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The exoskeleton of *Ungulaspis* and *Ateleaspis* (Osteostraci, Agnatha) from the Lower Devonian of Severnaya Zemlya, Russia

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ABSTRACT:

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The fragments of osteostracan exoskeleton from the Lower Devonian Severnaya Zemlya Formation of the Severnaya Zemlya archipelago, viz., *Ungulaspis arctoa* AFANASSIEVA & KARATAJŪTE-TALIMAA, 1998 and *Ateleaspis* sp., were studied. The structure of the exoskeleton of non-trematapsid osteostracans was investigated by SEM for the first time. A reconstruction of the structure of the *Ungulaspis arctoa* exoskeleton is suggested. Because of the poorer preservation of the *Ateleaspis* sp., only preliminary observations on the thin structure of its exoskeleton could be made. The forms under investigation are characterized by a similar type of sculpture on the surface of the shield (small tubercles) and on the body scales (thin crests). Some similarities in the structure of their shield exoskeleton (the presence of distinctly expressed tesserae, the presence of radiating canals, the probable absence of perforated septa and pore fields) were indicated. *Ungulaspis arctoa* is remarkable in the possessing macromorphological features typical of both the *Ateleaspis*- and *Scolenaspis*-like osteostracans. This similarity in the structure of exoskeleton of the investigated forms provides additional evidence in support of the affinity of these groups of osteostracans and their possible origin from common ancestors.

Key words: Osteostraci, Agnatha, Lower Devonian, Severnaya Zemlya.

INTRODUCTION

The presence of osteostracans in the Paleozoic fauna of the Severnaya Zemlya Archipelago was discovered more then twenty years ago during the expeditions (KARATAJŪTE-TALIMAA, *pers. comm.*). However, the first descriptions were made only recently (MARK-KURIK & JANVIER 1995, AFANASSIEVA 1998, AFANASSIEVA & KARATAJŪTE-TALIMAA 1998). The osteostracan material from Severnaya Zemlya comprises complete shields and parts of shields, as well as microfragments of the exoskeleton, which were extracted from the rock matrix by acid treatment. The characters of the exoskeleton can be used for taxonomic purposes (AFANASSIEVA 1995) and are necessary for the identification of fragmentary material.

MATERIAL AND METHODS

Ungulaspis arctoa and *Ateleaspis* sp. described by AFANASSIEVA and KARATAJŪTE-TALIMAA (1998), come from the upper part of the Severnaya Zemlya Formation of the Lower Devonian of October Revolution Island. The microfragments of

their exoskeleton, obtained by mechanical preparation of specimens, have been examined with an optical microscope and under SEM. The holotype of *Ungulaspis arctoa* is represented by the counterpart of the cephalic shield and by part of the body with fragments of the exo- and endoskeleton; the specimen of *Ateleaspis* sp. is represented by a fragment of the counterpart of the cephalic shield with a few fragments of the exoskeleton. The surfaces of their shields are not accessible for direct observation, but the exoskeleton itself can be seen from inside. The sculpture can therefore be studied only on fragments of the exoskeleton extracted from the matrix. Furthermore, the imprints of the tubercles of the shields and trunks commonly be seen under oblique illumination. The microfragments belonging to the holotype of *Ungulaspis arctoa* were taken from the anterolateral and marginal parts of the dorsal shield and from the trunk segments. The scarce microfragments of the exoskeleton of *Ateleaspis* were taken only from the lateral edge in the proximal part of the pectoral fin.

Material described in this paper is housed in the Institute of Geology of Lithuania in Vilnius (abbreviated GIL) and in the Paleontological Institute of the Russian Academy of Sciences in Moscow (PIN).

