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Exoskeleton Structure and the Distribution of *Aestiaspis viitaensis* (Agnatha) from the Silurian of Estonia

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Abstract—The exoskeleton of one of the earliest osteostracans, *Aestiaspis viitaensis* Janvier et Lelievre, 1994, from the Silurian of Saaremaa Island (Estonia) was studied using a scanning electron microscope. On the basis of the study of exoskeleton fragments by dissolving samples from different sites and their comparison with the holotype exoskeleton, it is concluded that the members of the genus *Aestiaspis* are distributed in the Viita and Vesiku Beds and, probably, Kuusnymme Beds all of the Rootsiküla Regional Stage and the Himmiste Beds of the Paadla Regional Stage.

INTRODUCTION

Estonian osteostracans (suborder Trematapidoidei), along with *Ateleaspis*-like osteostracans are the earliest known representatives of this agnathan group. Exoskeleton structure in *Trematapis*-like forms including the microstructure constantly attracts specialists attention and consequently is now rather well known (Denison, 1947, 1951; Gross, 1961, 1968; Afanassieva, 1985, 1986, 1991, 1995).

The object of this research was a recently described osteostracan *Aestiaspis viitaensis* Janvier, Leliévre, 1994 belonging to the Trematapididae occuring in the Rootsiküla Regional Stage deposits on Saaremaa Island. This is a small form; and its exoskeleton is known only in general features (Janvier and Leliévre, 1994; Afanassieva, 1996).

MATERIAL

This paper provides a detailed description of the holotype (no. Pi 7279, Institute of Geology, Tallinn) cephalothoracic shield ornament observed visually, as well as a fragment of the holotype exoskeleton and specimen PIN, no. 3257/607b consisting of fragments (Paleontological Institute of RAS, Moscow), studied using a scanning electron microscope (SEM).

The *Aestiaspis viitaensis* holotype was found by H. Leliévre close to the village of Viita in the middle part of the trench section referred to the Viita Beds of the Rootsiküla Regional Stage (Märss, 1990). The specimen PIN, no. 3257/607 presumably also came from the Viita or the Vesiku Beds of the same regional stage (Afanassieva, 1996).

Microremains (exoskeleton fragments) from different Silurian beds of Saaremaa Island were extracted by chemical preparation and studied using the SEM technique, all the material being collected and chemically processed by one of us (T.M). Scales similar in their ornamentation pattern to *Aestiaspis viitaensis* were found in the Viita, Kuusnymme and the Vesiku Beds of the Rootsiküla Regional Stage and in the Himmiste Beds of the Paadla Regional Stage (Fig. 3).

Viita Beds:

The type locality (Viita trench) yielded the trunk scales nos. Pi 7371 and Pi 7372, in which the sculpture is similar to that of *Aestiaspis viitaensis*. The trunk scale no. Pi 7373 came from the Vesiku 507 borehole drillcore (depth 8.65–8.80 m).

Kuusnymme Beds:

Trunk scales from the Elda Cliff, specimens Pi, nos. 7398–7406, 7408–7409.

Vesiku Beds:

Trunk scales from Vesiku Creek, specimens Pi, nos. 7376–7381.

Himmiste Beds:

Trunk scales from the Silma Cliff, specimens Pi, nos. 7374–7375 and from the Kuressaare (formerly Kingisepp) borehole drillcore, specimen Pi, nos. 7410–7412.

DISCUSSION

The surfaces of the dorsal and ventral shields in *Aestiaspis viitaensis* (Figs. 1, 2) bear narrow longitudinal ridges (crests) along the fused scales (tesserae). The crests vary in length and width and frequently widen slightly in the posterior part of each scale. Two types of crests are described on the cephalothoracic shield: the type includes large swollen crests situated lengthwise of the dorsomedial ridges and two pairs of lateral dorsal crests in addition to crests along the lateral fields; and the second type of crest consists of merged small and narrow crests which fill in the space between the ridges and sometimes bifurcate (Pl. 5, figs. 1–3). The ventral

