

The Early Devonian (Emsian) acrotretid microbrachiopod *Opsiconidion minor* Popov, 1981, from the Alaska/Yukon Territory border and Novaya Zemlya

Lars E. Holmer^{a,b}, Robert B. Blodgett^c, Yue Liang^{a,b} 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; yueliang_nwu@outlook.com, elizf@nwu.edu.cn

^b Institute of Earth Sciences, Palaeobiology, Uppsala University, SE-752 36 Uppsala, Sweden; lars.holmer@pal.uu.se

^c Blodgett & Associates, LLC (Geological & Paleontological Consultants) 2821 Kingfisher Drive Anchorage, Alaska 99502 USA; robertblodgett@gmail.com

Received 20 April 2020, accepted 29 May 2020, available online 18 June 2020

Abstract. New records of the poorly known acrotretid (Biernatidae) microbrachiopod *Opsiconidion minor* Popov are described from middle Emsian strata of the Ogilvie Formation in east-central Alaska and the adjacent Yukon Territory, Canada, and compared with new better-preserved topotypes from the late Early Devonian (Emsian) of Novaya Zemlya, Russia. In Alaska *O. minor* occurs together with fragmentary material of *Lingulipora* sp. and an indeterminate discinid. The only other previous record of *O. minor*, outside the type area, comes from the Early to ?Middle Devonian (Pragian to ?Givetian) of Australia (Victoria and NSW). *Opsiconidion* Ludvigsen is a stratigraphically extremely long-ranging and cosmopolitan acrotretid, which exhibits a remarkable conservatism; the morphology of the ventral valve remains essentially unchanged from the earliest Ordovician (Darrivilian) records to the Devonian.

Key words: Brachiopoda, Lingulata, Acrotretida, Biernatidae, Devonian, Emsian, Novaya Zemlya, Russia, Alaska, Yukon Territory.

INTRODUCTION

Devonian records of acrotretid lingulate brachiopods were for a long time comparatively uncommon, but recently our knowledge has increased significantly. Since the first possible reports by Rowell (1965, p. H276) and Langer (1971), numerous records of Devonian acrotretids have been described from many parts of the world (e.g. Ludvigsen 1974; Cocks 1979; von Bitter & Ludvigsen 1979; Popov 1981a; Brock et al. 1995; Huson & Over 2000; Mergl 2001, 2009, 2019; Mergl & Ferrova 2009; Mergl & Vodrážková 2012; Mergl & Jimenez-Sanchez 2015).

The only surviving acrotretid genera in the Devonian seem to be *Opsiconidion* Ludvigsen, 1974, *Concaviseptum* Brock et al., 1995, and *Havlicekion* Mergl, 2001, belonging within the Family Biernatidae Holmer, 1989. Although *Opsiconidion* has its main range in the Silurian and Devonian, it extends down also into the Ordovician (e.g. Popov et al. 1994; Holmer 2000; Sutton et al. 2000). Most previous important Devonian records of *Opsiconidion* have

been reviewed and discussed by Mergl (2001, 2019), in connection with comparative descriptions of faunas from Bohemia, which are presently the best-known occurrences of the genus and of other Devonian lingulates (see also Mergl 2009; Mergl & Ferrova 2009; Mergl & Jimenez-Sanchez 2015). The youngest possible report to date remains Langer (1971), who recorded some problematic and poorly known highly conical forms that possibly represent *Opsiconidion* from the early Late Devonian (Frasnian) of Germany; however, the youngest well-established occurrence is from the Givetian of Australia (Brock et al. 1995) and Southern Mongolia (Arno 2010).

The object of this study is to describe new material of the poorly known *Opsiconidion minor* Popov, 1981a, from middle Emsian strata of the Ogilvie Formation in east-central Alaska and the adjacent Yukon Territory, Canada. The original publication of Popov (1981a) is unfortunately poorly available and consequently new, well-preserved topotypes from the late Early Devonian (Emsian) of Novaya Zemlya, Russia, are illustrated for comparison with the new North American material.

GEOGRAPHICAL AND GEOLOGICAL SETTING

Novaya Zemlya

The illustrated topotypes of *O. minor* come from Valnev Island, Novaya Zemlya Archipelago (VSEGEI, St Petersburg, locality No. 39). They were etched from sample No. 39-31 (see Sobolev 1984, fig. 1), from the Lower Devonian (Emsian) *Polygnathus perbonus* Biozone (see Sobolev 1984, for further details).

Alaska and the Yukon Territory

Two middle Emsian (late Early Devonian) occurrences of *Opsiconidion minor* are known from two localities of the uppermost strata of the Ogilvie Formation exposed in the Jones Ridge–Squaw Mountain area along the Alaska–Yukon border, one on either side of the boundary. Both are in equivalent beds representing the uppermost Ogilvie Formation, and the associated fauna represents the deepest-water faunal association found in the Ogilvie Formation locally (Fig. 1). This association was termed the *Elythyra* cf. *E. kingi* palaeocommunity in Blodgett (1978) and characterized by an extreme abundance of the reticularid brachiopod *Elythyra* cf. *E. kingi*. Other associated brachiopods include *Athyrhynchus susanae*, *Phagmostrophia* cf. *P. merriami*, *Bifida* sp., *Linguopugnoides glabberhynchus*, ‘*Chonetes*’ spp., *Leptathyris* sp., *Orbiculoidea* sp. and *Opsiconidion minor*. The dacrocyonarid *Nowakia* is also seen in abundance here.

The University of Alaska (UA) Museum locality A-941 (Fig. 1) is from the base of Section D of Blodgett (1978). The section is situated in the Yukon Territory (latitude 65°05.2'N, longitude 140°59.56'W) and was measured in a small cliff composed of thinly bedded dark grey, petroliferous, micritic limestone. The cliff is located on the south side of Hard Luck Creek (also known as Harrington Creek), in its upper reaches approximately 0.805 km (0.5 mile) east of the Alaska–Yukon boundary, at the point where the creek makes a sharp bend to the north upstream. The total height of the section is 4.3 m (14 feet). The UA Museum locality A-941 represents the basal 1.22 m (4 feet) of section D. Conodonts from this locality include the age-diagnostic *Polygnathus inversus* Klapper & Johnson of middle Emsian age (Blodgett 1978).

