LATE ORDOVICIAN LINGULATE BRACHIOPODS FROM ESTONIA

by LEONID POPOV, JAAK NÕLVAK *and* LARS E. HOLMER

ABSTRACT. The lingulate brachiopod fauna from the Upper Ordovician Harju Series of southern Estonia consists of nine taxa, including the new acrotretid species *Rhinotreta laeta*, *Opsiconidion praecursor*, and *Scaphelasma scutula*. The unusual brachiopod-dominated assemblage was isolated by acid etching, mainly from a thin aphanitic limestone unit in the lower Pirgu Stage of the Viljandi core. The pitted micro-ornament on the larval and postlarval shell and the deep emarginature (pedicle notch) of the lingulide *Rowellella minuta* suggests that it belongs to the Zhanatellidae.

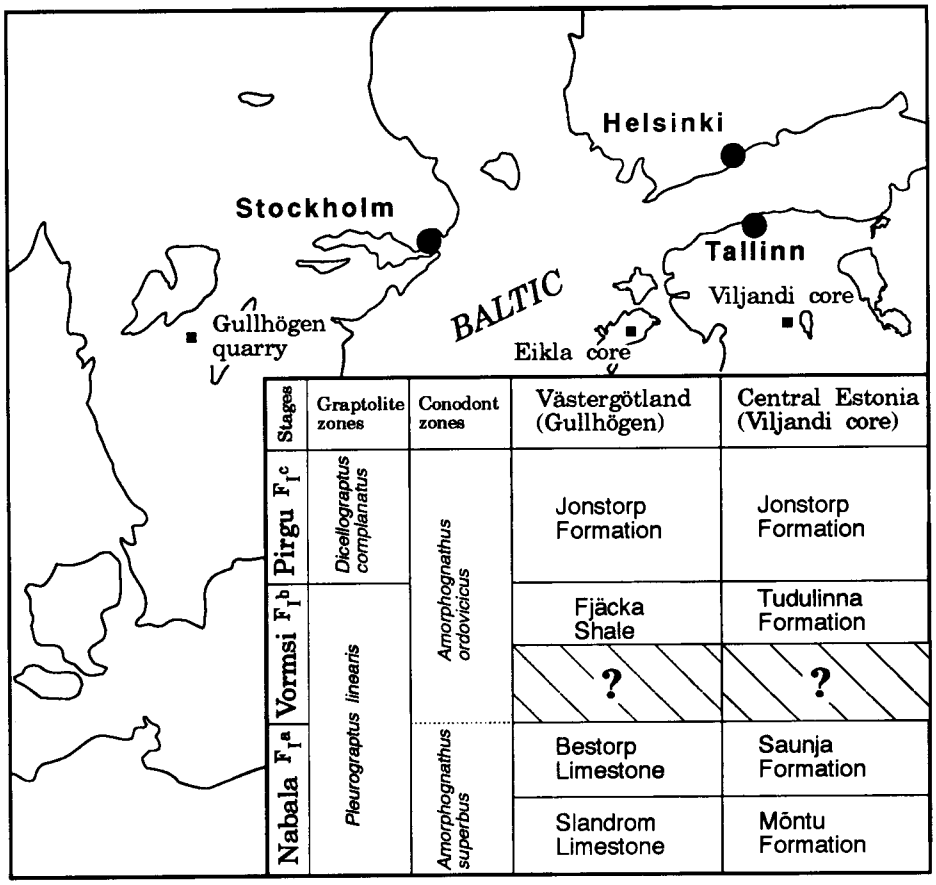
LINGULATE brachiopods, mainly lingulides and acrotretides, are known to be abundant in the early and middle Ordovician sequences of Baltoscandia (Gorjansky 1969; Biernat 1973; Holmer 1986, 1989), but less is known about the late Ordovician (Harju Series) faunas (e.g. Bergström 1968; Holmer 1986; Popov and Nõlvak 1987). The object of this paper is to describe a diverse assemblage of 'micro-brachiopods' (in the sense of Wright and McClean 1991) from the Upper Ordovician Nabala to Pirgu stages (lower–middle Ashgill; upper Pusgillian–lower Cautleyan) of southern Estonia. The described fauna is compared with other late Ordovician lingulate assemblages from Ireland and Sweden.

GEOLOGICAL SETTING, STRATIGRAPHY AND CORRELATION

Most of the lingulate assemblage described here comes from the Nabala–Vormsi interval in the Viljandi core, southern Estonia, but a few specimens originate from the same interval in the Eikla core on the island of Saaremaa (Text-fig. 1); the Upper Ordovician (Harju Series) succession in the latter core has been discussed by Nõlvak (1986), and Nõlvak and Grahn (in press). According to Põlma (1973, fig. 1), the Viljandi core is situated just at the southern boundary of the transitional zone between the Central Baltoscandian and North Estonian confacies belts, whilst the Eikla core is within the North Estonian confacies belt (see also Jaanusson 1976, text-fig. 7).

The upper Ordovician chitinozoan biostratigraphy of the Viljandi core was discussed by Nõlvak (1986), but the lithostratigraphical succession in the core has not been published. The lower part of the Nabala Stage is represented by the Mõntu Formation, consisting mainly of argillaceous limestone with some minor amounts of glauconite. Lingulates are rare, with only a few valves of *Rhinotreta laeta* sp. nov. and *Spondylotreta* cf. *parva* known; both these forms range almost throughout the entire sequence (Text-fig. 2). Above the Mõntu Formation lies a 0·4 m interval of aphanitic limestone (that is, a dense, high-carbonate calcilutite with a conchoidal fracture) belonging to the Saunja Formation; the lower and upper boundaries are marked by hardgrounds. In the unit, lingulates are extremely rare. The Tudulinna Formation of the Vormsi Stage, 6·3 m thick, is represented by spotted red argillaceous marlstones, with some beds of argillaceous and nodular argillaceous limestone; this part of the sequence has generally rare lingulates, but there is an increase in diversity and abundance towards the top, where the majority of the recorded species appear, including *Acanthambonia portranensis*, *Scaphelasma scutula* sp. nov. and *Eoconulus semiregularis*.

[Palaeontology, Vol. 37, Part 3, 1994, pp. 627–650, 7 pls]



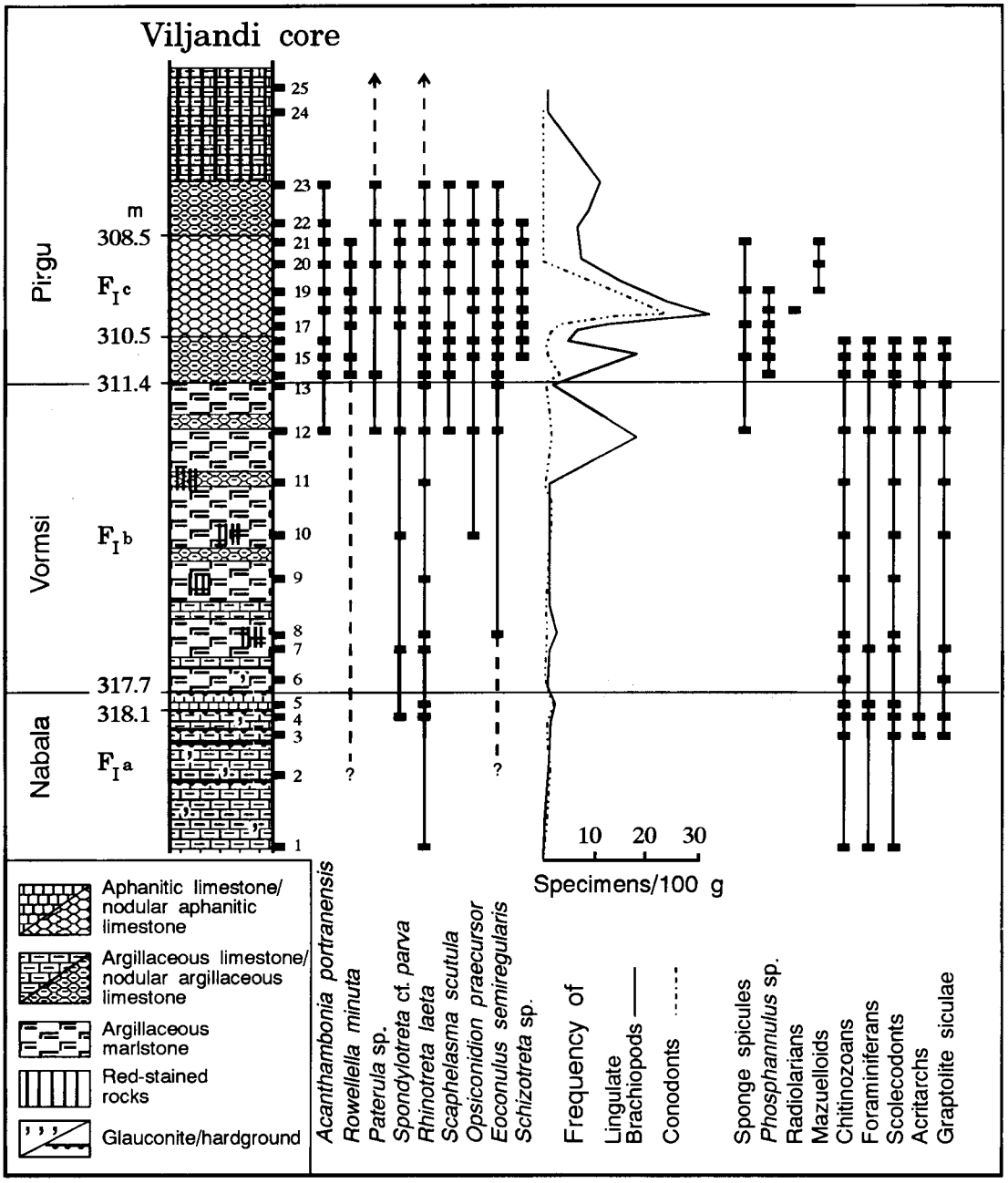
TEXT-FIG. 1. Map of Baltoscandia showing the location of Viljandi and Eikla cores, Estonia, and Gullhögen quarry, Sweden; stratigraphical scheme after Nõlvak and Grahn (in press).