DESCRIPTION AND DISCUSSION

Study of the cephalic shield of *Ungulaspis arctoa* under the optical microscope showed that its surface in the anterolateral parts was covered with small rounded and elongate tubercles (Text-fig. 1a). The shape of the tubercles changes to be more elongated in the direction of the body. Long and thin tubercles fusing into longitudinal ridges are located on the body scales (Text-fig. 1b). In the exoskeleton of the shield, tesserae (2.5-3 mm) can be distinctly seen, among which there are spaces for the circumareal canals (*sensu* GROSS 1961) of the sensory system. Radiating canals are preserved in some parts of the shield. In the lower parts of the exoskeleton there are some cavities and canals which can be interpreted as the basal cavities and ascending canals of the vascular system respectively.

SEM studies of the fragments of *Ungulaspis arctoa* exoskeleton from the anterolateral parts of the shield demonstrated that the tubercles have a ribbing on their surfaces (Pl. 1, Fig. 1). The upper part of the tubercles is made up of dense tissue, only in places pierced by tubules. The tissue of this type forms the main part of some tubercles, it is superficial to the vascular canals and can be identified as "a

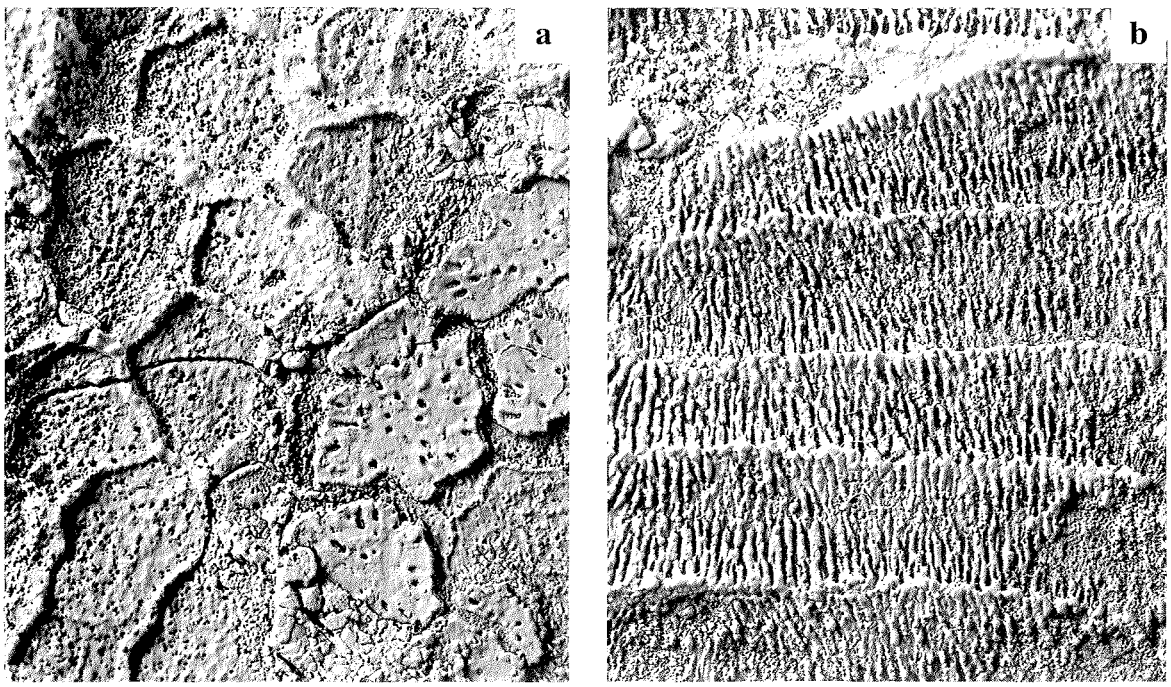

Fig. 1 – *Ungulaspis arctoa* AFANASSIEVA & KARATAJŪTE-TALIMAA, holotype GIL 35-670, Severnaya Zemlya Formation (Lochkovian), Lower Devonian, Severnaya Zemlya Archipelago, Russia; a – counterpart of cephalic shield with fragments of exoskeleton, × 9; b – counterpart of trunk with fragments of body scales, × 7 (a, b – view from the inner side of exoskeleton)