A second nearby locality in the Ogilvie Formation is situated in the Charley River A-1 1:63 360 scale quadrangle (latitude 65°06.2'N, longitude 141°01.1'W) in east-central Alaska (Fig. 1). This locality 83RB48 (USGS locality 11920-SD) consists of micritic to encrinoidal limestone from talus rubble slides on the south flank of Jones Ridge, elevation about 3000 feet (914.4 m), NW1/4, SW1/4 section 10, T. 3 N., R. 33 E. This locality is located

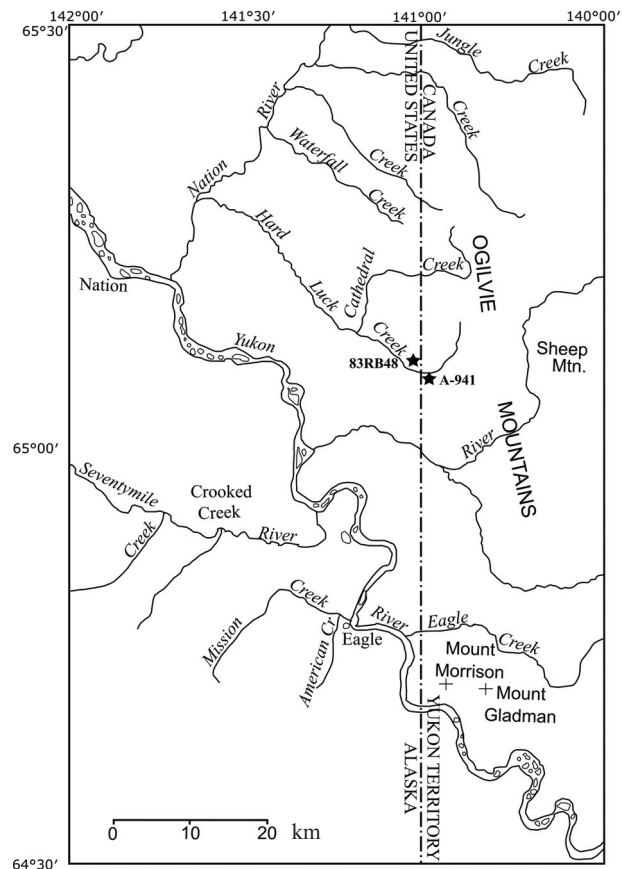


Fig. 1. Map showing localities 83RB48 (Alaska) and University of Alaska Museum locality A-941 (Yukon Territory) in the uppermost strata of the Ogilvie Formation exposed in the Jones Ridge–Squaw Mountain area along the Alaska–Yukon border. Locality 83RB48 is located approximately 0.8 mile (1.29 km) N10°W of the University of Alaska Museum locality A-941.

approximately 1.29 km (0.8 mile) N10°W of the first locality. Conodonts from this locality, identified by Audrey L. Orndorff and Anita G. Harris (written commun., 7 October 1988), contain two identifiable polygnathid species, *Polygnathus inversus* Klapper & Johnson and *Polygnathus laticostatus* Klapper & Johnson, indicating an Inversus/Laticostatus Zone (middle Emsian) age.

Brabb & Churkin (1969) and Churkin & Brabb (1968) included the above localities within the basal limestone and shale member (Emsian age) of the McCann Hill Chert established by Churkin & Brabb (1965). Blodgett (1978) recognized that these platformal carbonates exposed in the vicinity of Jones Ridge and Squaw Mountain are lithologically distinct from the deeper-water type basal limestone and shale member exposed to the south in Eagle D-1 1:63 360 scale quadrangle, and he assigned them rather to the Ogilvie Formation. The Ogilvie Formation is exposed widely to

the east and north in the Yukon Territory and ranges from late Early to Middle Devonian (Emsian to Givetian) in age (Perry et al. 1974). The outcrops discussed here represent the southwesternmost exposures of the Yukon Stable Block of Lenz (1972). Both to the south and west coeval Emsian strata grade from platformal carbonate facies of the Ogilvie Formation into basinal slope facies of the limestone and shale member of the McCann Hill Chert (Blodgett 1978; Blodgett et al. 1984; Clough & Blodgett 1984, 1987, 1988; Dover & Miyaoka 1988; Dover 1992).

SYSTEMATIC PALAEOLOGY

Measurements and repository. Measurements (in millimetres) were made with a binocular microscope on specimens oriented in the conventional manner: W = maximum width; L = maximum sagittal length; WI = maximum width of dorsal pseudointerarea; LI = maximum length of dorsal pseudointerarea; WM = maximum combined width of dorsal cardinal muscle scars; LM = maximum length of dorsal cardinal muscle scars; LS = maximum length of dorsal median septum, measured from the posterior sagittal margin. The mean values (X), standard deviation (S) and number (N) of measured specimens are given.

The specimens discussed and described here are deposited in the Swedish Museum of Natural History, Stockholm (NRM-PZ Br), the CNIGR (Central Scientific Geological Exploration) Museum, St Petersburg, and the University of Alaska Museum, Earth Sciences Collection, Fairbanks, Alaska (UAMES).

Class LINGULATA Gorjansky & Popov, 1985
Order ACROTRETIDA Kuhn, 1949
Family BIERNATIDAE Holmer, 1989

Diagnosis. See Holmer & Popov (2000, p. 130) and Sutton et al. (2000, p. 100).

Genera included. *Biernatia* Holmer, 1989; *Opsiconidion* Ludvigsen, 1974 [= *Caenotreta* Cocks, 1979]; *?Eschatelasma* Popov, 1981b; *Concaviseptum* Brock et al., 1995; *Bathmoleca* Sutton (in Sutton et al.), 2000; *Havlicekion* Mergl, 2001.

Occurrence. Ordovician (upper Tremadoc)–Middle Devonian (Givetian), ?Upper Devonian.

Remarks. The problematic Silurian genus *Eschatelasma* from Estonia was originally referred to the Subfamily Acrotretinae (Popov 1981b; Holmer & Popov 2000) but restudy of the type material (Holmer & Popov, unpublished information) indicates that it might be an aberrant biernatide. The morphology and pitting of the

metamorphic shell (see, e.g., Zhang et al. 2018) are identical to those of *Opsiconidion*, whilst the median septum lacks the upper septal rod and is quite unlike that of any biernatide.

Genus *Opsiconidion* Ludvigsen, 1974

Type species. *Opsiconidion arcticon* Ludvigsen, 1974, by original designation, from the Early Devonian (early Emsian) Michelle Formation, Yukon Territory.

Diagnosis. See Holmer & Popov (2000, p. 131) and Sutton et al. (2000, p. 100).

Species included. See Mergl (2001, 2009, 2018, 2019), Mergl et al. (2018), Sutton et al. (2000), Valentine et al. (2003).

Stratigraphic distribution. Ordovician (Darriwilian) to Middle Devonian (Givetian), ?Upper Devonian.

Remarks. *Opsiconidion* is a morphologically very conservative genus; the morphology of the ventral valve remains essentially unchanged from the earliest Ordovician records (Popov & Holmer in Popov et al. 1994; Holmer 2000; Sutton et al. 2000) to the Devonian. The genus probably originated directly from within *Biernatia* Holmer, 1989, and it is difficult to distinguish *Opsiconidion* from this genus on the basis of the ventral valve alone, because it has very few internal and external characters, and all forms seem to be strongly apsacline. The dorsal valve of *Opsiconidion* is usually more distinctive, and especially the median septum and pseudointerarea provide a possible means of taxonomic discrimination. As compared with species of *Biernatia*, it seems that the dorsal median septum and pseudointerarea of *Opsiconidion* are reduced; the complex, wide and convex surmounting plates of the former genus are never developed and instead simple septal rods or very narrow, flattened surmounting plates are present.