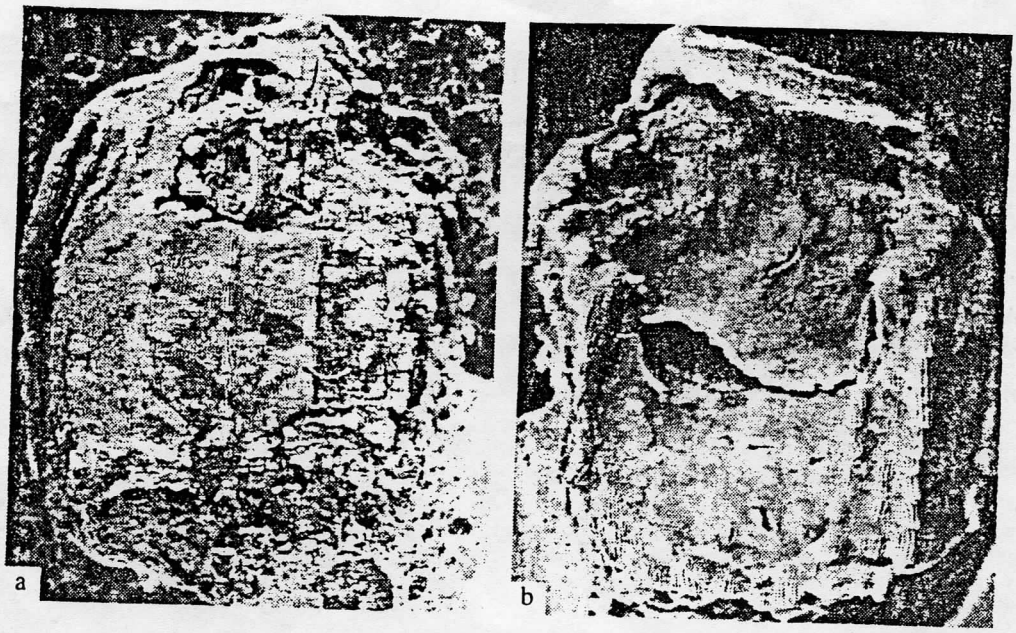


Fig. 1. *Aestiaspis viitaensis* Janvier et Leliévre, 1994, holotype no. Pi 7279; Institute of Geology of Estonia; Estonia, Saaremaa Island, Silurian, Upper Wenlockian, Viita Beds of the Rootsiküla Regional Stage; (a) cephalothoracic shield dorsally, (b) cephalothoracic shield ventrally; (a) and (b) ×6.