The major portion of the described fauna was isolated from the lower Pirgu Stage, within which an almost three metre thick interval (308·5–331·4 m) of nodular argillaceous limestone and light coloured, nodular aphanitic limestone yielded over thirty lingulate specimens per 100 g. The aphanitic interval is overlain by red argillaceous nodular limestones of the Jonstorp Formation.

Of the recorded lingulates, only *Acanthambonia portranensis* Wright, 1963 is not described below as the material of this species from the Vorsmi–Pirgu stages in the Viljandi core (Text-fig. 2) was described in detail by Popov and Nõlvak (1987). Gorjansky (1969, p. 49) described this species from the Pirgu Stage of southern Estonia.

The distribution of the associated fauna, including mazuelloids, radiolarians, conodonts, and sponge spicules is recorded in Text-figure 2, but is not discussed in detail here. However, it is of note that rich lingulate assemblages are commonly associated with sponge spicules (Text-fig. 2; see also Holmer 1986, 1987); possible sponge-lingulate associations have been described from the Cambrian by Whittington (*in* Conway Morris *et al.* 1982, p. 25, pl. R) and by Lenz (1993) from the Silurian of Canada, where numerous specimens of the lingulide *Paterula* (referred to as *Craniops* sp. by Lenz) are apparently attached around the oscular margin of sponges.

At the generic level, the Estonian lingulate assemblage has a composition similar to that of the Slandrom and Bestorp limestones at Gullhögen quarry, Västergötland (Text-fig. 1) described by



TEXT-FIG. 2. Stratigraphical column of the Nabala–lower Pirgu interval in the Viljandi core, showing the range of lingulates, frequency of lingulates and conodonts, and the range of associated groups of microfossils.

Holmer (1986); *Rowellella*, *Paterula*, *Rhinotreta*, *Scaphelasma*, *Eoconulus*, *Acanthambonia* and *Schizotreta* are present in the somewhat older Swedish fauna, which also contains numerous mazuelloids, radiolarians, sponge spicules and the problematic *Phosphannulus* (Holmer 1987). At the specific level, however, the Estonian and Västergötland assemblages are distinct. *Opsiconidion*

praecursor sp. nov. is the oldest known species of the genus and the most distinctive element of the Estonian assemblage; the genus is not known from the late Ordovician of Sweden.

The Estonian lingulate assemblage is also markedly similar to the assemblage described by Wright (1963) from the Portrane Limestone (Ashgill, Cautleyan) of Ireland, which includes *Rowellella minuta*, *Paterula* cf. *perfecta*, *Spondylotreta* cf. *parva*, *Eoconulus transversus*, *Schizotreta concava*, and *Acanthambonia portranensis*.

McClean (1988, 1989) and Wright and McClean (1991) described a diverse micro-brachiopod fauna from the Chair of Kildare Limestone (Ashgill, Rawtheyan), eastern Ireland, that includes *Acanthambonia portranensis*, although a formal description of this fauna has not been published (McClean 1988). As noted by Wright and McClean (1991), it has been assumed that there was a general decline in the number of lingulate species towards the end of the Ordovician (e.g. Cocks 1979), but the new Estonian and Irish assemblages indicate that this group remained diverse and abundant in beds of Ashgill age.

SYSTEMATIC PALAEONTOLOGY

The classification and terminology of lingulate brachiopods used here mainly follows that of Rowell (1965), Koneva (1986) and Holmer (1989). Measurements (in millimetres) were made with a binocular microscope at × 56 magnification. The method described by Krause and Rowell (1975) is followed in the presentation of the biometric data; vectors of means and variance-covariance matrices were calculated for each set of measurements (Tables 1–6; Text-figs 3–6). The mean, standard deviation (s), and number (N) of measured specimens are given.

All figured specimens are housed in the Institute of Geology, Estonian Academy of Sciences, Tallinn.

Class LINGULATA Gorjansky and Popov, 1985
Order LINGULIDA Waagen, 1885
Family ZHANATELLIDAE Koneva, 1986

Diagnosis. Shell subcircular to elongately suboval in outline; larval and postlarval shell with finely pitted micro-ornament. Ventral valve with flattened pseudointerarea, bisected by deep pedicle groove; flexure lines variably developed; beak with semicircular emarginature (pedicle notch). Dorsal pseudointerarea divided by median groove or undivided; umbonal muscle paired; mantle canals baculate in both valves, with submarginally placed *vascula lateralia* and well developed dorsal *vascula media*.

Genera included. Zhanatella Koneva, 1986; *Fossuliella* Popov and Ushatinskaya, 1992; ?*Kyrshbaktella* Koneva, 1986; *Rowellella* Wright, 1963.

Discussion. According to Koneva (1986), the zhanatellids are distinguished mainly by having a deep, semicircular pedicle notch, which was termed the 'emarginature'. Our unpublished studies into the

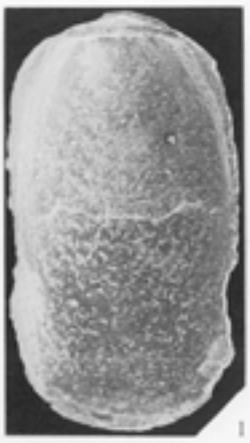
EXPLANATION OF PLATE 1

Figs 1–4. *Rowellella minuta* Wright, 1963; lower Pirgu Stage. 1, Br 1623, (depth 309·1 m); ventral interior; × 50. 2, Br 1624, (depth 310·9 m); dorsal exterior; × 50. 3, detail of the larval portion of shell shown in fig. 2; × 200. 4, detail of pitted micro-ornament of shell in 2; × 940.

Figs 5–7. *Spondylotreta* cf. *parva* Wright, 1963; lower Pirgu Stage. 5, Br 1627 (depth 310·1 m); juvenile dorsal interior; × 100. 6, Br 1628 (depth 310·3 m); ventral larval shell; × 150. 7, Br 1626 (depth 309·1 m); dorsal exterior; × 75.

Figs 8–9. *Schizotreta* sp.; lower Pirgu Stage. 8, Br 1632 (depth 308·7 m); dorsal exterior; × 50. 7, Br 1631 (depth 310·9 m); dorsal exterior; × 50.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.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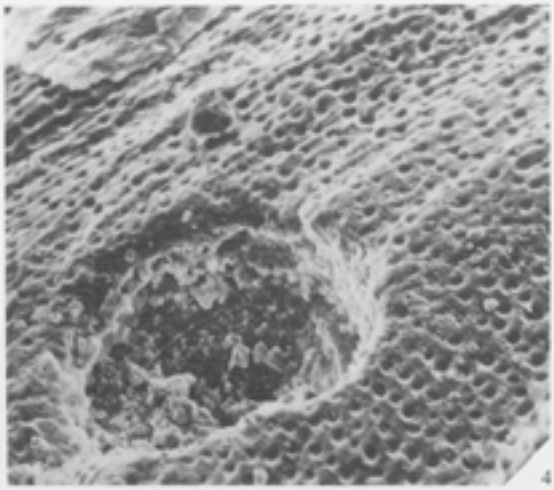
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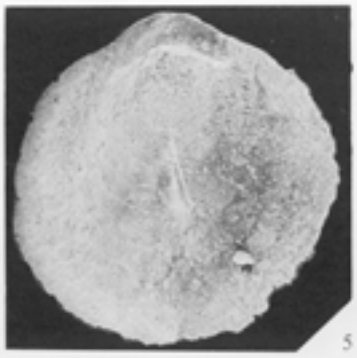
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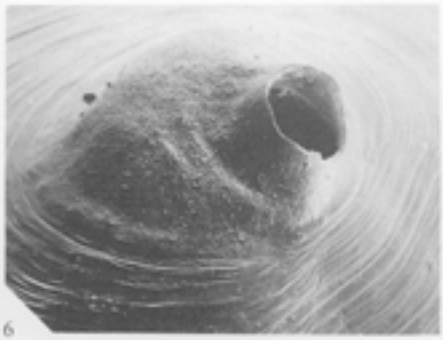
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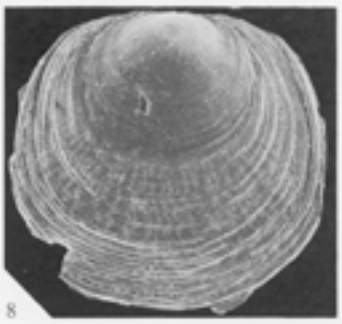
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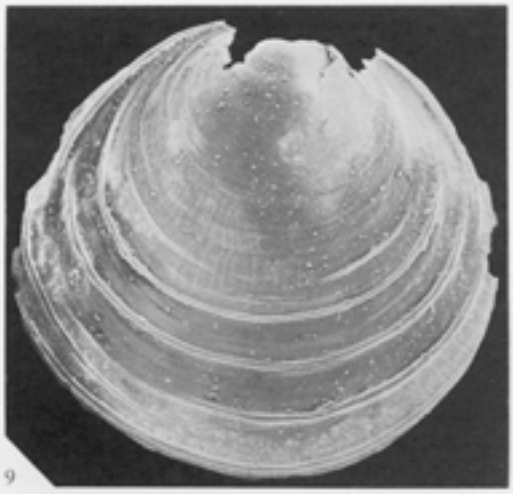
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POPOV *et al.*, *Rowellella, Spondylotreta, Schizotreta*

morphology of *Zhanatella* suggest that a pitted larval and postlarval shell also is a diagnostic character of the family. Both of these features are present in *Rowellella*, which is here referred to the zhanatellids. Koneva (1986) also suggested that *Kyrshabaktella* is a zhanatellid, but this is more problematic, since it is characterized by a smooth larval and postlarval shell.

Genus ROWELLELLA Wright, 1963

Type species. By original designation; *Rowellella minuta* Wright, 1963, from the Ashgill of Ireland.

Rowellella minuta Wright, 1963
Plate 1, figures 1–4

1963 *Rowellella minuta* sp. nov. Wright, p. 233, pl. 1, figs 8–12, 14–18.

Holotype. BB28223 (complete shell; in the Natural History Museum, London) from the Portrane Limestone (Ashgill, Cautleyan), Portrane, Co. Dublin, Ireland.

Estonian material. Seven ventral and five dorsal valves; figured: Br 1623, 1624.