The pitting and general shape of the metamorphic shell of *Opsiconidion* are also rather distinctive; the dorsal metamorphic shell usually has a very distinct sulcus, and the large pits of both valves are usually distinctly cross-cutting. The interpretation of the cross-cutting pits in *Opsiconidion* has been discussed repeatedly. According to Ludvigsen (1974) and von Bitter & Ludvigsen (1979), they were formed through a complex process involving resorption of shell material. However, Williams & Curry (1991, fig. 1) proposed a more likely model in which the cross-cutting relationships of the large circular pits are formed through overlapping vesicles or mineralized minute plates in the periostracum. The discovery of such mineralized siliceous plates in living and fossil discinoids (Holmer 1989, fig. 41; Williams et al. 1998; Baliński & Holmer 1999) further supports this interpretation, and protection from solar radiation has been suggested as a possible function (Williams 2003; Lüter 2004).

The possible life habits of *Opsiconidion* have also been the subject for various interpretations (see also Mergl & Vodrážková 2012; Mergl et al. 2018). Bassett (1984, p. 244) provided a review of the proposed lifestyles and suggested that minute, elongated microbrachiopods like *Opsiconidion* might have been interstitial. In contrast, Popov et al. (1994; see also Mergl 2002, p. 16 for discussion) noted that many assemblages dominated by microbrachiopods are associated with numerous sponge spicules. It is clear from the recently described (Lenz 1993) Canadian Silurian occurrence of the lingulid *Paterula* sp. (referred to as ‘*Craniops* sp.’) attached around the oscular margin of sponges that a sponge–lingulate association is a plausible possibility. This type of the secondary tiering mode of life on sponges and other epibionts is also clearly present in many other micromorphic Palaeozoic linguliform brachiopods (e.g. Wang et al. 2012; Topper et al. 2015a, 2015b).

Opsiconidion minor Popov, 1981a
 Figures 2, 3A–D, 4, 5A

1981a *Opsiconidion minor* Popov, p. 62, pl. 1, figs 1–7.
 1995 *Opsiconidion minor* Popov; Brock et al., p. 111, fig. 4G–L.

Holotype. Dorsal valve (L = 1.37, W = 1.51), CNIGR No. 1/11829 (Fig. 5A), from the upper Lower Devonian (Emsian) of Valnev Island, Novaya Zemlya (Popov 1981a, pl. 1, fig. 7).

Figured material. From Novaya Zemlya: RM Br 136300–136304. From east-central Alaska and closely nearby Yukon Territory: UAMES 5509, 5511, 5514, 5516 and 5520 (Yukon Territory), NRM-PZ Br 136305–136307 from 83RB48 (east-central Alaska).

Diagnosis. Dorsal valve gently convex to flattened; dorsal pseudointerarea with well-defined median groove and narrow propareas; surmounting plate well-developed, narrow, with fine median furrow; lower septal rod usually present; posterior platform well-developed; *vascula media* and *vascula lateralia* well-developed, closely spaced.

Description of the North American material. Shell transversely oval with maximum width placed somewhat anterior to mid-length.

Ventral valve strongly apsacline and acutely conical, on average about 1.5 times as high as wide in adult specimens. Ventral pseudointerarea undivided and poorly defined laterally. Ventral interior mainly lacking distinctive characters, but with some poorly developed traces of mantle canals.

Dorsal valve gently convex to flattened subcircular in outline, on average 87% (Table 1) as long as wide with poorly defined, shallow median sulcus. Dorsal pseudointerarea, broadly triangular in outline, anacline, occupying on average

39% (Table 1) of the maximum valve width; median groove well-defined in adults; propareas narrow. Dorsal median septum starting at a short distance from the pseudointerarea and extending on average 85% (Table 1) of the maximum valve length; maximum height placed at about 2/3 of the valve length from the posterior margin; surmounting plate, well-developed, narrowly triangular, up to 0.12 mm wide, extending and widening along posteroventral slope of septum to place of maximum height; with weakly defined median furrow ending in two node-like swellings at anterior end; anterior slope of surmounting plate slightly undercut near top, usually bounded by a single lower septal rod (which is lacking in some specimens); anterior apex of septal rod variably developed, projecting outwards as short node, or ending at sharp angulation from median septum, then declining to dorsal valve floor. Dorsal cardinal muscle scars well-defined in adults, occupying about 40–50% of the maximum shell valve width and length; scars diverging anteriorly, slightly raised and bounded laterally by ridges; dorsal anterior muscle scars apparently entirely lacking; dorsal *vascula media* and *vascula lateralia* well-developed and strongly impressed, very closely spaced and originating at a point about 1/5 of the total valve length from the posterior margin.

Metamorphic shell around 0.12–0.17 mm in diameter; well-developed median sulcus on dorsal metamorphic shell; metamorphic ornamentation with large circular, shallow flat-bottomed pits of somewhat varying size (up to about 5 µm across) showing cross-cutting relationships; clusters of extremely minute pits (less than 500 nm across) are sometimes developed between the flat-bottomed pits. Post-metamorphic shell ornamented by fine, closely spaced growth lines.

Discussion. The North American material is indistinguishable from the Russian type material; the only difference is that the recorded maximum width is slightly larger in the Russian material. The morphological details and relative size of the dorsal pseudointerarea, median septum, cardinal scars and mantle canals recorded by Popov (1981a) are all completely identical to the material described here. For ease of comparison, some topotypes from Novaya Zemlya are figured here (Fig. 4) along with a *camera lucida* drawing of the holotype (Fig. 5A).

The morphology of *O. minor* is closely similar to the Ludlowian *Opsiconidion ephemerus* (Mergl, 1982) in all important aspects; however, the maximum size of the Bohemian species is much smaller and the largest ventral valve is only 0.8 mm in width. The musculature and mantle canal system of *O. ephemerus* are unfortunately not known in detail.

Opsiconidion minor is also similar to Silurian *O. celloni* (Cocks, 1979), which also has a narrow, triangular surmounting plate with a median furrow. According to Cocks (1979), the surmounting plate actually consists of