modified osteo-dentine" (DENISON 1951, p. 211) of the superficial layer. The lower part of the tubercle consists of a relatively loose bony tissue, in which the cavities of osteocytes can be recognized (Pl. 1, Fig. 3). In broken surfaces of the exoskeleton it is possible to see relatively large cavities at the base of the tubercles (Pl. 1, Fig. 2). The tubercles are connected by bony tissue of the middle (spongy) layer (Pl. 1, Figs 2, 4). It has a large number of canals, 10-25 μm in diameter, which can be interpreted as the vascular canals, that are typical of osteostracans. The apertures of these canals are situated between the tubercles (Pl. 1, Fig. 1). No traces of perforated septa or pore fields were discovered. The spongy tissue of the middle layer gradually passes down into basal layer (Pl. 1, Fig. 2) with characteristic cross-laminated structure. Only the upper part of this layer is preserved in the exoskeleton fragments under study, but it is well developed in the tesserae of the cephalic shield.

A row of shiny elongate tubercles is found along the anterior and lateral edges of the cephalic shield of *Ungulaspis arctoa*. They are rather large, ca. 1 mm in length. Unlike the flattened marginal tubercles of some osteostracans (e.g. *Thyestes verrucosus* EICHWALD), they are strongly convex in *Ungulaspis arctoa*. In broken tubercles the inner structure is clearly seen (Pl. 1, Figs 4-5). A large number of canals and cavities of different sizes pierce the middle and, especially the lower parts of the tubercle, which are composed of bony tissue. In the upper and upper-lateral parts of the tubercle this tissue gradually turns into a mesodentine, typical of osteostracans (Pl. 1, Fig. 5). On the side surfaces of the tubercles there are thin parallel ribs (Pl. 1, Figs 4, 6).

A small fragment of body scale from the anterior part of the *Ungulaspis* trunk has also been studied. On the body scale the tubercles fuse, in some cases forming long branching ridges. The ridges are relatively thick (80-90 μm), and ca. 50 μk apart in the investigated part of the exoskeleton.

An attempt has been made to restore the structure of the exoskeleton of *Ungulaspis arctoa* on the basis of the data obtained (Text-fig. 2). It will be noted that the size of the tubercles can vary in different parts of the shield and they can also be more or less elongated. The thickness of the superficial layer and bony base of the tubercles is presumed to vary in accordance with the size of the tubercles in the different parts of the exoskeleton (as in the case of osteostracans with tubercles of different sizes, e.g. *Thyestes verrucosus*).

In the exoskeleton of the cephalic shield of *Ateleaspis* sp., 1-2 mm tesserae are clearly seen (AFANASSIEVA & KARATAJŪTE-TALIMAA 1998, Pl. 5, Fig. 3). They are covered with closely set small rounded tubercles. Between tesserae, there is a rather wide space for circumareal canals. Radiating canals are preserved in some part of the shield. As in the case of *Ateleaspis tessellata* TRAQUAIR (RITCHIE 1967), long narrow ridges are presented on the body scales of *Ateleaspis* sp.

