Estonian Journal Earth Sciences, 2019, **68**, 4, 206–224 https://doi.org/10.3176/earth.2019.15

The problematic lingulate brachiopod *Aulonotreta* from the Ordovician (Dapingian–Darriwilian) of Baltoscandia

Lars E. Holmer[a,b], Liang Yue[a], Zhiliang Zhang[a,c] and Zhifei Zhang[a]

[a] State Key Laboratory of Continental Dynamics, Shaanxi Key Laboratory of Early Life & Environments, Department of Geology, Northwest University, Xi'an, 710069 China; zhangtensor@hotmail.com, elizf@nwu.edu.cn
[b] Institute of Earth Sciences, Palaeobiology, Uppsala University, SE-752 36 Uppsala, Sweden; lars.holmer@pal.uu.se
[c] Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia

Received 12 August 2019, accepted 25 September 2019, available online 7 November 2019

Abstract. The enigmatic and aberrant lingulate brachiopod *Aulonotreta antiquissima* (Eichwald) from the Dapingian (Volkhov Stage) Toila Formation of northern Estonia and St Petersburg area (Historical Region of Ingria, Ingermanland, or Inkerinmaa; English, Swedish, Finnish) is re-described together with the new species, *Aulonotreta neptuni*, from the lower Darriwilian (Kunda Stage, lower Valastean Substage) Holen Limestone on the Island of Öland, southern Sweden. The genus is presently endemic to Baltoscandia. The new well-preserved material of *Aulonotreta* permits an account of the musculature, micro-ornamentation and siphonotretoid-like and non-baculate shell structure, all of which were previously poorly understood. The aberrant morphology and musculature of *Aulonotreta* suggest that it was adapted to an entirely epifaunal and most likely ambitopic adult mode of life.

Key words: Brachiopoda, Linguliformea, Lingulata, Ordovician, Dapingian, Darriwilian, Estonia, St Petersburg area, Sweden.

INTRODUCTION

The heavily ornamented, thick-shelled and strongly biconvex, lingulate brachiopod *Aulonotreta* differs strongly from most other lingulates and has hitherto been monotypic; the three species and subspecies that have been proposed are either junior synonyms or not congeneric. It is also seemingly endemic to Baltica and previously known almost exclusively from the glauconitic limestones of the Dapingian–lower Darriwilian Volkhov Regional Stage in northern Estonia and in the St Petersburg area (Historical Ingria), Russia (e.g. Mickwitz 1896; Walcott 1912). Although the type species *Aulonotreta antiquissima* (Eichwald, 1843) has attracted attention and been referred to comparatively frequently in the literature, especially during the latter part of the 19th century, it is still poorly understood; the description by Mickwitz (1896; translated by Walcott 1912; see also Holmer & Popov 2000) has remained the most modern account of this interesting and aberrant lingulate genus.

The object of this study is to re-describe *Aulonotreta antiquissima* based on new material, prepared with modern methods, and to draw comparisons with the new species *Aulonotreta neptuni* from the Darriwilian, Baltoscandian Kunda Stage on the northernmost part of the Island of Öland, southern Sweden. Although this occurrence of *Aulonotreta* has long been known (Jaanusson & Mutvei 1982, fig. 6), it has never been described or figured. The new material of *Aulonotreta* from both areas also permits a detailed account of its musculature, ontogeny, micro-ornamentation and shell structure.

GEOLOGICAL SETTING

The examined material originates from numerous Ordovician (Dapingian–Darriwilian) localities in the St Petersburg area, northern Estonia as well as from southern Sweden (Island of Öland; Fig. 1A), all situated on the Russian Platform (see, e.g., Männil 1966; Jaanusson & Mutvei 1982; Raukas & Teedumäe 1997; Dronov et al. 2005; Bauert et al. 2014).

The Dapingian and Darriwilian Baltoscandian Volkhov and Kunda stages consist almost exclusively of limestones. In northern Estonia and in the St Petersburg area most of the available specimens come from the Volkhov (Zheltyaki beds) and Toila formations, respectively (e.g. Raukas & Teedumäe 1997; Dronov et al. 2005); both consist of grey and reddish, glauconitic limestones with numerous discontinuity surfaces and

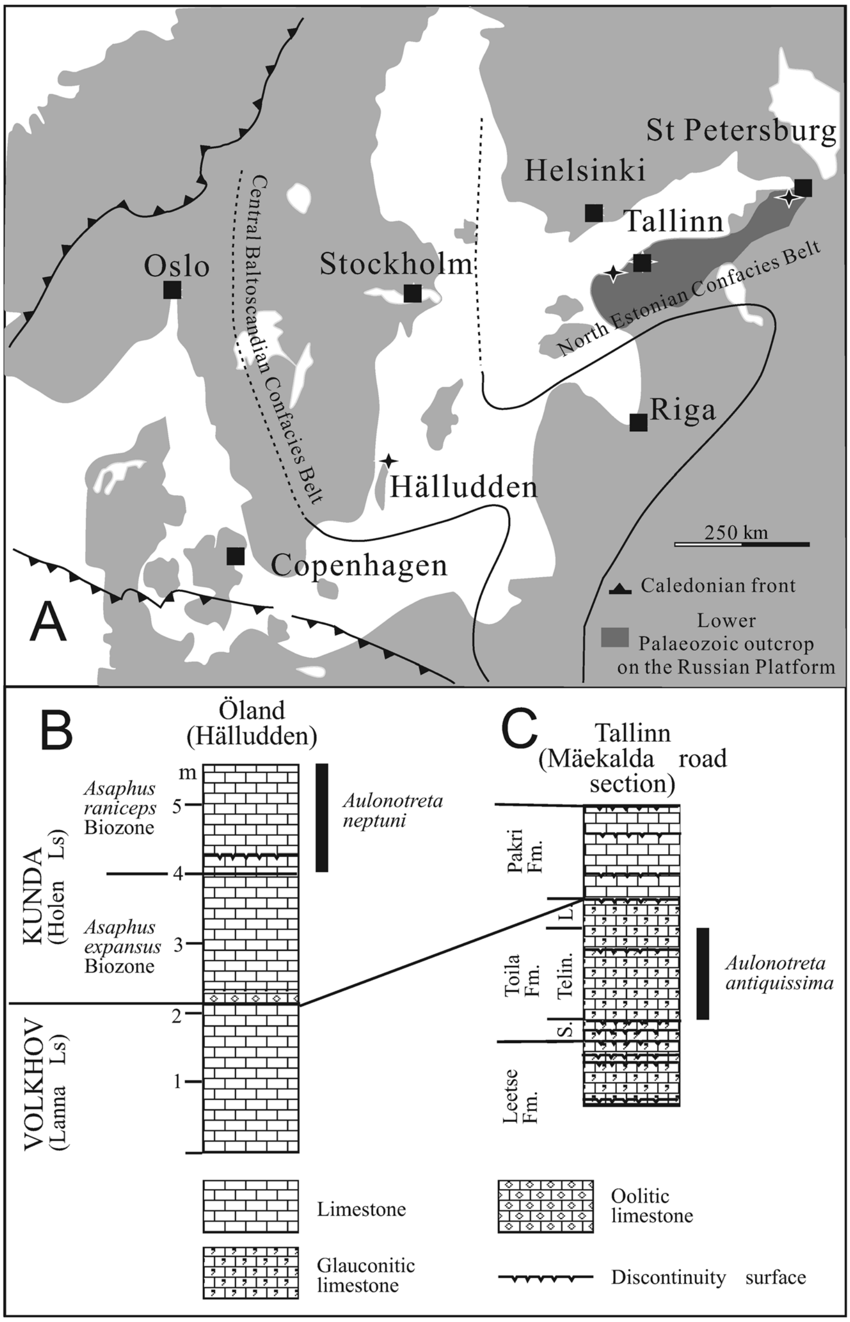


Fig. 1. A, regional overview of the early Palaeozoic on the Russian Platform with the collection sites marked by stars (map after Jaanusson 1976; Kröger et al. 2009, fig. 1); **B**, simplified lithological column through the Volkhov–Kunda interval in the Hälludden section, Northern Öland (after Jaanusson & Mutvei 1982, fig. 6); **C**, simplified lithological column through the Volkhov–Kunda interval in the Mäekalda road section, Tallinn (after Viira et al. 2001, fig. 2), S. = Saka Member, Telin. = Telinõmme Member, L. = Lahepere Member.

some intervals of marl (Fig. 1B). The Toila and Zheltyaki formations increase in thickness from northwestern Estonia eastwards towards the St Petersburg area, from about 0–3 m in northern Estonia to 2–6 m in the St Petersburg area (see, e.g., Lamansky 1905; Männil 1966). The available specimens of *Aulonotreta antiquissima* come from the following localities in Estonia (see also http://geokogud.info/ for details of the localities listed below) and the St Petersburg area: (1) Tallinn (in many old collections the various sections in the Tallinn area are not differentiated, but many may come from the classic Suhkrumägi outcrop or even from older outcrops inside the city walls on Tompea hill); (2) Mäeküla, Tallinn; (3) Mäekalda road section, Tallinn (Fig. 1); (4) Paldiski (Pakri Peninsula, an area with many outcrops along the coastal cliffs), Estonia; (5) Leetse, Estonia; (6) Popovka River gorge at southern outskirts of Pavlovsk (in early publications often referred to as vicinity of Tsarskoye Selo, today Pushkin), St Petersburg area.

On Öland, all the available specimens come from the Darriwilian Kunda Stage, which traditionally has been referred to the Holen Limestone (but see also Stouge 2004, for an alternative lithostratigraphy). The Holen Limestone consists entirely of calcarenites (Fig. 1A), which are up to about 8 m thick on northern Öland (see, e.g., Jaanusson & Mutvei 1982; Stouge 2004; Kröger et al. 2009, for more detailed descriptions and details on the localities listed below). The specimens of *Aulonotreta neptuni* sp. nov. come from the Hälludden, Torp, Byrum and Enerum localities on Öland.

METHODS

The material was isolated from the limestones by etching with weak buffered 10% acetic acid. The large shells of *Aulonotreta* are commonly fractured in the rock. To avoid complete fragmentation during the etching, the exterior (or interior) of the shell to be extracted was prepared mechanically from the rock and then covered with a layer of epoxy resin, before it was put in the acid. Due to the porous and poorly phosphatic interior of the lamellae, the use of acids clearly also dissolves part of the shell, leading to the hollowing out of the laminar secondary shell and exaggerating the depth of the valves. In fact, also Mickwitz (1896, pp. 49, 213) used acid in his attempts to observe the interior of *Aulonotreta*, but since he used diluted HCl, the shell was even more dissolved and the depth of the valves became even more exaggerated (Mickwitz 1896, pl. 3:24, 25). Due to the effect of the acid, it is in most cases difficult to get good interiors with this method and the muscle scars and other important features of the interiors may be strongly excavated to the extent that the scars of earlier growth stages are exposed.

For the study of shell structure, specimens embedded in epoxy resin were sectioned, polished and then etched with 4% HCl for 4 s. The counterparts were used to make thin sections for examination in transmitted light.

Measurements (in millimetres if not stated otherwise) have been performed on the material as follows: W, L, T, maximum width, length, thickness of complete articulated shell; LL, total number of growth lamellae; Lv, Ld, maximum length of ventral and dorsal valve; Hv, Hd, maximum height of ventral and dorsal valve; Iw, Il, maximum width, length of pseudointerarea; Pw, Pl, median width, length of median groove or pedicle groove; Uw, Ul, width, length of umbonal muscle scars; Talw, Tall, width, length of ventral transmedian/anterior lateral muscle scars; Tolw, Toll, width, length of dorsal transmedian/outside lateral muscle scars; Cw, Cl, width, length of central muscle scars; Aw, Al, width, length of dorsal anterior lateral muscle scars; Vwv, Vlv, width, length of median ventral visceral platform; Vwd, Vld, width, length of median dorsal visceral platform.