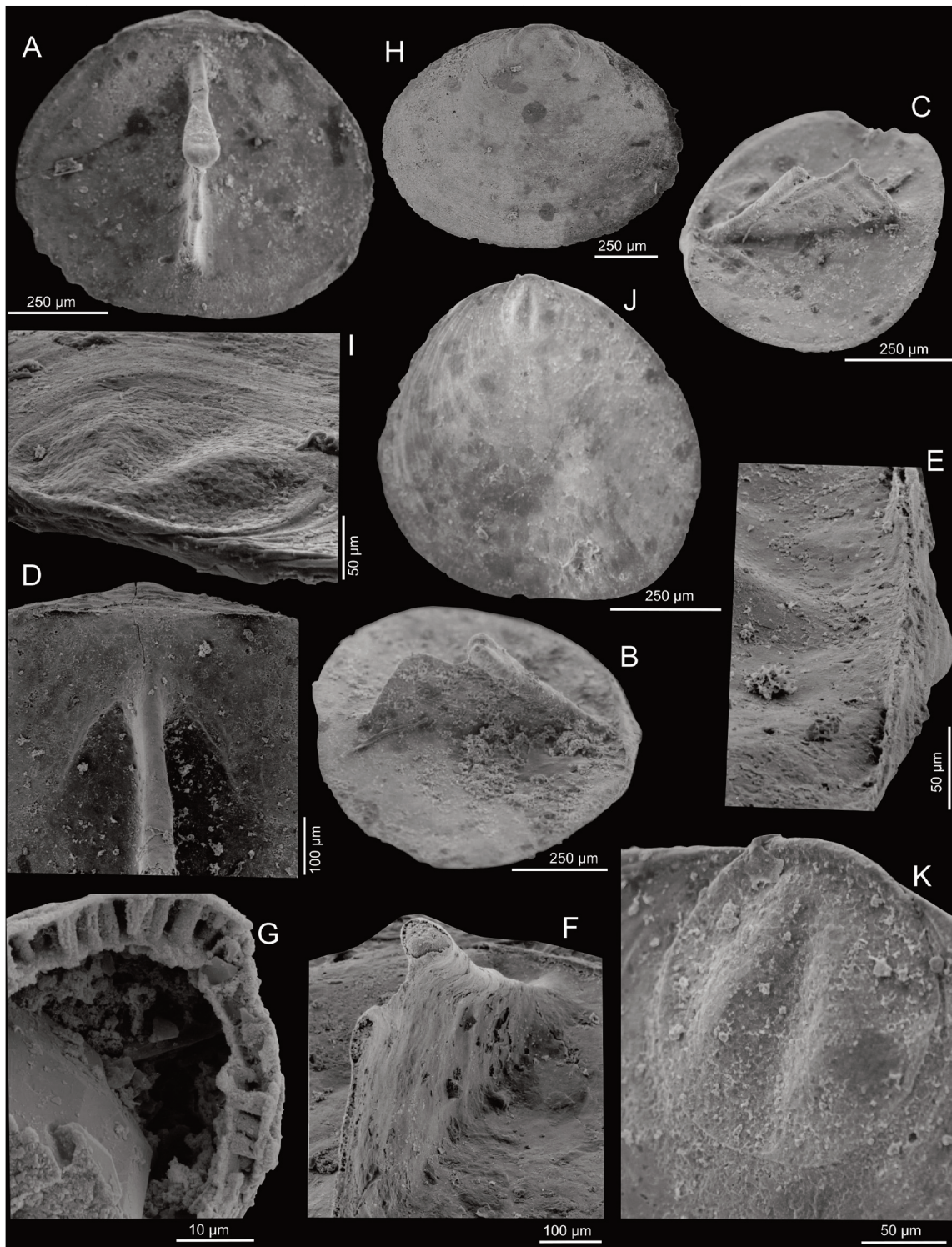


Fig. 2. *Opsiconidion minor* Popov, middle Emsian, all specimens from the Ogilvie Formation, east-central Alaska and the adjacent Yukon Territory. **A**, UAMES 5516, dorsal interior, from UA Museum locality A-941, Yukon Territory; **B**, UAMES 5511, lateral view of dorsal interior, from UA Museum locality A-941, Yukon Territory; **C**, UAMES 5514, lateral view of dorsal interior, from UA Museum locality A-941, Yukon Territory; **D**, NRM-PZ Br 136305, detail of dorsal pseudointerarea, from locality 83RB48, east-central Alaska; **E**, lateral view of **D**; **F**, oblique anterior view of dorsal median septum of **D**; **G**, detail of columnar shell structure in dorsal median septum of **D**; **H**, NRM-PZ Br 136306, dorsal exterior, from locality 83RB48, east-central Alaska; **I**, oblique anterior view of metamorphic shell of **H**; **J**, UAMES 5520, oblique anterior view of dorsal median septum, from UA Museum locality A-941, Yukon Territory; **K**, detail of metamorphic shell of **J**.

