Silurian and Devonian brachiopods from Severnaya Zemlya (Russian Arctic)

Tatiana L. MODZALEVSKAYA
All-Russia Geological Research Institute (VSEGEI),
Srednij pr. 74, St. Petersburg, 199106 (Russia)
modz@IB2567.spb.edu

Modzalevskaya T. L. 2003. — Silurian and Devonian brachiopods from Severnaya Zemlya (Russian Arctic). *Geodiversitas* 25 (1) : 73-107.

ABSTRACT
Silurian and Lower Devonian sequences of the carbonate sediments of the Severnaya Zemlya Archipelago, and adjacent territories, are rich in fossils, among which brachiopods are dominating. The association of brachiopods includes 25 taxa. Strophomenids, atrypids and spiriferids are the most diverse groups, although the most common are the rhynchonellids. Seven new species are described: *Brachyprion ruminatus* n. sp., *Lenatoechia octjabrensis* n. sp., *Anabaria*? *latens* n. sp., *Undispirifer*? *obsoletiplicatus* n. sp., *Grebenella laciniatus* n. sp., *Hyattidina remota* n. sp., and *Greenfieldia orbiculata* n. sp. Most of the brachiopod communities are characteristic of shallow water environments and represent BA-2, BA-3 or BA-4 benthic associations. They indicate the transition from open shallow-water shelf environments to fore-shoal facies. The brachiopod fauna is often monotaxic and is dominated by endemic species. At the generic level this fauna is 74% cosmopolitan, and 26% regional. This fact testifies the existence of palaeobiogeographic similarities between Severnaya Zemlya and the northern Baltica (Novaya Zemlya, Urals, and Baltic region) in the West, and between Severnaya Zemlya and East Siberia (Tajmyr, Siberian Platform) in the East in Silurian time. The assemblage of Devonian brachiopods from Severnaya Zemlya is most similar to the contemporaneous faunas from North-East Russia, Australia and Canadian Arctic Archipelago.

KEY WORDS
Brachiopoda,
Silurian,
Devonian,
Severnaya Zemlya,
East Siberia,
Urals,
Timan,
Russian Arctic,
Canadian Arctic,
biostratigraphy,
palaeobiogeography,
new species.

RÉSUMÉ
Les brachiopodes siluriens et dévoniens de Severnaya Zemlya (Arctique russe).
Les séquences de sédiments carbonatés du Silurien et du Dévonien de l'archipel de Severnaya Zemlya et des territoires adjacents sont riches en fossiles, où dominent les brachiopodes. Les assemblages de brachiopodes comprennent 25 taxons. Les strophoménides, atrypides et spiriférides sont les groupes les plus diversifiés, bien que les plus communs soient les rhynchonellides. Sept nouvelles espèces sont décrites : *Brachyprion ruminatus* n. sp., *Lenatoechia octjabrensis* n. sp., *Anabaria* ? *latens* n. sp., *Undispirifer* ? *obsoletiplicatus* n. sp., *Grebenella laciniatus* n. sp., *Hyattidina remota* n. sp. et *Greenfieldia orbiculata* n. sp. La plupart des commmunautés de brachiopodes sont caractéristiques d'environnements peu profonds et correspondent aux associations benthiques BA-2, BA-3 ou BA-4. Elles indiquent la transition entre les environnements d'eau ouverte peu profonde et le faciès sub-tidal. La faune de brachiopodes est souvent monotaxon et dominée par des espèces endémiques. Au niveau générique, elle est cosmopolite à 74 % et régionale à 26 %. Cela atteste l'existence de ressemblances paléobiogéographiques entre Severnaya Zemlya et le nord de la Baltica (Novaya Zemlya, Oural et région balte) à l'Ouest et Severnaya Zemlya et la Sibérie orientale (Taïmyr, Plateforme sibérienne) à l'Est, à la période silurienne. Ce sont des faunes contemporaines du Nord-Est de la Russie, de l'Australie et de l'Arctique canadien que l'assemblage de brachiopodes dévoniens de Severnaya Zemlya est le plus proche.

MOTS CLÉS
Brachiopoda,
Silurien,
Dévonien,
Severnaya Zemlya,
Sibérie orientale,
Oural,
Timan,
Arctique russe,
Arctique canadien,
biostratigraphie,
paléobiogéographie,
nouvelles espèces.

INTRODUCTION

B. Kh. Egiazarov (1959) was the first to collect Silurian and Devonian brachiopods from the Severnaya Zemlya and Sedov archipelagoes. The brachiopods were preliminary identified by O. I. Nikiforova. Her identifications were also used by M. S. Zhizhina (1965). During mapping in 1976-1979, brachiopods were collected by Yu. G. Samojlovich on the Samojlovich (Dlinnyj) Island, by A. F. Khapilin on October Revolution and Komsomolets islands, by E. I. Kachanov on Pioneer Island, by V. Vl. Menner (Matusevich and Ushakov rivers) and E. Yu. Kurik (Strojnaya River) on October Revolution Island, and by V. A. Markovskij on Komsomolets Island (Markovskij & Smirnova 1982). The brachiopods, collected bed by bed from the type section on the Matusevich River (October Revolution Island), are of particular importance for the regional stratigraphy.
The results of brachiopod studies have been previously used in Silurian and Devonian stratigraphy of the Severnaya Zemlya Archipelago (Kurik *et al*. 1982; Matukhin *et al*. 1999). The distribution of the Silurian and Devonian strata on Severnaya Zemlya, location of sections studied, and lithological characterization of Silurian and Devonian strata are given in Männik *et al*. (2002).
The purpose of this investigation is to describe new Silurian and Devonian brachiopods, to determine the age of the formations in the Severnaya Zemlya sequence, and to correlate it with other Silurian-Devonian sequences in the world. It should be noted that the Lower Devonian brachiopods available do not come from the type section on October Revolution Island but from three separated localities on Komsomolets Island. Unfortunately, the precise levels of the Devonian samples in the sequence are not known.
The material enabled to identify 25 different taxa, including seven new species. The preservation of brachiopods is highly variable. The mineralogical composition of most of the

brachiopod shells studied is calcitic, although some dolomitic ones were found. Many shells are abraded and preserved as moulds, sometimes as accumulations ("nests") with shells in living position. There are layers of coquina (composed of broken valves) embedded in limestone. Most of the pentameroids are difficult to identify, because they are usually represented by disarticulated ventral valves. Strophomenoids and spiriferoids are also preserved as rare disarticulated valves with little chance to study their internal structures. Thus, only rare specimens were suitable for detail morphological studies. New taxa are described in detail, others are characterized only briefly. All well preserved shells of pentameroids, atrypoids, rhynchonelloids, athyroids and spiriferoids were hand ground with measuring distances to the anterior margin. Serial sections at 0.05 mm intervals were examined in detail, better visible internal structures were drawn under magnification 8 or 16 times (depending on the size of shells). Also some peels were prepared. Descriptive terms used in this paper come from the *Treatise* (Williams & Brunton 1997) and from the paper by P. Racheboeuf (1987). Taxonomy is based on Popov *et al*. (1993) and Williams *et al*. (1996).

All collections studied are deposited in the CNIGR Museum, St. Petersburg, Russia, collection N 12991.

ABBREVIATIONS

L	length;
T	thickness of articulated shell;
W	width.

SYSTEMATICS

Subphylum CRANIIFORMEA
Popov, Bassett, Holmer & Laurie, 1993
Class CRANIATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order TRIMERELLIDA
Gorjansky & Popov, 1986
Family TRIMERELLIDAE Davidson & King, 1872
Genus *Trimerella* Billings, 1862

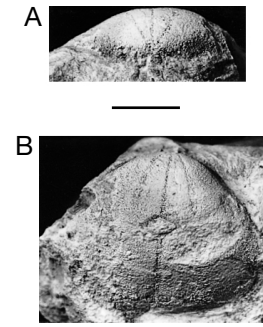

FIG. 1. — *Trimerella* sp., pedicle valve (N 1/12991), loc. 13e, Srednij Formation; **A**, posterior view; **B**, ventral view. Scale bar: 6 mm.

Trimerella sp.
(Fig. 1)

MATERIAL EXAMINED. — Numerous ventral shells (concentrated in shell bank) from the single locality, loc. 13e, Srednij Island (Sedov Archipelago, Männik *et al*. 2002: fig. 1); Srednij Formation.

REMARKS

Within the group of Telychian brachiopods assigned here to *Trimerella* are forms with ventral shells of medium size, longitudinally oval outline, and the convex umbo. The ventral pseudointerarea with homeochilidium is not visible. A low ventral muscle platform extends behind the middle of the valve. Short lateral septum occurs at less than 18° from the longer septum, which extends almost to the anterior margin. *Trimerella* is a common genus from the Ashgill through the Silurian of the North America, Europe, East Siberia, Australia, South China, Kazakhstan and Tuva. In their size and convexity, the shells resemble those of *Trimerella attenuata* Gorjansky, 1972 from the Donenzhal Formation of Kazakhstan (Tarbagataj ridge) (Gorjansky 1972: 171, pl. 45, figs 6, 7). The specimens from Severnaya Zemlya differ from those known from other regions in possessing a shell which is wider anteriorly and has a longer median septum. Larger but very similar shells are described from the Omnutakh and Mogokta formations in East Siberia (Lopushinskaya 1991: 51, pl. I, figs 1-5).

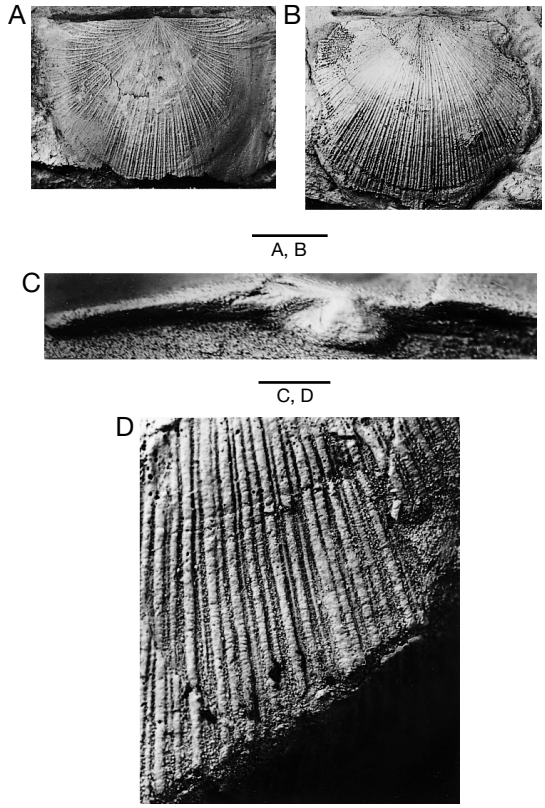

FIG. 2. — *Strophomena pectenoides* (Andreeva, 1961); **A**, dorsal view of a brachial valve (N 4/12991), loc. 13, bed 112, Vodopad Formation; **B**, **C**, brachial valve (N 3/12991); **B**, dorsal view; **C**, posterior view; **D**, surface sculptering of the specimen (N 5/12991), loc. 32, bed 21, Vodopad Formation. Scale bars: A, B, 10 mm; C, D, 2 mm.

Subphylum RHYNCHONELLIFORMEA Williams, Carlson, Brunton, Holmer & Popov, 1996
Class STROPHOMENATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order STROPHOMENIDA Öpik, 1934
Family STROPHOMENIDAE King, 1846
Genus *Strophomena* Rafinesque, 1825

Strophomena pectenoides
Andreeva *in* Nikiforova & Andreeva, 1961
(Fig. 2)

Strophomena? *pectenoides* Andreeva *in* Nikiforova & Andreeva, 1961: 184, pl. XXXIX, figs 1-6. — Lopushinskaya 1976: 39, pl. III, figs 16-19.

MATERIAL EXAMINED. — 10 isolated valves from loc. 13, beds 21, 112, Matusevich River, loc. 32, bed 21, Ushakov River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Vodopad Formation.

REMARKS

The specimens have a well developed narrow interarea, small chilidium, and narrow pseudodeltidium. There is a flattened dorsal umbo and a convex median part passing into a prominent sulcus. The shell is covered by fine rounded ribs which intercalate with even finer secondary ones. Low massive dental plates, teeth, and a large subquadrate muscle field with small oval adductors are developed in the ventral interior. The shells are similar to *Strophomena kulumbensis* Lopushinskaya, 1967 from Chamba, Talikit and Meik formations of East Siberia, but differ from that in possessing more frequent, unequal multicostellae and a chilidium larger than the pseudodeltidium (Lopushinskaya 1967: 89, pl. XX, figs 3-6). O. N. Andreeva (Nikiforova & Andreeva 1961: 185) attributed *pectenoides* to *Strophomena* with a query, because there were no specimens with a ventral muscle field, and noted their resemblance to *Coolinia pecten* (Linnaeus, 1758). However, the available facts show that the taxon belongs to *Strophomena*.

Genus *Rafinesquina* Hall & Clarke, 1892

Rafinesquina*? *stropheodontoides (Savage, 1913)
(Fig. 3)

Brachyprion stropheodontoides Savage, 1913: 119, pl. 6, fig. 4.

Rafinesquina? *inaequicostata* Lopushinskaya, 1967: 87, pl. XX, fig. 2.

Rafinesquina? *stropheodontoides* – Amsden 1974: 52, pl. 12, figs 2-4, pl. 13, fig. 1.

MATERIAL EXAMINED. — 13 specimens (separate ventral and dorsal valves and their fragments), from loc. 13A, bed 124, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Vodopad Formation.

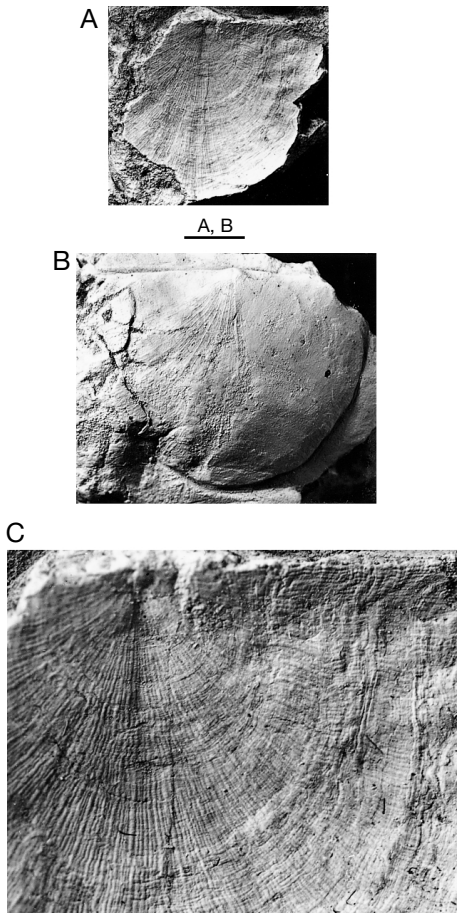

FIG. 3. — *Rafinesquina*? *stropheodontoides* (Savage, 1913); **A**, **C**, partly damaged dorsal valve, showing thickened costellae at different distances from the beak and short undulate rugae (N 6/12991); **A**, dorsal view; **C**, enlarged surface sculpturing; **B**, ventral view of a pedicle valve (N 7/12991), loc. 13A, bed 124, Vodopad Formation. Scale bars: A, B, 6 mm; C, 2 mm.