OR = observed range, N = number of measurements.

Terminology. There are some differences in how the terminology and reconstruction of the lingulate musculature have been used in the past, but here the terminology used by Bulman (1939, fig. 2; see also Holmer & Popov 2000, fig. 7) is followed.

Institutional abbreviations. All illustrated specimens are deposited in the Department of Palaeozoology, Swedish Museum of Natural History (Prefix: NRM-PZ Br), Stockholm; Geological Survey of Sweden (Prefix: SGU), Uppsala, Sweden; Central Science-Research Geological Exploration Museum (Prefix: CNIGR), St Petersburg State University Collections (Prefix: GUL), St Petersburg, Russia; British Museum of Natural History (Prefix: B), London, U.K.; Estonian Museum of Natural History, Tallinn, Estonia (Prefix: LMT).

SYSTEMATIC PALAEONTOLOGY

Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Family AULONOTRETIDAE Holmer & Popov, 2000

Emended diagnosis. Shell thick, almost equibiconvex, only somewhat dorsibiconvex, strongly lamellose; shell structure lacking baculae; prismatic, densely apatitic primary layer; secondary layer with thick hollowed laminae containing various loosely organized apatitic aggregates, including randomly oriented needles/rods; ornamentation with undulating, evenly spaced rugae; larval shell lacking pitted micro-ornament; adult shell with ornamentation of fine rhomboidal micro-pits; ventral pseudointerarea well developed, lacking flexure lines, with narrow, deep pedicle groove; dorsal pseudointerarea flattened, with straight posterior margin and poorly defined median groove; visceral area of both valves strongly thickened extending to mid-valve; ventral and dorsal umbonal scars on elevated processes from pseudointerarea; impression of pedicle nerve lacking; *vascula lateralia* of both valves submedian, slightly convergent; *vascula media* absent.

Remarks. Holmer & Popov (2000) recognized the new family Aulonotretidae within the Lingulida due to its aberrant morphology. Holmer (1993) and Holmer & Popov (1995) provisionally considered *Aulonotreta* to belong within the Elkaniidae, in view of its strongly biconvex ornamented shell. In the cladistics analysis of Cusack et al. (1999), *Aulonotreta* was considered as belonging within the linguloid-discinoid clade, as a sister taxon to the larger linguloid clade. The affinity of *Aulonotreta* remains problematic and the significance of the new data on the aberrant siphonotretoid-like shell structure, musculature and ontogeny is discussed below. The monotypic family is presently endemic to the Ordovician of Baltica (Sweden, Estonia, St Petersburg area).

Genus *Aulonotreta* Kutorga, 1848

1869 *Acritis* Volborth, p. 212 (obj.).
non 1972 *Aulonotreta* Andreeva, p. 46.
1983 *Rohonodus* Schallreuter, p. 108 [type, *R. vastorfensis*; OD].

Type species. Subsequent designation by Hall & Clarke 1894, p. 244; *Aulonotreta sculpta* Kutorga, 1848, p. 260 (= *Obolus antiquissimus* Eichwald, 1843, p. 143); Dapingian Volkhov Stage, Estonia and St Petersburg area (Ingria), Russia.

Diagnosis. Characters as for family.

Species included. *Aulonotreta antiquissima* (Eichwald, 1843); *A. neptuni* sp. nov.

Discussion. Apart from the two species presently placed within the genus, Mickwitz (1896, p. 213, pl. 3:23a,b) proposed *Obolus* (*Acritis*) *antiquissimus ventrosus*. However, it was based on a single dorsal valve, which is not distinguishable from the type species, and it is clearly a junior synonym (Walcott 1912). Walcott (1901, p. 694; see also Walcott 1912, p. 441, pl. 13:2) named *Obolus* (*Acritis*?) *rugatus*, from the Cambrian of Eureka County, Nevada, USA; however, as noted by himself, this probably represents a new genus. The only other named species, *Aulonotreta kuraganica* Andreeva (1972, p. 46, pl. 7:1–3), from the Lower Ordovician of the Ural Mountains was referred to the elkaniid *Lamanskya* by Holmer (1993, p. 158, fig. 8b–e). *Rohonodus vastorfensis* was described by Schallreuter (1983), as the dermal plates of new species of agnathan fish, but the illustrated specimens from Ordovician glacial erratic boulders are clearly just strongly fragmentary specimens of *Aulonotreta*, judging from the ornamentation of fine rhomboidal micro-pits.

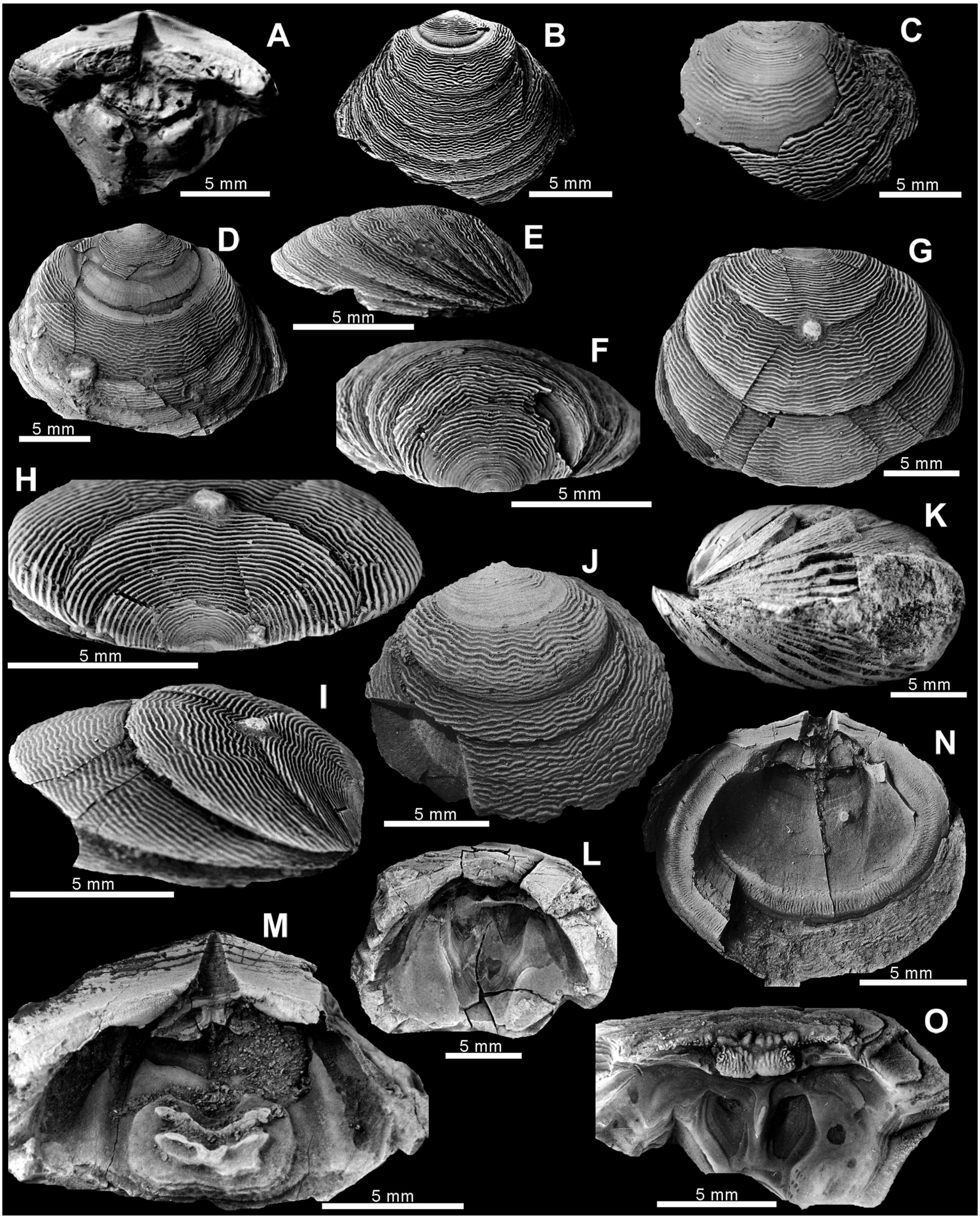
Stratigraphic distribution. Ordovician (Dapingian–Darriwilian).

Aulonotreta antiquissima (Eichwald, 1843)
Figures 2–5

v* 1843 *Obolus* (*Lucina*) *antiquissimus* Eichwald, p. 142, pl. 4:1a–c.
v. 1848 *Aulonotreta sculpta* Kutorga, p. 282, pl. 7:11a–d. [Lectotype selected here, CNIGR 81/3785, a fragmentary ventral valve from the Dapingian Baltoscandian Volkhov Stage (probably $B_{II\gamma}$), Popovka River, Tsarskoe Selo (today Pushkin), St Petersburg area, Russia, figured by Kutorga in pl. 7:11b.]
v. 1859 *Obolus antiquissimus* Eichwald, pl. 37:5a–d [pl. 37:5b is copied from Eichwald 1843, pl. 4:1a].
v. 1896 *Obolus antiquissimus* Eichwald; Mickwitz, p. 206, pl. 3:20–22, 24-2.
v. 1896 *Obolus antiquissimus* Eichwald *var. ventrosus* Mickwitz, p. 213, pl. 23. [Holotype by monotypy, CNIGR 116/10892, a complete dorsal valve from the Dapingian Volkhov Stage, Tallinn, Estonia.]
1905 *Obolus antiquissimus* Eichwald; Lamansky, p. 56.
v. 1912 *Obolus* (*Acritis*) *antiquissimus* (Eichwald); Walcott, p. 437, pl. 13:3, 15:2. [Full synonymy.]
v. 2000 *Aulonotreta antiquissima* (Eichwald); Holmer & Popov, p. 72, fig. 33,1a–g.

Lectotype. Selected here, GUL 4/32 (Fig. 2A), a fragmentary ventral valve from the Dapingian Volkhov Stage, Tallinn, Estonia; figured by Eichwald (1843, pl. 4:1a,b).