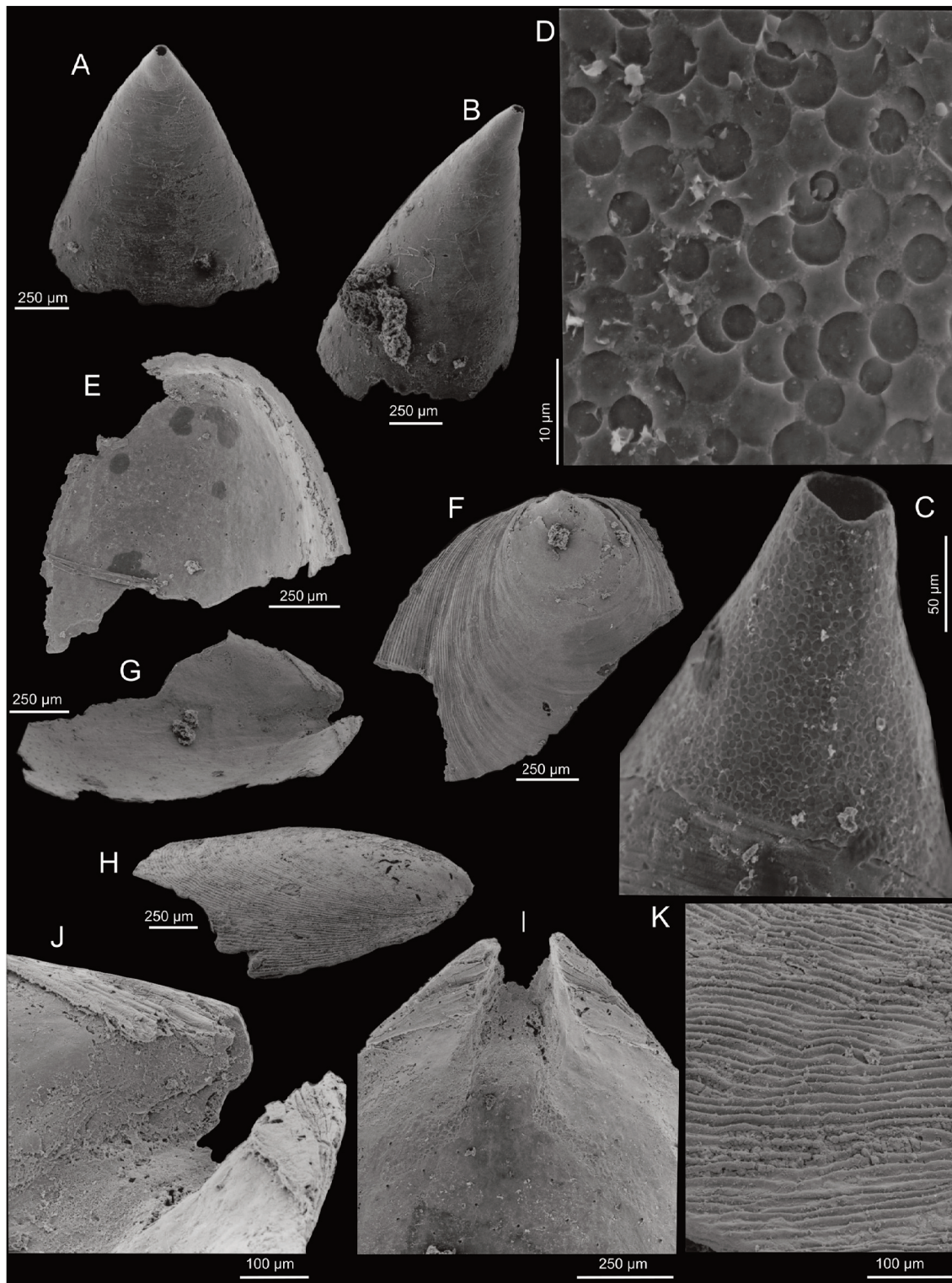


Fig. 3. A–D, *Opsiconidion minor* Popov, middle Emsian, both specimens from the Ogilvie Formation, east-central Alaska and the adjacent Yukon Territory: A, NRM-PZ Br 136307, posterior view of ventral exterior, from locality 83RB48, east-central Alaska; B, lateral view of A; C, UAMES 5509, detail of ventral metamorphic shell, from UA Museum locality A-941, Yukon Territory; D, detail of metamorphic pitting of C. E–K, *Lingulipora?* sp., all specimens from the Ogilvie Formation, locality 83RB48, east-central Alaska: E, NRM-PZ Br 136308, dorsal interior; F, NRM-PZ Br 136309, dorsal exterior; G, NRM-PZ Br 136310, lateral view of dorsal exterior; H, NRM-PZ Br 136311, lateral view of ventral interior; I, detail of pseudointerarea of H; J, oblique lateral view of pedicle groove of H; K, NRM-PZ Br 136312, detail of ornamentation of shell fragment.

two coalescing rods and the furrow is the junction between these, but this cannot be confirmed by the present study. *Opsiconidion minor* appears to differ from the Silurian species in having a relatively higher ventral valve, narrower propareas and a well-developed posterior platform (Fig. 5A). The mantle canals and musculature of *O. celloni* are not known.

The type species, *O. arcticon* Ludvigsen, 1974, is only slightly older than *O. minor* and comes from the early Emsian of the Yukon Territory, but it has also been recorded from the Middle Devonian of Ontario (von Bitter & Ludvigsen 1979). The dorsal valve of the type

species differs strongly from that of *O. minor* in lacking a surmounting plate and the pseudointerarea is completely undivided and forms a narrow rim along the posterior margin; the shape and relative size of the dorsal cardinal muscle scars appear to differ from *O. minor* (Fig. 5B). The maximum recorded size of *O. arcticon* from the Yukon Territory is only slightly less than that of *O. minor*, whilst the material from Ontario is considerably smaller (von Bitter & Ludvigsen 1979, text-fig. 2).

Opsiconidion aldridgei (Cocks, 1979) from the Llandovery of the Welsh Borderland and Estonia

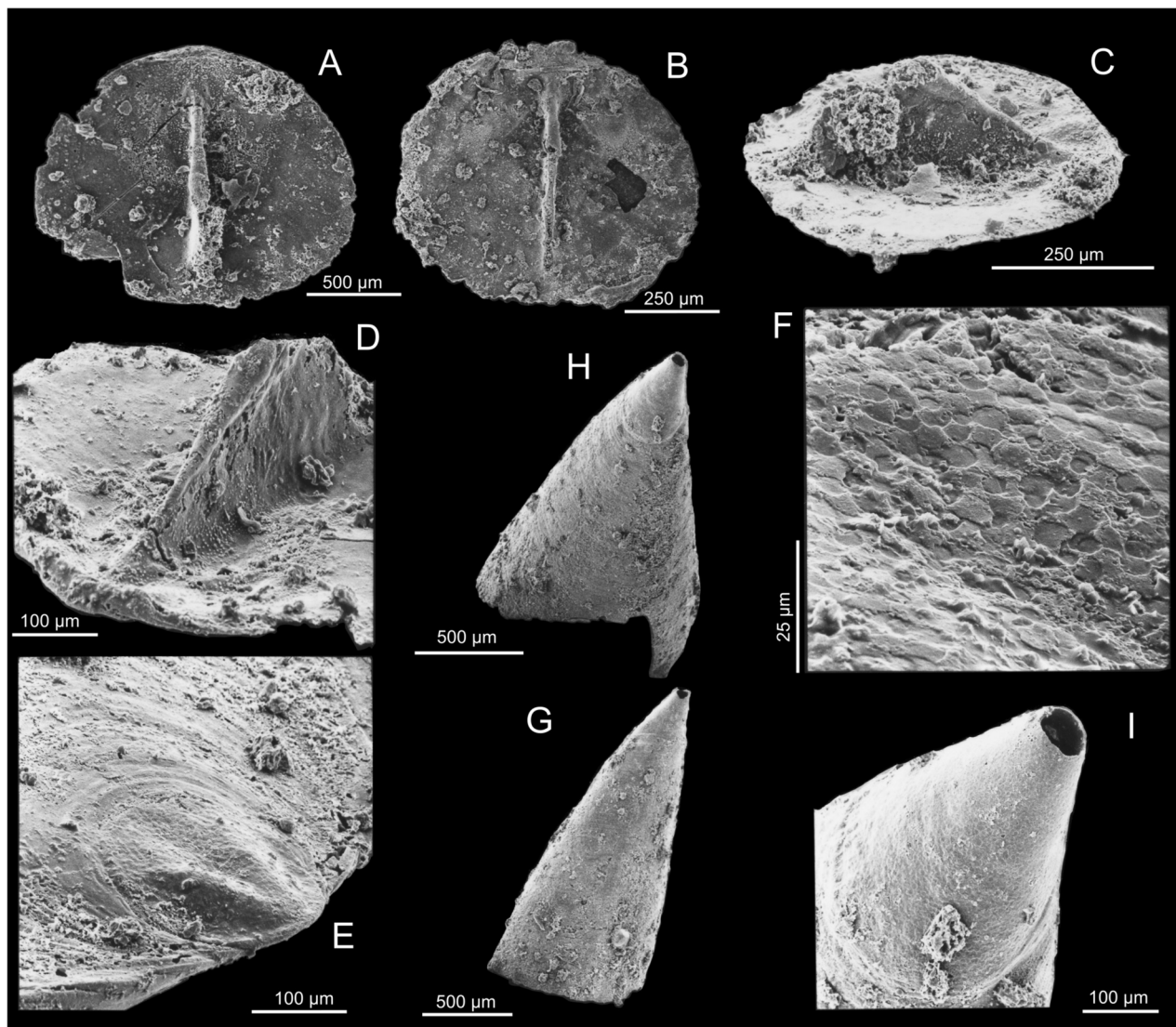
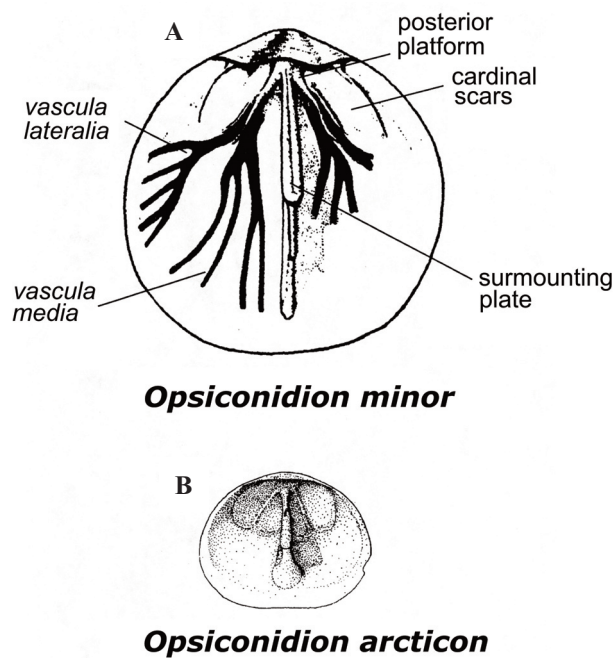


