

On the Morphology and Systematic Position of the Tremataspid Osteostracan *Aestiaspis viitaensis* (Agnatha)

Q17 247-1

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Received October 26, 1995

Abstract—Based on new material deposited at the Paleontological Institute of the Russian Academy of Sciences, and on the holotype, a redescription is made of *Aestiaspis viitaensis* Janvier et Lelievre, 1994, an osteostracan from the Silurian of Saaremaa Island (Estonia). A more precise and comprehensive diagnosis is given. The genus *Aestiaspis* is placed in the Tremataspidae, subfam. nov.

During my study of *Thyestes verrucosus* Eichwald, 1854, and *Witaaspis schrenkii* (Pander, 1856), from the collection of Academician F.B. Schmidt (PIN, nos. 1628, 3256, 3257), we noted a specimen radically different from the others in its smaller size. The shield was split transversally and labelled as two specimens (3257/607 a, b) of “*Thyestes verrucosus* Eichw., lower part of the body” from “Rotziküll auf Oesel” (modern Saaremaa Island, Estonia). My study of these specimens has shown that they can be assigned neither to the species indicated, nor to any known osteostracans. The above assignment, as well as those of other specimens in this collection, were made more than a hundred years ago, probably with the participation of Schmidt. The same locality is indicated on all the labels attached to specimens of *Thyestes verrucosus* and *Witaaspis schrenkii*. This information and, indirectly, the lithological similarity of the matrices, indicate that the specimens probably came from the same beds as *Thyestes verrucosus* and *Witaaspis schrenkii*, known only from ViitAsian and Vezikusian beds of the Rootsikula Horizon of the Lower Silurian of Saaremaa Island (Myarss, 1986).

The extremely small shield (its length and width are about 1 cm, length of the head approximately 0.5 cm) suggested that the specimen represents the remains of a juvenile individual. Relatively large orbits also testified to that. However, a study of the naso-hypophysial region revealed natural casts of the eye capsules on the imprint of the head of the shield that enabled me to establish the maximum diameter of the eye balls. The orbital openings, on the other hand, would normally have had smaller dimensions. Thus, the orbits had relative ratios (L/OI about 10) typical of osteostracans at a definitive developmental stage, in particular of *Saaremaaspis mickwitzii* (Rohon, 1892), *Thyestes verrucosus* Eichwald, 1854, and *Stesiopelta pustulata* Janvier, 1985.

A microscopic study indicated the presence of a well developed basal layer of exoskeleton in the ventral part of the shield. The relatively complete development of the layers of the exoskeleton, in our opinion, also indicate a definitive stage of development of the individual under study. These conclusions provide more solid grounds for comparison with the already known osteostracans that, but for some rare occasions, are represented by fossil remains of definitive individuals.

Even a superficial comparison allowed assignment of the new form to the order Tremataspiformes. The long consolidated cephalic shield with a convex ventral side and without cornual processes is also indicative of that. At the same time, the form clearly differs from the tannuaspid-like osteostracans of the suborder Tannuaspididae (Afanassieva, 1991) in the tight setting of the organs of the orbital-nasohypophysial complex, narrow lateral fields and position of the infraorbital canal (ifc) of the lateral sensory line. These characters suggest that this form belongs to the suborder Tremataspidae (Thyestidians, according to F. Janvier, see: Janvier, 1981, 1985), a very early osteostracan group. A long consolidated shield covering the head and a considerable part of the body and a well developed exoskeleton permit assignment of the form to the family Tremataspidae, i.e., typical tremataspis-like osteostracans. This diverse osteostracan family, according to contemporary views, comprises the following genera: *Tremataspis*, *Dartmuthia*, *Saaremaaspis*, *Tyriaspis*, *Oeselaspis*, *Timanaspis*, and, possibly, *Sclerodus*, the last according to Forey (1987). Analysis of the set of characters of the form described shows that it cannot be assigned to any known genus: very small size, well expressed segmentation of post-cephalic division of the shield, large naso-hypophysial depression surrounded by a rim, presence of narrow longitudinal ridges in the shield sculpture.