Examined material. All from the Dapingian Volkhov Stage. [Mickwitz's (1896) type material (now in the CNIGR) was examined and measured, but unfortunately cannot be re-photographed because the specimens are permanently mounted inside a sealed glass-covered container, which cannot be opened according to museum regulations] CNIGR 113/10892, partly exfoliated complete articulated shell (W = 22.6, Ld = 21.4, Lv = 22.0, Hd = 7.4, Hv = 6.8, T = 14.2, LL = 13), Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:20). CNIGR 114/10892, complete ventral exterior (W = 21.7, Lv = 20.0, Hd = 7.4, Hv = 5.25, LL = 13), Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:21). CNIGR 115/10892, deformed complete dorsal exterior (W = 21.5, Ld = 22.1, LL = 13), Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:22). CNIGR 116/10892 (Holotype of *Obolus antiquissimus* Eichwald *var. ventrosus*), partly exfoliated complete ventral exterior


A
5 mm
B
5 mm
C
5 mm
D
5 mm
E
5 mm
F
5 mm
G
5 mm
H
5 mm
I
5 mm
J
5 mm
K
5 mm
L
5 mm
M
5 mm
N
5 mm
O
5 mm

(W = 17.0, Lv = 16.0, Hd = 5.5, Hv = 5.25, LL = 7), Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:23). CNIGR 117/10892, fragmented ventral interior, Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:24). CNIGR 118/10892, fragmented dorsal interior, Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:25). CNIGR 119/10892, fragmented ventral interior, Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:26). CNIGR 120/10892, fragmented dorsal interior, Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:27). CNIGR 121/10892, fragmented ventral interior, Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:28). CNIGR 122/10892, complete juvenile ventral interior (W = 12.5, Lv = 10.5, Hv = 1.8, LL = 1, Pw = 0.7, Pl = 0.9, Iw = 7.0, Il = 1.5, Uw = 1.7, Ul = 1.2, Vlv = 3.6, Talw = 3.9, Tall = 2.0, Cw = 3.0, Cl = 3.6), Tallinn, Estonia; figured by Mickwitz (1896, pl. 3:29). CNIGR 81/3785 (Lectotype of *Aulonotreta sculpta* Kutorga), slightly fragmented and exfoliated ventral valve, Popovka River, St Petersburg area, Russia; figured by Kutorga (1848, pl. 7:11b). GUL 15/9 (Syntype of *Obolus* (*Lucina*) *antiquissimus* Eichwald), fragmentary dorsal valve (Fig. 2C), Tallinn, Estonia; figured by Eichwald (1843, pl. 4:1c). B5997, fragmentary dorsal valve (Fig. 2G–I), Paldiski, Estonia. B5998, fragmentary ventral internal mould, Tallinn. B5999, almost complete ventral valve (W = 16.0, Lv = 15.0, Hv = 5.0, LL = 10, Pw = 2.5, Pl = 1.6, Iw = 11.5, Il = 4.8; Fig. 2B), St Petersburg area, Russia. LMT1201gl, complete articulated shell (W = 21.0, Ld = 18.0, Lv = 21.0, Hd = 7.0, Hv = 4.8, T = 11.8, LL = 11; Fig. 2K), Leetse, Estonia. NRM-PZ Br133729, slightly exfoliated, fragmented dorsal valve (W = 18.0, Ld = 15.0, Hd = 6.5, LL = 6; Fig. 2D–F), Mäeküla, Estonia. NRM-PZ Br133718, fragmented dorsal valve (Figs 2O, 3H), Tallinn, Estonia. NRM-PZ Br65717, fragmented ventral valve (W = *c*. 13.7, Lv = *c*. 11.9, Hv = *c*. 4.7, LL = *c*. 4; Figs 2J, 3E, F), Tallinn, Estonia. NRM-PZ Br133532, fragmented dorsal valve (Fig. 2L), Estonia. NRM-PZ Br133529, fragmented ventral valve (Figs 2M, 3I), Tallinn, Estonia. NRM-PZ Br133527, fragmented ventral valve (Fig. 2N), Tallinn, Estonia. NRM-PZ Br65709, fragmented dorsal valve (Fig. 3B, G), Tallinn, Estonia. NRM-PZ Br65710, fragmented ventral valve (Fig. 3A, C, D, J–L), Tallinn, Estonia. NRM-PZ Br65706, sectioned fragmented ventral valves (Fig. 4A–E), Tallinn, Estonia. NRM-PZ Br133687, etched and sectioned fragmented dorsal valve (Fig. 4H–M), Mäekalda, Estonia. In addition to an undetermined number of more fragmentary valves.

Diagnosis. Shell very thick, with rounded, only slightly transversely oval outline and obtuse umbonal angle; shell almost equibiconvex with bulbous lateral profile, more than half as thick as wide, only somewhat dorsibiconvex and strongly lamellose; beaks of both valves with rounded lateral profile; dorsal beak somewhat recurved in lateral view, with ventral umbo curving over commissure; shell structure lacking baculae; thick hollowed laminae containing various apatitic units, microgranular to randomly oriented acicular; ornamentation with undulating, evenly spaced high rugae; larval shell lacking pitted micro-ornament, adult shell with ornamentation of fine rhomboidal micro-pits; ventral pseudointerarea unusually well developed, lacking flexure lines, with narrow, deep pedicle groove; dorsal pseudointerarea flattened, with straight posterior margin and poorly defined median groove; visceral area of both valves strongly thickened, forming terraced platforms, extending to mid-valve; ventral platform rectangular in outline; dorsal platform elongate oval in outline; dorsal central and anterior lateral muscle scars closely placed, bisected by low median ridge; dorsal transmedian scars elongate oval, completely underneath undercut pseudointerarea; *vascula lateralia* of both valves submedian, slightly convergent; *vascula media* absent.

Description. Shells large and very thick, on average 17.8 mm wide (OR = 12.5–22.6; N = 8), almost equibiconvex, 56–63% as thick as wide (N = 2), with bulbous lateral profile, only somewhat dorsibiconvex; height of dorsal valve only between 0.7 and 2.2 mm higher than ventral valve in two complete articulated shells (Figs 2K, 5E). Maximum thickness and height of both valves in posterior one third of total shell length. Outline of both valves broadly transversely oval to round; umbonal angle obtuse, on average 92% as long as wide (OR = 83–100%; N = 9), with greatest width anterior to mid-valve. Beaks of both valves rounded; dorsal beak somewhat recurved in lateral view, with

Fig. 2. *Aulonotreta antiquissima* (Eichwald, 1843), from the Dapingian Volkhov Regional Stage. **A**, Lectotype GUL 4/32, fragmentary ventral interior, Tallinn, Estonia (figured by Eichwald 1843, pl. 4:1a,b). **B**, B5999, almost complete ventral exterior, St Petersburg area, Russia. **C**, Syntype GUL 15/9, fragmentary dorsal exterior, Tallinn, Estonia (figured by Eichwald 1843, pl. 4:1c). **D–F**, NRM-PZ Br133729, slightly exfoliated, fragmented dorsal exterior, Mäeküla, Estonia: D, dorsal view; E, lateral view; F, posterior view. **G–I**, B5997, fragmentary dorsal exterior, Paldiski, Estonia: G, dorsal view; H, posterior view; I, lateral view. **J**, NRM-PZ Br65717, slightly fragmented ventral exterior, Tallinn, Estonia. **K**, LMT1201gl, complete articulated shell, Leetse, Estonia. **L**, NRM-PZ Br133532, oblique anterior view, fragmented dorsal interior, Estonia. **M**, NRM-PZ Br133529, fragmented ventral interior, Tallinn, Estonia. **N**, NRM-PZ Br133527, exfoliated juvenile ventral interior, Tallinn, Estonia. **O**, NRM-PZ Br133718, fragmented dorsal interior, Tallinn, Estonia.

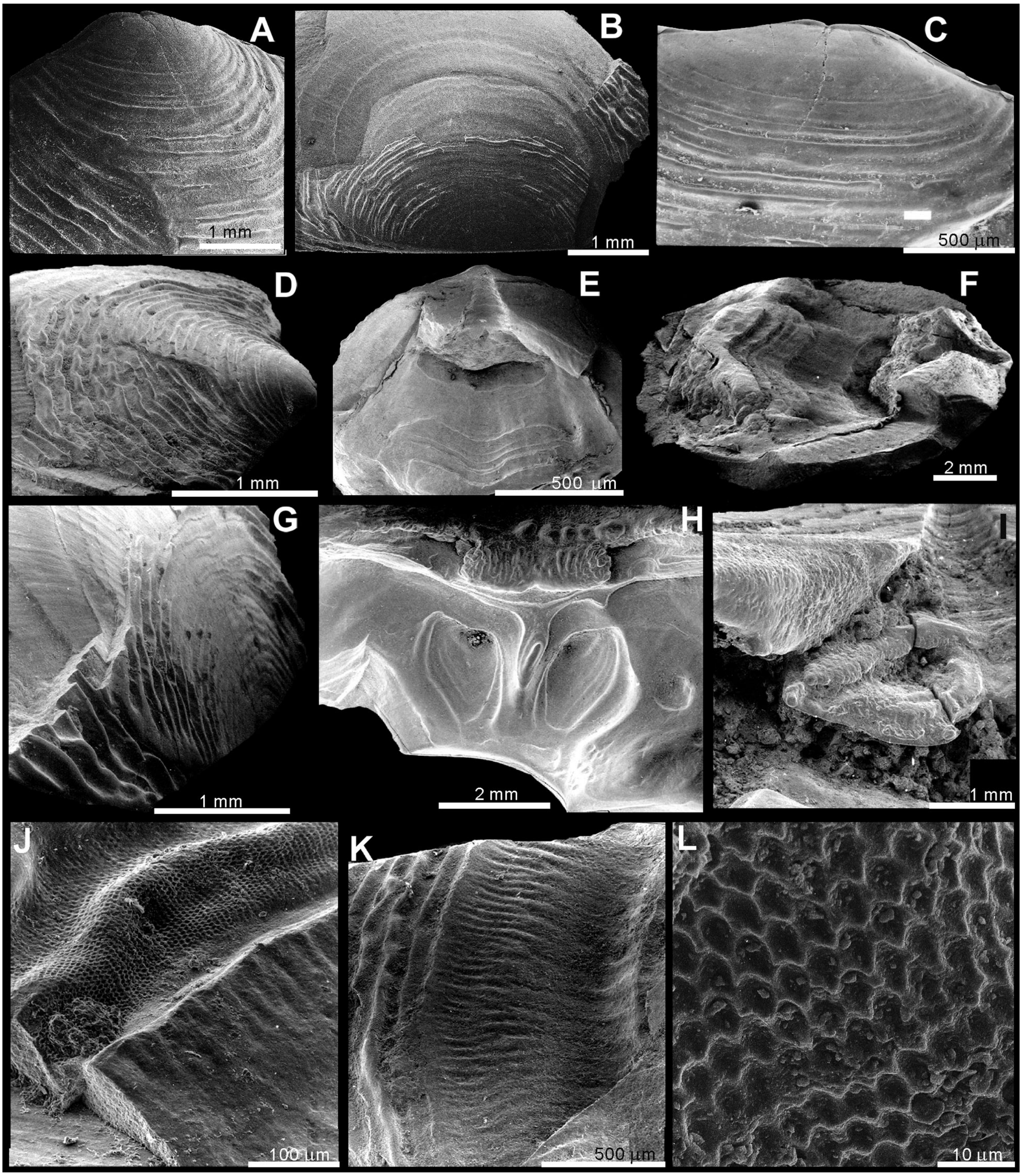


Fig. 3. *Aulonotreta antiquissima* (Eichwald, 1843), from the Dapingian Volkhov Regional Stage. **A**, NRM-PZ Br65710, fragmented ventral exterior, Tallinn, Estonia, detail of umbo. **B**, NRM-PZ Br65709, fragmented dorsal exterior, Tallinn, Estonia, posterior view. **C**, detail of larval shell of A. **D**, lateral view of umbo of A. **E, F**, NRM-PZ Br65717, fragmented ventral interior, Tallinn, Estonia: E, ventral view; F, lateral view. **G**, lateral view of umbo of B. **H**, NRM-PZ Br133718, fragmented dorsal interior, Tallinn, Estonia. **I**, NRM-PZ Br133529, detail of umbonal process of ventral interior, Tallinn, Estonia. **J**–**L**, detail of partly exfoliated exterior of A: J, showing post-larval rugae with micro-pits; K, detail of *vascula terminalia*; L, detail of rhomboidal micro-pits.

ventral umbo curving over the commissure in the largest shells (Fig. 5E). Shell strongly lamellose, with on average 8 major growth lamellae (OR = 1–13; N = 8); growth lamellae ornamented with strongly undulating, evenly spaced rugae (Fig. 2B–K). Adult shell with ornamentation of fine rhomboidal micro-pits (Fig. 3J–L). Pseudointerareas of both valves flattened, wide and deeply hollowed and undercut. Interior of both valves surrounded by distinctive flattened rim, around 1.5–2.5 mm across, starting directly anterior to pseudointerarea (Figs 2N, 5A, C, D).