REMARKS

The specimens are characterized by a concavo-convex, subquadrate general outline of shell, lack of a well defined geniculation, and a low interarea. The hinge line is straight, and the cardinal extremities are alate. The surface is finely costellated, with four to five minor costellae, presented in the interspaces between the major ribs. A single, straight, strong median costa extends along the whole shell length. Other costae curve near the cardinal extremities. The costellae are crossed by short and undulate rugae.

The shape and ornamentation of *R.*? *stropheodontoides* are similar to those of *R. crispa* Andreeva, 1961 studied from the Dolborian Stage of East Siberia (Nikiforova & Andreeva 1961: 159, pl. XXIX, figs 5, 6). The distinguishing features of the former include a median thickened rib and irregular thickening ribs. These are the earliest representatives of the genus found in the Arctic region. They have previously been known only from the Edgewood Formation (Ashgill-lowermost Llandovery) of North America.

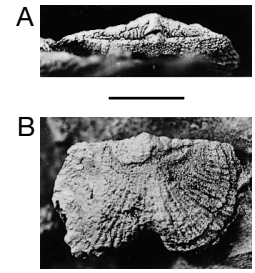

FIG. 4. — *Pentlandina*? sp., complete shell (N 8/12991), loc. 29a, ?Vodopad Formation; **A**, posterior view; **B**, ventral view. Scale bar: 5 mm.

Genus *Pentlandina* Bancroft, 1949

***Pentlandina*? sp.**
(Fig. 4)

MATERIAL EXAMINED. — A single shell, embedded in rock matrix, from loc. 29a, Lednikovaya River, October Revolution Island (Männik *et al*. 2002: fig. 1); Vodopad Formation.

REMARKS

A single small shell (L = 6.7 mm, W = 1.1 mm) with biconvex profile, semielliptical outline, deep ventral sinus, and prominent dorsal sulcus is attributed to *Pentlandina*? sp. The hinge line is shorter than the maximum width. The ventral interarea has a large delthyrium, closed by pseudodeltidium. A small chilidium is filled by a bilobate cardinal process. Ornament is parvicostellate with new ribs intercalating. Shells of *Pentlandina* from

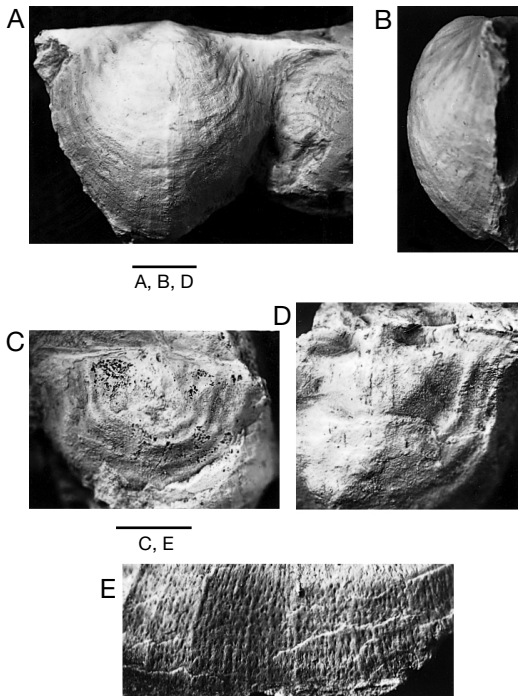

FIG. 5. — *Brachyprion ruminatus* n. sp.; **A**, **B**, pedicle valve (holotype N 9/12991), loc. 11, bed 14A, Samojlovich Formation; **A**, ventral view; **B**, lateral view; **C**, ventral view of an internal mould of a pedicle valve (N 10/12991), loc. 11, bed 14, Samojlovich Formation; **D**, ventral view of an internal mould of a pedicle valve with well developed impressions of concentric rugae (N 11/12991); **E**, note the radially arranged pseudopunctae at anterior margin (N 12/12991), loc. 11, bed 20, Samojlovich Formation. Scale bars: A, B, D, 6 mm; C, 5 mm; E, 2 mm.

the middle Llandovery of West Shropshire have the same size and shape (Cocks 1968: 293, pl. I, fig. 13). However, the specimens from Severnaya Zemlya lack any sign of the ventral muscle field well visible on the shells from Shropshire.

Family STROPHEODONTIDAE Caster, 1939
Genus *Brachyprion* Shaler, 1865

Brachyprion ruminatus n. sp.
(Fig. 5)

HOLOTYPE. — N 9/12991, CNIGR Museum, St. Petersburg (Fig. 5A, B), ventral valve; L = 20.1 mm, W = 26.1 mm.

ETYMOLOGY. — From *ruminatus* (Latin): chewed.

TYPE LOCALITY. — Loc. 11, Matusevich River, October Revolution Island.

FORMATION. — Samojlovich Formation.

AGE. — ?Llandovery, ?Telychian.

MATERIAL EXAMINED. — Seven ventral valves partly buried in matrix with only their disc exposed, and dorsal valve impressions from loc. 11, bed 14 (1-A), and three specimens from loc. 12, bed 9, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5).

MEASUREMENTS (IN MM). — L = 16.0-20.3, W = 17.4-26.1.

DIAGNOSIS. — Small concavoconvex strophedontids with subquadrate outline, unequally parvicostellate with strongly incurved rugae; cardinal extremities extended into acute ears.

DESCRIPTION

Shells small (less than 2 cm in length), concavoconvex of subquadrate outline, finely parvicostellate. Hinge line straight, cardinal extremities extended into acute ears. Ventral valve with sharply defined geniculation in midlength. Beak small, umbo convex. Ventral interarea narrow, long and orthocline. The hinge line denticulation occupies the middle of interarea. Diagnostic features include four to five strongly incurved rugae oriented parallel to each other. Radial ornament comprises unequally wavy parvicostellae, between there are two to seven fine, unequal striae. Thickened and more distinguished ribs are present anteriorly. A very weak fold is developed near the anterior border. Ventral muscle field is weakly impressed and divided by narrow median ridge. The cardinal process lobes on the inner side of dorsal valve are not joined at their base.

VARIATION

Young specimens have relatively flat ventral valves, but the rugae are clearly shown on the pedicle ring, which make them similar to leptaenids. The rugae of the adult specimens are smoother, and the shells are characterized by well distinguished geniculation.

COMPARISON

Megastrophia (Protomegastrophia) walmstedti (Lindström, 1861), described by Bassett &

Cocks (1974: 16, pl. 3, figs 5-9) from the lower Visby Beds (Telychian) of Gotland, is the closest species. Its specimens differ from those of *Brachyprion ruminatus* n. sp. in having larger size and well developed rugae on the ventral valve. *Brachyprion omnutakensis*, described by Lopushinskaya (1967: 90, pl. XX, figs 7-10) from the Omnutakh Formation, lacks rugae but possesses acute ears and bears unequal wavy striae of two orders. The pattern of ornamentation, including the form and distribution of rugae, on the ventral disc are similar to those of *Brachyprion polaris* Andreeva *in* Nikiforova & Andreeva, 1961 (Nikiforova & Andreeva 1961: 189, pl. XL, figs 6-10), but the new species is distinguished from the Siberian one by its sharp concentric rugae and cardinal ears.

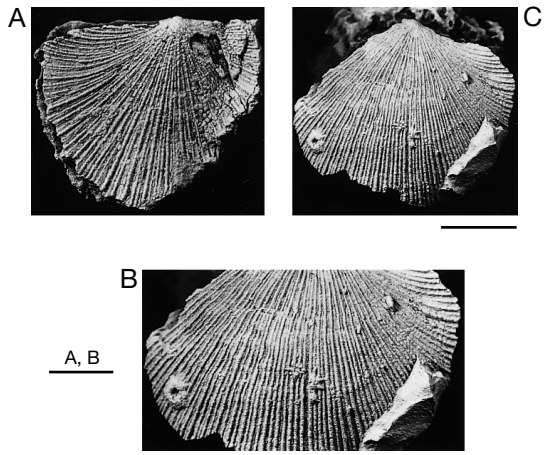

FIG. 6. — *Coolinia gracilis* (Andreeva *in* Nikiforova & Andreeva, 1961); **A**, ventral view of a pedicle valve (N 13/12991); **B**, **C**, dorsal view of a damaged brachial valve (N 14/12991), loc. 29a, ?Vodopad Formation. Scale bars: A, B, 6 mm; C, 10 mm.

Family CHILIDIOPSIDAE Boucot, 1959
Genus *Coolinia* Bancroft, 1949

Coolinia gracilis (Andreeva *in* Nikiforova & Andreeva, 1961)
(Fig. 6)

Schellwienella gracilis Andreeva *in* Nikiforova & Andreeva, 1961: 192, pl. XLI, figs 3-8.

Coolinia gracilis – Lopushinskaya 1991: 53, pl. I, fig. 6.

MATERIAL EXAMINED. — Four specimens embedded in rock matrix from loc. 13A, beds 124 and 140, Matusevich River; two specimens from loc. 32, beds 6-7, Ushakov River; and two specimens from loc. 29a, Lednikovaya River, October Revolution Island (Männik *et al*. 2002: figs 1, 2, 5, 6); Vodopad Formation.

REMARKS
The specimens are characteristically relatively large in size (L = 20.5-24.8 mm, W = 19.7-26.0 mm). Unequally biconvex or slightly convexo-concave shells are rounded in general outline, and possess a radial parvicostellate ornament with one or two new costellae arising exclusively by intercalation. Coarse concentric growth filae are presented across the costellae. The external morphology of the studied shells is typical of *C. gracilis*, but the dimensions of the chilidium and pseudodeltidium are not clear. O. N. Andreeva noted the low plane ventral unterarea with delthyrium bearing a small, flat pseudodeltidium in its apex on Siberian specimens (Nikiforova & Andreeva 1961: 192). *Coolinia gracilis* appears before *C. gorbiyatchensis* Lopushinskaya, 1976 from Talikit and Omnutakh formations, and differs in larger size and equally spaced ribs (Lopushinskaya 1976: 95, pl. XXI, figs 11-13). The species resembles *Coolinia propinqua* (Meek & Worthen, 1868), redescribed by Amsden (1974: 57, pl. 2, fig. 3, pl. 3, figs 1-5, pl. 4, fig. 1) from the Edgewood Formation in the Alexandrian Series of North America. The latter may be a senior synonym of *C. gracilis*.

Genus *Morinorhynchus* Havliček, 1965

Morinorhynchus proprius (Lopushinskaya, 1965)
(Fig. 7)

Schuchertella propria Lopushinskaya, 1965: 25, pl. I, figs 5-8.

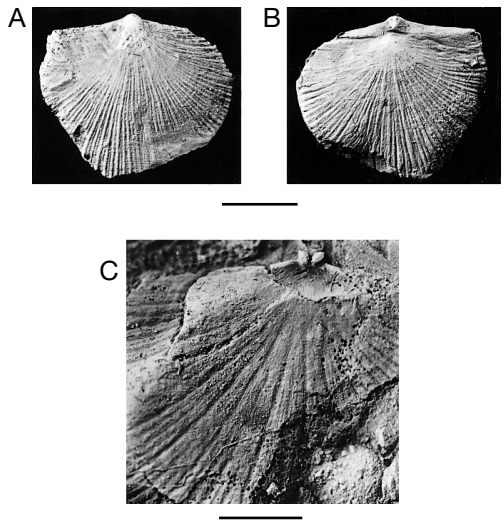

FIG. 7. — *Morinorhynchus proprius* (Lopushinskaya, 1965); **A**, **B**, complete shell (N 16/12991), loc. 11, bed 6B, Samojlovich Formation; **A**, ventral view; **B**, dorsal view; **C**, dorsal interior with bilobate cardinal process (N 17/12991), loc. 2, bed 66, Samojlovich Formation. Scale bars: A, B, 5 mm; C, 2 mm.

Morinorhynchus proprius – Lopushinskaya 1991: 55, pl. I, figs 9-12.

MATERIAL EXAMINED. — Seven specimens from loc. 2, bed 66, loc. 11, beds 6B and 11, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Srednij and Samojlovich formations.

REMARKS

These are small shells (L = 8.3-9.5 mm, W = 7.6?-11.6 mm, T = 1.4-1.9 mm). The delthyrium is closed by a large pseudodeltidium and a small, almost linear chilidium under which a bilobated cardinal process is situated. The radial ornament is multicostellate. The costellae are rounded, and are increasing by five orders of intercalation. Fine concentric growth-lines cross the costellae. That is why the specimens may be assigned to the genus *Morinorhynchus*. *M. proprius* was described by Lopushinskaya from the Omnutakh, Khukta, and Makus formations of East Siberia (Lopushinskaya 1965: 25). It can probably be mixed with *Schuchertella* cf. *subplana* Poulsen, 1943. The juvenile specimen illustrated by Poulsen (1943: 22, pl. 1, figs 22-24) from the Silurian of Greenland as *M.* cf. *plana* Conrad, 1842 is similar to *M. proprius* in having the same shell shape, and a similar pattern of costellae. *M.* cf. *plana* of Poulsen (1943) is also similar to *M. attenuatus* Amsden, 1951 from the Henryhouse Formation of North America (Amsden 1951: 84, pl. 17, figs 9-14), and from the Khatanzeya and Greben stages in the western Urals and Russian Arctic. However, *M. proprius* differs from *M.* cf. *plana* in having a rounded outline and lower number of costellae.

Superfamily CHONETOIDEA Bronn, 1862
Family CHONETIDAE Bronn, 1862
Genus *Sinochonetes* Wang, Boucot & Rong, 1981

Sinochonetes wangi Racheboeuf, 1987
(Fig. 8)

Sinochonetes wangi Racheboeuf, 1987: 11, pl. 3, figs 15-21.

MATERIAL EXAMINED. — Shells embedded in the coquina from loc. 21581, Krasnaya Bay, Komsomolets Island (Männik *et al.* 2002: fig. 1); Severnaya Zemlya or Pod"emnaya formations.