Diagnosis. Shell dorsi-biconvex, elongately subtriangular in outline with close to parallel lateral margins; ornamentation of well developed concentric lamellae; larval and postlarval shell finely pitted.

Discussion. The Estonian specimens are more or less identical to the Irish material in outline and ornamentation. However, the pitted micro-ornamentation has not previously been described from the type material. The semielliptical larval shell is about 0·2 mm wide and lacks growth lines (Pl. 1, fig. 3); it is ornamented by shallow and circular pits about 1·6–2·4 μm in diameter (Pl. 1, fig. 4). The postlarval shell has a similar type of micro-ornamentation with subcircular and transversely oval pits, 1·2–3·9 μm across. A similar type of pitting was described by Holmer (1986, 1989) from several species of *Rowellella*.

Family PATERULIDAE Cooper, 1956

Diagnosis. Shell dorsi-biconvex, inequivalved. Both valves with holoperipheral growth and lacking pseudointerareas; larval and postlarval shell finely pitted; visceral fields of both valves large, extended anterior to mid-valve; *vascular lateralia* of both valves submarginal, arcuate. Ventral valve with emarginature (pedicle notch).

Genera included. Paterula Barrande, 1879.

Discussion. Elliptoglossa Cooper and *Lingulops* Hall were previously included within the family; but they differ from paterulids in having a smooth larval and postlarval shell, marginal beaks in both valves, rudimentary pseudointerareas, and no pedicle notch. This suggests to us that *Elliptoglossa* and *Lingulops* are more closely related to the Obolidae. The Zhanatellidae is the only other lingulide stock that is characterized by having a deep pedicle notch (emarginature) and a pitted larval and postlarval shell.

Genus PATERULA Barrande, 1879

Type species. By original designation; *Paterula bohemica* Barrande, 1879, from the Caradoc of Bohemia.

Paterula sp.
Plate 2, figures 1–6

?1963 *Paterula* cf. *perfecta* Cooper; Wright, p. 235, pl. 2, figs 3–5, 8–10, 13, 16.

Material. Three ventral and twelve dorsal valves; Br 1620–1622 are figured.

Remarks. Paterula is a taxonomically complicated genus; without detailed knowledge concerning the micro-ornamentation and internal features, most species seem to be indistinguishable.

The valves examined are similar to the specimens described by Wright (1963) as *Paterula* cf. *perfecta* from the Portrane Limestone, but we have too few specimens to make a detailed comparison. The Estonian specimens are also somewhat similar to *Paterula* cf. *bohemica* figured by Henningsmoen (1948) from the Fjäcka Shale of the Kullatorp core, Kinnekulle, Sweden.

The subcircular larval shell of *Paterula* sp. is about 50–60 μm in diameter; it is covered by flat-bottomed, rounded to polygonal pits, each 2·4–3·6 μm across (Pl. 2, fig. 4). The pits are separated from one another by elevated ridges, but sometimes they show a cross-cutting relationship, similar to that found on the larval shell of the acrotretoid *Opsiconidion* (Bitter and Ludvigsen 1979). The outer boundary of the larval shell is poorly defined, and there is a gradual change to the net-like pattern of rhombic pits, each about 5·8 μm across, that covers the rest of the postlarval shell (Pl. 2, figs 4–5). An identical type of pitted micro-ornament was described by Holmer (1986) on *Paterula* spp. from the Slandrom Limestone of Sweden.

Order ACROTRETIDA Kuhn, 1949
Family ACROTRETIDAE Schuchert, 1893
Genus SPONDYLOTRETA Cooper, 1956

Type species. By original designation; *Spondylotreta concentrica* Cooper, 1956, from the middle Ordovician of Alabama.

Diagnosis. Ventral valve high to low conical; ventral pseudointerarea well defined, catacline or slightly procline, with distinct interridge; pedicle foramen forming short tube within larval shell; ventral interior with pedicle tube along posterior slope, continued as forked ridge, supported apically by median septum. Dorsal valve slightly convex; dorsal pseudointerarea wide, divided by median groove; dorsal interior with long and high, triangular median septum, and median buttress.

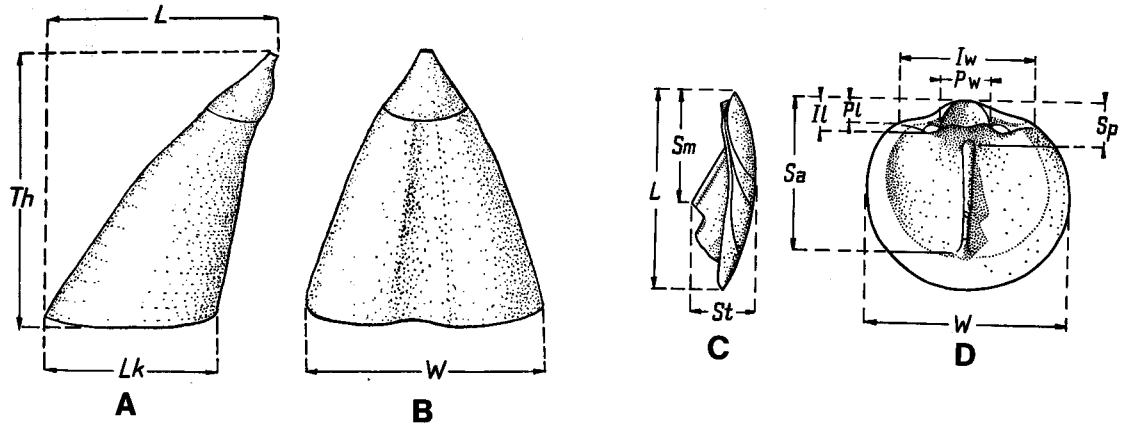
Discussion. Spondylotreta is most similar to *Acrotreta* Kutorga; the type species of the latter, *A. subconica* Kutorga was revised by Holmer and Popov (1994). Amongst other characters, *Acrotreta* differs from *Spondylotreta* in having a higher conical ventral valve, with a pedicle foramen that is not completely enclosed within the larval shell. *Acrotreta* appears to have its main range in the lower and middle Ordovician, whilst *Spondylotreta* is known primarily from the middle to upper Ordovician.

Spondylotreta cf. *parva* Wright, 1963
Plate 1, figures 5–7

cf. 1963 *Spondylotreta parva* sp. nov. Wright, p. 238, pl. 2, figs 17, 20–25; pl. 3, figs 1, 5, 9, 15.

Material. Five ventral and ten dorsal valves; Br 1626–1628 are figured.

Description. Shell transversely subcircular in outline. Ventral valve conical, with procline, slightly flattened pseudointerarea, bisected by distinct interridge. Pedicle foramen placed within the larval shell, and forming short external pedicle tube (Pl. 1, fig. 6). Ventral interior with internal pedicle tube, supported by apical process, forming high median septum; apical pits well developed, placed directly laterally to internal pedicle foramen.



TEXT-FIG. 3. *Opsiconidion praecursor* sp. nov. A–B, dorsal, and C–D, ventral valves, showing locations of measurements (Table 1). L, sagittal length; Lk, length of commissural plane; W, maximum width; Th, maximum depth of the valve; Il, length of dorsal pseudointerarea; Iw, width of dorsal pseudointerarea; Pw, width of median groove; Sp, point of origin of the median septum, measured from the sagittal posterior margin; Sm, point of maximum height of the median septum, measured from the sagittal posterior margin; Sa, length of median septum, measured from the sagittal posterior margin; St, height of median septum; Fa, distance from the anterior margin of the pedicle foramen to the sagittal posterior margin; Fp, distance from the posterior margin of the pedicle foramen to the sagittal posterior margin; A, distance from the sagittal posterior margin to the ventral apex.

Dorsal valve gently and evenly convex with shallow sulcus. Dorsal pseudointerarea orthocline with wide median groove. Dorsal interior with high triangular median septum buttressed posteriorly; dorsal cardinal muscle scars moderately large and transversely suboval in outline.

Shell is ornamented by fine, evenly spaced filae. Larval shell circular, about 130 μm in diameter (Pl. 1, fig. 7); larval ornamentation with large pits 2·4–4·0 μm in diameter, sometimes showing cross-cutting relationships, surrounded by clusters of small, irregularly distributed pits, 0·9–1·7 μm in diameter.

Discussion. There are virtually no differences between the Estonian specimens and those from Ireland. However, we do not have any well preserved adult valves and a closer comparison is not possible. Wright (1963) also described some large, poorly preserved fragments of *Spondylotreta* cf. *parva* that are equally difficult to compare closely with the Estonian form.

Family BIERNATIDAE Holmer, 1989

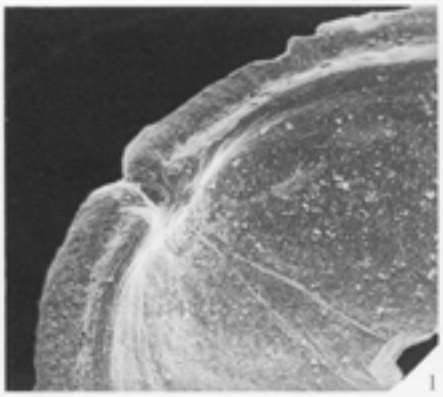
[*nom. trans.* Popov and Holmer, herein (*ex* Biernatinae Holmer, 1989, p. 131)]

EXPLANATION OF PLATE 2

Figs 1–6. *Paterula* sp. 1, Br 1620; Vormsi Stage; depth 312·5 m; ventral interior; × 75. 2, detail of emarginature of shell shown in fig. 1; × 150. 3, Br 1621; lower Pirgu Stage; depth 309·1 m; lateral view of dorsal exterior; × 50. 4, detail of apex of shell shown in fig. 3, showing pitted larval and postlarval shell; × 330. 5, detail of pitted postlarval portion of shell shown in fig. 3; × 1440. 6, Br 1622; lower Pirgu Stage; depth 311·3 m; ventral exterior; × 75.