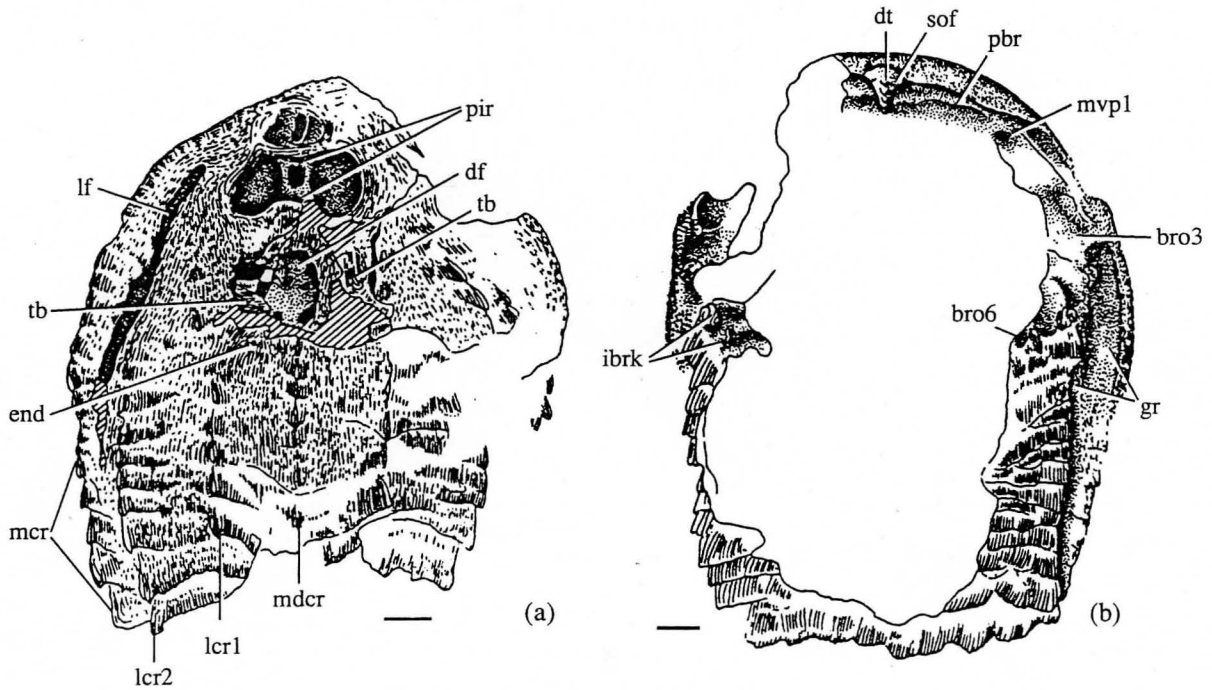


Fig. 1. *Aestiaspis viitaensis* Janvier et Lelievre, camera lucida drawing of the holotype Pi 7279: (a) dorsal side of the shield, (b) ventral side of the shield. Abbreviations: bro3, 6—branchial openings, df—dorsal field, dt—dentition of supraoral field, end—opening of endolymphatic passage, gr—ventrolateral grooves, ibrk—interbranchial thickenings (“interbranchial knobs”), lcr 1, 2—lateral dorsal crests, lf—lateral field, mcr—marginal crest, mdcr—median dorsal crest, mvpl—first medioventral process, pbr—prebranchial ridge, pir—pineal foramen, sof—supraoral field, tb—large tubercles beside dorsal field. Scale: 1 mm (from: Janvier and Lelievre, 1994).

Near the completion of my study I discovered an article by Janvier and Lelievre (1994) with a description of a new tremataspis-like osteostracan *Aestiaspis viitaensis* from the Silurian of Saaremaa. It was characterized by very small size and came from the Viita Beds of the Rootsikula Horizon. The shield was relatively well preserved, but strongly deformed. Certain fragments of the dorsal division of the shield and median part of its ventral part were missing (Fig. 1). Hence the authors reconstruction of the shield was only approximate.

I made a detailed study of the holotype deposited at the Institute of Geology of the Estonian Academy of Sciences (TAGI, Pi 7279). The study enabled clarification on some structural details that eliminate inaccuracies in the description by the above mentioned authors and discovery of some new features. As a result of this study and comparison of a relatively complete set of characters (Afanassieva, 1991) I believe that both specimens, the holotype and PIN, nos. 3257/607 a, b, belong to one and the same species, *Aestiaspis viitaensis* Janvier et Lelievre, 1994. Indicative of this are, firstly, precise coincidence of size, similar structure of organs, and relative positions of parts of the shield (parameters taken according to Denison and Afanassieva, see: Denison, 1951; Afanassieva, 1991), and a similar type of sculpture.