REMARKS

The dimensions of the shells vary from 6.5 to 9.6 mm in length and from 10.0 to 14.0 mm in width; the average L/W ratio is 0.63. Anderidia diverges anteriorly and fuses with cardinalia posteriorly at 60°. Cardinal process is internally bilobed with additional, poorly developed lateral lobes, and is posteriorly closed by chilidium. The external and internal morphology of both valves are typical of the genus *Sinochonetes*, and our specimens are morphologically identical with *S. wangi* described from the lower Emsian(?) strata of Ellesmere Island (Canadian Arctic). *S. wangi* differs from the type species, *S. minutisulcatus* Hou & Xian, 1975 (Siegenian of South China, Hou & Xian 1975: 25, pl. 1, figs 3, 4), in having finer costellae (7-10 per 1 mm), more numerous spines (five), and a poorly developed ventral sinus.

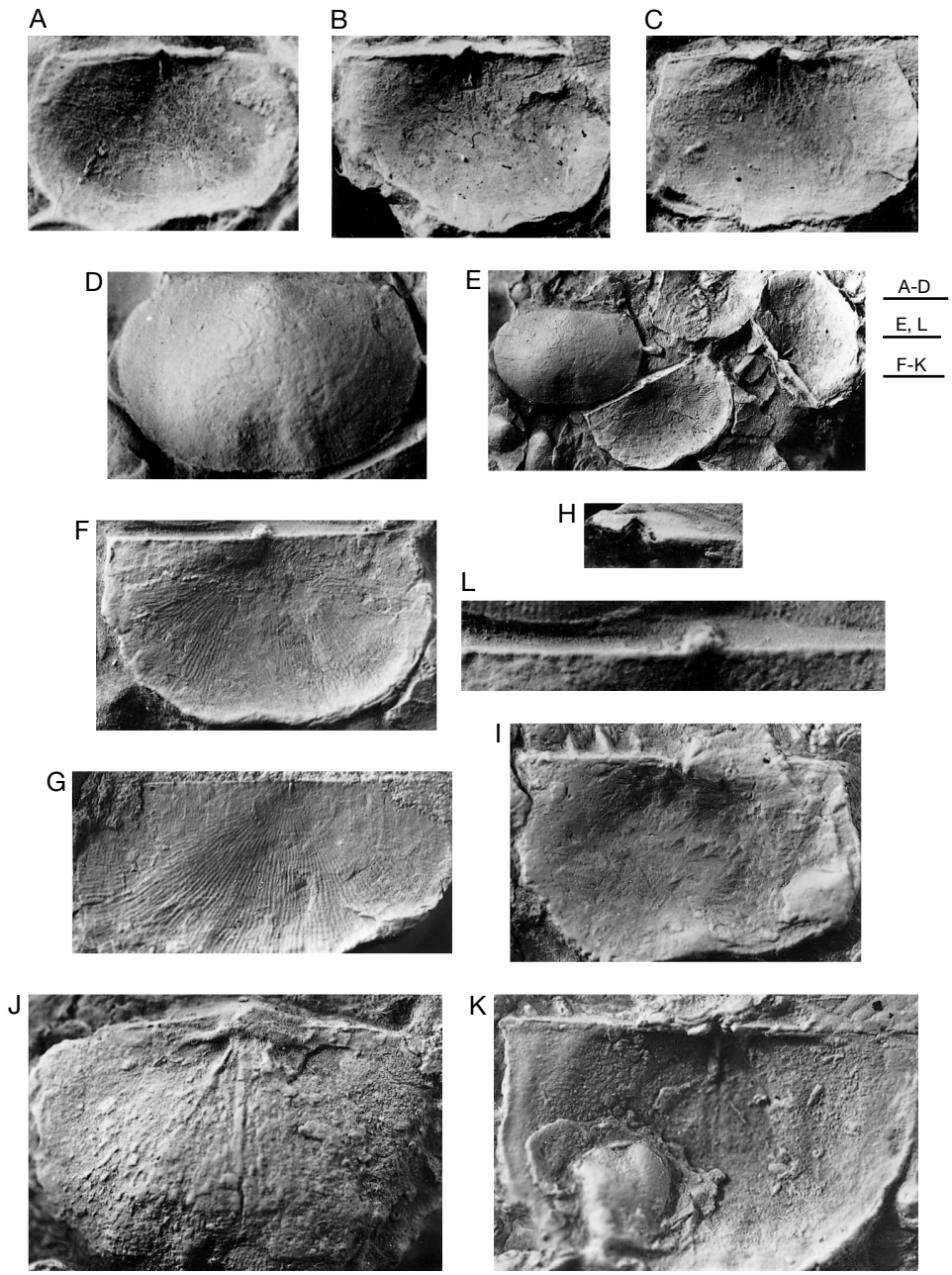

FIG. 8. — *Sinochonetes wangi* Racheboeuf, 1987; **A**-**C**, interior view of pedicle valves (N 18/12991, 19/12991, 20/12991), loc. 21581, Severnaya Zemlya or Pod''emnaya formations; **D**, ventral view of a complete valve (N 21/12991); **E**, external view of a shelly limestone with pedicle and brachial valves; **F**, **L**, complete valve (N 22/12991); **F**, dorsal view; **L**, posterior views with a pseudodeltidium and chilidium; **G**, dorsal valve, showing enlarged external surface with a fine striae (N 23/12991); **H**, posterior view of a pedicle valve, showing a delthyrium, covered by pseudodeltidium posteriorly (N 24/12991); **I**, **K**, dorsal valves with well preserved spines near cardinal margin (NN 25/12991, 26/12991); **J**, internal mould of a dorsal valve, showing a median septum and anderidia (N 27/12991). Scale bars: A-D, 2.5 mm; E, 5 mm; F-K, 2 mm; L, 1 mm.

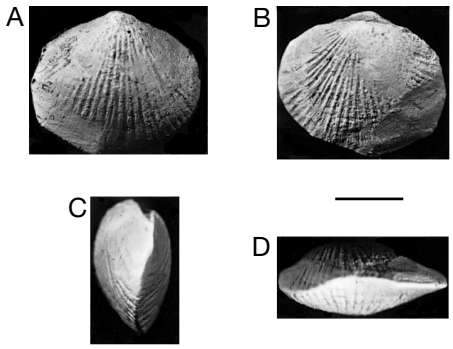

FIG. 9. — *Dalejina* ex gr. *hybrida* (Sowerby *in* Murchison, 1839), complete shell (N 2/12991), loc. 13, bed 89, Vodopad Formation; **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, anterior view. Scale bar: 3 mm.

Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order ORTHIDA Woodward, 1852
Family RHIPIDOMELLIDAE Schuchert, 1913
Genus *Dalejina* Havliček, 1953

Dalejina ex gr. ***hybrida***
(Sowerby *in* Murchison, 1839)
(Fig. 9)

ex gr. *Orthis hybrida* J. de C. Sowerby *in* Murchison, 1839: 630, pl. 13, fig. 11.

Rhipidomella ex gr. *hybrida* – Nikiforova & Andreeva 1961: 117, pl. XX, figs 1-4 .

MATERIAL EXAMINED. — One specimen from loc. 13, bed 89, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Vodopad Formation.

REMARKS

The combination of small size (L = 6.2 mm, W = 7.2 mm, T = 3.3 mm), rounded general outline, biconvex shell with fine ribs (about 45 at the anterior margin) which increase by intercalation of secondary or, seldom, preliminary ones, has generally been considered to be diagnostic features of *Dalejina*. The specimens from Severnaya Zemlya are more similar to those from the Omnutakh and Meik formations (Llandovery) of East Siberia (Nikiforova & Andreeva 1961: 117, pl. XX, fig. 2; Lopushinskaya & Doroshenko 1991). They were assigned to *D. hybrida*, although this species is known to be characteristic for the Wenlock Limestone in Britain. The lectotype of *D. pentlandica* (Davidson, 1869), described from the Telychian (Pentland Hills, Cocks 1978: 71), is characterized by a larger size, finer ribs, and a bigger convexity of dorsal valve.

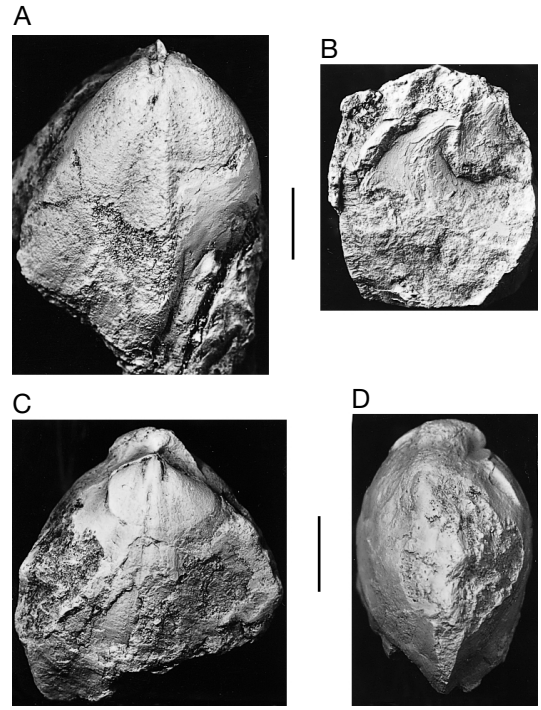

FIG. 10. — *Borealis cristiformis* (T. Modzalevskaya, 1985); **A**, dorsal view of a brachial valve (N 28/12991); **B**, internal longitudinal ventral septum (N 30/12991); **C**, **D**, complete slightly damaged shell (N 29/12991), loc. 14, bed 10b, Vodopad Formation; **C**, dorsal view; **D**, lateral view. Scale bars: A, B, 6 mm; C, D, 10 mm.

Order PENTAMERIDA
Schuchert & Cooper, 1931
Family PENTAMERIDAE McCoy, 1844
Genus *Borealis* Boucot, Johnson & Staton, 1971

Borealis cristiformis (T. Modzalevskaya, 1985)
(Figs 10; 11)

Pentamerus? *cristiformis* T. Modzalevskaya, 1985: 64, pl. II, figs 4, 5, pl. III, fig. 1.

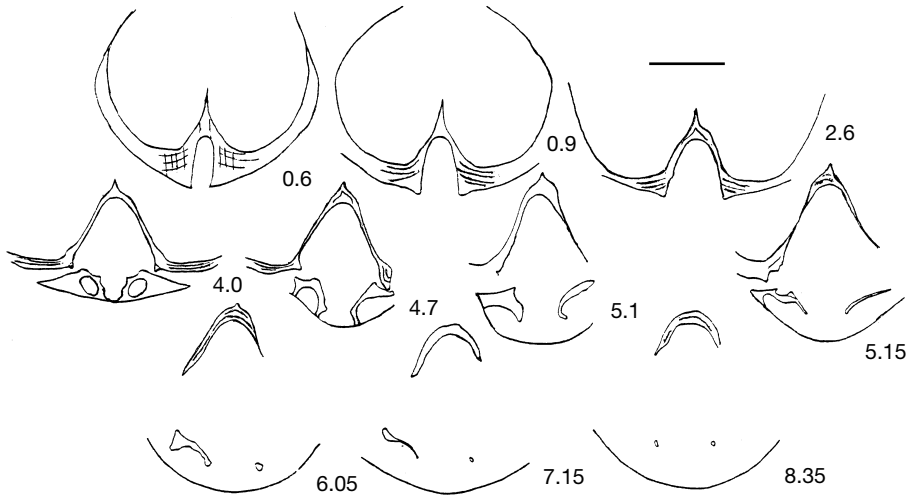

FIG. 11. — Selected transverse serial sections, illustrating the development of internal structures in *Borealis cristiformis* (T. Modzalevskaya, 1985) (N 31/12991). Measurements: length 29.1 mm, width 24.0 mm, thickness 22.2 mm; loc. 14, bed 10v, Vodopad Formation. Numbers on selected transverse sections indicate the distances (in mm) from ventral beak. Scale bar: 8 mm.

MATERIAL EXAMINED. — Two specimens from loc. 14, bed 10v, Matusevich River, and six specimens from loc. 51, sample 51-13f, Strojnaya River, October Revolution Island (Männik *et al.* 2002: figs 2, 5, 6); Vodopad Formation.

REMARKS

These are the oldest pentamerids found in the Circum-Arctic region, and were described from the lowermost Persej Formation of Novaya Zemlya for the first time. The diagnostic features (the medium size, the ventral acute ridge – like elevation –, and the subtriangular outline) occurring on the shells of pentamerids on Severnaya Zemlya indicate that they belong to *B. cristiformis*. The long spondylium (supported by a short septum); separated low brachial plates slightly inclined to each other by their internal ends, and sharply curved inner brachial plates, allow to assigne this species to genus *Borealis* (Fig. 11).

Borealis samojedicus (Keyserling, 1846) (Fig. 12)

Pentamerus samojedicus Keyserling, 1846: 235, pl. 9. — Lebedev 1892: 20.

Pentamerus oblongus Sowerby *in* Murchison, 1839 – Sapel'nikov & Beznosova 1980: 10, pl. V, figs 1-5. — Markovskij & Smirnova 1982: 40, 41. — Sapel'nikov 1985: 59, pl. XIX, figs 3, 4.

Borealis samojedicus – Modzalevskaya & Rubel 2000: 149, pl. I, figs 1-9, pl. II, figs 1-7.

MATERIAL EXAMINED. — Three specimens from loc. 18002-6, two specimens from loc. 18088-6, three specimens from loc. 18008-11, several specimens embedded in rock from loc. 18075-8, Komsomolets Island (Männik *et al.* 2002: fig. 1); Vodopad (lower Snezhinka) Formation.