Figs 7–8. *Opsiconidion praecursor* sp. nov.; Br 1646, holotype; lower Pirgu Stage; depth 310·1 m. 7, lateral view of dorsal interior; × 100. 8, plan view of dorsal interior; × 100.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.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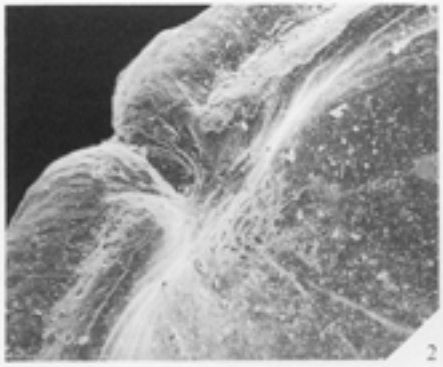
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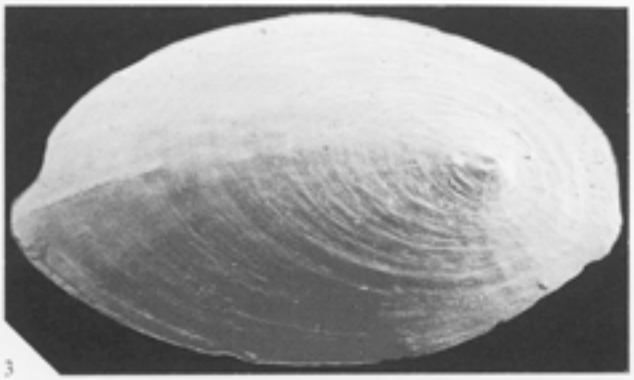
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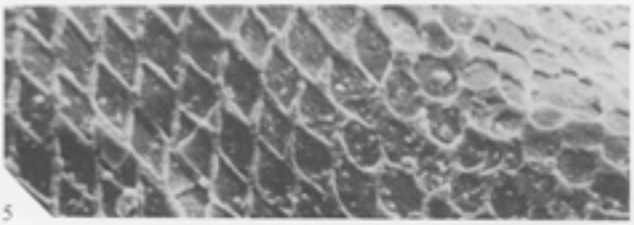
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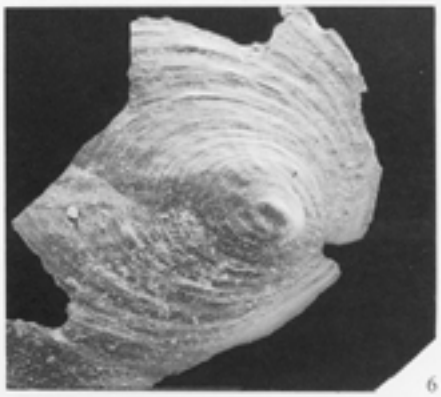
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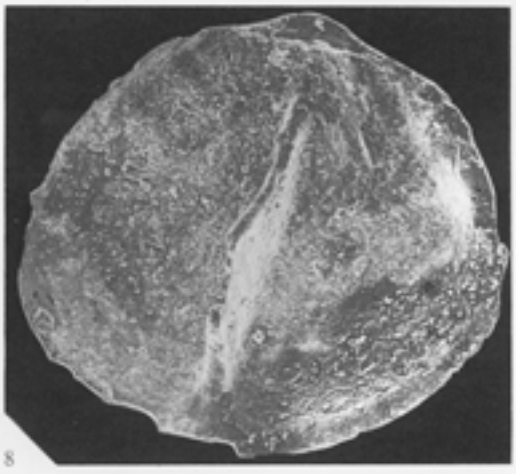
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POPOV *et al.*, *Paterula*, *Opsiconidion*

Diagnosis. Shell with narrow, curved posterior margin. Ventral valve strongly convex and apsacline. Ventral pseudointerarea poorly defined, usually lacking intertrough; apical process absent. Dorsal pseudointerarea small, with a tendency towards reduction; dorsal interior with median septum bearing convex surmounting plate or septal rod.

Genus OPSICONIDION Ludvigsen, 1974

Type species. By original designation, *Opsiconidion arcticon* Ludvigsen, 1974, from the Devonian of Yukon Territory.

Opsiconidion praecursor sp. nov.

Plate 2, figures 7–8; Plate 3; Text-figure 3

Derivation of name. Latin *praecursor* predecessor.

Type material. Holotype. Br 1646; dorsal valve from the lower part of Pirgu Stage, Viljandi core (depth 310·1 m), Estonia. Paratypes. Twenty seven ventral and twenty dorsal valves; Br 1644–1645, 1647–1649 are figured.

Diagnosis. Dorsal pseudointerarea reduced; dorsal median septum with single upper septal rod. Larval shell with pits of two sizes.

Description. Shell subcircular in outline, on average 91 per cent (s 3·4, N 10) as long as wide. Ventral valve highly conical, on average 110 per cent (s 13·5, N 5) as high as long. Ventral pseudointerarea apsacline, undivided or with poorly developed intertrough (Pl. 3, figs 1–3). Ventral interior without distinctive structures.

Dorsal valve gently convex and sulcate, with maximum height in the posterior one third of the valve length (Pl. 3, fig. 6). Dorsal pseudointerarea small, anacline, occupying on average 40 per cent (s 6·0, N 10) of valve width; median grove occupying on average 46 per cent (s 6·3, N 9) of the width of the pseudointerarea (Pl. 3, fig. 3). Dorsal interior with high, triangular median septum, originating on average 28 per cent (s 4·6, N 7) of the total length from the posterior margin, and extending for 85 per cent (s 4·1, N 10) of the length; single upper septal rod developed along the posterior slope of the septum; dorsal cardinal muscle scars poorly defined (Pl. 3, figs 4–5).

The larval shall is covered by pits of two sizes, with the larger ones, 2·9–4·9 μm in diameter, separated from one another by distinct elevated ridges, 0·7–2·1 μm in width, bearing clusters of extremely small pits (Pl. 3, fig. 7). The adult shell has a micro-ornamentation with concentric fila, forming radial rows of outwardly convex 'drapes' about 40 μm wide (Pl. 3, fig. 8).

Discussion. Opsiconidion praecursor sp. nov. is the oldest known species of the genus. It is very similar to *O. aldridgei* (Cocks 1979), from which it differs in having a proportionally smaller dorsal

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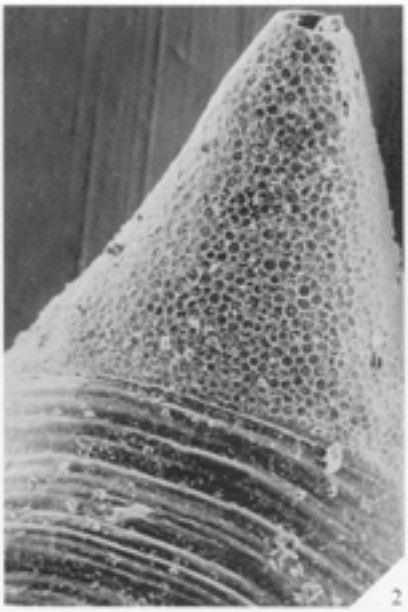
EXPLANATION OF PLATE 3

Figs 1–8. *Opsiconidion praecursor* sp. nov.; Viljandi core (1–7), Eikla core (8). 1, Br 1647; lower Pirgu Stage; depth 310·1 m; oblique posterior view of ventral exterior; × 100. 2, detail of shell shown in fig. 1, showing larval ornamentation; × 330. 3, Br 1644; Vormsi Stage; depth 312·5 m; posterior view of ventral exterior; × 100. 4, Br 1645; lower Pirgu Stage; depth 310·1 m; dorsal interior; × 100. 5, oblique lateral view of shell shown in fig. 4; × 200. 6, Br 1649; lower Pirgu Stage; depth 310·1 m; dorsal exterior; × 200. 7, detail of larval portion of shell shown in fig. 6; × 1120. 8, Br 1648; Nabala Stage; depth 284·7 m; detail of ornamentation of dorsal valve; × 720.

All scanning electron micrographs of specimens from the Upper Ordovician of Estonia.



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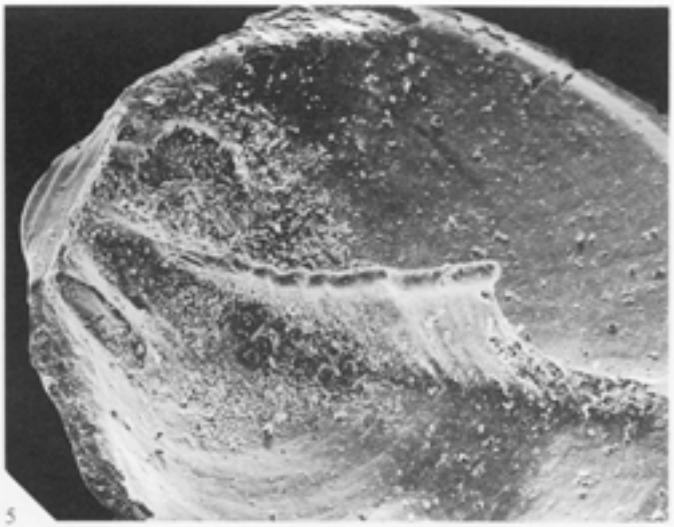

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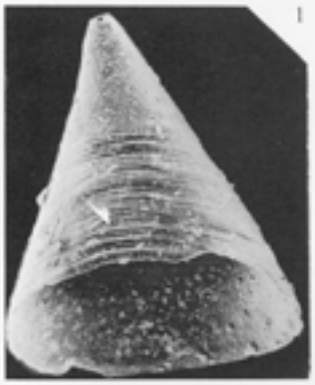

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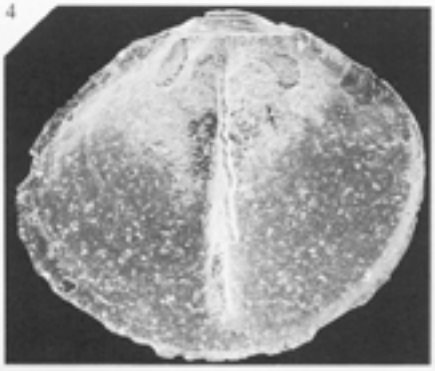

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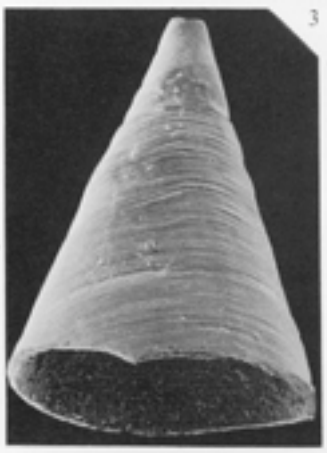