Fig. 4. *Opsiconidion minor* Popov, all specimens are topotypes from the Lower Devonian (Emsian) of Valnev Island, Novaya Zemlya, sample No. 39-31 (see Sobolev 1984, fig. 1). **A**, RM Br 136300, dorsal interior; **B**, RM Br 136301, dorsal interior; **C**, lateral view of B; **D**, oblique posterior view of B; **E**, RM Br 136302, oblique posterior view of dorsal metamorphic shell; **F**, detail of metamorphic pitting of E; **G**, RM Br 136303, lateral view of ventral exterior; **H**, RM Br 136304, lateral view of ventral exterior; **I**, detail of metamorphic shell of H.



Lingulipora? sp.
Figure 3E–K

Figured material. From east-central Alaska: NRM-PZ Br 136308–136312, from 83RB48 (east-central Alaska).

Remarks. The species is only represented by strongly fragmented material. The ventral valve has a very deep triangular pedicle groove and elevated propareas that lack flexure lines. The dorsal valve completely lacks a pseudointerarea. The interior of neither valve preserves any muscle scars or mantle canals. The micro-ornamentation consists of high, closely spaced and irregular, concentric wrinkles; the valve interior carries numerous perforations (up to about 10 µm across) that apparently continue through the shell and are visible as minute holes (some 1–3 µm across) also on the valve surface.

Lingulipora is a poorly known genus, and its systematic position is presently uncertain, in view of the lack of detailed information on the musculature, mantle canals, etc., from the type species. The specimens described here are somewhat similar to Devonian–Carboniferous forms that are usually assigned to the genus. It is possible that the deeply cut pedicle groove results from the fragmentation of the umbonal region and pedicle groove. Similar types of damages to the umbonal region were also noted by Baliński (1988), who studied the shell structure and ornamentation of Polish material from the Upper Devonian that he assigned to *Lingulipora*. However, it is to be noted that lingulids of the Family Lingulelloretidae Koneva & Popov, 1983, form an enclosed pedicle foramen which is somewhat similar to that of *Lingulipora* described by Baliński (1988), and it is not entirely impossible that the deeply cut and sometimes enclosed pedicle groove could be a feature of this genus.

The micro-ornamentation described by Baliński (1988, pp. 11–12) is similar to that illustrated here, but the perforations in the Polish species appear to be considerably wider. It is unclear if the perforations in *Lingulipora* represent true ‘articulate-like’ endopuncta as proposed by Baliński. Although considerably thicker, they are more likely comparable in structure and function with canals filled with extensions of the outer epithelium as present in Recent lingulates (see Williams et al. 1992).

Fig. 5. A, *Opsiconidion minor* Popov, CNIGR No. 1/11829, camera lucida drawing of the holotype; B, *Opsiconidion arcticon* Ludvigsen, drawing based on the dorsal interior figured by von Bitter & Ludvigsen (1979, pl. 90, fig. 7).

(Popov 1981b), *O. podlasiensis* Biernat, 1984, from the Wenlock of Poland and *O. praecursor* Popov & Holmer (in Popov et al. 1994) from the Late Ordovician of Estonia all differ from *O. minor* mainly in the lack of a surmounting plate.

Order LINGULIDA Waagen, 1885
Family UNCERTAIN
Genus *Lingulipora* Girty, 1898

Type species. *Lingula (Lingulipora) williamsana* Girty, 1898, p. 387, by original designation.

Diagnosis. See Holmer & Popov (2000, p. 78).

Occurrence. Devonian–Upper Carboniferous. North America; Europe.

Table 1. Dimensions (in millimetres) and ratios of dorsal valves of *Opsiconidion minor* (see p. 145 for abbreviations)

	L	W	LI	WI	LM	WM	LS	L/W	LI/L	LI/WI	WI/W	LM/L	WM/W	LS/L
N	6	6	6	6	1	1	6	6	6	6	6	1	1	6
X	0.93	1.07	0.06	0.42	0.40	0.52	0.79	87%	7%	15%	39%	42%	48%	85%
S	0.23	0.26	0.03	0.13			0.22	0.03	0.03	0.06	0.05			0.04
MIN	0.52	0.60	0.02	0.20	0.40	0.52	0.40	84%	3%	7%	33%	42%	48%	77%
MAX	1.20	1.32	0.08	0.60	0.40	0.52	1.04	91%	10%	17%	45%	42%	48%	89%

Acknowledgements. Leonid Popov (Wales) kindly made available the specimens from Novaya Zemlya. 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. Robert B. Blodgett wishes to thank ARCO ALASKA (especially William Grether and Michael Churkin, Jr) for graciously providing helicopter logistical support during field work conducted on the south flank of Jones Ridge in 1983. Zhifei Zhang acknowledges 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 Linda Hints. The publication costs of this article were covered by the Estonian Academy of Sciences.