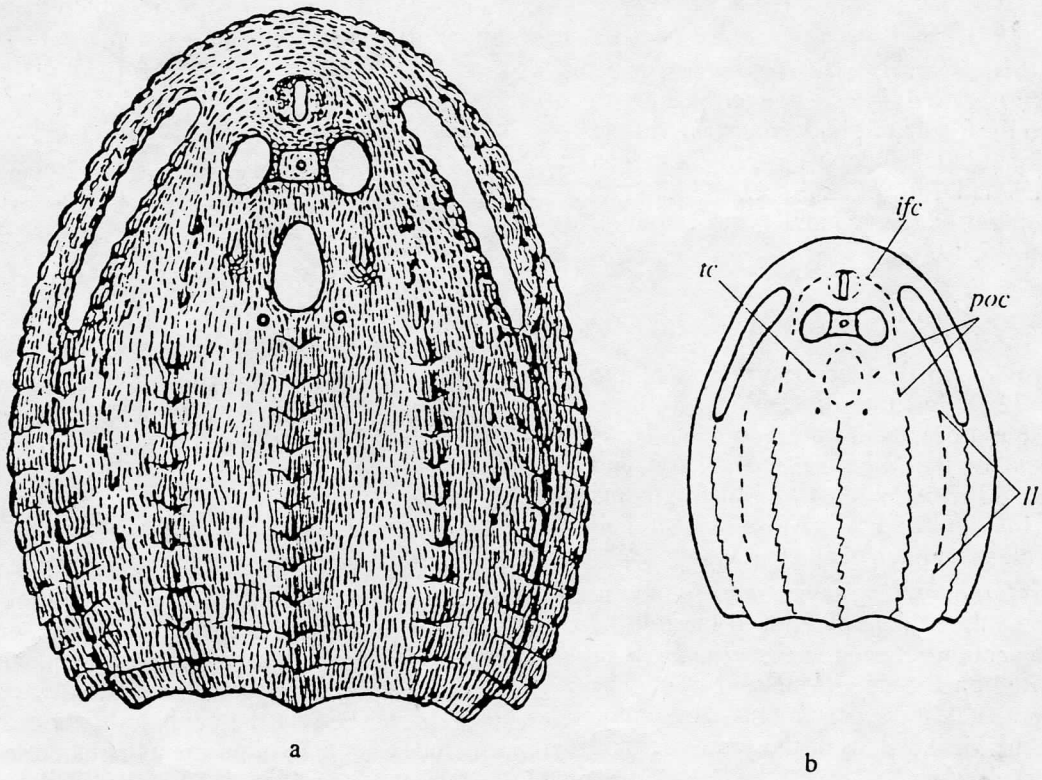
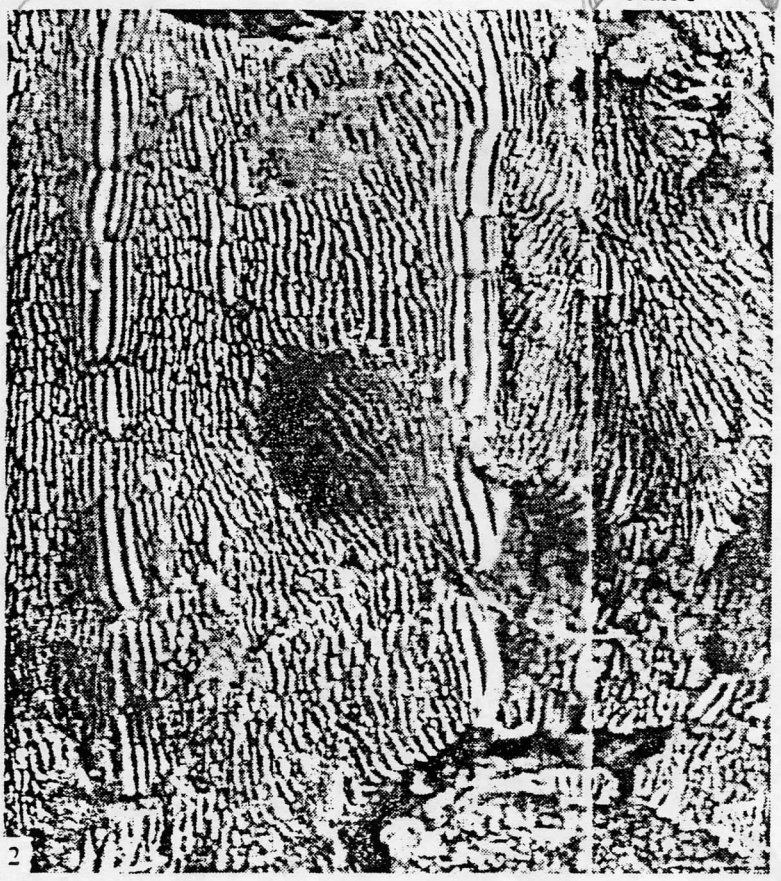


Fig. 2. *Aestiaspis viitaensis* Janvier et Leliévre, 1994; (a) a reconstruction of the dorsal side of the shield ornament, ×8; (b) major sensory line canals distribution pattern. *ll*—main lateral, *ifc*—infraorbital, *poc*—postorbital, *tc*—transversal.