The new data make it possible to define more accurately the taxonomic position of the genus *Aestiaspis*. A peculiar combination of features of high taxonomic rank, i.e., one pair of lateral fields, a shorter, in compar-

ison with other tremataspids, segmented shield (cf. Tremataspidae Woodward, 1891; Oeselaspidinae Robertson, 1935; Timanaspidae Obruchev, 1962), convex ventral division of the shield, peculiar type of ornamentation, and small size, in our opinion allow one to assign the new form to a separate subfamily Aestiaspidinae.

In a book dedicated to osteostracans from the territory of the Soviet Union (Afanassieva, 1991) I proposed sets of diagnostic characters for taxa at different levels. According to that scheme, I propose a more precise and comprehensive diagnosis of the genus, as well as a detailed description of *Aestiaspis viitaensis*.

SYSTEMATIC PALEONTOLOGY

Order Tremataspidiformes

Suborder Tremataspidoidei

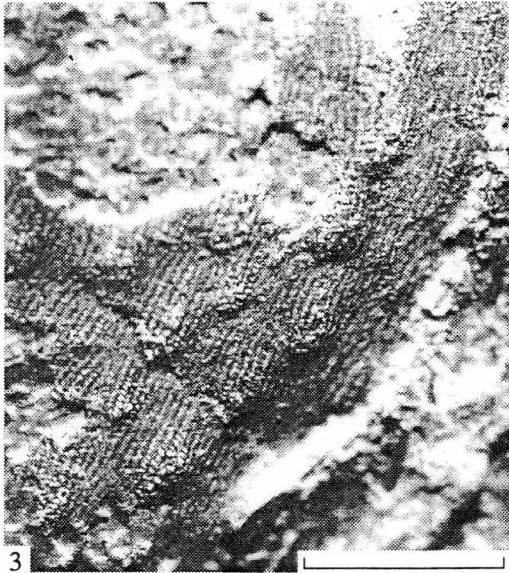
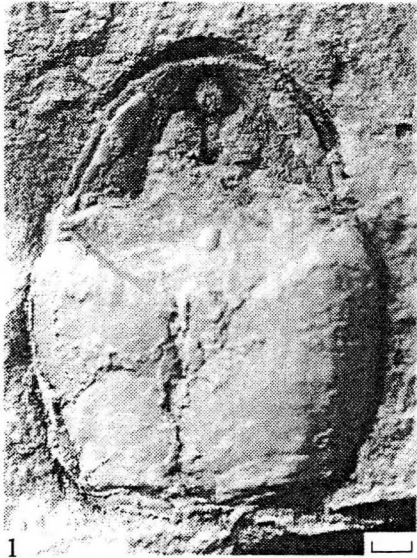
Family Tremataspidae Woodward, 1891

Subfamily Aestiaspidinae Afanassieva, Subfam. Nov.

Type genus. *Aestiaspis* Janvier et Lelievre, 1994.

Diagnosis. Small form. Cephalic shield relatively long (L/A^1 —approximately 4.5). Ventral divi-

¹ Following indices are: L—length of the shield, S—width of the shield, indices A–H according to Denison (Denison, 1951), indices Si, Q, Ol, Os according to Afanassieva (Afanassieva, 1991, pp. 7–8).



sion of shield convex. One pair of lateral fields, moderate length. Shield surface covered with narrow longitudinal ridges. Upper layer of exoskeleton not represented in some regions of shield surface.

Genus composition. One genus—*Aestiaspis* Janvier et Lelievre, 1994, Upper Wenlockian, Saaremaa Island, Estonia.

Comparison. Differs from all subfamilies in extremely small size, in type of ornamentation (except Timanaspidae, dorsal division of the shield). In addition, differs from Tremataspidae, Oeselaspidinae, and Timanaspidae in a shorter cephalic shield, from Tremataspidae and Oeselaspidinae in presence of only one pair of lateral fields, from Tremataspidae in less developed exoskeleton, from Dartmuthiinae, Oeselaspidinae, and Timanaspidae in more convex ventral shield.