REFERENCES

- Arno, Z. 2010. Givetian (Middle Devonian) *Opsiconidion* (Phylum Brachiopoda, Class Inarticulata, Order Acrotretida) from the Gobialtai Formation, Shine Jinst Region, Southern Mongolia. *Geological Society of America, Abstracts with Programs*, **42**, 65.
- Baliński, A. 1988. Shell morphology and structure in *Lingulipora* Girty. *Acta Palaeontologica Polonica*, **33**, 123–133.
- Baliński, A. & Holmer, L. E. 1999. The late Devonian trematid lingulate brachiopod *Schizobolus* from Poland. *Acta Palaeontologica Polonica*, **44**, 335–346.
- Bassett, M. G. 1984. Life strategies of Silurian brachiopods. *Special Papers in Palaeontology*, **32**, 237–263.
- Biernat, G. 1984. Silurian inarticulate brachiopods from Poland. *Acta Palaeontologica Polonica*, **29**, 91–103.
- Blodgett, R. B. 1978. *Biostratigraphy of the Ogilvie Formation and Limestone and Shale Member of the McCann Hill Chert (Devonian), East-Central Alaska and Adjacent Yukon Territory*. Unpublished M.S. thesis, University of Alaska, Fairbanks, 142 pp.
- Blodgett, R. B., Potter, A. W. & Clough, J. G. 1984. Upper Ordovician–Lower Devonian biostratigraphy and paleoecology of the Jones Ridge-Squaw Mountain area, east-central Alaska. *Geological Society of America, Abstracts with Programs*, **16**, 270.
- Brabb, E. E. & Churkin, M., Jr. 1969. Geologic map of the Charley River quadrangle, east-central Alaska. *United States Geological Survey Miscellaneous Geologic Investigations*, Map I-573, Scale: 1:250,000.
- Brock, G. A., Engelbretsen, M. J. & Dean-Jones, G. 1995. Acrotretoid brachiopods from the Devonian of Victoria and New South Wales. In *Papers from the First Australian Palaeontological Convention* (Jell, P. A., ed.), *Memoir of the Association of Australasian Palaeontologists*, **18**, 105–120.
- Churkin, M., Jr. & Brabb, E. E. 1965. Ordovician, Silurian and Devonian biostratigraphy of east-central Alaska. *American Association of Petroleum Geologists Bulletin*, **49**, 172–185.
- Churkin, M., Jr. & Brabb, E. E. 1968. Devonian rocks of the Yukon-Porcupine Rivers area and their tectonic relation to other Devonian sequences in Alaska. *International Symposium on the Devonian System. Calgary, Alberta Society of Petroleum Geologists, Calgary, Alberta*, **2**, 227–258 (dated 1967).
- Clough, J. G. & Blodgett, R. B. 1984. Lower Devonian basin to shelf carbonates in outcrop from the western Ogilvie Mountains, Alaska and Yukon Territory. In *Carbonates in Subsurface and Outcrop, 1984 C.S.P.G. Core Conference, October 18–19, 1984* (Eliuk, L. S., ed.), pp. 57–81. Canadian Society of Petroleum Geologists, Calgary, Alberta.
- Clough, J. G. & Blodgett, R. B. 1987. Lower Devonian carbonate facies and platform margin development, east-central Alaska and Yukon Territory. In *Alaskan North Slope Geology*, **1** (Tailleur, I. & Weimer, P., eds), pp. 349–354. Pacific Section, Society of Economic Paleontologists and Mineralogists and Alaska Geological Society.
- Clough, J. G. & Blodgett, R. B. 1988. Late Early Devonian coral–stromatoporoid reef complex and associated facies, Ogilvie Formation of east-central Alaska and adjacent Yukon Territory. In *Devonian of the World* (McMillan, N. J., Embry, A. F. & Glass, D. J., eds), *Canadian Society of Petroleum Geologists Memoir*, **14**, 519–525.
- Cocks, L. R. M. 1979. New acrotretacean brachiopods from the Palaeozoic of Britain and Austria. *Palaeontology*, **22**, 93–100.
- Dover, J. H. 1992. *Geologic Map and Fold- and Thrust-Belt Interpretation of the Southeastern Part of the Charley River Quadrangle, East-Central Alaska*. U.S. Geological Survey Miscellaneous Investigations Series Map I-1942, 14 p., 2 sheets, scale 1:100,000.
- Dover, J. H. & Miyaoka, R. T. 1988. *Reinterpreted Geologic Map and Fossil Data, Charley River Quadrangle, East-Central Alaska*. U.S. Geological Survey Miscellaneous Field Studies Map MF-2004, 2 sheets, scale 1:250,000.
- Girty, G. H. 1898. Description of a fauna found in the Devonian black shale of eastern Kentucky. *American Journal of Science*, **4**, 384–395.
- Gorjansky, V. Y. & Popov, L. E. 1985. Morphology, systematic position and origin of inarticulate brachiopods with carbonate shells. *Paleontologicheskij Zhurnal*, **1985**, 3–14 [in Russian].
- Holmer, L. E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata*, **26**, 1–172.
- Holmer, L. E. 2000. Redescription of the Ordovician acrotretoid brachiopod *Conotreta* Walcott, 1889. *GFF*, **122**, 313–318.
- Holmer, L. E. & Popov, L. E. 2000. Lingulata. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Revised*, **2** (Kaesler, R. L., ed.), pp. 30–146. Geological Society of America and University of Kansas Press, Lawrence.
- Huson, R. & Over, D. J. 2000. Youngest acrotretids (Phylum Brachiopoda, Class Inarticulata, Order Acrotretida) from the Upper Devonian Hanover Shale in western New York State. *Geological Society of America, Abstracts with Programs*, **32**, 370.
- Koneva, C. P. & Popov, L. E. 1983. Some new lingulids from the Upper Cambrian and Lower Ordovician of Malyi