Ventral valve only somewhat longer (around 1–3 mm difference in the largest complete articulated shells) and strongly convex, on average 31% as high as long (OR = 17–43%; N = 8) and 91% (OR = 83–100%; N = 8) as wide as long (Figs 2B, D, J, K, 5E). Ventral pseudointerarea lacking flexure lines, but with strongly developed growth lines, flattened and orthocline to somewhat anacline, with an obtuse umbonal angle; unusually strongly developed, undercut and raised high above the valve floor, very wide, around one fifth to half as long as wide, and occupying about half the valve width in juveniles and close to all of valve width in the largest specimens; propareas extending far out to the lateral borders of valve, and extending for around one third of the valve length in the largest specimens; pedicle groove very deep and narrow, widening anteriorly and occupying around one fifth to less than half of the width and length of the pseudointerarea, respectively (Figs 2A, M, N, 5A, D).

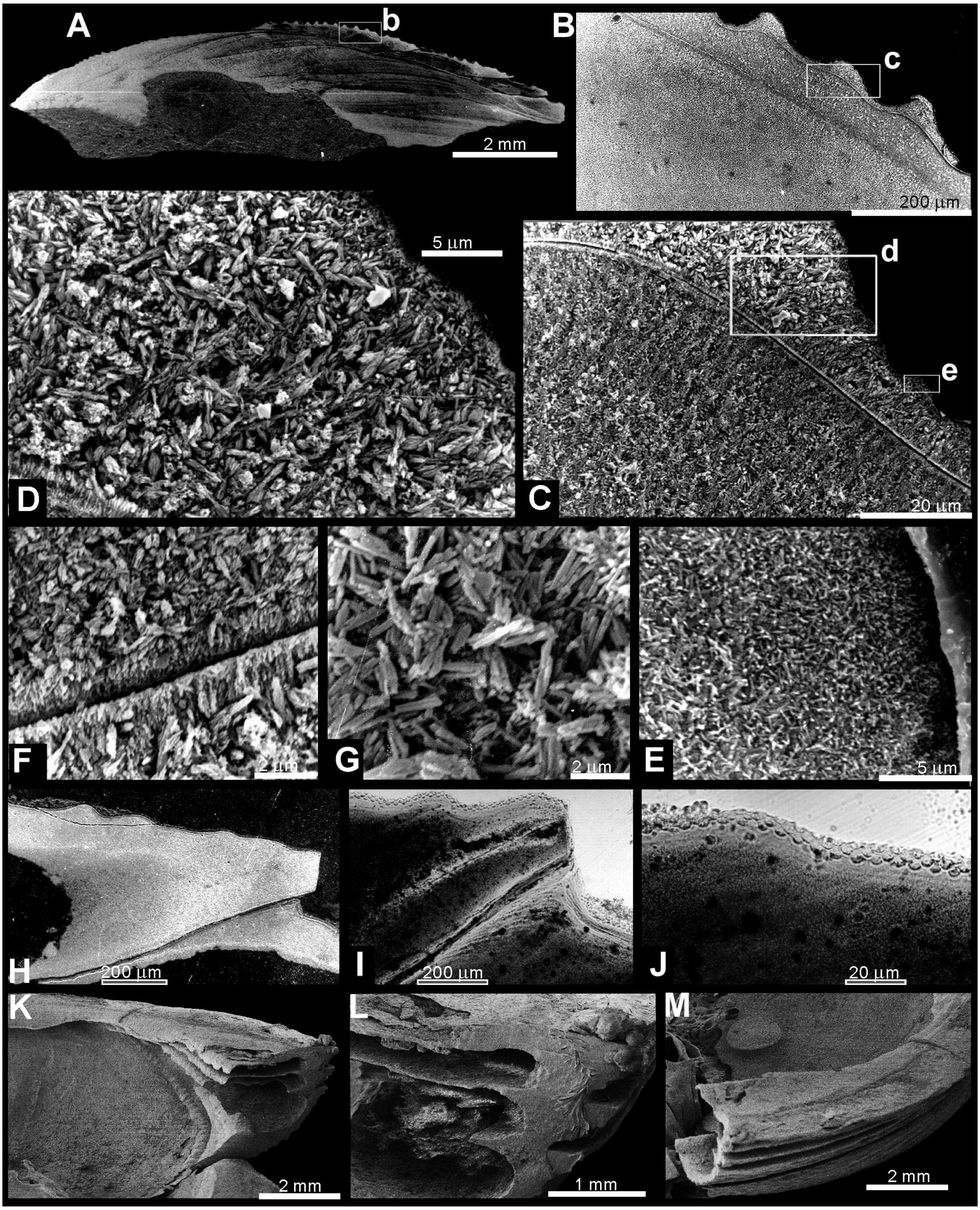
Dorsal valve strongly convex, on average 37% as high as long (OR = 35–39%; N = 2) and 94% (OR = 86–103%; N = 3) as wide as long (Figs 2E, F, H, K, 5E). Dorsal pseudointerarea with straight posterior margin, occupying more than one third of the width of the pseudointerarea, lacking flexure lines, but with strongly developed growth lines, flattened orthocline to anacline; dorsal pseudointerarea unusually strongly developed, undercut and raised high above the valve floor, very wide, around half as long as wide, and occupying all of the valve width in the largest specimens; propareas extending far out to the lateral borders of valve, and extending for around one third of the valve length; median groove very poorly defined (Figs 2L, 5C).

Visceral area, musculature and mantle canals. The visceral areas of both valves are strongly thickened and form distinctive terraced platforms supporting the central body cavity. The body cavity has deeply impressed and closely spaced muscle scars and extends deep underneath the rim-like projecting pseudointerareas and lateral posterior borders of both valves in adults. The body cavities of both valves are comparatively small and are placed in the posterior half of both valves (Figs 2L–O, 3E, F H, 5A–D).

The ventral scars of the umbonal muscle form two very unusual tooth-like processes (= 'pedicle muscles' in Walcott 1912), which are placed directly at the anterior end of the pedicle groove and extend freely into the visceral cavity (Figs 2M, 3I, 5A, B). The two strongly impressed scars directly anterior to and beneath the umbonal scars are assumed to represent the central and outside lateral scars, but the exact placement of these is not entirely clear (Figs 2M, 3E, F, 5A, B). The ventral body cavity is supported by a thickened central large elevated platform, bearing a long median depression (Figs 2M, 3E, F, 5A). The wide platform has a rather rectangular, almost square outline and occupies around one third of the valve width; it becomes thickened anteriorly, where it extends to around the mid-valve. Although the platform lacks clear imprints of muscle scars, it is possible that the middle lateral muscles were attached to this area (Fig. 5D); however, it is also possible that, e.g. the middle lateral muscles were absent. The possible ventral scars of the transmedian and anterior lateral muscles form an elongate and deeply impressed area directly anterior to the propareas, and extend somewhat underneath the elevated propareas and marginal rim (Figs 2M, 5A, B).

The dorsal scars of the umbonal muscle form a single buttressed process, directly anterior to the poorly defined median groove, which occupies just around one tenth of the width of the pseudointerarea; the process has two closely spaced elevated oval scars with rows of minute pustules (Figs 2O, 3H, 5B, C). In some specimens the umbonal process partly extends freely into the visceral cavity (Fig. 2L). The two large, strongly impressed and elongate kidney-shaped scars, directly anterior to and beneath the umbonal scars are assumed to represent the central scars; they are separated by a low ridge (Figs 2O, 3H) and supported laterally by the elongated oval central visceral platform, surrounded by a raised rim. The anterior lateral muscle scars are placed very close to the central scars at the thickened anterior end of the platform, occupying around one third of the valve width and extending to around mid-valve (Figs 2L, O, 3H, 5B, C). The dorsal scars of the outside and middle lateral (if present) muscles form an elongate and deeply impressed area directly anterior to the propareas, whereas the possible smaller separate scars of the dorsal transmedian muscle are placed underneath and hidden by the elevated and undercut dorsal pseudointerarea (Figs 2L, O, 3H, 5B, C).

The *vascula lateralia* of both valves are deeply impressed, submedian, forming with two main gently arcuate, convergent trunks, beginning at the posterior section of the visceral area and extending for almost most of the length of the shell. The main secondary trunks are only ramified distally, radiating inwardly and outwardly almost perpendicular to the main trunks, becoming strongly and finely ramified, closely spaced branches of the *vascula terminalia* extending onto the distinctive flattened rim surrounding the valve interiors (Figs 2N, 3J, K, 5A, C, D). The *vascula media* are absent.



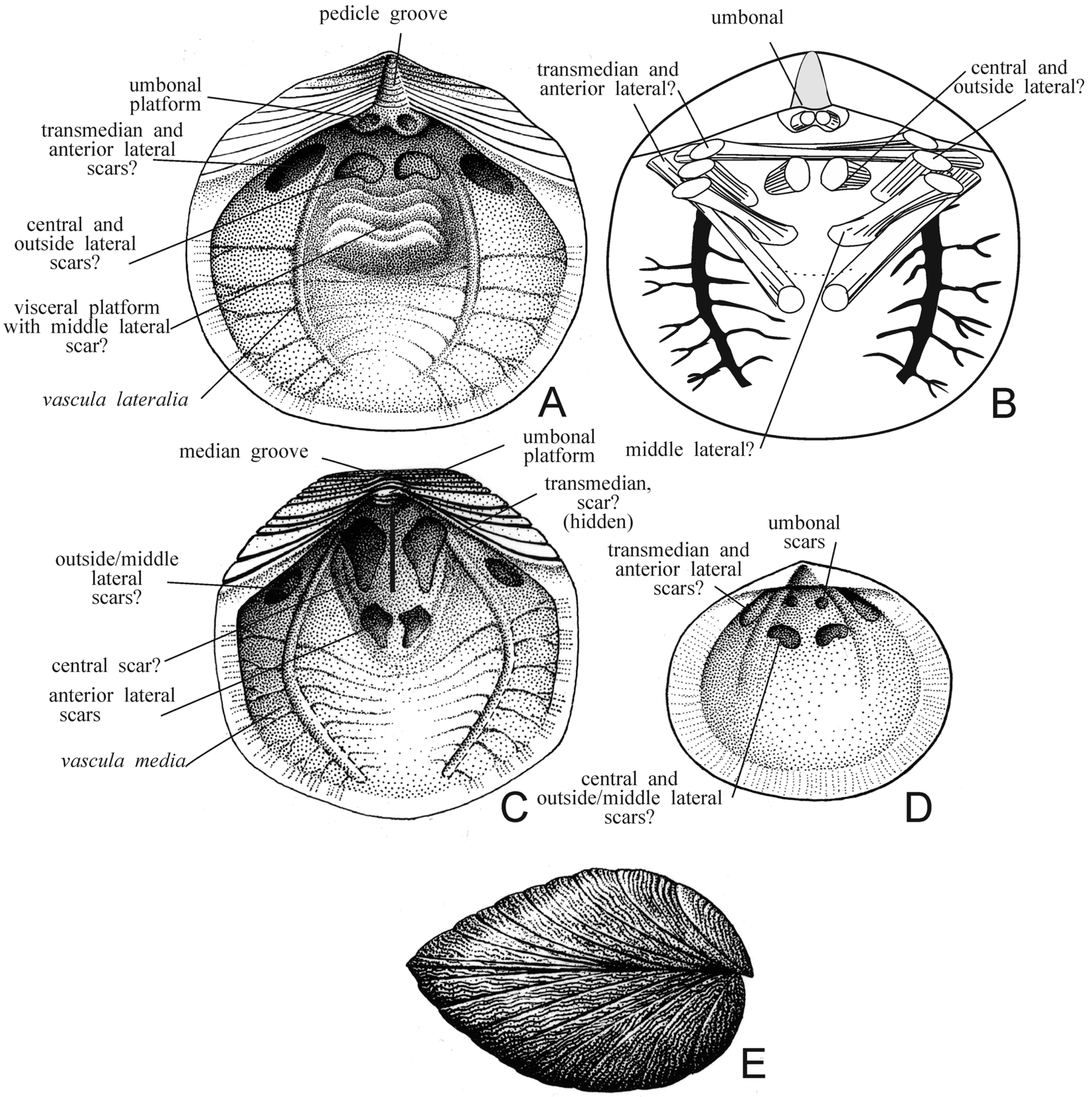


Fig. 5. *Aulonotreta antiquissima* (Eichwald, 1843), from the Dapingian Volkhov Regional Stage, reconstructions are based on multiple specimens, all drawn at approximately 2.5 times. **A**, reconstruction and interpretation of the ventral interior; **B**, reconstruction and interpretation of the musculature; **C**, reconstruction and interpretation of the dorsal interior; **D**, reconstruction and interpretation of the ventral interior of a juvenile valve (based on examination of CNIGR 122/10892, figured by Mickwitz 1896, pl. 3:29); **E**, reconstruction and interpretation of profile of a complete articulated shell (based mainly on LMT1201gl; Fig. 2K).