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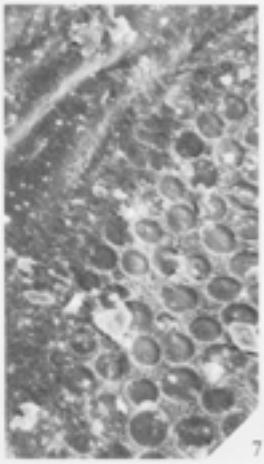

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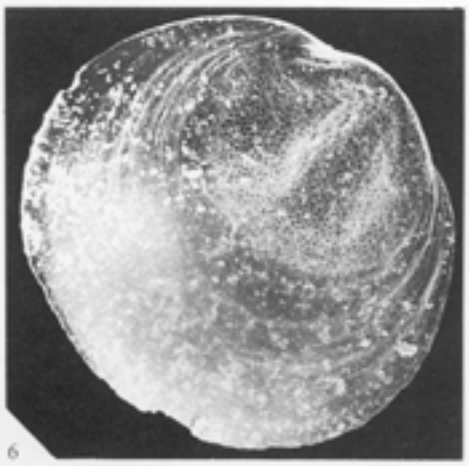

6

POPOV *et al.*, *Opsiconidion*

TABLE 1. Statistics for ten dorsal valves of *Opsiconidion praecursor* sp. nov., from the Viljandi core (lower Pirgu Stage; depth 308·7 m and 310·1 m). Measurements in mm. Location of measurements as in Text-figure 3.

	Vector of Means					
	L	W	Iw	Pw	Sm	Sa
	0·42	0·47	0·18	0·08	0·28	0·36
	Variance–covariance matrix					
L	0·008					
W	0·0065	0·008				
Iw	0·002	0·002	0·002			
Pw	0·001	0·001	0	0		
Sm	0·004	0·004	0·001	0·001	0·004	
Sa	0·005	0·005	0	0·001	0·003	0·005

pseudointerarea, and a more centrally placed maximum height of the dorsal median septum. Moreover, the mean size (length and width) of *O. praecursor* is about half that of *O. aldridgei*. *O. praecursor* is also distinguished from all other species of the genus by having large larval pits surrounded by clusters of minute ones; all other species seem to have only one size of pits, usually showing cross-cutting relationships (e.g. Bitter and Ludvigsen 1979; Cocks 1979; Popov 1981). In this respect it is similar to species of *Biernatia* (Holmer 1986, 1989).

Williams and Holmer (1992) suggested that radial sets of 'drapes' identical to those described above are formed due to stresses in the outer mantle lobe induced by the setal muscles.

Family EPHIPPELASMATIDAE Rowell, 1965

[*nom. trans.* Popov and Holmer, herein (*ex* Ephippelasmatinae Rowell, 1965, p. H279)]

Diagnosis. Shell with narrow, straight posterior margin; larval shell with unequally distributed pits of varying size. Ventral valve recurved conical; ventral pseudointerarea catacline to strongly apsacline with intertrough; foramen within larval shell, usually forming external tube; internal pedicle tube usually present along posterior slope; apical process reduced, usually forming low ridge near apex. Dorsal valve slightly convex to concave; dorsal pseudointerarea divided by short, lens-like median groove; dorsal median septum variably developed; median buttress commonly absent.

Genera assigned. See Holmer (1986, p. 112; 1989, p. 112).

EXPLANATION OF PLATE 4

Figs 1–8. *Rhinotreta laeta* sp. nov. 1, Br 1639; depth 310·3 m; dorsal exterior; × 100. 2, Br 1640; depth 311·3 m; dorsal exterior; × 200. 3, Br 1635; depth 310·3 m; detail of ventral exterior, showing possible predatory borehole penetrating the larval shell; × 260. 4, detail of shell shown in fig. 3, showing edge of larval shell; × 1120. 5, detail of larval pitting of shell shown in fig. 3; × 5600. 6, Br 1638; depth 310·8 m; oblique posterior view of the ventral larval shell; × 310. 7, Br 1641; depth 310·3 m; ventral interior; × 330. 8, Br 1637; depth 309·1 m; ventral interior; × 360.

All scanning electron micrographs of specimens from the Upper Ordovician Pirgu Stage of the Viljandi core, Estonia.

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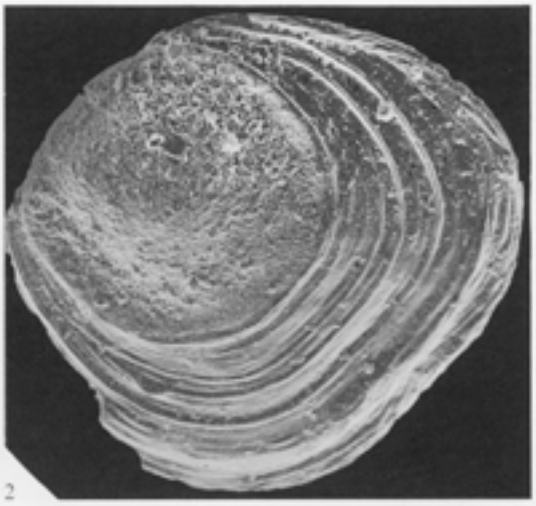

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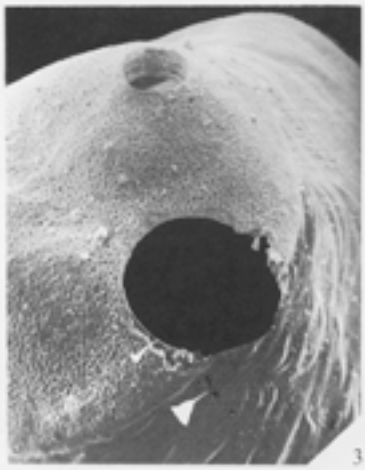

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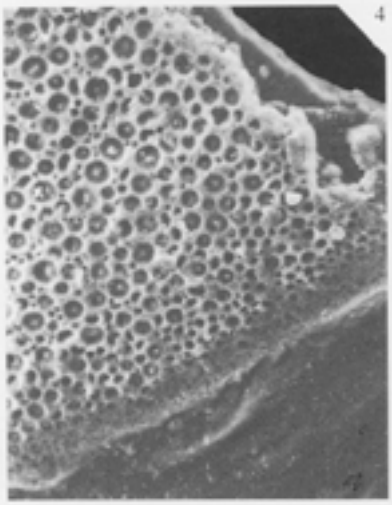

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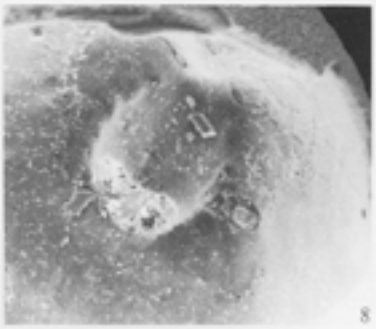

8

POPOV *et al.*, *Rhinotreta*

Genus RHINOTRETA Holmer, 1986

Type species. By original designation; *Rhinotreta muscularis* Holmer, 1986, from the upper Viru Series, Gullhögen quarry, Västergötland, Sweden.

Diagnosis. Shell subcircular to subquadrate in outline. Ventral valve with long exterior pedicle tube. Dorsal valve flat, with low median ridge or septum.

Species assigned. Rhinotreta muscularis Holmer, 1986; *Rhinotreta davidi* Holmer, 1989; *Rhinotreta laeta* sp. nov.

Rhinotreta laeta sp. nov.

Plate 4; Plate 5, figures 1–4; Text-figure 4

1982 *Viljandia laeta* Popov *et al.*, p. 95, pl. 1, figs 5–6 [*nomen nudum*].

Derivation of name. Latin *laetus*, pleasant.

Type material. Holotype. Br 1634; complete shell (dorsal and ventral valves separated during preparation), from the Vormsi Stage, Viljandi core (depth 312·5 m), Estonia. Paratypes. Two complete shells, fifty five ventral and fifty three dorsal valves; Br 1635–1636, 1638–1640, 1642 are figured.

Diagnosis. Shell subquadrate in outline; ventral valve about 80–90 per cent as high as long; ventral pseudointerarea catacline to apsacline, bisected by indistinct intertrough; internal pedicle tube well developed. Dorsal valve flattened with raised umbo; dorsal pseudointerarea narrow, occupying about half of valve width.

Description. Shell subquadrate in outline (Pl. 4, figs 1–2), on average 87 per cent (s 8·8, N. 25) as long as wide. Ventral valve highly conical (Pl. 5, fig. 1), on average 88 per cent (s 17, N 17) as high as long. In lateral profile, the anterior slope of the valve is strongly and unevenly convex; the lateral slopes are evenly convex in transverse profile. Ventral pseudointerarea catacline to apsacline, with poorly developed, shallow intertrough (Pl. 5, fig. 1). Ventral interior with short pedicle tube along the posterior slope of the valve, supported by small, ridge-like apical process; the pedicle tube is covered by irregular polygonal pits, and the apical pits are placed directly lateral to the pedicle tube (Pl. 4, fig. 7).

Dorsal valve nearly flat with raised umbo. Dorsal pseudointerarea narrow, occupying on average 50 per cent (s 4·8, N 20) of the valve width; the median groove is gently concave, occupying on average 51 per cent (s 9·7, N 20) of the width of the pseudointerarea (Pl. 5, figs 2–3). Dorsal interior with large, but poorly defined

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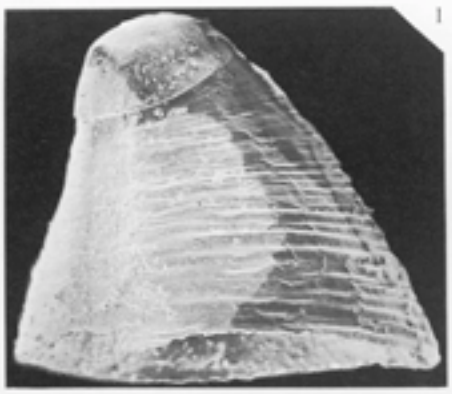
EXPLANATION OF PLATE 5

Figs 1–4. *Rhinotreta laeta* sp. nov. 1, Br 1634, holotype; Vormsi Stage; depth 312·5 m; oblique lateral view of ventral exterior (the dorsal and ventral valves of the complete shell were separated before photography); × 100. 2, oblique lateral view of dorsal interior of shell shown in fig. 1; × 130. 3, Br 1642; lower Pirgu Stage; depth 310·9 m; dorsal interior; × 100. 4, Br 1636; lower Pirgu Stage; depth 311·3 m; detail of pitted dorsal larval micro-ornament; × 1120.