- Karatau. In *Stratigrafiya i paleontologiya nizhnego paleozoya Kazakhstana* [Lower Palaeozoic Stratigraphy and Palaeontology of Kazakhstan] (Apollonov, M. K., Vandaletov, S. & Ivshin, N. K., eds), pp. 110–124. Izdatel'stvo Nauka, Alma-Ata [in Russian].
- Kuhn, O. 1949. *Lehrbuch der Paläozoologie*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 326 pp.
- Langer, W. 1971. Acrotretidae (Brachiopoda) im Devon des Sauer- und Bergischen Landes. *Decheniana*, **123**, 328–329.
- Lenz, A. C. 1972. Ordovician to Devonian history of northern Yukon and adjacent District of Mackenzie. *Bulletin of Canadian Petroleum Geology*, **20**, 321–361.
- Lenz, A. C. 1993. A new Silurian sponge–inarticulate brachiopod life? association. *Journal of Paleontology*, **67**, 138–139.
- Ludvigsen, R. 1974. A new Devonian acrotretid (Brachiopoda, Inarticulata) with unique protegular ultrastructure. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **3**, 133–148.
- Lüter, C. 2004. How brachiopods get covered with nanometric silicon chips. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **271**, S465–S467.
- Mergl, M. 1982. *Caenotreta* (Inarticulata, Brachiopoda) in the Upper Silurian of Bohemia. *Věstník Ústředního ústavu geologického*, **57**, 115–116.
- Mergl, M. 2001. Lingulate brachiopods of the Silurian and Devonian of the Barrandian (Bohemia, Czech Republic). *Acta Musei Nationalis Pragae, Series B – Historia Naturalis*, **57**, 1–49.
- Mergl, M. 2002. Linguliformean and craniiformean brachiopods of the Ordovician (Trenice to Dobrotiva Formations) of the Barrandian, Bohemia. *Acta Musei Nationalis Pragae, Series B, Natural History*, **58**, 1–82.
- Mergl, M. 2009. Lingulate brachiopods from Acanthopyge Limestone (Eifelian) of the Barrandian, Czech Republic. *Bulletin of Geosciences*, **83**, 281–298.
- Mergl, M. 2018. The late Emsian association of weakly plicate brachiopods from Hamar Laghdad (Tafilalt, Morocco) and their ecology. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, **290**, 153–182.
- Mergl, M. 2019. Lingulate brachiopods across the Kačák Event and Eifelian–Givetian boundary in the Barrandian area, Czech Republic. *Bulletin of Geosciences*, **94**, 169–189.
- Mergl, M. & Ferrova, L. 2009. Lingulate brachiopods from the Chýnice Limestone (upper Emsian, Barrandian; Czech Republic). *Bulletin of Geosciences*, **84**, 525–546.
- Mergl, M. & Jimenez-Sanchez, A. 2015. Lingulate brachiopods from the Suchomasty Limestone (upper Emsian) of the Barrandian, Czech Republic. *Bulletin of Geosciences*, **90**, 173–193.
- Mergl, M. & Vodrážková, S. 2012. Emsian–Eifelian lingulate brachiopods from the Daleje–Třebotov Formation (Třebotov and Suchomasty limestones) and the Choteč Formation (Choteč and Acanthopyge limestones) from the Prague Basin. *Bulletin of Geosciences*, **87**, 315–332.
- Mergl, M., Frýda, J. & Kubajko, M. 2018. Response of organophosphatic brachiopods to the mid-Ludfordian (late Silurian) carbon isotope excursion and associated extinction events in the Prague Basin (Czech Republic). *Bulletin of Geosciences*, **93**, 369–400.
- Perry, D. G., Klapper, G. & Lenz, A. C. 1974. Age of the Ogilvie Formation (Devonian), northern Yukon: based primarily on the occurrence of brachiopods and conodonts. *Canadian Journal of Earth Sciences*, **11**, 1055–1097.
- Popov, L. E. 1981a. The first record of inarticulate brachiopods of the family Acrotretidae from the Lower Devonian of the USSR. In *Paleontologicheskaya osnova stratigraficheskikh skhem paleozoya i mezozoya ostrovov Sovetskoy Arktiki* [Palaeontological Basis of Palaeozoic and Mesozoic Stratigraphical Charts of Islands of the Soviet Arctic] (Bondarev, V. I., ed.), pp. 61–65 [in Russian].
- Popov, L. E. 1981b. The first record of microscopic inarticulate brachiopods of the family Acrotretidae from the Silurian of Estonia. *Eesti NSV Teaduste Akadeemia Toimetised, Geoloogia*, **30**, 34–41 [in Russian].
- Popov, L. E., Nölvak, J. & Holmer, L. E. 1994. Late Ordovician lingulate brachiopods from Estonia. *Palaeontology*, **37**, 627–650.
- Rowell, A. J. 1965. Inarticulata. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (Moore, R. C., ed.), pp. 260–296. Geological Society of America and University of Kansas Press, Lawrence.
- Sobolev, N. N. 1984. Conodonts from the Lower and Middle Devonian deposits of Novaya Zemlya. In *Novaya Zemlya na rannikh etapakh geologicheskogo razvitiya* [Novaya Zemlya at the Early Stages of Its Geological Evolution] (Bondarev, V. I., ed.), pp. 58–85. PGO “Sevmorgeologiya”, Leningrad [in Russian].
- Sutton, M. D., Bassett, M. G. & Cherns, L. 2000. Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh Basin, Part 2. *Monograph of the Palaeontographical Society*, **153**, 61–114.
- Topper, T. P., Strotz, L. C., Holmer, L. E., Zhang, Z. F., Tait, N. N. & Caron, J. B. 2015a. Competition and mimicry: the curious case of chaetae in brachiopods from the middle Cambrian Burgess Shale. *BMC Evolutionary Biology*, **15**, 42.
- Topper, T. P., Strotz, L. C., Holmer, L. E. & Caron, J. B. 2015b. Survival on a soft seafloor: life strategies of brachiopods from the Cambrian Burgess Shale. *Earth-Science Reviews*, **151**, 266–287.
- Valentine, J. L., Brock, G. A. & Molloy, P. D. 2003. Linguliformean brachiopod faunal turnover across the Ireviken Event (Silurian) at Boree Creek, central-western New South Wales, Australia. *CFS Courier Forschungsinstitut Senckenberg*, **242**, 301–327.
- von Bitter, P. V. & Ludvigsen, R. 1979. Formation and function of protegular pitting some North American acrotretid brachiopods. *Palaeontology*, **22**, 705–720.
- Waagen, W. H. 1885. Salt Range Fossils, Pt. 4 (2), Brachiopoda. *Memoirs, Palaeontologia Indica, Series 13*, **1**(5) 729–770.
- Wang, H. Z., Zhang, Z. F., Holmer, L. E., Hu, S. X., Wang, X. R. & Li, G. X. 2012. Peduncular attached secondary tiering acrotretoid brachiopods from the Chengjiang fauna: Implications for the ecological expansion of brachiopods during the Cambrian explosion. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **323**, 60–67.
- Williams, A. 2003. Microscopic imprints on the juvenile shells of Palaeozoic linguliform brachiopods. *Palaeontology*, **46**, 67–92.

- Williams, A. & Curry, G. B. 1991. The microarchitecture of some acrotretide brachiopods. In *Brachiopods Through Time* (MacKinnon, D. I., Lee, D. E. & Campbell, J. D., eds), pp. 133–140. Balkema, Rotterdam.
- Williams, A., Mackay, S. & Cusack, M. 1992. Structure of the organo-phosphatic shell of the brachiopod *Discina*. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **337**, 83–104.
- Williams, A., Cusack, M., Buckman, J. O. & Stachel, T. 1998. Siliceous tablets in the metamorphic shells of apatitic discinid brachiopods. *Science*, **279**, 2094–2096.
- Zhang, Z. L., Popov, L. E., Holmer, L. E. & Zhang, Z. F. 2018. Earliest ontogeny of early Cambrian acrotretoid brachiopods – first evidence for metamorphosis and its implications. *BMC Evolutionary Biology*, **18**, 42.

Vara-Devoni (Emsi) akrotretiidne mikrobrahhiopood *Opsiconidion minor* Popov, 1981 Alaskal ja Yukoni territooriumil ning Novaja Zemljal

Lars E. Holmer, Robert B. Blodgett, Yue Liang ja Zhifei Zhang

On kirjeldatud Vara-Devoni senini vähetuntud väikesemõdulisi brahhiopode seltsist Acrotretida (klass Lingulata). Uuritud materjal kuulub liiki *Opsiconidion minor* Popov, mille topotüübiline materjal on kirjeldatud Novaja Zemlja arhipelaagist. Kirjeldatud materjal pärineb Põhja-Ameerika kahest leiukohast, mis asuvad Alaska (USA) ja Kanada Yukoni territooriumi piirialal, kus on esindatud Alam-Devoni (Emsi) Ogilvie kihistu. Kirjeldatud brahhiopoodid esinevad kihtides, mis kuuluvad konodondi *Polygnathus inversus* Klapper & Johnson biotsooni. Akrotretiidi *Opsiconidion minor* koonilise kujuga ventraalsel (selgmisel) poolmikul pole liigispetsiifilisi tunnuseid. Välisskulptuuris eristub selgelt algse arengustaadiumi (diameetriga kuni 0,17 mm) “võrkjas” skulptuur poolme tipus (*metamorphic shell*) ja hilisema arengu jooksul kujunenud peen kasvujootest moodustunud muster. Nõrgalt kumer või lame subsirkulaarne dorsaalne poolmik laiusega kuni 6 mm on aga iseloomustatud rea spetsiifiliste kesksepti ja musklite kinnitusaluselise iseloomustavate tunnustega. Liigi Ameerika esindajad on praktiliselt identsed topotüüpiliste eksemplaridega Novaja Zemljalt, olles neist ainult veidi väiksemad. Kaasneva Alam-Devoni liigina on artiklis lühidalt kirjeldatud veel linguliid *Lingulipora?* sp., mille täpne taksonoomiline kuuluvus on ebaselge eksemplaride halva säilimise tõttu.