Fig. 4. *Aulonotreta antiquissima* (Eichwald, 1843), from the Dapingian Volkhov Regional Stage. **A**–**E**, NRM-PZ Br65706, fragmented ventral valve, embedded in epoxy resin, Tallinn, Estonia: A, polished and etched sagittal section through centre with location of B indicated; B, detail of primary shell and outer secondary shell with location of C indicated; C, detail of primary layer and outermost lamina of secondary layer with location of D, E indicated; D, detail of primary layer with apatitic aggregates; E, detail of primary layer with nanometric-sized granular apatite; F, detail of the double lamina with stacked acicular apatite and median slit, separating primary and secondary layers; G, detail of variously shaped apatitic aggregates in primary layer. **H**–**M**, NRM-PZ Br133687, etched and sectioned fragments of a dorsal valve, Mäekalda, Estonia: H, exfoliated fragment embedded in epoxy resin, polished and etched, showing contact between two hollowed lamellae in the secondary layer; I, thin-section of same fragment, viewed through transmitted polarized light, showing the birefingent apatitic laminae at the boundary between lamellae; J, detail of I, showing birefingent apatite in the primary layer; K, anterior view of the dorsal interior, showing the loss of the visceral platform and the hollowed lamellae of the secondary layer; L, detail of K, showing the compact apatitic layers surrounding the hollowed lamellae and the primary layer; M, detail of K, showing the flattened rim surrounding the interior and the lamellose exterior.

Ontogeny and ornamentation. The earliest ontogeny is poorly preserved on both valves in the available material, but the beak of one ventral valve (NRM-PZ Br65710; Fig. 3A, C, D) has a smooth, poorly defined transversely oval area, about 1 mm wide and 0.4 mm long, which appears to represent the earliest larval shell; it lacks any kind of structures and the rugose ornamentation starts directly outside this area (Fig. 3A–C). The rugose ornamentation on the earliest juvenile shell is regularly concentric with evenly spaced rugae, around 60 µm apart (Fig. 3C), and the ornamentation with undulating rugae generally starts outside the first growth lamellae (Figs 2B–J, 3A–D, G). However, the post-larval ontogeny is also poorly understood and although there are hundreds of adult specimens in the investigated museum collections in Estonia, Sweden and St Petersburg, it is remarkable that only one well-preserved slightly more juvenile ventral valve has been found so far (illustrated by Mickwitz 1896, pl. 3:29). This juvenile ventral valve (CNIGR 122/10892) just has two growth lamellae and shows the well-preserved interior with muscle scars and the early *vascula lateralia*, as described above (Fig. 5D). The strongly lamellose adult shells have up to about 13 major growth lamellae in the largest available (W = 23) well-preserved ventral valve (CNIGR 114/10892). The growth lamellae have a tendency to become easily exfoliated in most available valves (Figs 2C–F, 3B, D, G). The first growth lamella is generally formed when the valve is around 8.0–10.0 mm wide and 2.5–5 mm long, and lamellae are subsequently added at a rather variable rate of around 1–6 mm apart, during the growth of the shell, with a tendency of the last lamellae to become more closely spaced (Figs 2B–K, 4A, 5E). The growth lamellae are ornamented with strongly undulating, rather evenly spaced, high and rounded rugae, up to 70 µm high and around 100–200 µm apart (Fig. 2B–K). However, there are frequent disturbances to the regular rugose ornamentation and the curved ribs at times flow together or become disturbed (Fig. 2B–J); other irregularities could be due to injuries (Fig. 3A, D). The entire post-larval lamellose and rugose shell is pitted and has an ornamentation of fine micro-pits, which are generally rounded to elongate rhomboidal, in general about 6–8 µm long and 4–5 µm across, but vary in size and shape as they are distributed and deformed over the crest of the high rugae (Fig. 3J, L). The pits are separated by low ridges, generally 1–2 µm across (Fig. 3L).

Shell structure. The total thickness of an adult shell can be up to more than 4–5 mm in the thickest lamellose part of the visceral area of both valves (Fig. 4A). The outermost rheomorphic primary layer is also comparatively thick, around 10–70 µm thick over the rugose adult surface (Fig. 4B–C), and has a tendency to break with a conchoidal fracture. The layer is well-defined and separated from the underlying secondary shell by a thin slit, which causes it to be easily exfoliated (Figs 2B, C, 4A–F). In transmitted polarized light the primary layer is seen as a dense and birefingent apatitic layer (Fig. 4I, J). Under SEM the primary layer has a densely micro-crystalline structure, with a very varying array of randomly organized and oriented apatitic units and aggregates, including nanometric-sized granular, spherulitic, plate-like structures, as well as needles, rods and acicular shapes of very varying sizes (Fig. 4B–E). The largest rod-like units in the lower part of the primary layer are up to around 20 µm long and a couple of micrometres across, but the size decreases rapidly towards the upper 6–7 µm of the primary layer, which is made up of nanometric-sized acicular to granular units. The primary layer carries the finely pitted ornamentation and all the fine rheomorphic variation with undulating rugae (Fig. 4E, I, J). The lower boundary to the secondary layer is formed by a distinctive lower lamina, around 5–7 µm thick, which is made up of acicular units that are closely stacked perpendicular relative to the shell exterior and the top of the underlying secondary shell has an identical upper lamina, separated from the primary layer by a thin slit (Fig. 4D–I). The secondary layer can be up to 5–6 mm thick, underneath the thickened visceral platforms (Fig. 4A). It is made up of a series of stacked growth lamellae, all of which are roughly wedge-shaped in sagittal sections; the interior lamellae, up to around 0.5 mm thick and usually somewhat laminated internally (Fig. 4A), are becoming gradually more inclined (up to around 10–30 degrees) relative to the exterior of the valve. The outermost secondary lamellae (corresponding to the up to 13 major growth lamellae as described above) form separate wedge-shaped packages that vary in size through ontogeny, but generally around up to around 0.5 mm thick and 1–4 mm long. The easily exfoliated major growth lamellae are also separated from the underlying lamellae by a 1 µm slit, marked by two thin laminae of acicular units that are closely stacked perpendicular relative to the shell exterior (Fig. 4A, H, I). The underlying interior secondary growth lamellae are only densely apatitic in the upper- and lowermost parts (as well as in the internal lamination; Fig. 4A), whereas the central core of the lamellae only has areas of loosely distributed, dispersed apatitic units and aggregates as described above, in a surrounding matrix that mainly now consists of calcium carbonate (Fig. 4A, I, J). This causes the lamellae of the secondary shell to become hollowed-out, with only the upper and lower apatitic laminae standing proud, after treatment with weak acetic acid (Fig. 4K–M). During the process, both the calcium carbonate and the dispersed apatitic grains set within the calcium carbonate matrix are dissolved and disarticulated, respectively, and in many cases the acid treatment also almost completely removes the internal lamellar thickenings of the visceral area (Fig. 4H, K–M).

Stratigraphic distribution. Ordovician (Dapingian, Volkhov Stage).

Aulonotreta neptuni sp. nov.
Figures 6, 7

1982 *Aulonotreta*; Jaanusson & Mutvei, fig. 6. [Listed].

Derivation of name. From the type locality at Hälludden, close to the so-called 'fields of Neptune' on northern Öland (e.g. Jaanusson & Mutvei 1982)

Holotype. SGU9919 (Fig. 6H, J, K), a fragmentary ventral valve from the lower Darriwilian Kunda Stage (*Asaphus raniceps* Zone), Hälludden, northern Öland, Sweden.

Examined material. All from the lower Darriwilian Kunda Stage, Sweden. SGU9920 (Fig. 6E), completely exfoliated complete articulated shell (W = 23.0, Ld = 21.0, Lv = 22.0, T = 11.0, LL = 8, Vld = 7.2, Vwd = 6.4, Vlv = 5.6, Vwv = 6.4), Hälludden, northern Öland, Sweden. NRM-PZ Br14925 (Fig. 6A), slightly exfoliated, fragmented dorsal valve (W = 18.0, Ld = 15.0, Hd = 3.5, LL = 4; Fig. 2D), Hälludden, northern Öland, Sweden. NRM-PZ Br20075 (Fig. 6B), internal mould of fragmented dorsal valve, Hälludden, northern Öland, Sweden. NRM-PZ Br14920 (Fig. 6C), slightly exfoliated, fragmented dorsal exterior, Hälludden, northern Öland, Sweden. NRM-PZ Br14934 (Fig. 6D), slightly exfoliated, fragmented dorsal exterior, Torp, northern Öland, Sweden. NRM-PZ Br20908 (Fig. 6F), internal mould of ventral interior, Byrum, northern Öland, Sweden. NRM-PZ Br20121 (Fig. 6G), fragmented ventral interior, Hälludden, northern Öland, Sweden. NRM-PZ Br2019 (Fig. 6I), internal mould of dorsal interior, Hälludden, northern Öland, Sweden. NRM-PZ Br18408 (Fig. 6L), fragmented dorsal interior, Enerum, northern Öland, Sweden. In addition to an undetermined number of more fragmentary valves. NRM-PZ Br14938 (Fig. 6M–O), fragmented dorsal exterior, Hälludden, northern Öland, Sweden.

Diagnosis. Shell thick, somewhat transversely oval; posterior outline triangular with close to right umbonal angle in adults, close to equibiconvex, less than half as thick as wide; lamellose; shell structure completely recrystallized; ornamentation with undulating, evenly spaced rugae; adult shell with ornamentation of fine rhomboidal micro-pits; ventral pseudointerarea well developed, lacking flexure lines, with narrow, deep pedicle groove; dorsal pseudointerarea flattened, with straight posterior margin and poorly defined median groove; visceral area of both valves thickened with terraced platforms, rather wide and triangular in outline, almost extending to mid-valve; dorsal central and anterior lateral muscle scars closely placed, completely bisected by high median ridge, extending to anterior edge of visceral area; *vascula lateralia* of both valves submedian, slightly convergent; *vascula media* absent.