Genus *Aestiaspis* Janvier et Lelievre, 1994

Aestiaspis: Janvier et Lelievre, 1994, p. 123.

Type species. *Aestiaspis viitaensis* Janvier et Lelievre, 1994, Silurian, Upper Wenlockian, Rootsikula Horizon, Saaremaa Island, Estonia.

Diagnosis. Very small osteostracans, length of cephalic shield about 1 cm. Shield width slightly less than length. Posterolateral parts of shield form small prominences. Traces of expressed segmentation on abdominal division of shield. Orbits medium in size. Dorsal field relatively short. Endolymphatic passage openings spaced, situated behind the field. Lateral field moderately long, slightly widened anteriorly. Shield surface covered with narrow longitudinal ridges.

Composition. Type species.

Notes. In their genus and species diagnosis Janvier and Lelievre include presence of "broad longitudinal grooves" extending from the third and fourth external branchial openings toward lateral prominences of the abdominal division (Janvier and Lelievre, 1994, p. 123). Presence of such grooves is dubious. In our opinion, certain flattening observed on the only preserved part of the ventral division in the holotype might be the consequence of deformation of the shield.

Aestiaspis viitaensis Janvier et Lelievre, 1994

Plate 12, figs. 1–5

Aestiaspis viitaensis: Janvier and Lelievre, 1994, pp. 123–125.

Holotype. TAGI, Pi 7279, cephalic shield; Silurian, Upper Wenlockian, Viita Beds, Rootsikula Horizon; Saaremaa Island, Estonia.

Description (Figs. 1 and 2). Cephalic shield elongated (L/A—approx. 4.5), moderate width (L/S—1.3; S/A—approx. 3.5). Maximum shield width behind midlength level. Prepineal part of shield very short (B/A—approx. 1), postpineal relatively long (C/A—approx. 3.5). Contour of cephalic shield ovate, rostral edge rounded, lateral margins convex, posterior edge forms blunt medial prominence. Posterolateral prominences small, their length on dorsal side of shield possibly equals that of medial process, on ventral side shorter. Posterior part of medium width shield (Si/A—approx. 2.6) bears traces of expressed segmentation over entire postcranial part of shield.

Nasohypophysial depression large, deep, ovate (almost circular), surrounded with wide bolster with three protuberances: small anterior and two higher pre-orbital, situated very close to rostral edge (about 1 mm. distance that makes 1/10 of shield length). Bean-shaped nasohypophysial opening relatively long and wide, occupies entire length of nasohypophysial depression.

Orbits ovate, almost circular (in holotype), medium sized (Ol—approx. 0.12 cm, L/Ol—approx. 10), relatively closely set (distance between them, corresponding to position of pineal plate, equals about 0.6 mm). Pineal foramen round, relatively large.

Size and position of dorsal field known only approximately. Ovate, small in size (Ld/A—approx. 0.65), separated from pineal plate. Openings of endolymphatic ducts were beyond its posterior edge.

Lateral fields of moderate length (about 0.5 cm), rounded at the margins, slightly widened in the anterior half (width about 0.7 mm). Fields originate at mid-level of nasohypophysial depression, ends somewhat anteriorly of shield midlength, distance from lateral margins slightly shorter than field width.

Dorsal and ventral divisions of shield similar in structure, covered with narrow longitudinal ridges. Low median crest consisting of separate scales extends along the dorsal division of the shield, with two lateral crests on each side. Flattened crest of scale rows extends along the shield edge.

The lateral sensory line system is well developed in *Aestiaspis* and, evidently, represented by lines typical of this osteostracan group. We revealed an infraorbital line (ifs) closely adjoining the orbito-nasohypophysial complex. It is noteworthy that in the given species

Plate 12

Figs. 1–5. *Aestiaspis viitaensis* Janvier et Lelievre, cephalic shield: (1) PIN, no. 3257/607a, imprint of cephalic division and mold of ventral division of the shield; (2) PIN, no. 3257/607b, mold of cephalic division and imprint of ventral shield of the same individual, casts of internal organs and fragments of exoskeleton are in evidence; (3) PIN, no. 3257/607b, fragment of preserved part of exoskeleton on ventral division of the shield (internal view); (4) PIN, no. 3257/607b, ventral division of the shield, basal layer of exoskeleton is in evidence; (5) PIN, no. 3257/607a, imprint of cephalic part of the shield with casts of organs, Saaremaa Island, Estonia; Lower Silurian, Rootsikula Horizon. Scale (all photos): 1 mm.