Plate 5

1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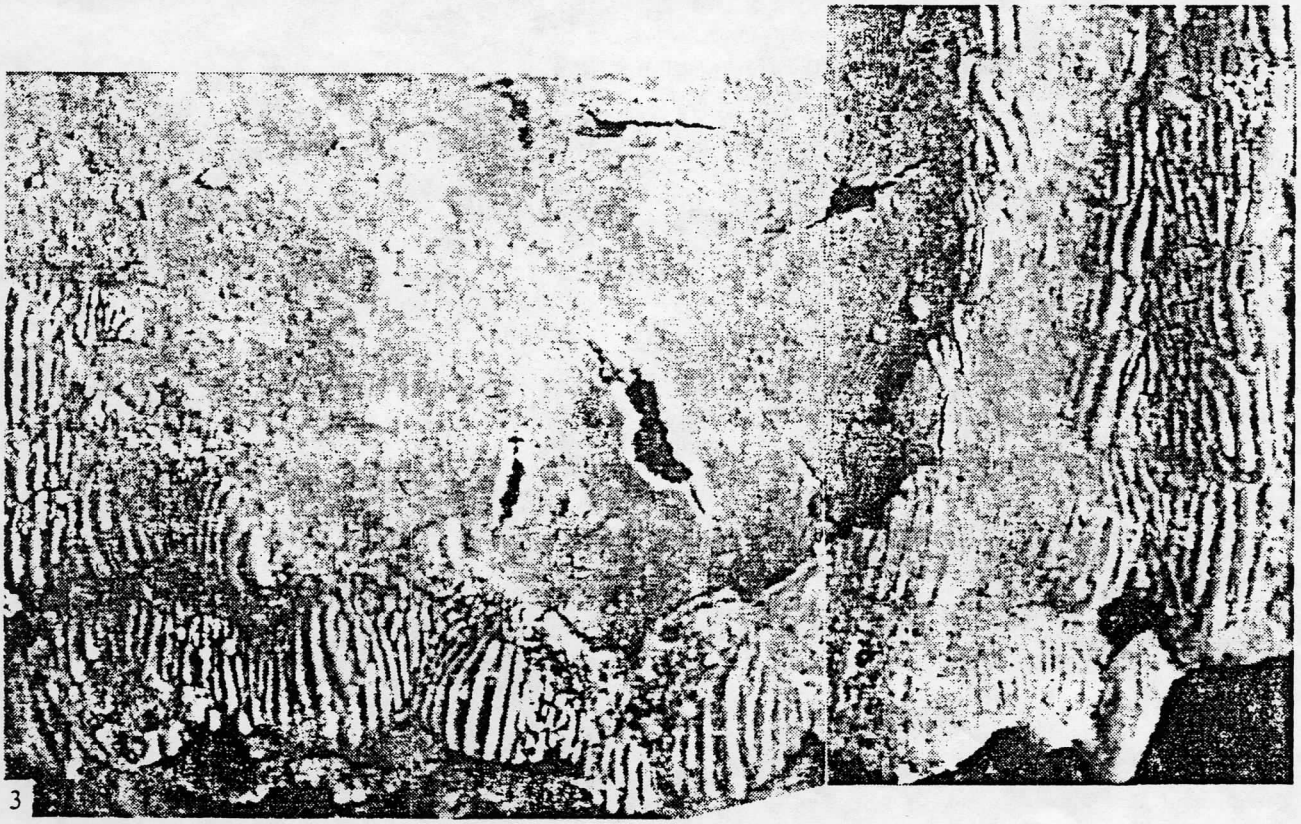
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Silurian	Ludlovian	Pnadla Regional Stage	Uduvere Beds	–
			Himmiste Beds	Silma Cliff Silma coast Kuressaare (Kingisepp) borehole
			Sauvere Beds	–
	Wenlockian	Rootsiküla Regional Stage	Soeginina Beds	–
			Vesiku Beds	Vesiku Creek
			Kuusnymme Beds	Elda Cliff
			Viita Beds	Viita trench Vesiku borehole

Fig. 3. The stratigraphic distribution of *Aestiaspis osteostracan* remains in the Silurian of Saaremaa Island.

side of the shield demonstrates a smooth transition between these two crest types.

In *Aestiaspis viitaensis* the exoskeleton is well developed at the whole cephalothoracic shield surface and is basically composed of the bony tissue of the middle (spongy) and basal (laminar) layers. The superficial layer is possibly present only in the distal parts of the crests and is especially swollen. Enameloid tissue may be observed in the marginal flattened denticles and possibly on the surface of the large shiny crests and swollen distal parts of the interbranchial septa ("interbranchial knobs": Janvier and Leliévre, 1994).