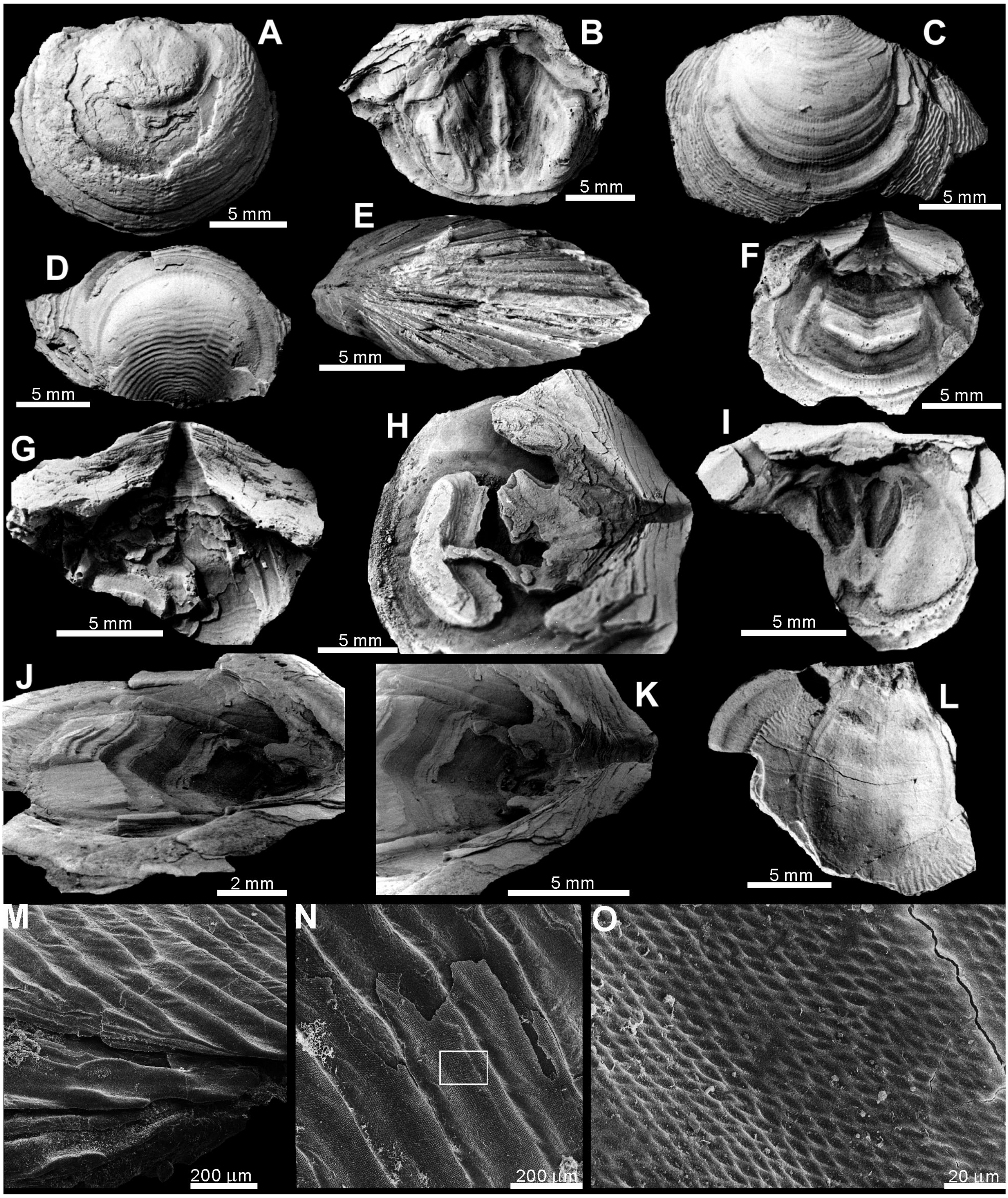
Description. Shells large and thick, less than half as wide as thick in one complete shell, nearly equibiconvex, with flattened convex lateral profile, only somewhat dorsibiconvex; height of dorsal valve only less than 1 mm higher than ventral valve in one complete articulated shell (Figs 6E, 7C). Maximum thickness and height of both valves at mid-valve. Outline of both valves broadly transversely oval; posterior outline triangular, with distinctive almost right umbonal angle in adults; greatest width somewhat anterior to mid-valve (Fig. 7A, B). Shell lamellose, with up to about eight major growth lamellae in one complete shell; growth lamellae ornamented with strongly undulating, evenly spaced rugae (Fig. 6C, D, M–O). Adult shell with ornamentation of fine rhomboidal micro-pits (Fig. 6M–O). Pseudointerareas of both valves flattened, wide and deeply hollowed and undercut. Interior of both valves surrounded by distinctive flattened rim, starting directly anterior to pseudointerarea (Figs 6L, 7A, B).

Ventral valve only somewhat longer, less than 1 mm difference in the largest complete articulated shell, and gently convex (Figs 6E, 7C). Ventral pseudointerarea lacking flexure lines, but with strongly developed growth lines, flattened and orthocline, with close to right umbonal angle; strongly developed, somewhat undercut and raised above the valve floor, very wide and occupying close to all of valve width in adults; propareas extending far out to the lateral borders of valve; pedicle groove deep and narrow, widening anteriorly (Figs 6G, H, K, 7A).

Dorsal valve gently convex (Figs 6E, 7C). Dorsal pseudointerarea with straight posterior margin, lacking flexure lines, but with strongly developed growth lines, flattened orthocline; not distinctly undercut, but, raised above the valve floor, wide, occupying all of valve width in largest specimens; propareas extending far out to the lateral borders of valve and extending for around one third of the valve length; median groove very poorly defined (Figs 6A, D, E, I, 7B).

Visceral area, musculature and mantle canals. The visceral areas of both valves are thickened and form distinctive terraced platforms, with rather wide and triangular outlines, supporting the central body cavity. The body cavity has deeply impressed and closely spaced muscle scars and extend only somewhat underneath the rim-like projecting pseudointerareas and lateral posterior borders in the ventral valve. The body cavities of both valves are comparatively small and placed in the posterior half of both valves (Figs 6B, F–K, 7A, B).

The ventral scars of the umbonal muscle are poorly preserved in most specimens, but appear to form two tooth-like processes, directly at the anterior end of



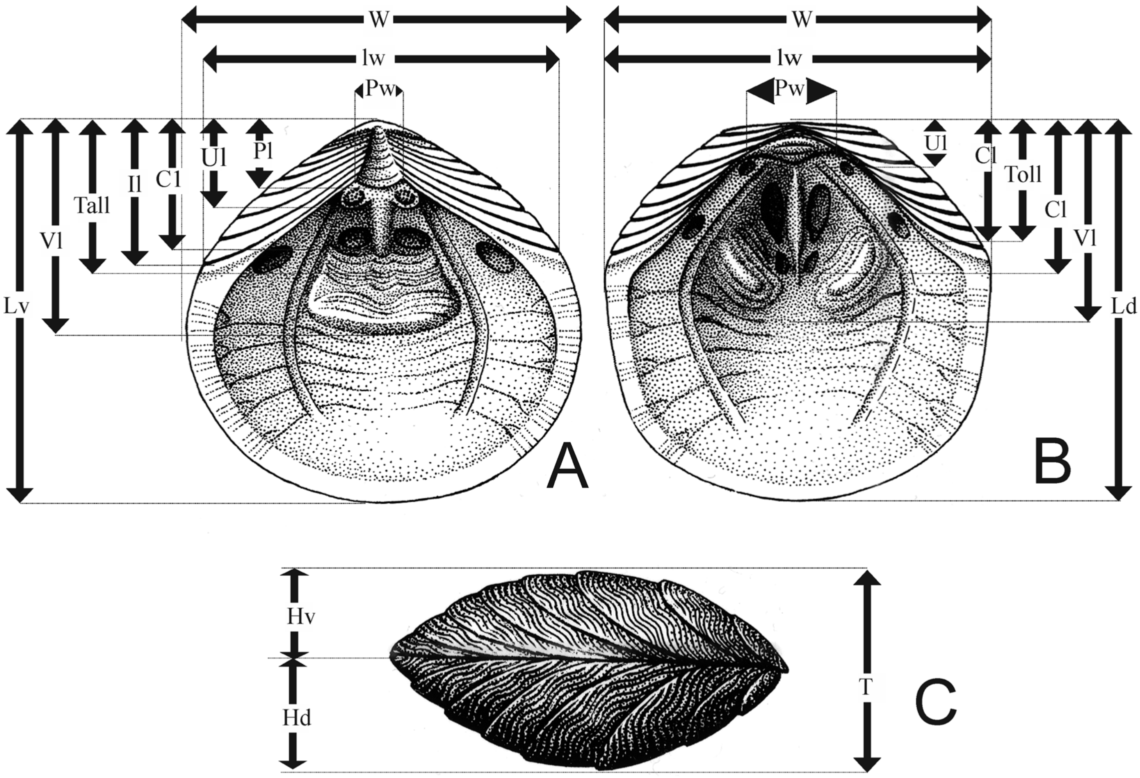


Fig. 7. *Aulonotreta neptuni* sp. nov., all from the lower Darriwilian Kunda Stage (*Asaphus raniceps* Biozone), Öland. The reconstructions are based on multiple specimens, all drawn at approximately 2.5 times. **A**, reconstruction and interpretation of the ventral interior, with explanation of measurement; **B**, reconstruction and interpretation of the dorsal interior with explanation of measurement; **C**, reconstruction and interpretation of the profile of a complete articulated shell (based mainly on SGU9920; Fig. 6E).

the pedicle groove (Figs 6F, 7A). The assumed scars of the central and outside lateral muscles are difficult to interpret; in one specimen they seem to be elevated and extending anteriorly from the umbonal process, but this could possibly be an effect of recrystallization (Fig. 6H, J, K). In other specimens there are indistinct imprints directly anterior and beneath the umbonal scars (Figs 6F, G, 7A). The ventral body cavity is supported by a thickened central large elevated platform, bearing a faint median depression, which in some specimens is ridge-like posteriorly (Figs 6F, G, 7A). The wide platform becomes thickened anteriorly, where it almost extends to around mid-valve. The possible ventral scars of the transmedian and anterior lateral muscles form elongate areas directly anterior to the propareas, but do not seem to extend underneath the elevated propareas and marginal rim (Figs 6F, H, 7A).

The dorsal scars of the umbonal muscle form a single poorly defined buttressed process, directly anterior to the poorly defined median groove (Figs 6B, I, 7B).

Fig. 6. *Aulonotreta neptuni* sp. nov., all from the lower Darriwilian Kunda Stage (*Asaphus raniceps* Zone). **A**, NRM-PZ Br14925, slightly exfoliated, fragmented dorsal exterior, Hälludden, northern Öland, Sweden. **B**, NRM-PZ Br20075, latex cast internal mould of fragmented dorsal interior, Hälludden, northern Öland, Sweden. **C**, NRM-PZ Br14920, slightly exfoliated, fragmented dorsal exterior, Hälludden, northern Öland, Sweden. **D**, NRM-PZ Br14934, posterior view of slightly exfoliated, fragmented dorsal exterior, Torp, northern Öland, Sweden. **E**, SGU9920, lateral view of almost completely exfoliated complete articulated shell, Hälludden, northern Öland, Sweden. **F**, NRM-PZ Br20908, latex cast of ventral internal mould, Byrum, northern Öland, Sweden. **G**, NRM-PZ Br20121, fragmented ventral interior, Hälludden, northern Öland, Sweden. **H**, SGU9919 (Holotype), lateral view of a fragmentary ventral interior, Hälludden, northern Öland, Sweden. **I**, NRM-PZ Br2019, latex cast of dorsal internal mould, Hälludden, northern Öland, Sweden. **J**, detail of lateral view of H, showing visceral area. **K**, detail of lateral view of H, showing pseudointerarea and posterior part of visceral area. **L**, NRM-PZ Br18408, fragmented dorsal interior, Enerum, northern Öland, Sweden. **M**–**O**, NRM-PZ Br14938, fragmented dorsal exterior, Hälludden, northern Öland, Sweden: M, lateral view of exterior, showing contact between two rugose lamellae; N, detail of M, showing partly exfoliated rugose primary layer and location of O; O, detail of rhomboid micro-pits.