REMARKS

Large smooth shells (L = 72.4 mm, W = 49.5 mm, T = 35.0 mm) have inconspicuous radial furrows in the anterior part, and frequently developed concentric growth lines. The outline of the shell varies from rounded to subtriangular. Development of the median fold is variable, especially on the ventral valve. The specimens from coquinas, with high population frequency, have more laterally flattened shells and narrow spondylium. *B. samojedicus* has the same interior as *B. borealis* (Eichwald, 1842) (Rubel 1970). The narrow longitudinal shells, with distinctly developed ventral sulcus and strongly posteriorly

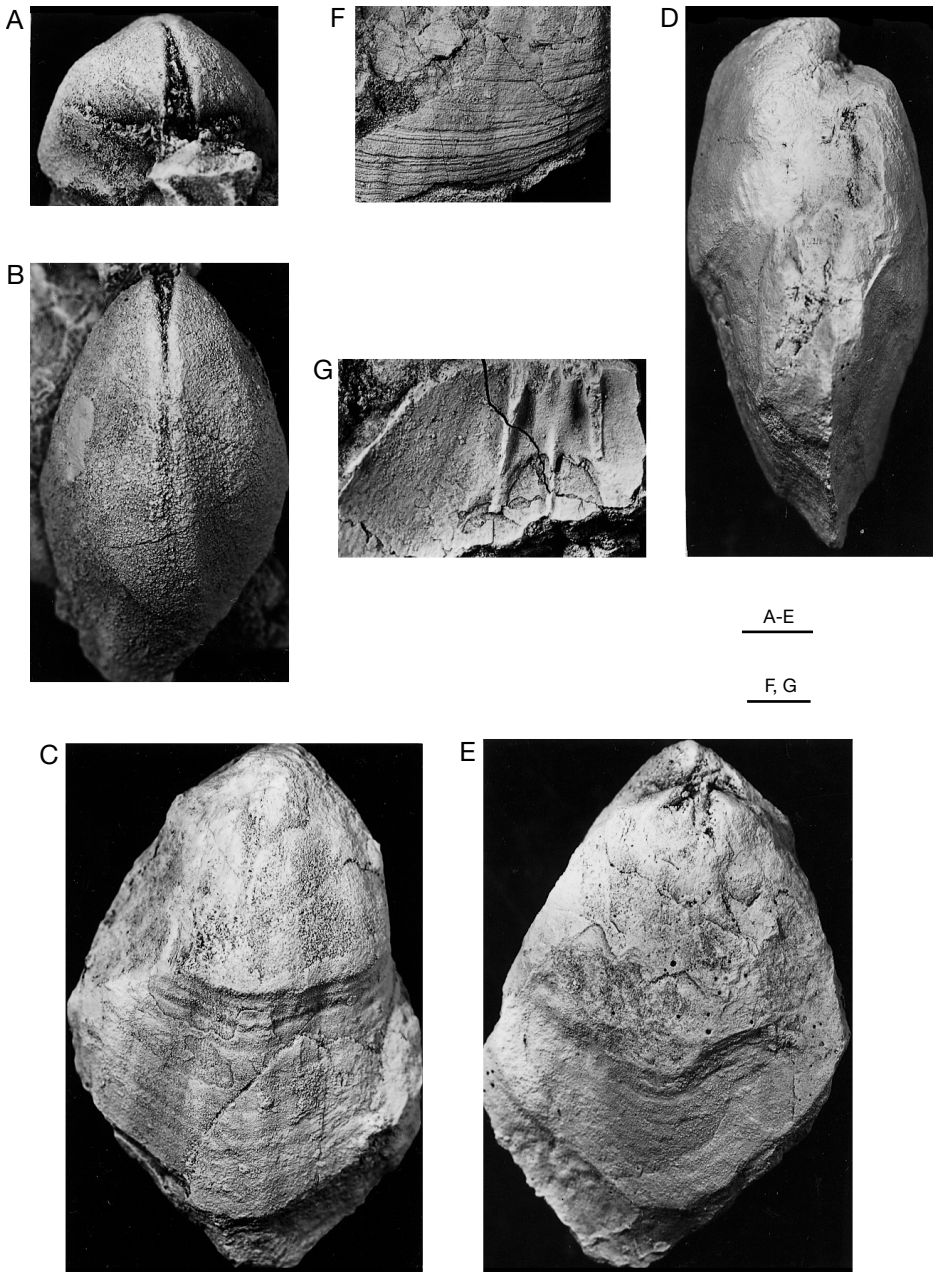

FIG. 12. — *Borealis samojedicus* (Keyserling, 1846); **A**, **B**, largely exfoliated shell (N 32/1299), loc. 18088-6, Vodopad (Snezhinka) Formation; **A**, posterior view; **B**, dorsal view; **C**-**E**, complete shell (N 33/12991), loc. 18002-6, Vodopad (Snezhinka) Formation; **C**, ventral view; **D**, lateral view; **E**, dorsal view; **F**, enlarged anterolateral view of the external surface of a broken pedicle valve (N 34/12991); **G**, interior of a pedicle valve (N 35/12991), loc. 18008-11, Vodopad (Snezhinka) Formation. Scale bars: A-E, 10 mm; F, G, 6 mm.

widened septum, are very similar to *B. schmidti* (Lebedev, 1892) from the Llandovery of Nizhnyaya Tunguska (East Siberia), and could be assigned to this species (Lebedev 1892: 22). However, these specimens were found together with some subtriangular shells which possess a flattened dorsal valve, undulating surface, and sharp concentric lines. These features are typical of *B. samojedicus* (Keyserling 1846: 235, pl. IX, fig. 2) from the Chernaya Rechka Formation (Llandovery) of the Timan Ridge. But the clearly developed lobate external shape, and the narrowing of the shell anteriorly and posteriorly, make them similar to the Norwegian species *B. borealis osloensis* Mørk, 1981, which is characteristic of bed 7a/b (Llandovery) in the Oslo region (Mørk 1981: 544, pl. 84, figs 9-11).

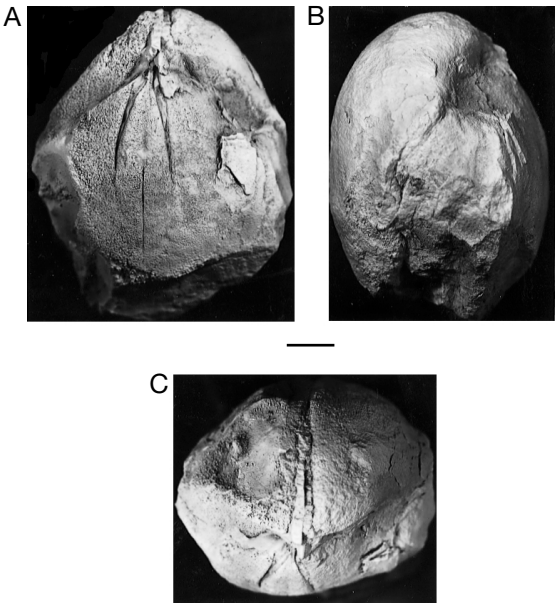

FIG. 13. — *Harpidium* sp., complete shell (N 37/12991), loc. 13, bed 27, Vodopad Formation; **A**, dorsal view; **B**, lateral view; **C**, posterior view. Scale bar: 10 mm.

Genus *Harpidium* Kirk, 1925

Harpidium sp.
(Fig. 13)

MATERIAL EXAMINED. — Five poorly preserved specimens from loc. 13, beds 87 and 102 (coquina), Matusevich River, October Revolution Island, and five external moulds from loc. 20533, Komsomolets Island (Männik *et al.* 2002: figs 1, 2, 5); Vodopad (lower Snezhinka) Formation.

REMARKS
Shells are large (up to 60 mm in length), with a massive incurved ventral umbo and a rectimarginate anterior margin. Inside the pedicle valve there are double septum extending to the anterior third of the shell, and supporting long spondylium with a moderately wide floor. The dorsal interior consists of a discrete brachial plate which extends for the length of the valve and is gently divergent anteriorly. The ventral muscle field is divided deeply by septum. The dorsal muscle field is longitudinal in outline, limited by brachial plates laterally and divided by a narrow low crest. The specimens cannot be assigned to *Pentamerus* J. de C. Sowerby, 1813 because of the strongly convex valves and lack of a trilobate external structure. The specimens from Severnaya Zemlya resemble those studied by Poulsen (1943: 35, pl. 3, fig. 21) and by Boucot & Johnson (1979) from the Offley Island Formation (Greenland). V. P. Sapel'nikov (1985) proposed that these specimens, but also some other species of *Harpidium*, may be assigned to one of the forms of *H. angustum* Poulsen, 1943. *Harpidium* occurs in the upper Llandovery to Ludlow in the Urals, Central Asia, Kazakhstan, Altaj Mountains, North East Russia, North America (Alaska, Iowa, Wisconsin, Ohio, Illinois), and Greenland.

Order RHYNCHONELLIDA Kuhn, 1949
Family RHYNCHOTREMATIDAE Schuchert, 1913
Genus *Stegerhynchus* Foerste, 1909

Stegerhynchus*? *decemplicatus duplex
Nikiforova & T. Modzalevskaya, 1968
(Figs 14A-E; 15)

Stegerhynchus decemplicatus duplex Nikiforova & T. Modzalevskaya, 1968: 54, pl. I, figs 4-7.

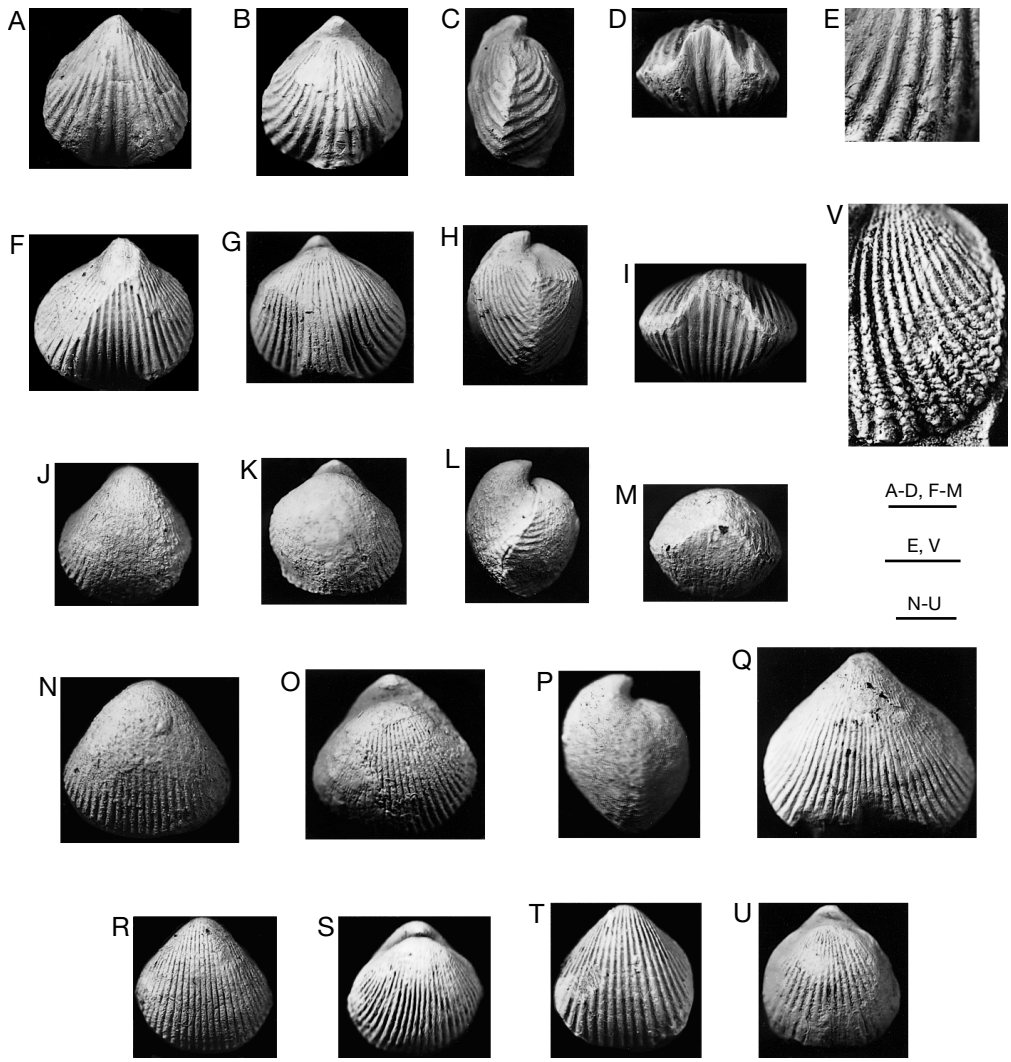

FIG. 14. — **A**-**E**, *Stegerhynchus*? *decemplicatus duplex* Nikiforova & T. Modzalevskaya, 1968; **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, anterior view; **E**, enlarged external surface of a complete shell (N 38/12991), loc. 13, bed 89, Vodopad Formation; **F**-**I**, **V**, *Anabaria*? *latens* n. sp.; **F**, dorsal view; **G**, ventral view; **H**, lateral view; **I**, anterior view of a complete shell (holotype N 50/12991), loc. 11, bed 6B, Samojlovich Formation; **V**, enlarged external surface of a poorly silicified shell (N 51/12991), loc. 29a, ?Vodopad Formation; **J**-**P**, **R**, **S**, *Lenatoechia octjabrensis* n. sp.; **J**, ventral view; **K**, dorsal view; **L**, lateral view; **M**, anterior views of a complete shell (N 41/12991), loc. 11, bed 6B, Samojlovich Formation; **N**, ventral view; **O**, dorsal view; **P**, lateral view of a complete shell (holotype N 40/12991), loc. 2, bed 66, Samojlovich Formation; **R**, ventral view; **S**, dorsal view of complete shell (N 42/12991), loc. 117v, ?Samojlovich Formation; **Q**, **T**, **U**, *Anabaria*? *latens* n. sp.; **Q**, pedicle valve of a complete shell (N 52/12991), loc. 13, bed 27, Srednij Formation; **T**, ventral view; **U**, dorsal view of a complete shell (N 53/12991), loc. 13, bed 64, Golomyannyj Formation. Scale bars: A-D, F-M, 5 mm; E, V, 2 mm; N-U, 3 mm.

Stegerhynchus (*Stegerhynchus*) *decemplicatus duplex* – Lopushinskaya & Yadrenkina 1987: 119, pl. 25, fig. 6.

MATERIAL EXAMINED. — 16 specimens and fragments from loc. 13, bed 89, Matusevich River, October Revolution Island (Männik *et al*. 2002: figs 2, 5); Vodopad Formation.