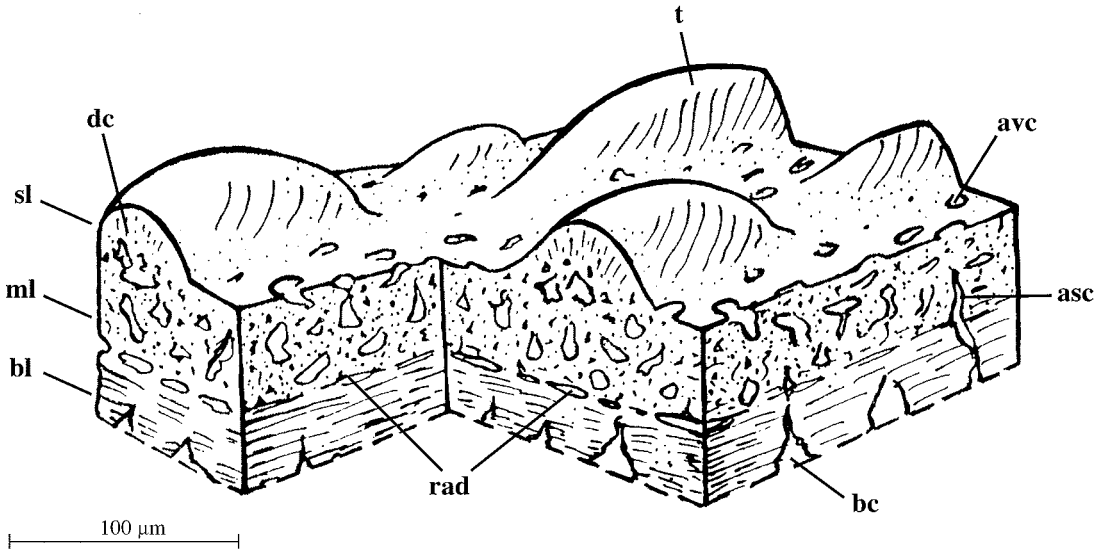

Fig. 2 – Three-dimensional diagram of the structure of the cephalic shield (dorsal side) of *Ungulaspis arctoa* AFANASSIEVA & KARATAJŪTE-TALIMAA

Abbreviations: asc – ascending vascular canal, avc – aperture of vascular canal, bc – basal cavity, bl – basal layer, dc – tubules of dentine, ml – medial layer, rad – radiating canal, sl – superficial layer, t – tubercle on the surface of tessera

Unfortunately, it is not possible to describe in detail the thin structure of the *Ateleaspis* sp. exoskeleton due to its bad preservation at a microstructural level. Study of the fragment under SEM has revealed the presence of elongate tubercles 150-300 μm long (Pl. 1, Fig. 7) on the surface of the part of the shield examined (the margin of the proximal part of the pectoral fin). Ribbing was found on the surface of some tubercles (Pl. 1, Fig. 8). Between the tubercles there are apertures 15-30 μm in diameter that presumably lead to vascular canals. In fractures between the tubercles, loose structure of a bony tissue of the middle layer could be seen. No traces of perforated septa or pore fields were found. Unfortunately, nothing can be said about the thickness and, therefore, the degree of development of the superficial layer of *Ateleaspis* sp.

Comparison of the two forms shows that *Ateleaspis* sp. is similar to *Ungulaspis arctoa* in the characters of the exoskeleton (presence of distinctly expressed tesserae, the type of sculpture of the shield and the trunk, presence of radiating canals, and the probable absence of perforated septa and pore fields in the middle layer of the exoskeleton). At the same time it should be taken into account that this statement is of a preliminary nature, as the exoskeleton of *Ateleaspis* sp. has not been properly studied and the fragments of exoskeleton investigated represent only small areas of the body.

At present, the thin structure of the exoskeleton has been most comprehensively studied for the *Trematapis*-like forms (Thyestidiens, sensu JANVIER 1985; Trematapidoidei, sensu AFANASSIEVA 1991) of osteostracans (DENISON 1951; GROSS 1961, 1968a, b; AFANASSIEVA 1986, 1995; AFANASSIEVA & MÄRSS 1997). Comparison of the exoskeleton structure of *Ungulaspis arctoa* with that of Trematapidoidei shows that they differ not only in the shield sculpture, but also in a number of microstructural features. The presence of small tubercles on the surface of the exoskeleton of *Ungulaspis arctoa* makes it comparable with *Saaremaaspis*, *Oeselaspis* and *Thyestes*. However, it differs from them in the absence of the pore fields that characterize most of the Trematapidoidei. It is evident that comparison of *Ungulaspis arctoa* with each representative of the given group will reveal the difference in whole combination of exoskeleton characters.

Among non-trematapid osteostracans, the exoskeleton of *Waengsjoeaspis excellens* (WÄNGSJÖ) (= *Zenaspis excellens* by GROSS 1961) was described rather completely (WÄNGSJÖ 1952). However, the position of *W. excellens* in the systematics of osteostracans has not yet been specified (*Osteostraci cornuates* incertae sedis: JANVIER 1985). It should be noted that it differs from *Ungulaspis arctoa* in possessing a better developed superficial layer of the exoskeleton which "...forms a covering to the middle layer and is pierced by fairly wide pores or grooves of the mucous canal system" (WÄNGSJÖ 1952, p. 41).

