatives possess numerous and variable micromeric elements which were only slightly connected with their mesomeric (?) and macromeric elements. The tubercles or ornamental ridges of the branchial plates are an exception. The result is that the medial plates, in particular the dorsal and ventral plates, generally lack any ornamentation. They show nothing but polygonal traces of platelets or "tesserae" on the rough external surface of the middle spongy layer of the plates. The platelets were detached from the larger skeletal plates before burial.
- (5) Evidently, both single and complex micromeric elements of *Psammosteus* were confined not only to the larger exoskeletal plates forming "tesserae", but they could also occupy the surface of the area between meso- and macromeric skeletal elements. They might have also fulfilled the function of scales in the posterior part of the body and tail.
- (6) The loss of platelets seems to be specific to the genus *Psammosteus* and probably depends upon the remodelling on the top of the middle spongy aspidin layer of the carapace. Therefore, it is difficult to support the view that *Psammosteus* is derived from a psammosteid such as *Psammolepis* in which the ornamental tubercles are firmly attached to their meso- and macromeric skeletal elements before and after burial.
- (7) Discovery of micromeric exoskeletal elements in psammosteid heterostracans supposes that, even in very young individuals, independent minute elements could form in the skin between macromeric elements. Consequently the area between the larger elements was not necessarily devoid of an exoskeleton. The derivation of psammosteids from pteraspids and the secondary nature of psammosteid "tesserae" are concepts that remain equivocal.

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