REMARKS

The discrete cardinal plate supported by a massive dorsal platform, median elevation strengthened by shell thickening and merging with a low broad septum or myophragm are the characteris-

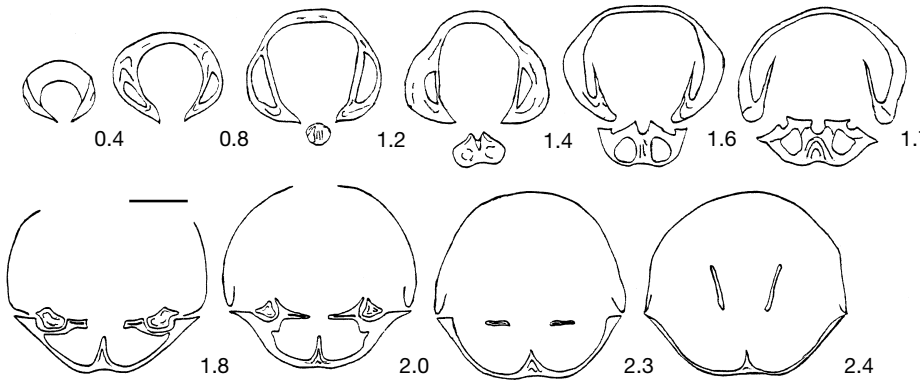

FIG. 15. — Selected transverse serial sections, illustrating the development of internal structures in *Lenatoechia octjabrensis* n. sp. (N 43/12991). Measurements: length 8.1 mm, width 8.2 mm, thickness 5.9 mm; loc. 2, bed 66, Samojlovich Formation. Numerical designations are the same as on Fig. 11. Scale bar: 3 mm.

tic features of *Stegerhynchus* (Fig. 15). The linear cardinal process is absent, probably due to the poor preservation. The outline, size, two ribs in the ventral sinus, three ribs on the dorsal fold, and well preserved concentric ornament of the specimens suggest that these specimens can be refered to *S.*? *decemplicatus duplex* Nikiforova & T. Modzalevskaya, 1968 described from the Talikit, Omnutakh, and Meik formations of East Siberia. Small size, and weakly developed sinus and fold distinguish a somewhat similar genus *Nikolaevirhynchus* Baranov, 1988 identified from Ryabininskaya Formation (Wenlock) on North East Russia. Moreover, the representatives of genus *Nikolaevirhynchus* are characterized by an absence of the median longitudinal elevation, which is broadened posteriorly and strengthened by shell thickening.

Family TRIGONIRHYCHIIDAE McLaren, 1965
Genus *Lenatoechia* Nikiforova, 1970

Lenatoechia octjabrensis n. sp.
(Figs 14J-P, R, S; 16)

HOLOTYPE. — N 40/12991, CNIGR Museum, St. Petersburg (Fig. 14N-P), conjoined valves; L = 8.8 mm, W = 8.3 mm, T = 7.2 mm.

ETYMOLOGY. — After the October Revolution Island.

TYPE LOCALITY. — Loc. 11, Matusevich River, October Revolution Island; Samojlovich Formation.

AGE. — ?Llandovery-Wenlock.

MATERIAL EXAMINED. — Mainly conjoined valves of good preservation, one specimen from loc. 11, bed 6B, 10 specimens from loc. 2, bed 66, Matusevich River; 65 specimens from loc. 117v, Ushakov River, October Revolution Island (Männik *et al.* 2002: figs 1, 2, 5); Samojlovich Formation.

MEASUREMENTS (IN MM). — L = 4.7-8, W = 5.7-8.3, T = 4.6-7.2.

DIAGNOSIS. — Shells subtriangular in outline, strongly biconvex in lateral profile; costae rounded, low and numerous; anterior margin uniplicate.

DESCRIPTION

Shells small, equally (strongly) biconvex, with subtriangular outline and numerous ribs. Ventral umbo and pointed beak incurved, narrow, with delthyrium closed by deltidial plates. Ventral sinus and dorsal fold weakly developed, anterior margin uniplicate. Surface covered by rounded, equal and high ribs (in total 35) with the width of the ribs exceeding their interspaces. Ventral valve with long dental plates and massive teeth. The dorsal interior contains a discrete cardinal plate and septalium, supported by broad, massive, short septum, that extends approximately half the valve length (Fig. 16).

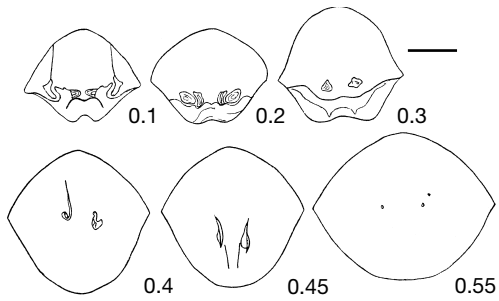

FIG. 16. — Selected transverse serial sections, illustrating the development of internal structures in *Stegerhynchus*? *decemplicatus duplex* Nikiforova & T. Modzalevskaya, 1968 (N 39/12991). Measurements: length 7.7 mm, width 10.3 mm, thickness 4.9 mm; loc. 13, bed 89, Vodopad Formation. Numerical designations are the same as on Fig. 11. Scale bar: 2 mm.

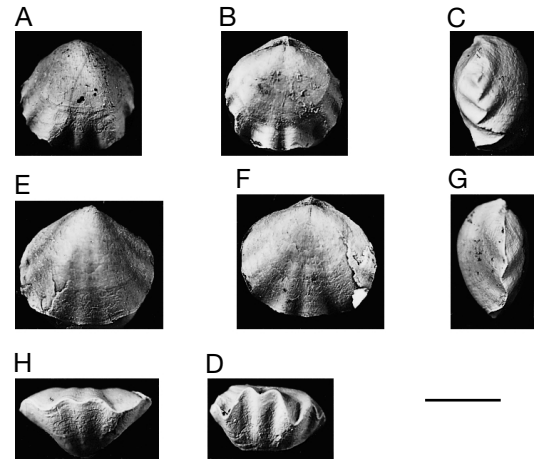

FIG. 17. — *Sibiritoechia convexa* Alekseeva, 1966, complete shells (NN 44/12991, 45/12991), loc. 21581, Severnaya Zemlya or Pod''emnaya formations; **A**, **E**, ventral view; **B**, **F**, dorsal view; **C**, **G**, lateral view; **D**, **H**, anterior view. Scale bar: 5 mm.

COMPARISON

The pattern of the ribs, weakly developed sinus, fold, and uniplicated anterior margin are similar to those of *Lenatoechia ramosa* (Nikiforova, 1961) from the Talikit and Omnutakh formations of East Siberia (Nikiforova & Andreeva 1961: 207, pl. XLIV, figs 8, 9). The new species differs from *L. ramosa* by having smaller size and possessing a subtriangular outline.

Family PLECTORHYNCHELLIDAE
Rzhonsnitskaya, 1956
Genus *Sibiritoechia* Alekseeva, 1966

Sibiritoechia convexa Alekseeva, 1966
(Figs 17; 18)

Sibiritoechia convexa Alekseeva, 1966: 1148, fig. 1; 1967: 60, pl. VIII, fig. 7. — Alekseeva *et al.* 1970: 89, pl. IX, figs 6-8.

Sibiritoechia lata Alekseeva, 1966: 1149, figs 1, *2*; 1967: 62, pl. VIII, fig. 8. — Alekseeva *et al.* 1996: 108, pl. XII, fig. 5.

Sibiritoechia oblonga Alekseeva, 1966: 1149, figs 1, *3*; 1967: 63, pl. IX, figs 8-11. — ?Alekseeva *et al.* 1970: 87, pl. IX, figs 4, 5.

MATERIAL EXAMINED. — Specimens are embedded in shelly limestone from which 50 complete shells of different sizes have been prepared. Southeastern Komsomolets Island, southern bank of Krasnaya Bay (loc. 21581) (Männik *et al.* 2002: fig. 1); Severnaya Zemlya or Pod"emnaya formations.

REMARKS

There is a wide variation in the outline (from longitudinally oval to isometrical), and in convexity (equally biconvex or ventribiconvex) of the shell. The ribs arise at different distances from the beak, and their number varies from 9 to 11. One rib on the ventral sinus and two on the dorsal sulcus are constant but they are developed differently depending upon the outline and convexity of the shells. The internal structure is characterized by thin, short dental plates, divided cardinal plates, and obliquely inclined crura (Fig. 18). The valve outline, and the other external features of these brachiopods of the same population, do not permit detailed systematic comparison. They can be assigned to species "*convexa*", "*lata*", and "*oblonga*", studied by Alekseeva (1966: 147). V. V. Baranov concluded that "*lata*" and "*oblonga*" are, in reality, the same taxon (Alekseeva *et al.* 1970). In fact, it is difficult to find distinctions between "*convexa*" and "*lata*", except in the convexity of the ventral valve. Since these more convex valves are often seen in only a few members of a population, "*convexa*" is not examined here separately. *Sibiritoechia* is known from the Lochkovian and Pragian of Salair (Tom'chumysh Beds), and

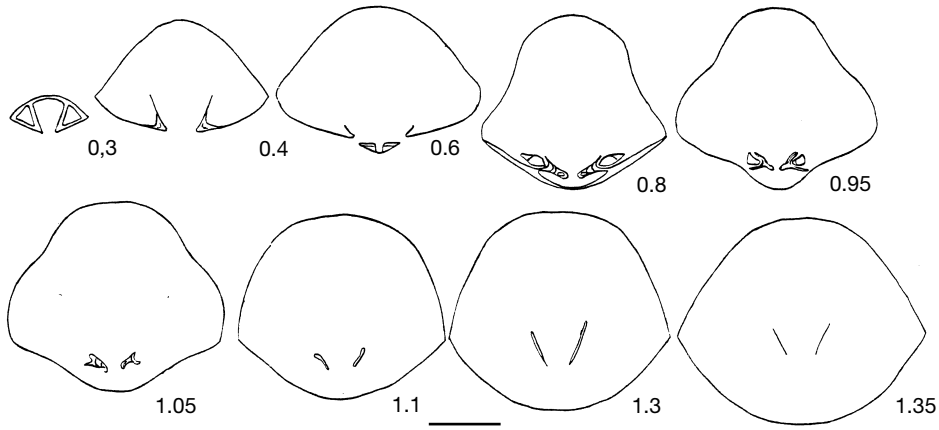

FIG. 18. — Selected transverse serial sections, illustrating the development of internal structures in *Sibiritoechia convexa* Alekseeva, 1966 (N 46/12991). Measurements: length 6.4 mm, width 6.6 mm, thickness 4.1 mm; loc. 21581, Severnaya or Pod''emnaya formations. Numerical designations are the same as on Fig. 11. Scale bar: 1.9 mm.

North East Russia (Sette-Daban Ridge, Sette-Daban Formation; Selennjakh Ridge, Sagyr Formation; Tas-Khayakhtakh Ridge, Datnin Formation).

Order ATRYPIDA Rzhonsnitskaya, 1960
Family ATRYPIDAE Gill, 1871
Genus *Dihelictera* Copper, 1995

Dihelictera* cf. *lepidota
(Nikiforova & T. Modzalevskaya, 1968)
(Figs 19; 21I)

cf. *Protatrypa lepidota* Nikiforova & T. Modzalevskaya, 1968: 61, pl. II, figs 8, 9.

MATERIAL EXAMINED. — Eight specimens from loc. 11, beds 14 and 14-A, and loc. 2, beds 74 and 79 (only fragments), Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Samojlovich Formation. Two poorly preserved specimens from samples 2zh/76, 2i/76, Pioneer Island (Männik *et al.* 2002: fig. 1); Srednij Formation.

REMARKS

Specimens are small, with a ventral keel-like ridge and dichotomous ribs. Ribs are crossed by concentric growth lamellae which are most pronounced anteriorly. The internal structure is typical of the genus *Dihelictera* to which *Protatrypa lepidota* Nikiforova & T. Modzalevskaya, 1968 (Nikiforova & Modzalevskaya 1968: 61, pl. II, figs 8, 9) is assigned by P. Copper (1995: 855) (Fig. 19). This species is widespread in the Omnutakh and Khukta formations of East Siberia and Gora Gjiaden' Formation of Salair (Ivanovsky & Kul'kov 1974: 59, pl. XX, figs 6, 7).

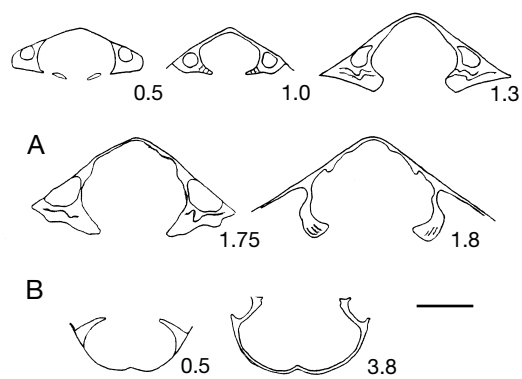

FIG. 19. — Selected transverse serial sections, illustrating the development of internal structures in *Dihelictera* cf. *lepidota* (Nikiforova & T. Modzalevskaya, 1968); **A**, ventral valve (N 48/12991), length 10.2 mm, loc. 2, bed 79, Samojlovich Formation; **B**, dorsal valve (N 49/12991), length 10.0 mm; loc. 11, bed 14, Samojlovich Formation. Numerical designations are the same as on Fig. 11. Scale bar: 2.3 mm.

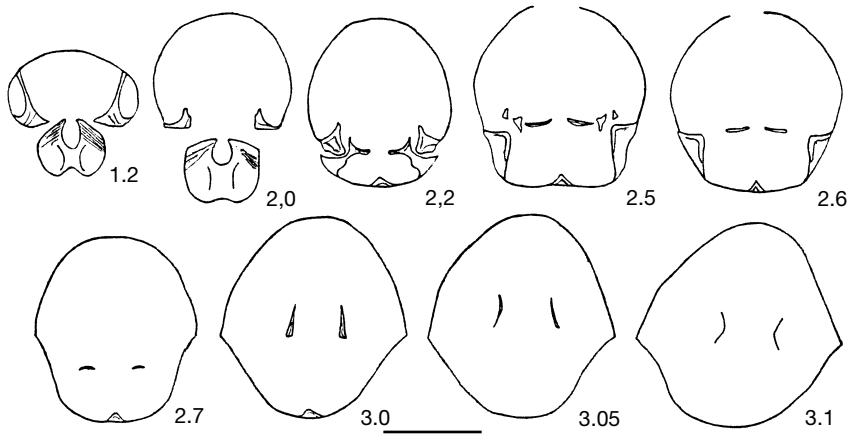

FIG. 20. — Selected transverse serial sections, illustrating the development of internal strutures in *Anabaria*? *latens* n. sp. (N 54/12991). Measurements: length 8.7 mm, width 8.7 mm, thickness 6.2 mm; loc. 13, bed 64, Golomyannyj Formation. Numerical designations are the same as on Fig. 11. Scale bar: 3.2 mm.

Genus *Alispira* Nikiforova, 1961

Alispira gracilis (Nikiforova *in* Nikiforova & Andreeva, 1961)

Zygospira (Alispira) gracilis Nikiforova *in* Nikiforova & Andreeva, 1961: 244, pl. LIII, figs 1-8.