As for the non-cornuate forms, only incomplete data on the microstructure of the exoskeleton of *Hemicyclaspis* and *Aceraspis* are available. It is known that *H. murchisoni* (EGERTON) has a well developed continuous superficial layer (STENSIÖ 1932). This layer is less developed in the rarer *H. lightbodii* STENSIÖ, as well as in *Aceraspis robusta* KIAER. Their cephalic shields are covered with tubercles consisting of dentine (STENSIÖ 1932, HEINTZ 1939).

The microstructural characters of the exoskeleton of the osteostracans belonging to other major groups have been rather poorly studied. Consequently, we can note only some similarity with the sculpture of the shield of the Cephalaspispidoidei (small tubercles) and the Scolenaspispidoidei (small tubercles or tubercles of different size). Distinctly expressed tesserae are also characteristic of the latter group.

Ateleaspis represents a relict form within the association of osteostracans discovered in the Severnaya Zemlya Formation of the Lower Devonian of the Severnaya Zemlya Archipelago. Until now, it has been known only from the Silurian of Scotland (and, according to RITCHIE, probably, of Norway: RITCHIE 1967). As was observed previously (AFANASSIEVA & KARATAJŪTE-TALIMAA, 1998) *Ungulaspis arctoa* was noteworthy in possessing macromorphological characters typical of both the *Ateleaspis*- and *Scolenaspis*-like osteostracans. The similarity in the structure of exoskeleton of the forms investigated supports the presumed affinity of these groups of osteostracans and their possible origin from common ancestors.

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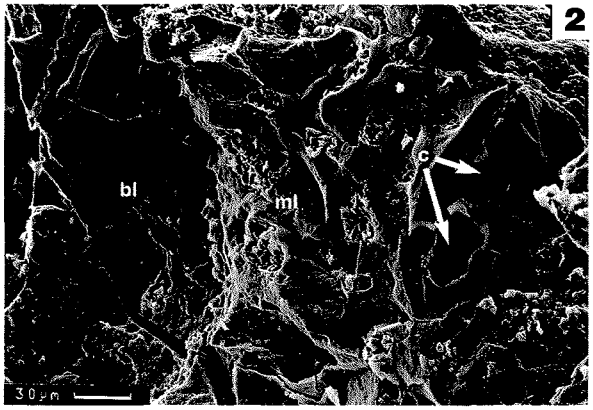
PLATE 1

1-6 – *Ungulaspis arctoa* AFANASSIEVA & KARATAJŪTE-TALIMAA, Severnaya Zemlya Formation (Lochkovian), Lower Devonian, Severnaya Zemlya Archipelago, Russia; microfragments of the holotype GIL 35-670; **1** – PIN 4766/1, tubercles on the surface of the cephalic shield; **2** – PIN 4766/2, horizontal break of the tessera; **3** – PIN 4766/1, bony tissue of the middle layer; **4-5** – PIN 4766/5, vertical break of marginal tubercle; **6** – PIN 4766/5, small marginal tubercle

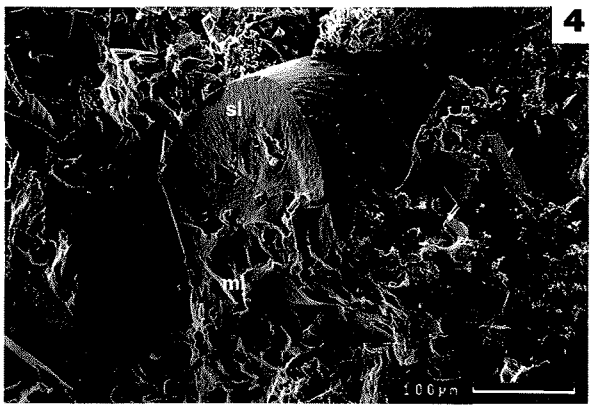
7-8 – *Ateleaspis* sp., Severnaya Zemlya Formation (Lochkovian), Lower Devonian, Severnaya Zemlya Archipelago, Russia. Microfragment PIN 4766/8 of specimen GIL 35-669; **7** – Tubercles on the surface of exoskeleton (proximal part of pectoral fin); **8** – Ribbing on the surface of tubercle