As noted above, in *Aestiaspis viitaensis* the dorsal and ventral parts of the shield are similar in structure. Exoskeletal fragments of the ventral shield (specimen PIN, no. 3257/607b) preserved in the counterpart were studied by SEM.

The ventral side of the shield exoskeleton is well expressed and is composed of fused scales arranged in longitudinal rows. Separate scales are clearly visible in the specimen investigated using a SEM, since in numerous places the exoskeleton cracked along the middle layer. The size of the scales is approximately 0.5 × 0.5 mm. The exoskeleton is basically composed of a comparatively dense bony tissue, penetrated by canals and cavities. The shield edge bears a row of small (about 0.25 mm long) flattened denticles, similar to those of *Thyestes verrucosus* (Afanassieva, 1991, pl. 11, fig. 3). As in this species, they are obliquely striated (Pl. 6, fig. 1). Variously sized cavities (sometimes large) are present at the bases of the denticles in *Aestiaspis* and *Thyestes*, which may include the cutaneous soft tissues.

The exoskeleton cracked surface shows canals and cavities situated below the crests and between them (Pl. 6, fig. 2). The canal diameter is about 20 μm and in the cavities it reaches 30 μm. A radial pattern was not noted in the distribution of the canals similar to some other Trematraspididae: *Trematraspis*, *Saaremaaspis*, and, probably, *Timanaspis*. The canals and cavities are more numerous between the crests and less abundant directly below them. The walls of the canals are dense and the bony cell lacunae are quite rare.

The perforated septa are described here in *Aestiaspis viitaensis* for the first time. These structures are typical for the major part of the members of the Trematraspidoidei suborder (*Trematraspis*, *Dartmuthia*, *Saaremaaspis*, *Oeselaspis*, *Procephalaspis*, *Thyestes*). It should be noted that as far as we know the exoskeleton microstructure in *Sclerodus* and *Tyriaspis* was never investigated and in *Witaaspis* similar structures were not found (Afanassieva, 1991). Their absence in *Witaaspis* is probably due to incomplete exoskeleton development in this form (cephalothoracic shield is composed only from a part of the middle and basal layers). The caps (septa) closing the foramina of the vascular canals in *Aestiaspis viitaensis* appear as pore zones (Pl. 6, fig. 3), their diameter being 10–20 μm. They are so closely spaced in the central part of the ventral division of the ventral shield, that they fuse in places to form a perforated horizontal septum (Pl. 6, fig. 4) similar to that of *Trematraspis* and *Dartmuthia*. However, in contrast to *Trematraspis* (Afanassieva, 1991, pl. 2, figs. 4–5), in *Aestiaspis* this septum is not continuous and most of its microforamina are grouped as isolated pore fields. The diameter of the microforamina in the septum is 1–3 μm, that is slightly less than in other trematraspidids. This probably results from the smaller size of *Aestiaspis viitaensis*.

A well developed canal system of the middle layer communicates through the perforated septa with the grooves located between the crests at the exoskeletal surface. Thus, taking into account the distribution of these canals in relation to the perforated septa and the shield surface it is possible to conclude that the former contained the lower vascular plexus (Stensiö, 1932; Denison, 1947, 1951; Gross, 1961). The sensory (mucous according to Stensiö, 1932) system canals are likely to be situated in the grooves between the crests.