The very elongated and narrow dorsal central and anterior lateral muscle scars are closely placed, completely bisected by a well-developed high median ridge, extending to the anterior edge of the visceral area; the scars seemingly are placed completely outside the very wide central visceral platform (Figs 6B, I, 7B). The small dorsal scars of the outside and middle lateral muscles are poorly impressed, directly anterior to the propareas, and the possible scars of the dorsal transmedian muscle are even less well developed (Figs 6B, I, 7B).

The *vascula lateralia* of both valves are well developed in some specimens, submedian, forming with two main gently arcuate, convergent trunks, beginning at the posterior section of the visceral area and extending for almost most of the length of the shell. The main secondary trunks are only ramified distally, radiating inwardly and outwardly almost perpendicular to the main trunks, becoming strongly and finely ramified, closely spaced terminal branches extending onto the distinctive flattened rim surrounding the valve interiors (Figs 6L, 7A, B). The *vascula media* are absent.

Ontogeny and ornamentation. There are no juvenile valves at all represented in the hundreds of fragmented specimens examined. Moreover, the growth lamellae have a tendency to become exfoliated in almost all available valves and it is not possible to trace the development of the shell growth in any detail (Fig. 6A, C–E, M–O). The adult lamellose shell has around eight major growth lamellae in the only available (W = 23) large, well-preserved complete shell (SGU9920), and judging by this specimen, the growth lamellae are added at around 1–4 mm apart during the growth of the shell (Figs 6E, 7C). The growth lamellae are ornamented with strongly undulating, rather evenly spaced, high and rounded rugae, around 0.2–0.4 mm apart (Fig. 6C, D, M, N). The entire post-larval lamellose and rugose shell is pitted and has an ornamentation of fine micro-pits, which are generally rounded to elongate rhomboidal, in general about 6–10 µm long and 4–5 µm across, but vary in size and shape as they are distributed over the high rugae (Fig. 6N–O).

Shell structure. The fragmented shells are invariably completely recrystallized. A sectioned shell (not figured) revealed that it is composed of a compact finely apatitic mass, which does not preserve any recognizable structures.

Discussion. Unfortunately the poor preservation of the strongly fragmented and recrystallized material of *Aulonotreta neptuni* makes it difficult to compare it in detail with the much better preserved Baltic type species [The broken preservation seems to be a general factor in the fauna from this level on northern Öland (e.g. Kröger et al. 2009).] However, it is clear that the new species from Öland mainly differs from *A. antiquissima* in being considerably less biconvex and more flattened in lateral profile. The Swedish species is less than half as thick as wide in specimens of the same size, while the much more bulbous *A. antiquissima* at the same size is close to 70% as thick as wide. Moreover, *A. neptuni* has a distinctly triangular posterior outline, with close to right umbonal angle in adults, whereas the type species is characterized by a distinctly obtuse umbonal angle and rounded posterior outline. The shell of *A. neptuni* is also considerably less lamellose as compared to the type species, and the pseudointerareas of both valves are not as highly raised and undercut as in the Baltic species. The musculature of *A. neptuni* is less well-preserved, but the assumed scars of the dorsal transmedian muscle is not placed underneath the dorsal propareas as in *A. antiquissima.* The dorsal anterior lateral scars in *A. neptuni* appear to be more anteriorly placed as compared with *A. antiquissima*, but this could be an effect of shell exfoliation. Moreover, the visceral platforms in the Swedish species are much wider and have more triangular outlines than the type species, where the dorsal and ventral visceral platforms have more rectangular and oval outlines, respectively.

Stratigraphic distribution. Ordovician (lower Darriwilian Kunda Stage).

DISCUSSION

Musculature and visceral area

In the only previous detailed description, Mickwitz (1896; translated by Walcott 1912) already noted that the muscle scars of *Aulonotreta* can be directly compared with the scars of other Obolidae. Like most early Palaeozoic representatives, *Aulonotreta* appears to have the following six pairs of symmetrically arranged scars (see Bulman 1939; Holmer & Popov 2000): (1) central, (2) umbonal, (3) anterior lateral, (4) middle lateral, (5) outside lateral and (6) transmedian (Fig. 5B). However, the identification and location of individual scars are not always completely straightforward and Mickwitz (1896; Walcott 1912) mistook the scars on the umbonal process for a ‘pedicle muscle’, which, as noted by Bulman (1939), is not present in any fossil or recent linguliform. It is possible that some of the oblique muscles (like the middle lateral) may have been absent in *Aulonotreta* and the individual scars of each muscle suggested here are tentative, but the reconstruction is based on the assumption that it had a full set of muscles (Fig. 5A–D). *Aulonotreta* differs from most other species of Lingulida in its bulbous, strongly dorsibiconvex shell and in having a very short visceral cavity with the muscle scars placed closely together in the posterior part of the valves, where some of the oblique muscles are attached to areas lying underneath the pseudointerareas (Fig. 5A–D). As noted by Holmer (1993) and Holmer & Popov (1995), the morphology and shape of *Aulonotreta* are only similar to two equally aberrant possible members of the Elkaniidae, *Lamanskya* and *Volborthia*, from the Baltic Ordovician. Both these taxa also have strongly dorsibiconvex shells (up to 90% and 70% as thick as wide in *Volborthia* and *Lamanskya*, respectively), in addition to short visceral areas. However, the musculatures of both these problematic taxa are extremely poorly known and cannot be compared in detail, but *Volborthia* clearly has an elevated ventral umbonal process with the possible scars of the umbonal muscles, which is similar to that of *Aulonotreta* (see Holmer & Popov 1995, fig. 3c–e).

Ontogeny and ornamentation

The early ontogeny is very poorly preserved in both species described above, but a single specimen of *A. antiquissima* preserves a possible ventral larval shell (about 1 mm wide and 0.4 mm long), which appears to be completely smooth and lacks all identifiable structures (Fig. 3A–C). In contrast, the otherwise similar *Volborthia* and *Lamanskya* both have much smaller and distinctly pitted larval shells with micro-pits (Holmer 1993, figs 6a, b, 8i–k). However, it is possible that the pitting in the early ontogeny of *Aulonotreta* has been lost during fossilization. The post-larval lamellose growth of *Aulonotreta* is much more strongly developed as compared with *Volborthia* and *Lamanskya* and the up to 13 major growth lamellae of *Aulonotreta* (Figs 2K, 5E) are clearly associated with more major mantle retractions during the ontogeny (Fig. 4B). As noted by Holmer & Popov (1995, p. 220), these types of periods of major mantle retractions invariably form up to a dozen or so major growth bands on a great number of linguloids and siphonotretoids and it is most likely that they are related to the stress and cessation in shell growth associated with regular spawning. The characteristic undulating rugose ornamentation of *Aulonotreta* is largely unlike that of any other linguliform. However, Mickwitz (1896, pl. 3:104) noted that the spinose and lamellose shell of *Thysanotos* has a somewhat similar strong rugose ornamentation but lacks the characteristic undulations (see also Popov & Holmer 1994, fig. 43). The pitted post-larval ornamentation of *Aulonotreta* with elongate, 6–8 µm long rhomboidal micro-pits (Figs 3L, 6O) is somewhat similar to that of *Volborthia* and *Lamanskya* and many more typical Ordovician elkaniids, such as, e.g., *Tilasia* (Holmer 1991), but the pits are invariably larger in these taxa. In *Volborthia*, *Tilasia* and *Lamanskya*, the rhomboidal pits are up to around 400, 100 and 50 µm long, respectively (Holmer 1991, 1993; Holmer & Popov 1995). In size and shape, the rhomboidal pits of *Aulonotreta* are very similar to those found on the postlarval shells of the minute lingulid *Paterula*, where they are up to 8–10 µm long (e.g. Holmer & Popov 2000, fig. 35; Williams 2003, text-fig. 2). The various types of micro-pits in obolids (such as the Eoobolidae and Zhanatellidae; Holmer & Popov 2000) have generally been interpreted as negative imprints of vesicular or mineralized structures in the periostracum (see, e.g., Williams & Holmer 1992; Williams 2003). However, Williams (2003, p. 83) noted that the deformed rhomboids as present in *Paterula* are unlikely to represent imprints of mineralized tablets and suggested that they represent a cast of an ornamented periostracum. Holmer et al. (2017) recently discussed the nature and formation of larger rhomboid pits (0.15–0.3 mm long) in linguliform brachiopods, similar to those present in *Volborthia* and *Lamanskya*, and it is also unlikely that these rhomboids represent imprints of mineralized tablets.

Shell structure

The unique poorly mineralized apatitic structure in the lamellose secondary shell of *Aulonotreta* was also already noted and illustrated by Mickwitz (1896), who wrote (here quoted from the translation by Walcott 1912, p. 439) that ‘A noteworthy appearance, which has only been noticed with *0. antiquissimus*, deserves to be emphasized. The ring-shaped lamellae of the anterior part of the shell consist of rock-mass (limestone), but are, as all lamellae, clothed with a homogeneous (corneous) layer, so that it gives the impression that the individual lamellae had been hollow and after the death of the animal had been filled with calcareous mud. It is, however, more likely that the inner layer of the canal, which is less capable of resistance, was dissolved after the death of the animal and restored by the penetrating calcareous mud.’ The shell structure and the contact between the outer homogeneous layer (= primary layer) and the mostly mud-filled secondary layer is also well illustrated by Mickwitz (1896, pl. 3:35). Thus, a shell of *A. antiquissima* that is dissolved out of the limestone with acid will invariably result in the hollowing out of the secondary lamellae as the matrix of calcareous mud is dissolved, which also results in the disintegration of most of the loosely organized apatitic grains (Fig. 4H–M). This unique shell structure is most similar to that of, e.g., *Siphonotreta*, where the hollowed out equally lamellose secondary shell contains almost identical chambers with loosely organized very similar apatitic grains (Williams et al. 2004, text-fig. 1). Williams et al. (2004) interpreted the hollows (termed chambers) in the secondary lamellose shell structure of living *Siphonotreta* as having once been filled with organic glycosaminoglycans (or GAGs) with dispersed apatitic grains. This interpretation, which is similar to that proposed by Mickwitz (1896), is also adopted for understanding the hollowed structures in the secondary lamellae of *A. antiquissima*. During the taphonomy of *A. antiquissima*, the empty GAGs chambers, with dispersed remaining apatitic grains would have been largely filled by calcium carbonate. Williams & Cusack (2007, p. 2473, fig. 1631) suggested that this type of shell structure with GAGs chambers may be an important synapomorphy for a group that also includes some of the paterinates (see Williams et al. 1998), which are among the oldest known Cambrian brachiopods. In contrast to *Aulonotreta*, the secondary shell structure of the morphologically similar *Volborthia* and *Lamanskya* lacks all evidence of this siphonotretoid-like shell structure and both taxa preserve a baculate secondary shell, like the majority of all lower Palaeozoic obolids (Holmer 1993; Holmer & Popov 1995).