Figs 5–10. *Scaphelasma scutula* sp. nov.; lower Pirgu Stage. 5, Br 1653 holotype; depth 308·7 m; lateral view of complete shell; × 75. 6, detail of pedicle opening of shell shown in fig. 5; × 330. 7, Br 1652; depth 311·3 m; lateral view of dorsal interior; × 100. 8, detail of structure of shell shown in fig. 7; × 420. 9, Br 1654; depth 311·3 m; dorsal exterior of shell shown in fig. 7; × 50. 10, detail of larval portion of shell shown in fig. 7; × 150.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.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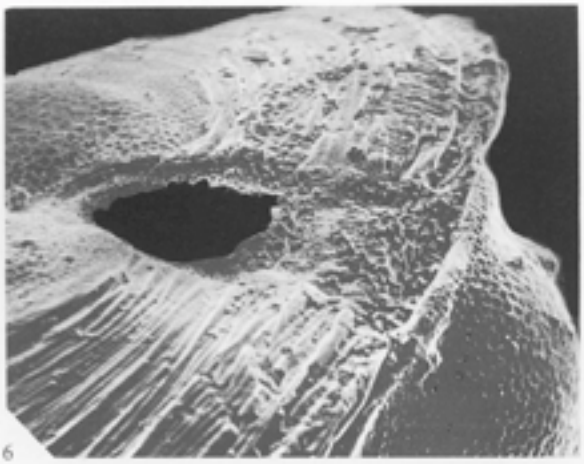
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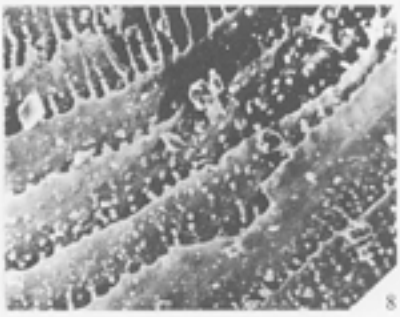
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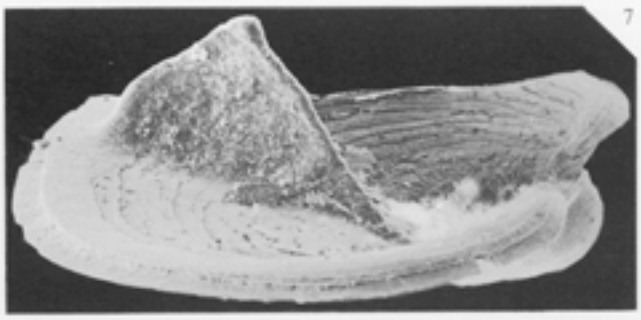
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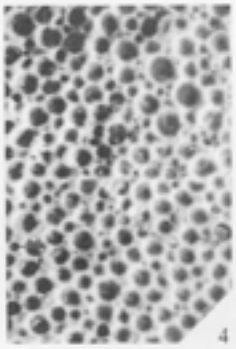
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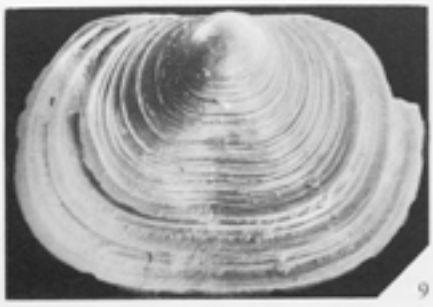
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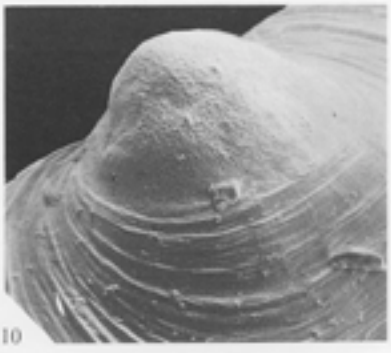
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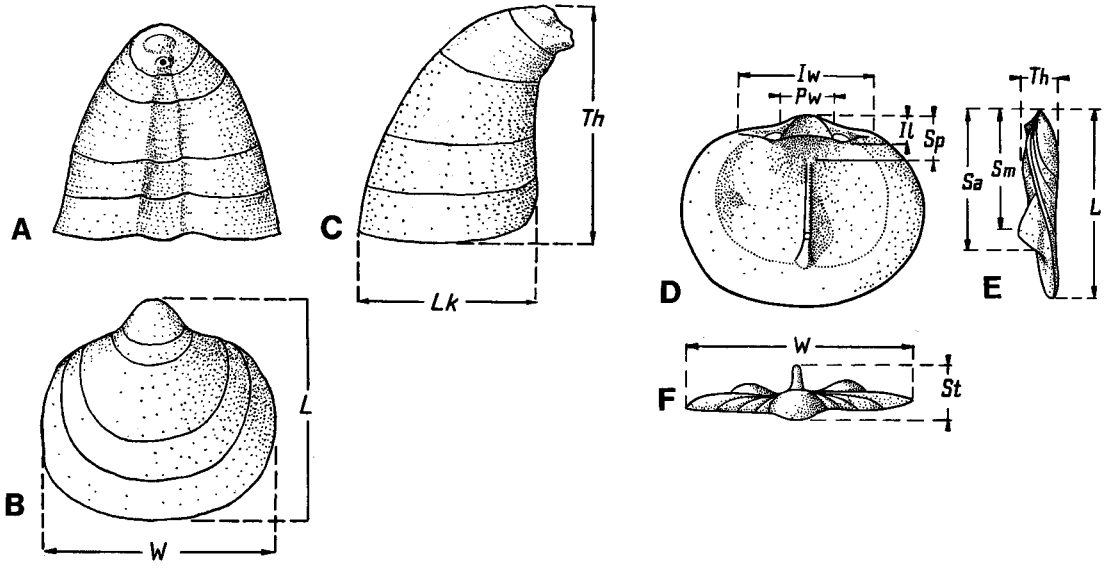
POPOV *et al.*, *Rhinotreta, Scaphelasma*



TEXT-FIG. 4. *Rhinotreta laeta* sp. nov. A–C, dorsal, and D–F, ventral valves, showing locations of measurements (Tables 2–3). See Text-figure 3 for legend.

TABLE 2. Statistics for ventral valves of *Rhinotreta laeta* sp. nov., from the Viljandi core. Measurements in mm. Location of measurements as in Text-figure 4.

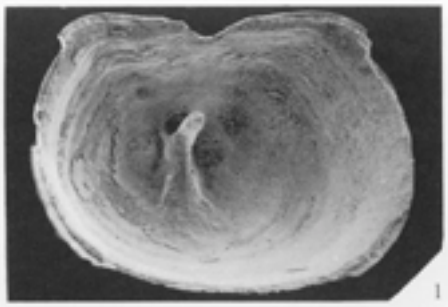
	(Depth 310·1 m, N 25) Vector of Means				(Depth 310·9 m, N 18) Vector of Means			
	L	W	Th	Lk	L	W	Th	Lk
	0·46	0·46	0·40	0·40	0·50	0·54	0·43	0·46
	Variance–covariance matrix				Variance–covariance matrix			
L	0·011				0·009			
W	0·011	0·013			0·009	0·006		
Th	0·013	0·014	0·016		0·007	0·006	0·011	
Lk	0·007	0·008	0·010	0·0065	0·006	0·005	0·0065	0·0065

EXPLANATION OF PLATE 6

Figs 1–4. *Scaphelasma scutula* sp. nov.; Viljandi core (1, 4), Eikla core (2–3). 1, Br 1656; lower Pirgu Stage; depth 310·9 m; ventral interior; × 90. 2, Br 1651; Nabala Stage; depth 285·9 m; dorsal interior; × 100. 3, oblique anterior view of shell shown in fig. 2; × 100. 4, Br 1655; lower Pirgu; depth 310·9 m; ventral exterior; × 65.

Figs 5–10. *Eoconulus semiregularis* Biernat, 1973; lower Pirgu Stage. 5, Br 1657; depth 310·3 m; lateral view of dorsal exterior; × 100. 6, Br 1660; depth 310·9 m; ventral exterior; × 50. 7, detail of attachment scar of shell shown in fig. 6; × 300. 8, Br 1659; depth 311·3 m; ventral exterior; × 50. 9, Br 1664; depth 308·7 m; ventral exterior; × 50. 10, detail of attachment scar of shell shown in fig. 9; × 250.