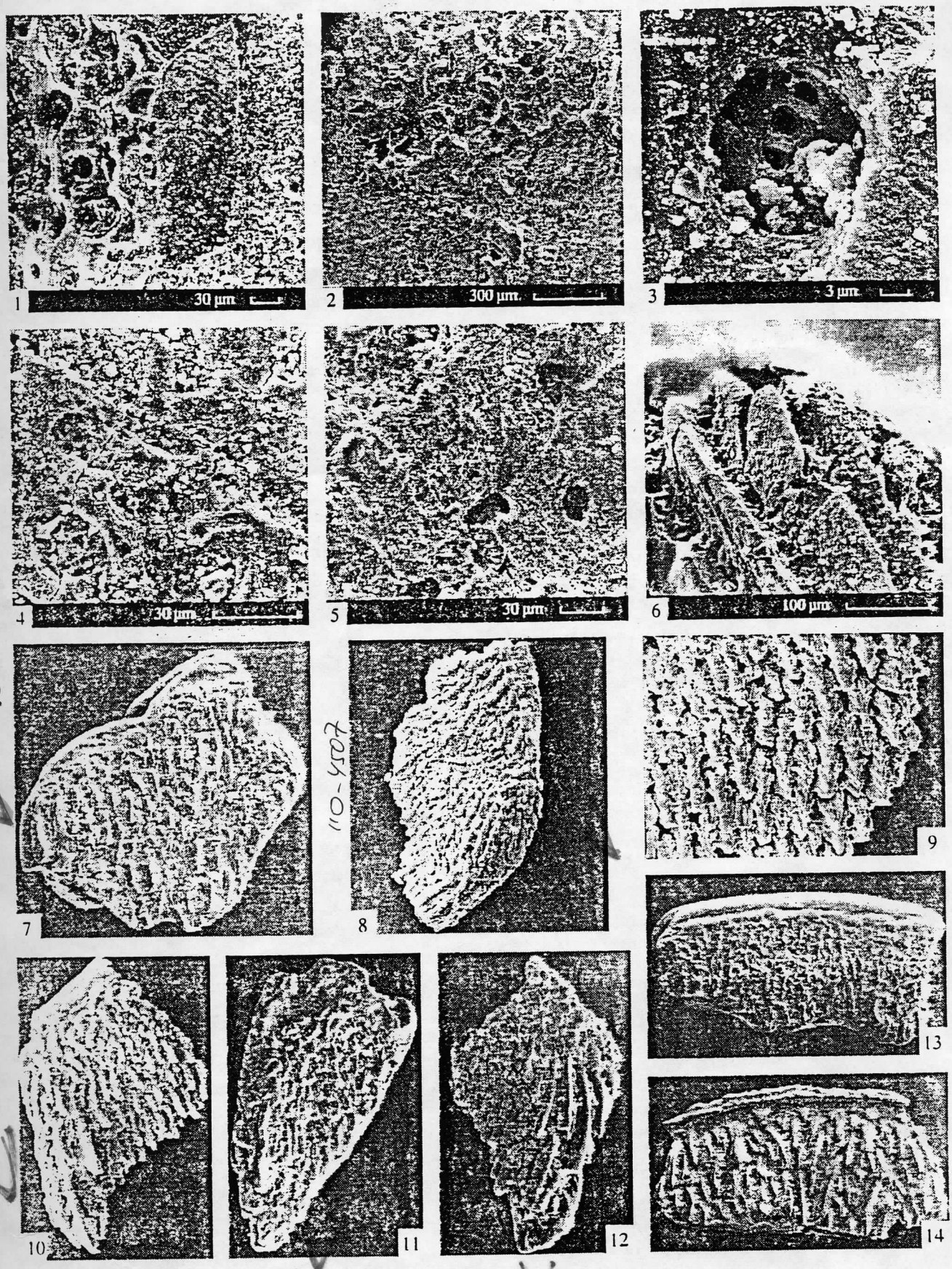
Explanation of Plate 5

Aestiaspis viitaensis Janvier et Leliévre, 1994. Holotype no. Pi 7279, Institute of Geology of Estonia; Estonia, Saaremaa Island, Silurian, Upper Wenlockian, Viita Beds of the Rootsiküla Regional Stage.

Figs. 1 and 2. Dorsal surface of the cephalothoracic shield sculpture, postcephalic division: (1) ×30, (2) ×28. *T*—dorsal ridge tubercle; *t*—a tubercle situated along the sensory canal.

Fig. 3. Ventral surface of the cephalothoracic shield sculpture, posterolateral part of the ventral division, ×31.

Plate 6



1 2 3 4 5 6 7 8 9 10 11 12 13 14

The basal layer is well developed and has a typical structure in being rather dense, in some places penetrated by canals, and rarely having cavities, or basal chambers (Pl. 6, fig. 5).