Environment and life habit

The Volkhov Toila Formation in Estonia consists of argillaceous glauconitic limestones, including intervals with more soft argillaceous marls, like in the Telinõmme Member (e.g. Raukas & Teedumäe 1997), which has yielded almost all of the available well-preserved material of *A. antiquissima* (Fig. 1). These marly limestones usually contain a very well-preserved fauna, with many still-articulated shells of brachiopods, including some articulated shells of *A. antiquissima*. The fauna has probably not been transported very far and sometimes even the delicate spinose shells of siphonotretoids are articulated with perfectly preserved spines embedded in the soft marls (Holmer, unpublished observations). Although it is commonly assumed that lingulids and obolids were active burrowing animals, comparable to the living lingulids, this has been repeatedly shown to be inaccurate for most early Palaeozoic lingulids, and it should not be assumed that all fossil lingulids were burrowing organisms (see discussion in Zhang et al. 2005). It is also unlikely that *A. antiquissima* had a burrowing life habit as all its characters (shape of shell, ornamentation and musculature) make it poorly adapted for burrowing (e.g. Savazzi 1986) and it most likely belonged to the epifauna. The heavy and thick bulbous shell could probably not be supported by the pedicle in the adult stage and it may have adopted an ambitopic mode of life (e.g. Bassett 1984). The strong rugose ornamentation could have functioned for mechanical reinforcement and to decrease sediment scour around the valves on the soft marly substrate of the Toila Formation (e.g. Savazzi 1986, p. 59). As noted above, there are virtually no well-preserved juveniles among the hundreds of adult specimens, representing both species, in the investigated museum collections in Estonia, Sweden and St Petersburg. The reason for this is not obvious, but it is possible that the early growth stages of *Aulonotreta* were somehow less mineralized and thus had a much lower preservation potential.

Affinity and systematic position

In most of the previous published works on the type species of *Aulonotreta* it has been considered to belong within the Obolidae, and *Obolus* (e.g. Eichwald 1843; Mickwitz 1896; Walcott 1912). Holmer (1993, p. 152) and Holmer & Popov (1995, p. 219) considered *Aulonotreta* to be more related to the aberrant and problematic, possible elkaniids *Lamanskya* and *Volborthia*, respectively. Cusack et al. (1999) placed *Aulonotreta* within the linguloid-discinoid clade, forming a sister taxon to the linguloid clade; however, this was based on the erroneous assumption that *Aulonotreta* has a regular baculate secondary shell. To date the siphonotretid-like non-baculate secondary shell structure of *Aulonotreta* has not been clearly identified within any undoubted linguloid-discinoid. However, the shell structures of most lingulid groups have not been sufficiently investigated, so the distribution of this character is not known in details and it is also possible that the non-baculate shell in *Aulonotreta* simply represents a secondary loss. Pending further detailed study, *Aulonotreta* and the Aulonotretidae are kept within the Lingulida.

Acknowledgements. Lars Holmer's work was supported by a grant from the Swedish Research Council (VR 2018-03390); part of the work was carried out at the Early Life Institute, State Key Laboratory of Continental Dynamics, Northwest University, Xi'an, China, and made possible through a Zhongjian professor scholarship. Zhifei Zhang and Zhiliang Zhang acknowledge the research programmes from the National Natural Science Foundation of China (NSFC 41425008, 41720104002, 41772002, 41621003 and 41890844) and 111 projects of China (P201102007). The manuscript benefited from comments from the referees Michal Mergl and Leonid Popov. This work is a contribution to IGCP 653. The publication costs of this article were partially covered by the Estonian Academy of Sciences.

REFERENCES

Andreeva, O. N. 1972. Brachiopods from the Ordovician Kuragan Suite in the southern Urals. *Paleontologicheskij Zhurnal*, **1972**, 45–56.

Bassett, M. G. 1984. Life strategies of Silurian brachiopods. *Special Papers in Palaeontology*, **32**, 237–263.

Bauert, H., Hints, O., Meidla, T. & Männik, P. (eds). 2014. *4th Annual Meeting of IGCP 591. The Early to Middle Paleozoic Revolution. Estonia, 10–19 June 2014. Abstracts and Field Guide*. University of Tartu, Tartu, 202 pp.

Bulman, O. M. B. 1939. Muscle systems of some inarticulate brachiopods. *Geological Magazine*, **76**, 434–444.

Cusack, M., Williams, A. & Buckman, J. 1999. Chemico-structural evolution of the shell of linguloid brachiopods. *Palaeontology*, **42**, 799–840.

Dronov, A., Tolmacheva, T. J., Raevskaya, E. & Nestell, M. 2005. *Cambrian and Ordovician of St. Petersburg Region – Guidebook of Pre-Conference Field Trip*. St. Petersburg State University, St. Petersburg, 15 pp.

Eichwald, E. de, 1843. Über die Obolen und der silurischen Sandstein von Esthland und Schweden. *Beiträge zur Kenntnis des russischen Reichs*, **8**, 139–156.

Eichwald, E. de, 1859. *Lethaea rossica au paléontologie de la Russie, décrite et figurée*. Ancienne Période Atlas, Stuttgart, 681 pp.

Gorjansky, V. Yu. & Popov, L. E. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shell. *Paleontologicheskij Zhurnal*, **1985(3)**, 3–14 [in Russian].

Hall, J. & Clarke, J. M. 1894. *An Introduction to the Study of the Genera of Palaeozoic Brachiopoda, Natural History of New York, Palaeontology, Vol. 8, Part 2*. New York Geological Survey, Charles van Benthuysen & Sons, Albany, 394 pp.

Holmer, L. E. 1991. The taxonomy and shell characteristics of a new elkaniid brachiopod from the Ashgill of Sweden. *Palaeontology*, **34**, 195–204.

Holmer, L. E. 1993. The Lower Ordovician brachiopod genus *Lamanskya* and the Family Elkaniidae. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **85**, 151–160.

Holmer, L. E. & Popov, L. 1995. The elkaniide brachiopod *Volborthia* from the Lower Ordovician of Baltoscandia. *Paläontologisches Zeitschrift*, **69**, 213–221.

Holmer, L. E. & Popov, L. E. 2000. Lingulata. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda. 2 (revised). Linguliformea, Craniiformea, and Rhynchonelliformea (part)* (Kaesler, R. L., ed.), pp. 30–146. Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.

Holmer, L. E., Popov, L. E., Ghobadi Pour, M., Zhang, Z. & Zhang, Z. 2017. Unusual pitted Ordovician brachiopods from the East Baltic: The significance of coarsely pitted ornamentation in linguliforms. *Papers in Palaeontology*, **3**, 387–399.

Jaanusson, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Baltoscandia. In *The Ordovician System. Proceedings of Palaeontological Association Symposium, Birmingham, 1974* (Bassett, M. G., ed.), pp. 301–326. Cardiff.

Jaanusson, V. & Mutvei, H. 1982. *Ordovician of Öland. Guide to Excursion 3. IV International Symposium on the Ordovician System, Oslo*. Swedish Museum of Natural History, Stockholm, 23 pp.

Kröger, B., Zhang, Y. & Isakar, M. 2009. Discosorids and Oncocerids (Cephalopoda) of the Middle Ordovician Kunda and Aseri Regional Stages of Baltoscandia and the early evolution of these groups. *Geobios*, **42**, 273–292.

Kutorga, S. S. 1848. Ueber die Brachiopoden-Familie der Siphonotretaceae. *Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersbourg, Verhandlungen*, **1847**, 250–286.

Lamansky, W. 1905. Die Aeltesten Silurischen Schichten Russlands (Etage B). *Mémoires du Comité Géologique, Nouvelle série, Livraison*, **20**, 1–203.

Männil, R. 1966. *Evolution of the Baltic Basin During the Ordovician*. Valgus Publishers, Tallinn, 200 pp. [in Russian].

Mickwitz, A. 1896. Uber die Brachiopodengattung *Obolus* Eichwald. *Memoires de l'academie imperiale des sciences de St.-Petersbourg*, **4**, 1–215.

Popov, L. & Holmer, L. E. 1994. Cambrian–Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata*, 35, 1–166.

Raukas, A. & Teedumäe, A. (eds). 1997. *Geology and Mineral Resources of Estonia*. Estonian Academy Publishers, Tallinn, 436 pp.

Savazzi, E. 1986. Burrowing sculptures and life habits in Paleozoic lingulacean brachiopods. *Paleobiology*, **12**, 46–63.

Schallreuter, R. 1983. Vertebratenreste aus einem unter ordovizischen Geschiebe. *Neues Jahrbuch für Geologie und Paläeontologie Monatshefte*, **1983**, 101–112.

Stouge, S. 2004. Ordovician siliciclastics and carbonates of Öland, Sweden. *Erlanger Geologische Abhandlungen, Sonderband*, **5**, 91–111.

Viira, V., Löfgren, A., Mägi, S. & Wickström, J. 2001. An Early to Middle Ordovician succession of conodont faunas at Mäekalda, northern Estonia. *Geological Magazine*, **138**, 699–718.

Volborth, A. F. 1869. Über *Schmidtia* und *Acritis*, zwei neue Brachiopoden-Gattungen. *Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersbourg, Verhandlungen, series 2*, **4**, 1–12.

Waagen, W. 1885. Salt-Range Fossils. I. Productus-limestone fossils. *Palaeontologia Indica*, Series 13, 1, part 4(5), 329–770.

Walcott, C. D. 1901. Cambrian Brachiopoda: *Obolella*, subgenus *Glyptias*; *Bicia*; *Obolus*, subgenus *Westonia*; with descriptions of new species. *Proceedings of the United States National Museum*, **23 (1229)**, 669–695.

Walcott, C. D. 1912. Cambrian Brachiopoda. *Monograph of the U.S. Geological Survey*, **51**, 1–872.

Williams, A. 2003. Microscopic imprints on the juvenile shells of Palaeozoic linguliform brachiopods. *Palaeontology*, **46**, 67–92.

Williams, A. & Cusack, M. 2007. Chemicostructural diversity of the brachiopod shell. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda. Volume 6: Supplement* (Williams, A. et al., eds), pp. 2396–2521. Geological

Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.

Williams, A. & Holmer, L. E. 1992. Ornamentation and shell structure of acrotretoid brachiopods. *Palaeontology*, **47**, 1313–1337.

Williams, A., Popov, L. E. & Holmer, L. E. 1998. The diversity and phylogeny of the paterinate brachiopods. *Palaeontology*, **41**, 221–262.

Williams, A., Holmer, L. E. & Cusack, M. 2004. Chemicostructure of the organophosphatic shells of siphonotretide brachiopods. *Palaeontology*, **35**, 657–692.

Zhang, Z., Shu, D., Han, J. & Liu, J. 2005. Morpho-anatomical differences of the Early Cambrian Chengjiang and Recent lingulids and their implications. *Acta Zoologica*, **86**, 277–288.

Problemaatiline käsijalgne *Aulonotreta* Baltoskandia Kesk-Ordoviitsiumist

Lars E. Holmer, Liang Yue, Zhiliang Zhang ja Zhifei Zhang

On kirjeldatud Põhja-Eestis ja Ingerimaal Toila kihistus (Volhovi lade) levinud lingulaatset käsijalgset *Aulonotreta antiquissima* (Eichwald) ning püstitatud uus liik *Aulonotreta neptuni*, mis esineb Rootsis Ölandi saarel Holeni lubjakivis (Kunda lade). *Aulonotreta* on Baltoskandia jaoks endeemiline perekond. Uus hästi säilinud materjal võimaldab iseloomustada selle taksoni lihaskonda, koja mikrostruktuure ning teisi spetsiifilisi tunnuseid, mis olid seni puudulikult tuntud. *Aulonotreta* ebaharilik morfoloogia ja lihaskond viitavad sellele, et perekond oli täiskasvanuna kohastunud elamiseks merepõhjas sette pinnal, kuuludes tõenäoliselt ambitoopse ehk vabalt lebava epifauna koosseisu.