All scanning electron micrographs of specimens from the Upper Ordovician of Estonia.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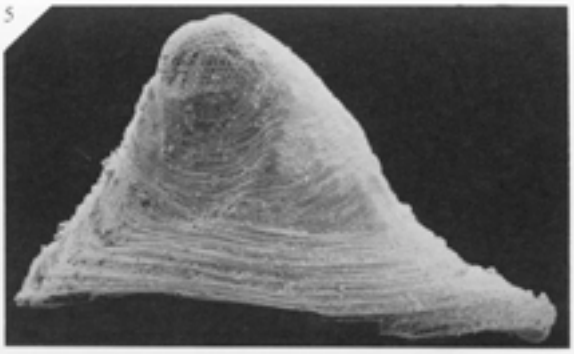
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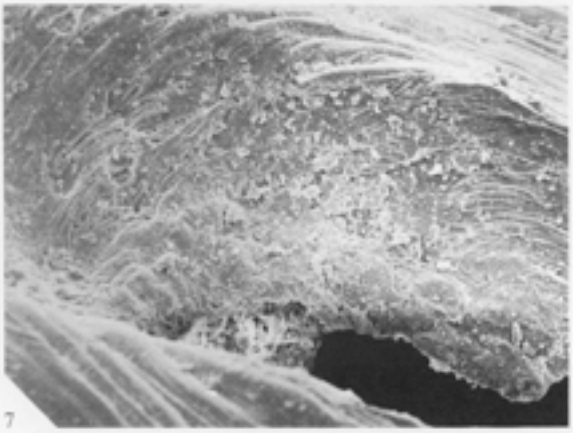
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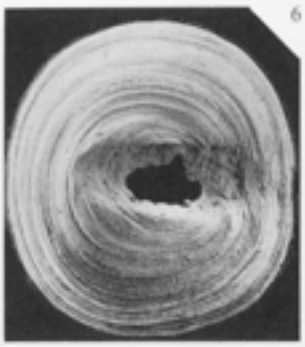
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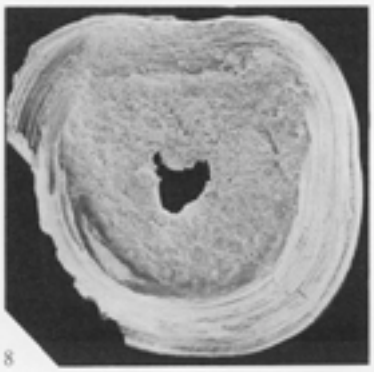
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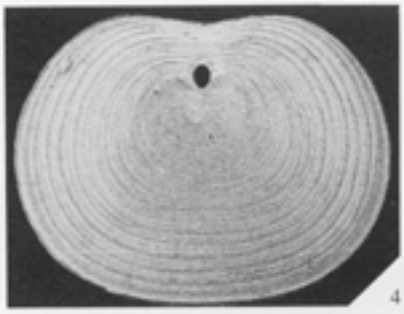
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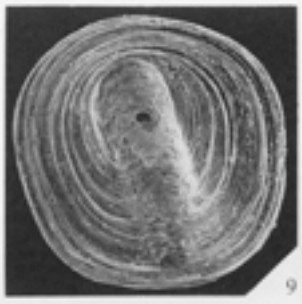
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10

POPOV *et al.*, *Scaphelasma*, *Eoconulus*

TABLE 3. Statistics for eighteen dorsal valves of *Rhinotreta laeta* sp. nov., from the Viljandi core (lower Pirgu Stage; depth 310·1 m). Measurements in mm. Location of measurements as in Text-figure 4.

	Vector of Means									
	L	W	Th	Il	Iw	Pw	Sp	Sm	Sa	St
	0·62	0·72	0·09	0·07	0·36	0·19	0·18	0·34	0·45	0·13
	Variance–covariance matrix									
L	0·008									
W	0·011	0·020								
Th	0·001	0·003	0·001							
Il	0·001	0·001	0	0						
Iw	0·005	0·010	0·001	0·001	0·001					
Pw	0·003	0·005	0·001	0·001	0·003	0·003				
Sp	0	0	0	0	0	0	0·001			
Sm	0·002	0·005	0	0	0·001	0	0	0·001		
Sa	0·004	0·007	0·001	0·001	0·004	0·002	0	0·001	0·004	
St	0·003	0·004	0·0005	0	0·002	0·001	0	0	0·002	0·0015

cardinal muscle scars; dorsal median septum low, triangular, originating on average 33 per cent (s 7·8, N 17) of the valve width from the posterior margin, and extending for 60 per cent (s 7·8, N 17) of the length (Pl. 5, figs 2, 3). Valves ornamented by closely spaced, ridge-like, filae or lamellae; those of the dorsal valve are more widely spaced (Pl. 4, figs 1–2).

Discussion. *Rhinotreta laeta* differs from the other two described species, in having a more subquadrate outline, an ornamentation with high, ridge-like filae or lamellae, and a greater maximum size. It also differs from the type species *R. muscularis* in having a shorter external pedicle tube. It is distinguished from *R. davidi* by the poorly defined intertrough and somewhat shorter and higher dorsal median septum.

Family SCAPHELASMATIDAE Rowell, 1965

[*nom. trans.* Popov and Holmer, herein (*ex* Scaphelasmatinae Rowell, 1965, p. H278)]

Genus SCAPHELASMA Cooper, 1956

Type species. By original designation; *Scaphelasma septatum* Cooper, 1956, from the middle Ordovician of Alabama.

Scaphelasma scutula sp nov.

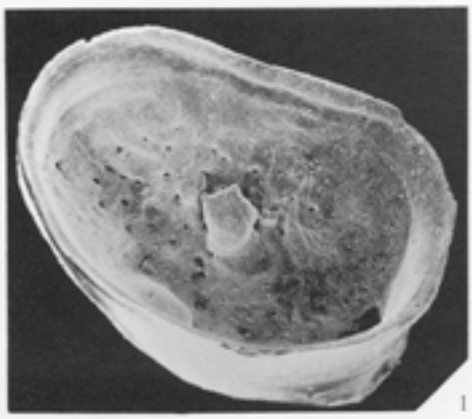
Plate 5, figures 5–10; Plate 6, figures 1–4; Text-figure 5

Derivation of name. Latin *scutula*, small plate.

EXPLANATION OF PLATE 7

Figs 1–7. *Eoconulus semiregularis* Biernat, 1973. 1, Br 1661; lower Pirgu Stage; depth 310·1 m; ventral interior; × 50. 2, detail of apical process of shell shown in fig. 1; × 200. 3, Br 1658; lower Pirgu Stage; depth 310·9 m; dorsal exterior; × 100. 4, detail of larval portion of shell shown in fig. 3; × 330. 5, detail of larval pitting of shell shown in fig. 3; × 940. 6, Br 1662; Vormsi Stage; depth 312·5 m; juvenile dorsal exterior; × 200. 7, lateral view of shell shown in fig. 6; × 235.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.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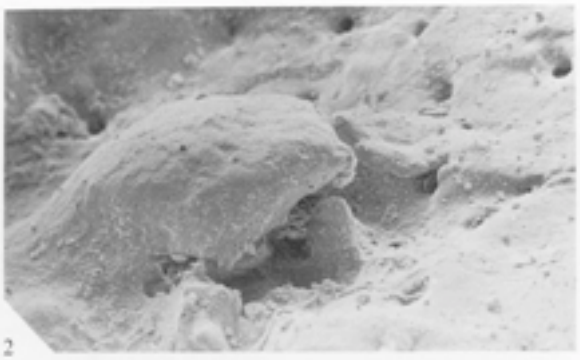
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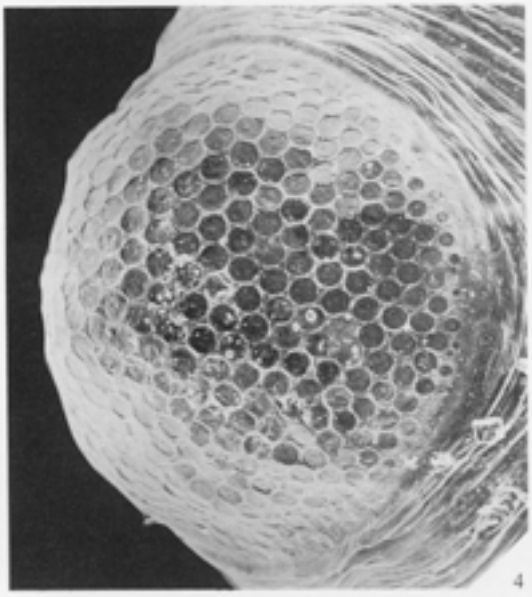
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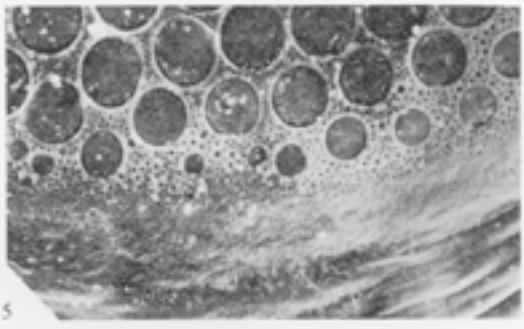
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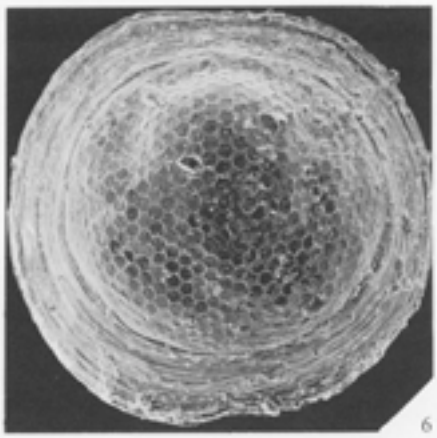
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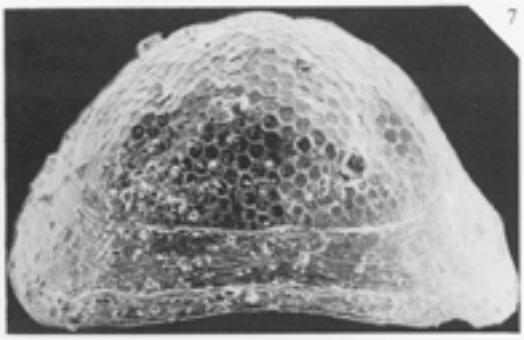

7

POPOV *et al.*, *Eoconulus*

Type material. Holotype. Br1653, complete shell, from the Vormsi Stage of the Viljandi core (depth 308·7 m), Estonia. Paratypes. Three complete shells, twenty ventral and twenty dorsal valves; Br 1651–1652, 1654–1656 are figured.

Diagnosis. Ventral interior with apical process forming a rod-like projection directly anterior of pedicle opening.

Description. Shell transversely oval in outline. Ventral valve widely conical, on average 83 per cent (s 3·9, N 12) as long as wide, and 48 per cent (s 1.2, N 13) as high as long; the maximum height is placed on average 36 per cent (s 3·2, N 13) of the valve length from the slightly concave posterior margin. Ventral pseudointerarea strongly procline with well defined intertrough (Pl. 6, fig. 4). Pedicle foramen elongately oval, about 60 μm long and 40 μm wide (Pl. 5, fig. 6). Apical process forming rod-like projection, placed directly in front of the pedicle opening (Pl. 6, fig. 1).