Unfortunately, preservation of the holotype exoskeleton after acid treatment (Janvier and Leliévre, 1994) was poor and unsuitable for delicate SEM research. Nevertheless, an oblique striation at the surface of the large crests over the holotype fragment (a scale from posterior edge of the ventral division) was readily observable (Pl. 6, fig. 6). In our view, a similar striation suggests that the hardest hypermineralized layer, the enameloid, could be present on the surface of the large crests, the upper part of which is composed of compact dentinoid tissue. The surface between the crests is very much destroyed. However, in some areas there are foramina through which apparently the external canals communicated with those of the lower vascular plexus.

In our opinion, the arrangement of the main sensory lines in the exoskeleton of *Aestiaspis viitaensis* is marked by large tubercles, disposed in rows along the sensory canals (Pl. 5, t). These tubercles, each associated with a separate scale, bear well developed swollen crests separating wide grooves. The main structure of the sensory canals and distribution pattern, marked by such tubercles, are characteristic of this osteostracan group. It is possible to identify the infraorbital (ifc), postorbital (poc), main lateral (ll), and, probably, transversal (tc) sensory line canals on the holotype (Fig. 2b).

As noted by Janvier and Leliévre (1994), the ornamentation pattern of *Aestiaspis viitaensis* only seldom occurs in the osteostracans. Similar sculpture is known in *Timanaspis kossovoii* Obruchev and probably in *Ilemoraspis kirkinskayae* Obruchev. Besides this, small crests on the *Aestiaspis* shield surface may be similar to those over the tubercle surface of *Thyestes verrucosus*, although not over the large tubercles, as indicated by Janvier and Leliévre (1994, p. 123) but over the small tubercles. This condition is essential, since in our point of view relatively large "crests", situated around large tubercles in *Thyestes verrucosus* are homologous to those in *Dartmuthia gemmifera* (or in other trematapid osteostracans possessing radial canals in their exoskeleton) and housed the radial canals in the middle layer. Similar "crests" are found only in some *Thyestes verrucosus* specimens in which the armor growth in our opinion was not completed. At the same time the narrow crests on the small tubercles of *Thyestes*, as well as the narrow crests of *Aestiaspis* are present in all the studied specimens, i.e., they are a typical ornamentation element in these genera.

The topographical variability of the osteostracan trunk scales is practically unknown since complete specimens of these agnathans are only rarely found. In the suborder Trematapidoidei only a partially preserved *Trematapis schmidti* Rohon, 1892 trunk skeleton (Märss, 1986) and trunk exoskeleton fragments of some other osteostracans (Janvier, 1985) are described. As no special classification for the osteostracan scales exists, the terminology accepted in the scale descriptions of other lower vertebrates is used here.

Unfortunately, in this short paper it is not possible to illustrate all the studied scales. Only the exoskeleton fragments (Pl. 6, figs. 7–14) possessing in our opinion the most characteristic type of sculpture for each layer are selected here.

The most interesting scales for comparison came from the Viita type locality.

The scale Pi 7372 (Pl. 6, fig. 7) is tessera-shaped and could probably be situated in the caudal part of the trunk. The overlapping area is short and smooth. The non-overlapping zone bears rather short, slightly winding crests.

The scale Pi 7371 is asymmetric and subtriangular-shaped; it possibly came from the marginal trunk areas (rigidity fins). A relatively large overlapping surface is found anteriorly. The posterior scale edge is serrated. It is covered by rather short, slightly winding crests. Narrow crests are well marked over the ridges. The

Explanation of Plate 6

Figs. 1–6. *Aestiaspis viitaensis* Janvier et Leliévre, 1994: (1–5) specimen PIN, no. 3257/607b; Estonia, Saaremaa Island; Silurian, Upper Wenlockian, Viita or Vesiku Beds of the Rootsiküla Regional Stage: (1) a flattened denticle from the edge of the cephalothoracic shield (the upper part of the denticle is broken off), (2) canals and cavities of the middle and basal layers of the ventral side of the shield exoskeleton, (3) perforated septum, same location, (4) a group of perforated septa, same location, (5) basal layer of an exoskeleton, same location; (2–5) viewed from the internal side of the exoskeleton, (6) holotype no. Pi 7279, a scale fragment from the posterolateral shield edge.