Alispira gracilis – Rubel 1970: 25, pl. XIII, figs 16-22. — Lopushinskaya 1976: 63, pl. XI, figs 1, 2.

MATERIAL EXAMINED. — Two specimens from loc. 12, bed 112, Matusevich River, October Revolution Island (Männik *et al*. 2002: figs 2, 5); Vodopad Formation.

REMARKS

Specimens have a ventral valve with a keel on the umbo, and an acute, weakly incurved beak. The sinus is well defined: arising at the umbo, it is bordered by larger ribs and commonly bears one or two weaker ones. The lateral ribs increase in width anteriorly. The number of ribs multiplies by bifurcation and intercalation. Based on these features the specimens are assigned to *Alispira gracilis* which is typical of the Chamba and Talikit formations of East Siberia. *Homeospira*? sp. (Poulsen 1934: 19, pl. 2, figs 21, 22) from the Cape Schuchert Formation of Greenland resembles *A. gracilis*. O. I. Nikiforova thought that, in reality, the last one should also be assigned to *A. gracilis* (Nikiforova & Andreeva 1961).

Genus *Anabaria* Lopushinskaya, 1965

Anabaria*? *latens n. sp. (Figs 14F-I, Q, T-V; 20)

HOLOTYPE. — N 50/12991, CNIGR Museum, St. Petersburg (Fig. 14F-I), conjoined valves; L = 9.2 mm, W = 10.0 mm, T = 7.5 mm.

ETYMOLOGY. — From *latens* (Latin): hidden.

TYPE LOCALITY. — Loc. 11, Matusevich River, October Revolution Island.

FORMATION. — Samojlovich Formation.

AGE. — ?Llandovery, ?Telychian.

MATERIAL EXAMINED. — 19 discrete specimens (and specimens embedded in rock) from loc. 13, beds 27, 30-31, 64 and 89, and one specimen (and some fragments) from loc. 11, bed 6B, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Vodopad, Golomyannyj, Srednij and Samojlovich formations.

MEASUREMENTS (IN MM). — L = 8.2-9.2, W = 8.7-11.0, T = 3.7-7.5 mm.

DIAGNOSIS. — Shells of small size, almost biconvex in lateral profile; isometrical or subpentagonal in outline, with coarse costae; ventral sinus wide and flat.

DESCRIPTION

Shells small, pentagonal in outline, unequally biconvex, isometrical or with the width slightly larger than the length. Ventral beak high,

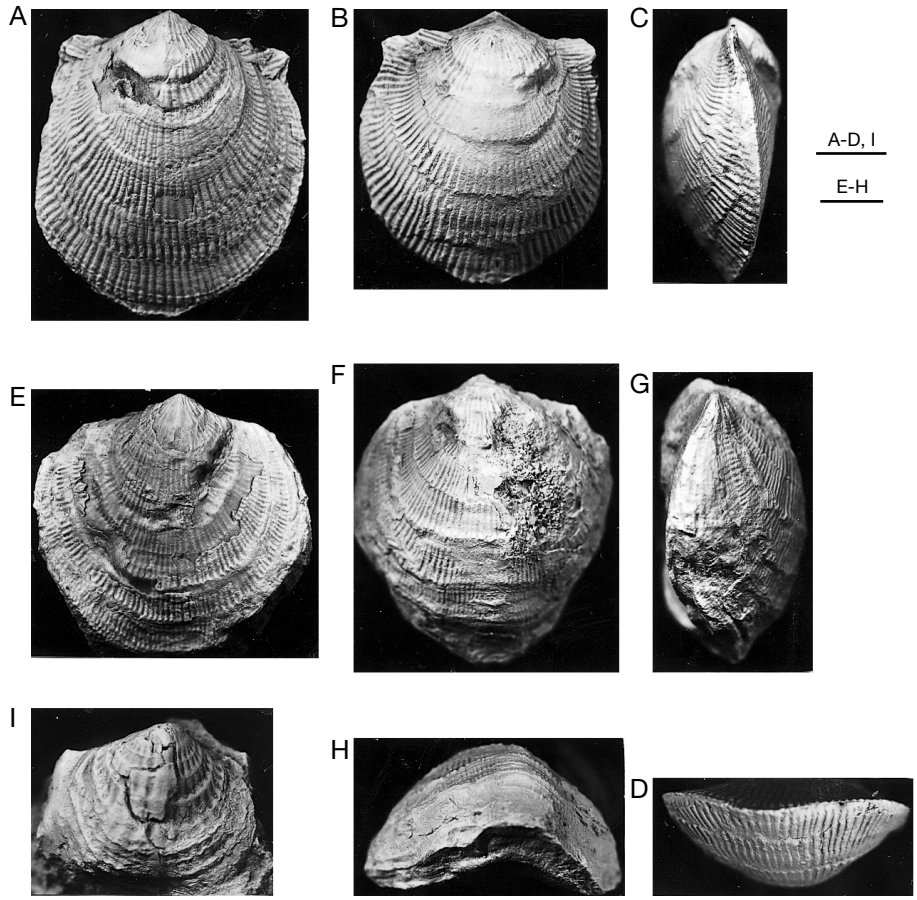

FIG. 21. — **A**-**H**, *Anulatrypa nieczlawiensis tenuicostata* Tcherkesova *in* Modzalevskaya & Cherkesova, 1994; **A**, **E**, ventral view; **B**, **F**, dorsal view; **C**, **G**, lateral view; **D**, **H**, anterior view of a young and adult complete shells (N 55/12991, 56/12991), loc. 18095, Rusanov Formation; **I**, *Dihelictera* cf. *lepidota* (Nikiforova & T. Modzalevskaya, 1968), ventral view of a pedicle valve (N 47/12991), loc. 2, bed 79, Samojlovich Formation. Scale bars: A-D, I, 5 mm; E-H, 6 mm.

incurved, with delthyrium, closed by deltidial plates posteriorly. Ventral sinus flat and wide. Dorsal fold not high, fluently merging in lateral flanks of the valve. Anterior margin uniplicate. Rounded, low costae gradually widened anteriorly and increased by intercalation from 24 to 40 with concentric growth lines. Interior of ventral valve with long, thin dental plates, placed closely to the shell walls; teeth small. Discrete horizontal cardinal plate supports vertically flattened crura. Myophragm extends on two thirds of the valve length. Spiralia are not found (Fig. 20).

COMPARISON AND REMARKS

Anabaria? *latens* n. sp. resembles small ribbed atrypids and rhynchonellids. That is why the lack of spiralia makes difficult to attribute these brachiopods to any genus exactly. The almost isometrical biconvex shells with rounded ribs and shallow ventral sinus found in the studied material allow to assign them to genus *Anabaria*? The specimens from Srednij Formation possess dorsally curved anterior margin and fine ribs which make them similar to *Anabaria rara* (Nikiforova, 1961) from the Talikit and Omnutakh formations of East Siberia (Nikiforova & Andreeva

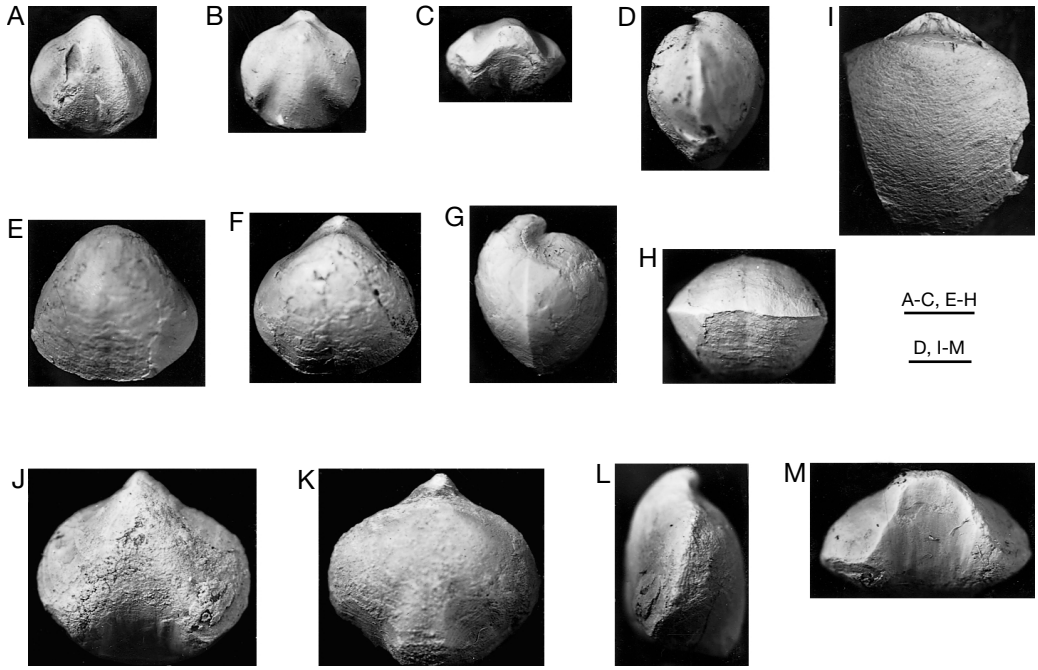

FIG. 22. — **A**-**D**, *Hyattidina remota* n. sp.; **A**, ventral view; **B**, dorsal view; **C**, anterior view of a complete shell (holotype N 58/12991); **D**, lateral view of a complete shell (N 59/12991), loc. 13, bed 48, Golomyannyj Formation; **E**-**H**, *Greenfieldia orbiculata* n. sp.; **E**, ventral view; **F**, dorsal view; **G**, lateral view; **H**, anterior view of a complete shell (holotype N 62/12991), loc. 2, bed 66, Samojlovich Formation; **I**, *Meristina*? *norilica* (Nikiforova *in* Nikiforova & Andreeva, 1961), ventral view of a complete shell (N 61/12991), loc. 13, bed 27, Srednij Formation; **J**-**M**, *Dubaria tenera* Nikiforova & T. Modzalevskaya, 1968; **J**, ventral view; **K**, dorsal view; **L**, lateral view; **M**, anterior view of a complete shell (N 57/12991), loc. 13, bed 89, Vodopad Formation. Scale bars: A-C, E-H, 5 mm; D, J-M, 3 mm; I, 6 mm.

1961: 248, pl. LIV, figs 1-7). The differences include rounded pentagonal outline, more acute apical angle, and coarser ribs on *Anabaria*? *latens* n. sp. than on *Anabaria rara*.

The new species is indistinguishable in the pattern of ribs, and number of ribs in the ventral sinus, from *Lenatoechia elegans* (Nikiforova, 1961) from the Omnutakh Formation of East Siberia (Nikiforova & Andreeva 1961: 205, pl. XLIV, figs 1-7). Despite their small size, the specimens from the Golomyannyj Formation are characterized by isometrical outline and well defined flat ventral sinus. They are also similar to *Pseudocamarotoechia*? *gljadensis* Kul'kov, 1974 from the Gora Gljaden' Formation (Ivanovsky & Kul'kov 1974: 55, pl. XIX, figs 11, 12) but differ in having well developed dental plates and undeveloped dorsal septum.

Genus *Anulatrypa* Havliček, 1987

Anulatrypa nieczlawiensis (Kozlowski, 1929)

Anulatrypa nieczlawiensis tenuicostata
Tcherkesova *in* Modzalevskaya & Cherkesova, 1994
(Fig. 21A-H)

Anulatrypa nieczlawiensis tenuicostata Tcherkesova *in* Modzalevskaya & Cherkesova, 1994: 56, pl. V, figs 3-5.

MATERIAL EXAMINED. — Five specimens from loc. 18095, Komsomolets Island (Männik *et al*. 2002: fig. 1); Rusanov Formation.

REMARKS

The external features, such as ventral beak overlapping the top of dorsal beak; the absence of ventral interarea, fold and sulcus, numerous slen-

der ribs; concentric lamellae extending into short trails allow to assign the specimens to the genus *Anulatrypa*. The sizes of adult specimens varie within the ranges: L = 11.2-28.6 mm, W = 9.3-22.0 mm, T = 4.4-16.5 mm. The number of ribs is more than 30 at a distance of 5 mm from the ventral apex. These features characterize the specimens collected from the uppermost Tolbat and lower Daksan beds of Central Tajmyr, and allow to assign these to the subspecies *A. nieczlawiensis tenuicostata*. The Severnaya Zemlya specimens differ from those from Tajmyr (Modzalevkaya & Cherkesova 1994: 56) by possessing weakly longitudinal outline, and straight hinge line ending in the rounded ears. The specimens from Severnaya Zemlya have some similarities in size, in outline, and in ornamention with *Anulatrypa hyperanulata* Havliček, 1987 from Zlichovian of Central Bohemia (Havliček 1987: 75, pl. 1, fig. 5). Specimens from both regions possess a narrow tongue in the anterior margin, but those from Severnaya Zemlya lack a ventral sinus.
A. nieczlawiensis tenuicostata has been found from Central Tajmyr, from the Delorm Formation in the Canadian Arctic Cathedral Mountains, and in the Bystrin Formation on Novaya Zemlya (Modzalevskaya & Cherkesova 1994).

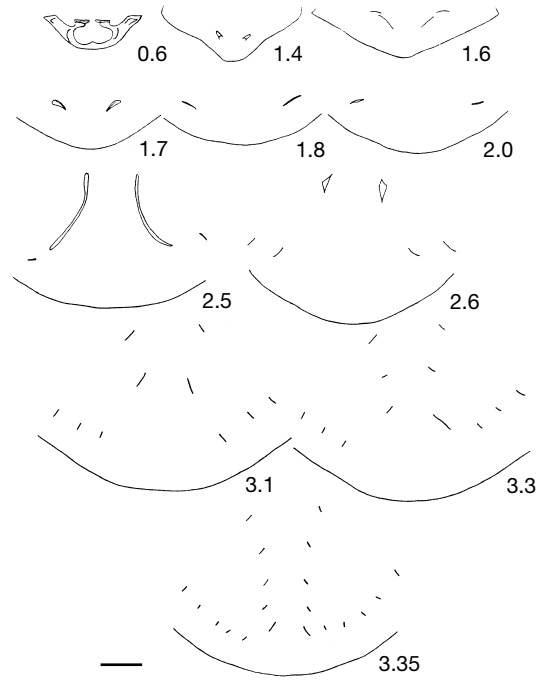

FIG. 23. — Selected transverse serial sections, illustrating the development of internal structures in *Dubaria tenera* Nikiforova & T. Modzalevskaya, 1968 (N 15/12991). Measurements: length 5.6 mm, width 8.0 mm, thickness 4.5 mm; loc. 13, bed 64, Golomyannyj Formation. Numerical designations are the same as on Fig. 11. Scale bar: 10 mm.