Abbreviations: avc – apertures of vascular canal, bl – basal layer, c – cavities in the base of tubercles, dc – tubules of mesodentine, ml – middle layer, sl – superficial layer


1
avc
100µm


2
bl
ml
c
30µm


3
10µm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sl
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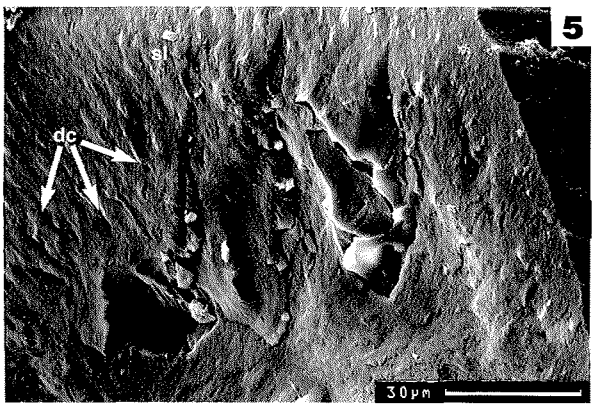
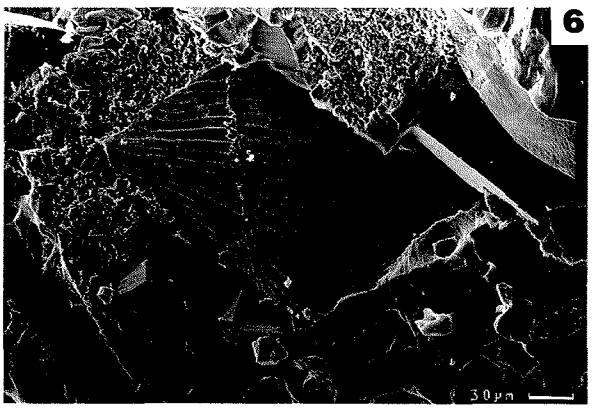

5
sl
dc
30µm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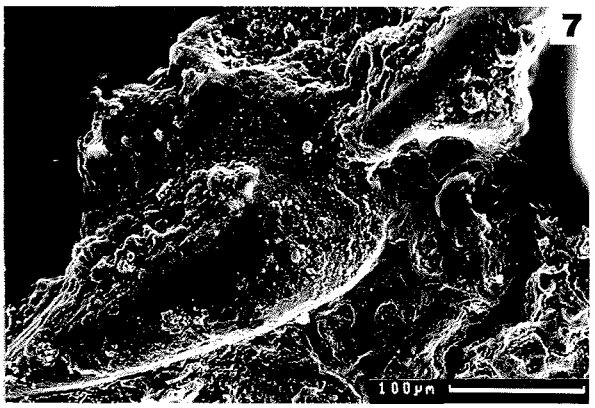
30µm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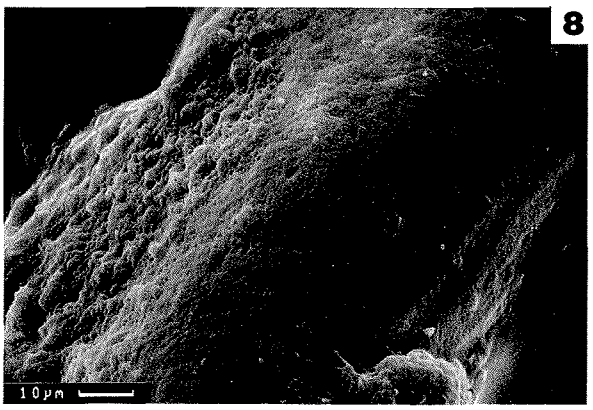
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