Fig. 7. *Aestiaspis viitaensis* Janvier et Leliévre, 1994: the trunk scale Pi 7372; Estonia, Saaremaa Island; Silurian, Upper Wenlockian, Viita Beds of the Rootsiküla Regional Stage; ×38.

Figs. 8–10. *?Aestiaspis viitaensis* Janvier et Leliévre, 1994: the trunk scale; Estonia, Saaremaa Island; Silurian, Upper Wenlockian, Kuusnymme Beds of the Rootsiküla Regional Stage; (8) specimen Pi, no. 7399, ×30, (9) specimen Pi, no. 7401, sculpture fragment, ×88, (10) specimen Pi, no. 7398, ×17.

Figs. 11–13. *?Aestiaspis viitaensis* Janvier et Leliévre, 1994: the trunk scale; Estonia, Saaremaa Island; Silurian, Upper Wenlockian, Vesiku Beds of the Rootsiküla Regional Stage; (11) specimen Pi, no. 7379, ×32, (12) specimen Pi, no. 7381, ×32, (13) specimen Pi, no. 7380, ×28.

Fig. 14. *?Aestiaspis* sp., trunk scale; Estonia, Saaremaa Island; Silurian, Lower Ludlovian, Himmiste Beds of the Paadla Regional Stage; specimen Pi, no. 7374, ×25.

right scale margin demonstrates two comparatively large ridges.

The scale Pi 7373 from the Vesiku borehole drillcore (correlated to the Viita Beds) differs from the scales described above and that of the holotype by its ornament (tubercles possessing a wide base) and may probably be referred to another (? new) osteostracan species.

A significant number of the studied scales (more than 10) came from the Kuusnõmme Beds of the Elda Cliff. The fragments of deep and short trunk scales with short overlapping surfaces (specimen Pi, nos. 7400, 7405, 7406 and probably 7403) were found here. These scales are covered by narrow comparatively short crests, infrequent long and swollen ridges being situated between them. There are also asymmetric (marginal) scales with well expressed overlapping surfaces and swollen crests on the left and right edges (Pl. 6, fig. 10: specimen Pi, no. 7398). Tessera-shaped scales (specimen Pi, no. 7401) are also found, that were possibly situated in the caudal region. It should be noted, that in all studied scales from these beds the ridges are peculiarly crested to different degrees (Pl. 6, fig. 9).

Three previously mentioned types of scales are found in the Vesiku Beds: deep and short trunk scales (scale fragment Pi 7380), asymmetric from the marginal areas (Pl. 6, figs. 11, 12: Pi 7379, 7381 and probably scale fragments Pi 7377 and 7378) and tessera-shaped from the caudal region (possibly a fragment Pi 7376). It is worth pointing to the scale sculpture similarity from the Viita type locality (Pi 7372: Pl. 6, fig. 7) and the Vesiku Beds (Pi 7380: Pl. 6, fig. 13): both scales are covered by short, slightly winding crests. A thin crest ribbing is characteristic of the other scales.

The trunk scale fragment Pi 7374 ornament (Pl. 6, fig. 14) from the Silma Cliff (Himmiste Beds) differs from that of the scales from the beds mentioned above by larger and infrequent winding crests. A delicate crest ribbing is not distinctive, but the scale is worn and the exoskeleton surface preservation makes impossible a description of minute structures. Ridge sculpturing in scale fragment Pi 7375, from the same locality, is much better preserved. Thin short crest striations are well expressed, the crests themselves being similar to the tubercles. By their shape, size, arrangement and density they are similar to those of the scale Pi 7374. The scale fragments from the Kuressaare borehole (specimen Pi, nos. 7410, 7411) differ significantly from those described above by larger and more infrequent crests. Thus, the scales from the Himmiste Beds definitely differ from the scales from other beds and in our opinion may be assigned to a new osteostracan genus.

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