Family LISSATRYPIDAE Twenhofel, 1914
Genus *Dubaria* Termier, 1936

Dubaria tenera Nikiforova & T. Modzalevskaya, 1968
(Figs 22J-M; 23)

Dubaria tenera Nikiforova & T. Modzalevskaya, 1968: 68, pl. III, figs 8-10.

MATERIAL EXAMINED. — Three specimens from loc. 13, beds 64, 89, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Vodopad and Golomyannyj formations.

REMARKS
The specimens assigned to this species show some characteristics of external and internal structures identical to those of *Dubaria tenera*, illustrated by Nikiforova & Modzalevskaya from the Talikit Formation of East Siberia (Fig. 23). Possibly, this species is a junior synonym of *Atrypopsis varians* Poulsen, 1943 described from the Offley Island Formation of Greenland (Poulsen 1943: 44, pl. 5, figs 13-16). These two taxa are morphologically very similar. However, the identification of our specimens is quite problematic due to the lack of the dorsal myophragm on them. This structure is one of the main diagnostic features of *Atrypopsis* and *Dubaria* Boucot, Johnson & Staton, 1964 (Rubel 1970). P. Copper (1991: 37), restudying the atrypids, concluded that *Atrypopsis*, *Dubaria*, *Rhynchatrypa* Siehl, 1962, and *Barkolia* Zhang, 1983 are junior synonyms of *Septatrypa* Kozlowski, 1929. Hence, the occurrence of a short dorsal septum is an essential feature to identify *Septatrypa* (Nikiforova *et al.* 1985: 44, pl. 11, fig. 9).

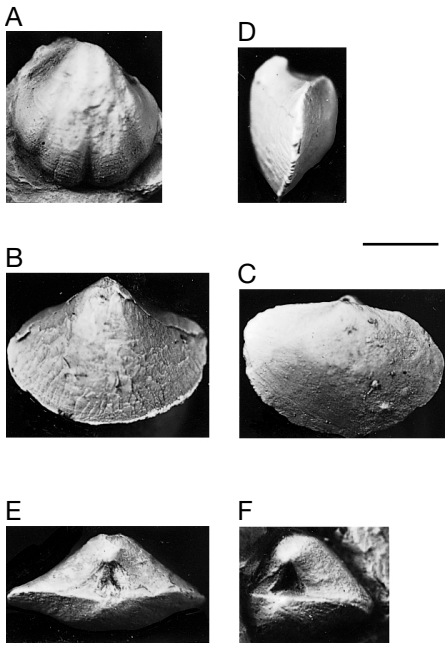

FIG. 24. — **A**, *Eohowellella* sp., ventral view of a pedicle valve (N 64/12991), loc. 2, bed 79, Samojlovich Formation; **B**-**F**, *Reticulariopsis talenti* Lenz & Johnson, 1985; **B**, ventral view; **C**, dorsal view; **D**, lateral view; **E**, posterior view of a complete shell (N 65/12991); **F**, posterior view of a complete shell (N 66/12991), showing delthyrium, loc. 21581, Severnaya Zemlya or Pod''emnaya formations. Scale bar: A, 5 mm; B-E, 2 mm; F, 2.5 mm.

Order SPIRIFERIDA Waagen, 1883
Family DELTHYRIDIDAE Waagen, 1883
Genus *Eohowellella* Lopushinskaya, 1976

Eohowellella sp.
(Fig. 24A)

MATERIAL EXAMINED. — Four specimens from loc. 11, bed 14, and coquina from loc. 2, beds 74, 79, Matusevich River, October Revolution Island (Männik *et al*. 2002: figs 2, 5); Samojlovich Formation.

REMARKS

Small, subrhomboidal shells of the genus *Eohowellella* are widely variable. They have rounded cardinal extremities, four plicae arising near the beak and rapidly widening anteriorly. The width of the plicae is four times more than the interspaces. The shells studied possess a combination of features characteristic of two different species of *Eohowellella*. The size and weakly developed plicae on the both valves are characteristic of *E. yadrenkinae* Lopushinskaya, 1976, whilst the flat dorsal valve with distinctly developed trilobite external structure, and numerous concentric growth lines, are typical to *E. minimus* Lopushinskaya, 1976. Both of these species occur in the Talikit, Omnutakh, Khukta and Makus formations in the East Siberia (Lopushinskaya 1976: 80). Small size, plicae wider than interspaces, and almost flat dorsal valve are also characteristic of *Howellella elegans* (Muir-Wood, 1925), the holotype of which comes from the Mulde Beds of Gotland (Bassett & Cocks 1974: 38, pl. 10, fig. 5). The Severnaya Zemlya specimens have an erect ventral umbo, subrhombical outline and more numerous plicae than *H. elegans*.

Family RETICULARIIDAE Waagen, 1883
Genus *Reticulariopsis* Fredericks, 1916

Reticulariopsis talenti Lenz & Johnson, 1985
(Figs 24B-F; 25)

Reticulariopsis talenti Lenz & Johnson, 1985: 91, pl. 15, figs 1-11.

Reticulariopsis? sp. – Lenz & Johnson 1985: 91, pl. 15, figs 12-16.

MATERIAL EXAMINED. — Four isolated shells, mainly embeded in the rock matrix, from loc. 21581, Komsomolets Island (Männik *et al*. 2002: fig. 1); Severnaya Zemlya or Pod"emnaya formations.

REMARKS

Small specimens (L = 5.1-5.5 mm, W = 6.3-6.9 mm, T = 3.7-4.0 mm) are characterised by ventribiconvex as well as biconvex shells with poorly developed sinus and fold. Serially sectioned internal structure shows small triangular teeth supported by short anteriorly divergent dental plates. Dental sockets are longitudinal and narrow. Crural plates are wide, triangular, jointed near the bottom of the shell. Crura are thin, fluently merging with primary lamellae of spiralia. The coils of

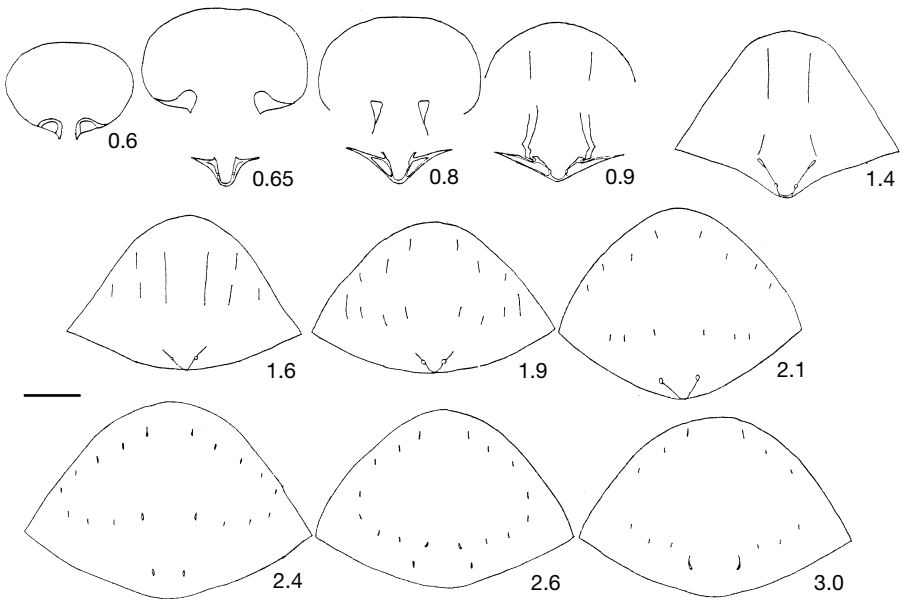

FIG. 25. — Selected transverse serial sections, illustrating the development of internal structures in *Reticulariopsis talenti* Lenz & Johnson, 1985 (N 67/12991). Measurements: length 5.1 mm, width 6.3 mm, thickness 4.0 mm; loc. 21581, Severnaya Zemlya or Pod''emnaya formations. Numerical designations are the same as on Fig. 11. Scale bar: 1.4 mm.

spiralia are directed laterally and comprise four whorls. No ctenophoridium is found (Fig. 25). Shells of similar size, with laterally ovate outline, are characteristic of *Reticulariopsis*? sp. (Lenz & Johnson 1985: 91). In the Garra Formation (Wellington area in New South Wales, Australia), this type of shells occurs 4 m below *R. talenti*. There is no evidence of its co-occurrence together with *R. talenti* also from Severnaya Zemlya. Smaller size, acute apical angle, weakly developed sinus and fold are reliable criteria for discriminating *R. talenti* from *Reticulariopsis*? *warreni* Perry, 1984 described from the Delorme Formation, Mackenzie District of the Yukon (Perry 1984: 121, pl. 41, figs 29-46).

Genus *Undispirifer* Havliček, 1957

Undispirifer*? *obsoletiplicatus n. sp.
(Figs 26; 27)

Non *Howellella pauciplicata* Waite, 1956: 17, pl. XII, fig. 1.

Howellella pauciplicata – Alekseeva 1967: 78, pl. XI, figs 7-12, pl. XII, fig. 1.

HOLOTYPE. — N 68/12991, CNIGR Museum, St. Petersburg (Fig. 26B), ventral valve; L = 14.2 mm, W = 16.7 mm.

ETYMOLOGY. — From *obsoletiplicatus* = *obsoletus* (Latin): decayed, and *plicatus*: folded.

TYPE LOCALITY. — Loc. 21581, southern bank of Krasnaya Bay, Komsomolets Island.

FORMATION. — Spokojnaya or Pod"emnaya formations.

AGE. — Lower Devonian.

MATERIAL EXAMINED. — 10 disarticulated shells and their external moulds from loc. 21581, Komsomolets Island (Männik *et al.* 2002: fig. 1); Spokojnaya and/or Pod"emnaya formations.

MEASUREMENTS (IN MM). — Ventral valve: L = 14.6, W = 18.0-20.0?; dorsal valve: L = 13.7-14.7, W = 16.5-19.2.

DIAGNOSIS. — Shells moderately large, pentagonal in outline with inconspicuous plications; ventral sinus weakly developed, dorsal fold sharply limited anteriorly.

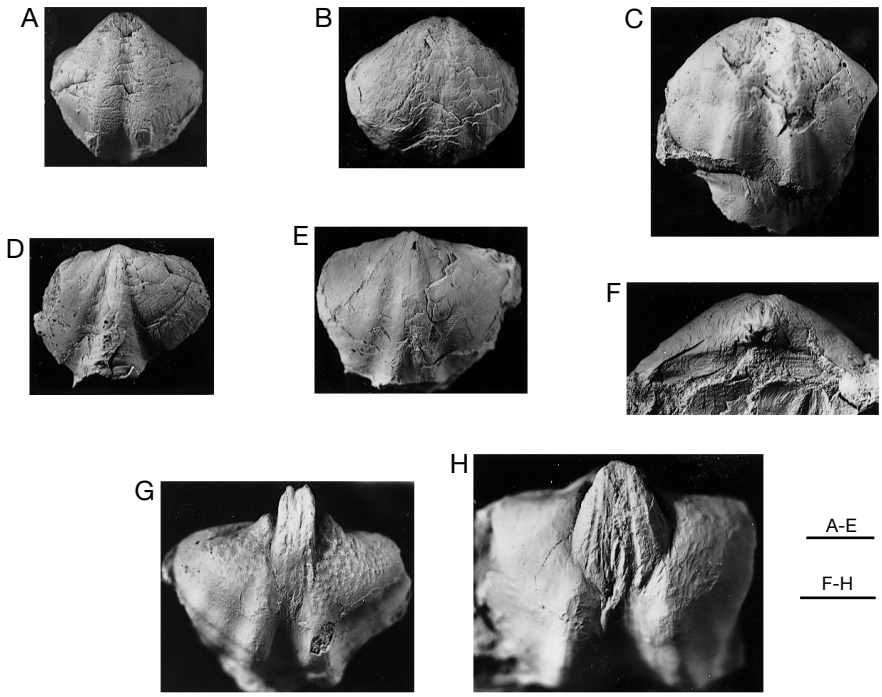

FIG. 26. — *Undispirifer*? *obsoletiplicatus* n. sp.; **A**-**C**, ventral view of different sizes pedicle valves; **A**, N 69/12991; **B**, holotype (N 68/12991); **C**, N 70/12991; **D**, **E**, dorsal view of a brachial valve (NN 71/12991, 72/12991); **F**, posterior view of a pedicle valve with interarea and open delthyrium (N 73/12991); **G**, **H**, external moulds of pedicle valves, showing a well developed muscle field and gonad impressions (NN 74/12991, 75/12991), loc. 215581, Severnaya Zemlya or Pod''emnaya formations. Scale bars: A-E, 6 mm; F-H, 5 mm.

DESCRIPTION

Moderate size, biconvex shells of pentagonal outline with inconspicuous plications, gentle sinus and fold. Isometrical ventral valve with suberect beak. Maximum width of valve is located close to its midlength. Interarea trigonal, weakly concave, apsacline, low. Delthyrium open with narrow deltidial plates. The sinus on ventral valve is shallow. It originates at umbo and widens gently towards the anterior margin of the valve. Here, the margins of the sinus are well defined and it forms a deep tongue. The width of the dorsal valve is greater than its length, and it bears a distinctly developed fold which widens towards the anterior margin Here, a median furrow is sometimes observed. Surface is smooth with hardly visible plicae on the lateral flanks anteriorly. Microornament is not visible.

In the ventral interior, short dental plates are thickened by callus, which fills the beak. Muscle field is longitudinally oval, sharply outlined, well impressed. Adductors are indistinctly limited, diductors are radially striated. There are ovarian impressions lateral to the muscle field. In the dorsal interior crural plates do not reach the valve walls. Jugum and spiralia are not observed (Fig. 27).