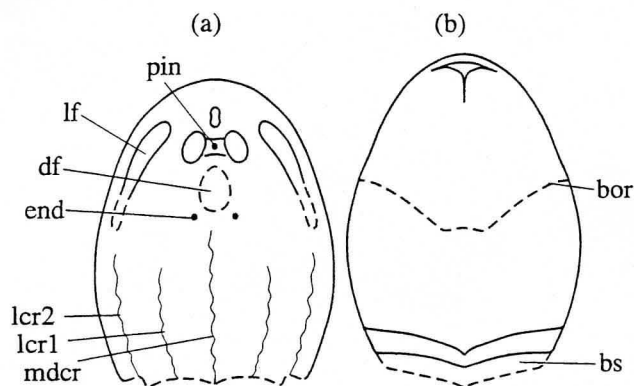


Fig. 2. *Aestiaspis viitaensis* Janvier et Lelievre, schematic reconstruction of the shield: (a) dorsal side, (b) ventral side. Abbreviations: bor—posterior limit of oralobranchial cavity, bs—body segment, pin—pineal plate; other abbreviations see: Fig. 1. Scale: 1 mm.

determination of positions of main sensory lines is complicated since the lines “disappear” in between the narrow ridges of the shield.

On the dorsal side, carapace is consolidated in its cephalic part. Traces of segmentation are clearly seen in the post-cephalic part of the shield. Segments are represented by rows of merged scales. Segmentation expressed better toward the caudal part of the shield.

Shield consolidated on the ventral side, however merged tesserae are clearly seen. Along posterior edge of the shield in specimen no. 3257/607b clearly visible trace of segment occupies entire width. Besides, a segment of the caudal part merged with the shield is discernible.

Ventral division of the shield is convex. Oralobranchial cavity of oligobranchiate type, relatively large, shape of covering scales unknown. Anterior edge of ventral shield bordering on it posteriorly evidently forms median process. Supraoral field well developed and houses a row of teeth (holotype). Branchial cameras separated by interbranchial septae with thickened distal parts—“interbranchial knobs” according to Janvier and Lelievre (1994). Traces of six pairs of branchial pouches are clearly seen on the holotype: evidently there were at least 10 pairs of them.

Unlike in *Aestiaspis viitaensis* as in the reconstruction by Janvier and Lelievre (Janvier and Lelievre, 1994, figs. 5 and 6), in specimen no. 3257/607b only slight flattening of lateral parts of abdominal division of the shield is seen (Plate 12, figs. 2 and 4). Strongly flattened region on the right side of the shield in the holotype is, in our opinion, the consequence of strong deformation of the carapace.

Among other data on the structure of internal organs of *Aestiaspis viitaensis* the following may be empha-

sized. In our material, traces of canals approaching lateral fields are seen, but nothing can be inferred about the ramification point of the sell canal. Positions of anterior divisions of the brain (olfactory organ, telencephalon, mesencephalon), vestibular apparatus (its posterior limits permit us to reconstruct the approximate position of openings of the endolymphatic passages), and anterior parts of oralobranchial cavity of oligobranchiate type are clearly seen.

Exoskeleton well developed. Superficial layer represented in ridges and nodes in the region of the oralobranchial cavity. Basal layer well developed and has a typical structure of crossed bundles of bony fibers.

Measurements. Shield length about 1.2 cm, width about 0.9 cm.

Note. The values of A and Ld in diagnoses above are known for *Aestiaspis viitaensis* only approximately. In connection with this all ratios of the shield in the diagnoses were additionally checked for relations x_i/Ol , where x_i are shield measurements according to Denison and Afanassieva (Denison, 1951; Afanassieva, 1991).

Material. Holotype, and well preserved shield split into two specimens, PIN, no. 3257/607a, b.

ACKNOWLEDGMENTS

I am grateful to T.I. Myårss of the Institute of Geology, Estonian Academy of Sciences, for making available the material and facilitating my research in Tallinn.

I acknowledge the support of the International Science Foundation and the Russian Foundation for Basic Research.

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