Dorsal valve strongly convex in apical region, flattening marginally; on average 86 per cent (s 7·2, N 19) as long as wide (Pl. 5, figs 9–10). Dorsal pseudointerarea narrow, occupying on average 23 per cent (s 4·0, N 18) of the valve width; median groove lens shaped, slightly concave, occupying on average 43 per cent (s 12, N 18) of the width of the pseudointerarea (Pl. 6, figs 2–3). Dorsal interior with high, triangular median septum occupying starting on average 48 per cent (s 11, N 19) of the valve length from the posterior margin and extending for 88 per cent (s 5·0, N 18) of the length; the maximum height is placed at 72 per cent (s 7·4, N 18) of the valve length from the posterior margin (Pl. 5, fig. 7; Pl. 6, figs 2–3).

Discussion. Scaphelasma scutula differs from all other known species of the genus in having a well developed, rod-like apical process.

Family EOCONULIDAE Cooper, 1956
Genus EOCONULUS Cooper, 1956

Type species. By original designation; *Eoconulus rectangulatus* Cooper, 1956, from the middle Ordovician of Alabama.

Eoconulus semiregularis Biernat, 1973
Plate 6, figures 5–10; Plate 7; Text-figure 6

1973 *Eoconulus semiregularis* sp. nov. Biernat, p. 112, pl. 36, figs 1–8.
1982 *Eoconulus semiregularis* Biernat; Popov *et al.* p. 101, pl. 2, fig. 6.
?1989 *Eoconulus* cf. *semiregularis* Biernat; Holmer, p. 150, figs 39I, 106–107, 111.

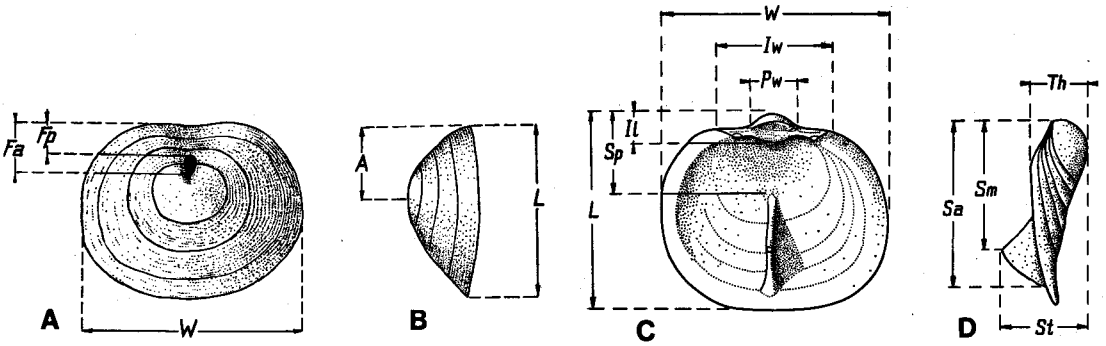
Holotype. Bp VI/6*b* (dorsal valve; in the Palaeobiological Institute, Polish Academy of Sciences, Warszawa), from an Upper Ordovician erratic boulder (no. 0·247). Jarosławiec, Baltic coast, Poland.

Material. Four ventral and eighty six dorsal valves; Br 1657–1658, 1660–1662, 1664 are figured.

Diagnosis. Shell irregularly subcircular in outline. Dorsal valve usually highly conical. Ventral valve truncatedly cylindrical in profile, with large, flattened to irregularly shaped, or cylindrical attachment scar; ventral interior with well developed apical process directly anterior to pedicle opening.

Description. Ventral valve truncate-cylindrical in profile. Attachment scar commonly forming a mould of a cylindrical object, more rarely flat or irregular (Pl. 6, figs 6–9). Pedicle foramen small, circular, about 40 μm in diameter, placed at about the centre of the attachment scar (Pl. 6, fig. 10). Ventral interior has a wart-like apical process, slightly overhanging the internal pedicle opening; three or five 'papillae' surround the apical process (Pl. 7, fig. 2). Ventral cardinal muscle scars strongly raised. Ventral interior surface with deep, cylindrical pores that do not reach the external valve surface (Pl. 7, figs 1–2).

Dorsal valve usually highly conical, on average 93 per cent (s 13, N 24) as long as wide and 68 per cent



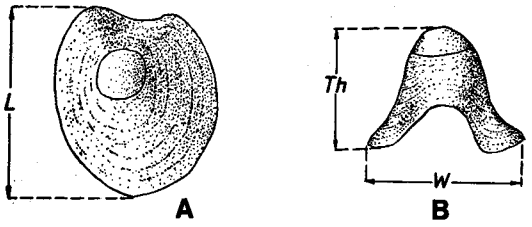
TEXT-FIG. 5. *Scaphelasma scutula* sp. nov. A–B, dorsal, and C–D, ventral valves, showing locations of measurements (Tables 4–5). See Text-figure 3 for legend.

TABLE 4. Statistics for thirteen ventral valves of *Scaphelasma scutula* sp. nov., from the Viljandi core (Vormsi–lower Pirgu stages; depth from 308·7 to 312·5 m). Measurements in mm. Location in mm. Location of measurements as in Text-figure 5.

	Vector of means					
	L	W	Th	Fp	Fa	A
	0·66	0·79	0·32	0·13	0·18	0·24
	Variance–covariance matrix					
L	0·022					
W	0·026	0·038				
Th	0·014	0·019	0·013			
Fp	0·0085	0·011	0·005	0·004		
Fa	0·008	0·010	0·005	0·0035	0·004	
A	0·007	0·009	0·004	0·003	0·003	0·003

TABLE 5. Statistics for sixteen valves of *Scaphelasma scutula* sp. nov., from the Viljandi core (Vormsi–lower Pirgu stages; depth from 308·7 to 312·5 m). Measurements in mm. Location of measurements as in Text-figure 5.

	Vector of means									
	L	W	Th	Il	Iw	Pw	Sa	Sm	Sp	St
	0·61	0·72	0·13	0·075	0·32	0·14	0·54	0·44	0·27	0·22
	Variance–covariance matrix									
L	0·022									
W	0·033	0·052								
Th	0·002	0·004	0·001							
Il	0·003	0·004	0	0·001						
Iw	0·016	0·016	0·0015	0·002	0·018					
Pw	0·0075	0·007	0·001	0·001	0·006	0·003				
Sa	0·024	0·033	0·003	0·003	0·017	0·007	0·026			
Sm	0·016	0·022	0·002	0·002	0·012	0·006	0·013	0·013		
Sp	0·001	0·003	0	0	0·001	0	0·001	0·001	0·001	
St	0·015	0·015	0·001	0·002	0·010	0·005	0·014	0·012	0·001	0·010



TEXT-FIGURE. 6. *Eoconulus semiregularis* Biernat, 1973. Dorsal valve, showing locations of measurements (Table 6). See Text-figure 3 for legend.

TABLE 6. Statistics for twenty four dorsal valves of *Eoconulus semiregularis* Biernat, from the Viljandi core (lower Pirgu Stage; interval 310·1–311·3 m). Measurements in mm. Location of measurements as in Text-figure 6.

	Vector of Means			
	L	W	Th	A
	0·78	0·85	0·53	0·22
	Variance–covariance matrix			
L	0·067			
W	0·076	0·112		
Th	0·041	0·045	0·037	
A	0·025	0·025	0·017	0·018

(s 9·8, N 24) as high as long. The maximum height is placed on average 28 per cent (s 12, N 25) of the valve length from the posterior margin (Pl. 6, fig. 5). Dorsal interior lacking distinctive features.

The dorsal larval shell is about 0·2 mm in diameter, ornamented by two grades of pits; the larger ones are flat-bottomed, 9·0–10·0 μm in diameter, separated from one another by flattened ridges that are covered by clusters of minute pits, 0·3–0·6 μm in diameter (Pl. 7, fig. 4). Towards the edge of the larval shell, the diameter of the larger pits decreases to 2·3–7·4 μm and the finer pits increase in number; outside of this zone, the larval shell is surrounded by a band, 12–15 μm wide, ornamented only by minute pits (Pl. 7, fig. 5). The ventral larval shell is not defined; the attachment scar is ornamented only by fine, concentric filae (Pl. 6, fig. 7).

Discussion. As noted by Holmer (1989), it is difficult to make meaningful definitions of species of *Eoconulus*, since the outline and convexity of the valves are almost completely dependent upon the shape of the substrate. Moreover, most described species of the genus are known only from the dorsal valve, as is the case with the Polish type material of *E. semiregularis*. However, the dorsal valves in the Estonian material are identical to the Polish specimens in all available characters. Our material is also closely comparable with *E.* cf. *semiregularis* Biernat described by Holmer (1989) from the mid-Ordovician of Sweden, but the Estonian dorsal valves have a higher dorsal valve and a greater maximum size.

Order DISCINIDA Waagen, 1885
Family DISCINIDAE Gray, 1840
Genus SCHIZOTRETA Kutorga, 1848

Type species. By original designation; *Orbicula elliptica* Kutorga, 1846, from the Lower Ordovician of Ingria, St Petersburg district, Russia.

Schizotreta sp.
Plate 1, figures 8–9

Material. Two ventral and six dorsal valves; Br 1631, Br 1632 are figured.

Remarks. There are only a few specimens of *Schizotreta* in the collection, none of which allows a specific determination. They are, however, very similar to *S. concava* Wright, 1963, in having the dorsal apex placed close to the posterior margin and ornamentation with coarse, ridge-like, concentric filae.

Acknowledgements. We are grateful to Madis Rubel (Tallinn), Anne McClean (Belfast), Valdar Jaanusson (Stockholm) and two anonymous reviewers for comments on the manuscript. We are also grateful to Mr E. P. Klimov (Tallinn) for carrying out the scanning electron microscopy. The work has been supported by grants (to L. Holmer) from the Swedish Natural Science Research Council (NFR). Leonid Popov gratefully acknowledges three NFR visiting scientist grants, and a grant from the Swedish Institute, that have enabled him to work extensively at the Institute of Earth Sciences, Department of Historical Geology and Palaeontology, Uppsala University, Sweden.

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Typescript received 27 April 1993
Revised typescript received 7 September 1993