REMARKS

The species of *Undispirifer* are in need of revision. As was noted by Johnson (1975), this genus includes Lower Devonian spiriferids (among which there are many poorly plicated forms) with morphologies intermediate between *Howellella* and *Undispirifer*. As a result, *laeviplicata* resembles both genera (Kozlowski 1929: 195; Smith 1980: 180; Lenz & Johnson 1985: 92). The

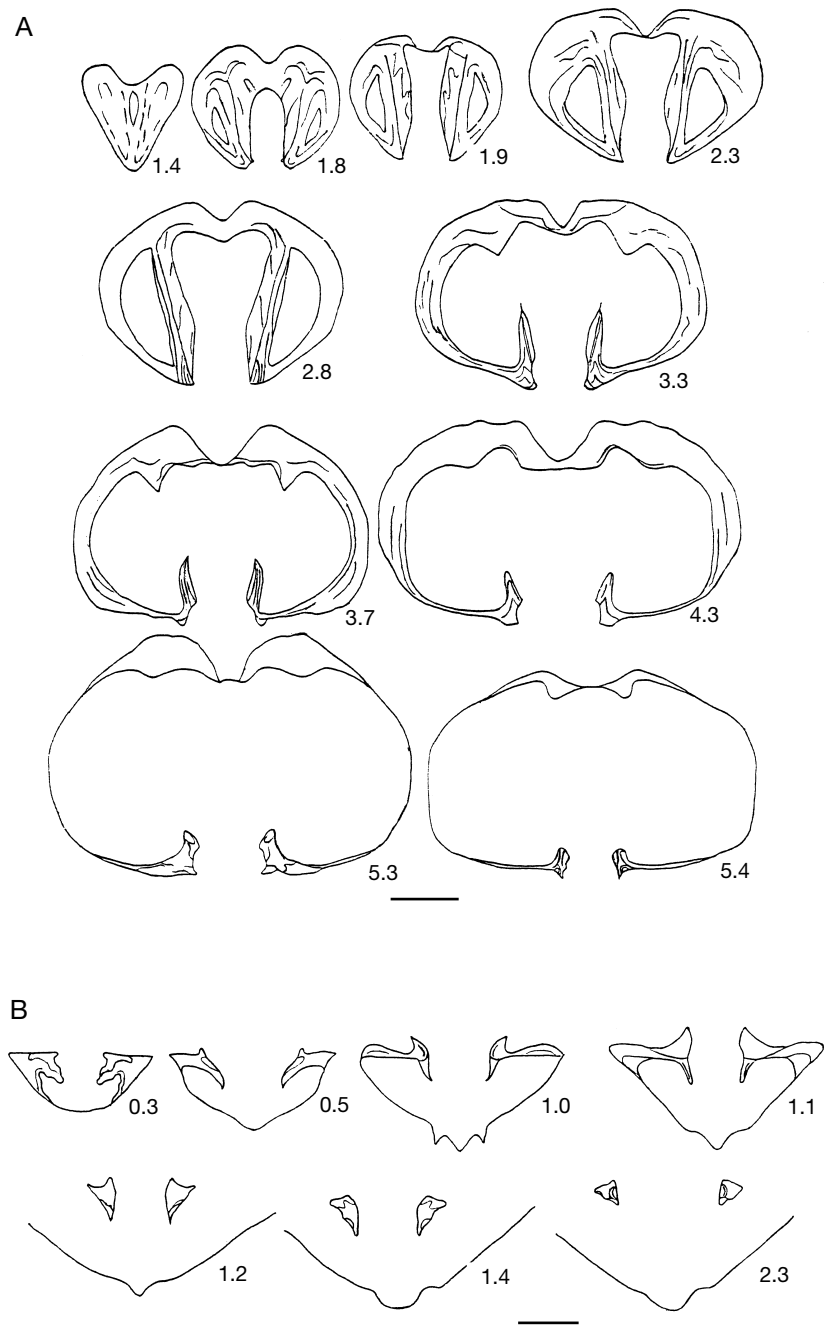

FIG. 27. — Selected transverse serial sections, illustrating the development of internal structures in *Undispirifer*? *obsoletiplicatus* n. sp.; **A**, ventral valve (N 76/12991), length 17.3 mm, width 12.0? mm; **B**, dorsal valve (N 77/12991), length 14.7 mm, width 19.9 mm; loc. 21581, Severnaya Zemlya or Pod''emnaya formations. Numerical designations are the same as on Fig. 11. Scale bar: 2.3 mm.

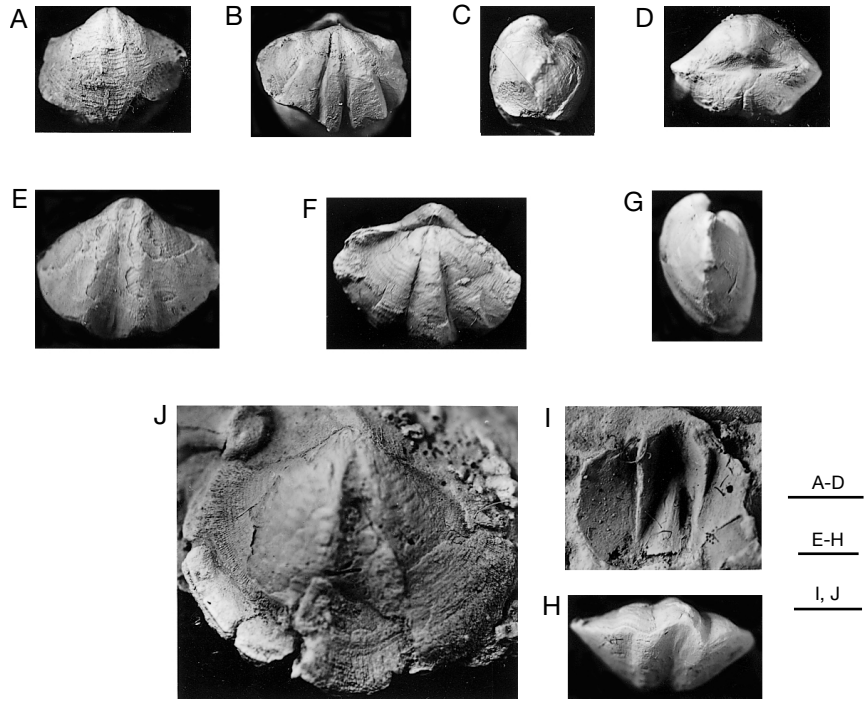

FIG. 28. — *Grebenella laciniatus* n. sp.; **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view of a complete shell (N 79/12991), loc. 21581, Severnaya Zemlya or Pod''mnaya formations; **E**, ventral view; **F**, dorsal view; **G**, lateral view; **H**, anterior view of a complete shell (holotype N 78/12991); **I**, ventral interior with dental lamellae and muscle field (N 80/12991), Severnaya Zemlya or Pod''emnaya formations; **J**, enlarged external surface of a ventral valve, showing concentric growth lines with the impressions of the spines (N 81/12991), loc. 20399, Rusanov or Al'banov formations. Scale bars: A-D, 5 mm; E-H, 3 mm; I, J, 2 mm.

specimens from Severnaya Zemlya are assigned here to *Undispirifer* on the basis of clearly developed ventral muscle field and the callus-filled beak. The last feature is missing on *Howellella*. The ventral valve of *U.*? *obsoletiplicatus* n. sp. differs from that of *U. laeviplicatus* (Kozlowski, 1929) (Lochkovian of Prince of Wales Island, Canadian Arctic) by its smooth lateral plicae and weakly developed sinus (Smith 1980: 71, pl. 33, figs 6-36). The similarity to *Howellella pauciplicata*, found from the Settedaban Formation (Alekseeva 1967: 78, pl. XI, figs 7-12, pl. XII, fig. 1), suggests that the Severnaya Zemlya and North East specimens are conspecific. This species differs from *Howellella prima* Alekseeva, 1967 in its sharply limited, anteriorly widening dorsal fold, high, rounded dorsal tongue, and weak outlines of the dorsal muscle field (Alekseeva 1967: 82, pl. XII, figs 2-11).

Genus *Grebenella* Modzalevskaya & Besnosova, 1992

Grebenella laciniatus n. sp. (Figs 28; 29)

HOLOTYPE. — N 78/12991, CNIGR Museum, St. Petersburg (Fig. 28E-H), conjoined valves; L = 6.0 mm, W = 8.0 mm, T = 4.1 mm.

ETYMOLOGY. — From *laciniosus* (Latin): shredded.

TYPE LOCALITY. — Loc. 20399, source of the left tributary of the Snegovaya River, Komsomolets Island.

FORMATION. — Rusanov or Al'banov formations.

AGE. — Lower Devonian.

MATERIAL EXAMINED. — Shelly limestone, two conjoined and 10 separated valves from loc. 20399 (source of the left tributary of the Snegovaya River) and loc. 21581 (southern bank of Krasnaya Bay), Komso-

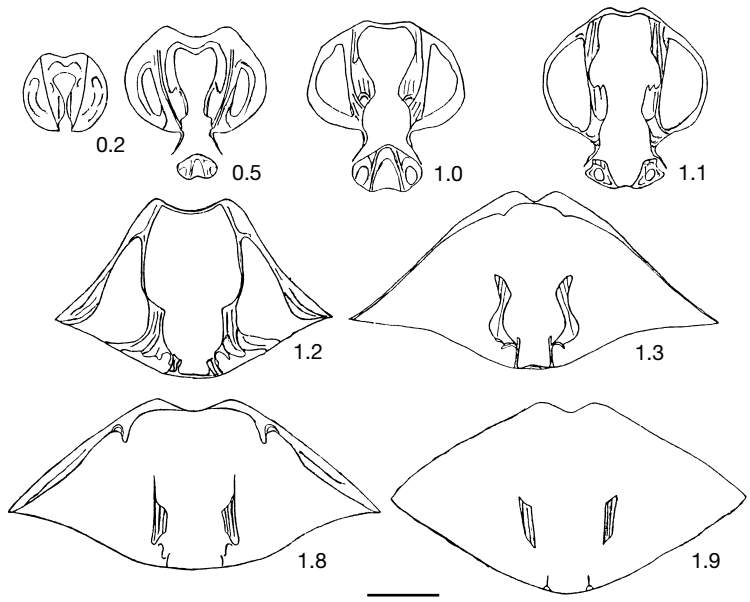

FIG. 29. — Selected transverse serial sections, illustrating in the development of internal structures in *Grebenella laciniatus* n. sp. (N 82/12991). Measurements: length 6.8 mm, width?, thickness?; loc. 20399, Rusanov or Al'banov formations. Numerical designations are the same as on Fig. 11. Scale bar: 1.6 mm.

molets Island, Severnaya Zemlya (Männik *et al.* 2002: fig. 1); Rusanov or Al'banov formations.

MEASUREMENTS (IN MM). — L = 4.8-8.5, W = 6.6-8.0, T = 3.6-4.3.

DIAGNOSIS. — Small shells, transversally oval in outline and ventribiconvex in lateral profile; dorsal fold with deep narrow furrows on the flanks; plicae weakly developed.

DESCRIPTION

Shells small, transversally oval, ventribiconvex with developed sinus and fold, and with smooth flanks. Ventral valve is the most convex in its umbonal part. Apex acute, hanging over the dorsal valve, delthyrium partly closed by deltidial plates, interarea triangular, low. Cardinal extremities rounded, sinus is well limited, arises from the beak, widening anteriorly, anterior tongue pronounced. Dorsal valve with sharply outlined fold bordered by deep narrow furrows. Fold originates at the beak. Broad plicae on flanks arise at about one third of valve length. Concentric growth lamellae are rhythmical, and bear the impressions of spines on their anterior edges in the mould. Ventral umbonal chambers filled by callus. Dental plates high, long, strongly thickened, widely situated and divergent; teeth massive. Ventral muscle field triangular with a triangular furrow near its anterior margin. Callus also well developed in dorsal valve, where thickened crural plates are widely divergent posteriorly and rest on short septum at the valve floor. Crura extend to near the valve floor. Dental sockets well limited medially by inner socket ridges (Fig. 29).

COMPARISON

The flattened dorsal valve, transverse outline, and weakly developed plications suggest the comparison with *Grebenella impalpabilis* T. Modzalevskaya, 1994 from the Tolbat Beds, Tajmyr (Modzalevskaya & Cherkesova 1994: 87, pl. X, figs 11-14). However, the fewer plicae, comparatively weak dorsal fold with deep narrow furrows on the flanks support assignment of Severnaya Zemlya specimens to a new species.

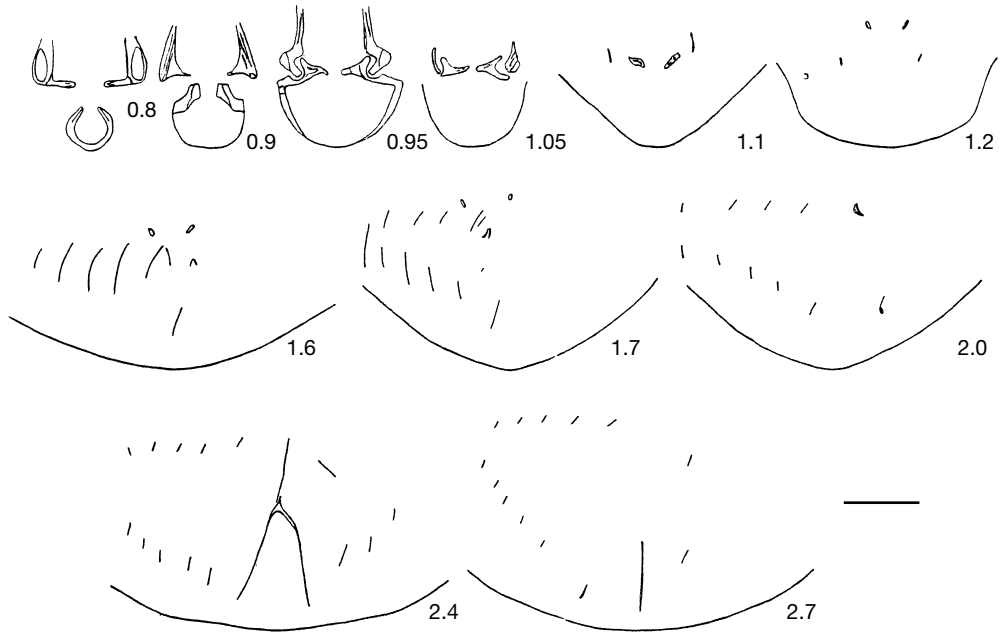

FIG. 30. — Selected transverse serial sections, illustrating the development of internal structures in *Hyattidina remota* n. sp. (N 60/12991). Measurements: length 6.8 mm, width 8.4 mm, thickness 5.0 mm; loc. 13, bed 48, Golomyannyj Formation. Numerical designations are the same as on Fig. 11. Scale bar: 5 mm.

Order ATHYRIDIDA Boucot, Johnson & Staton, 1964
Family MERISTELLIDAE Waagen, 1883
Genus *Hyattidina* Schuchert, 1913

Hyattidina remota n. sp.
(Figs 22A-D; 30)

HOLOTYPE. — N 58/12991, CNIGR Museum, St. Petersburg (Fig. 22A-C), conjoined valves; L = 8.4 mm, W = 8.4 mm, T = 5.6 mm.

ETYMOLOGY. — From *remotus* (Latin): far.

TYPE LOCALITY. — Loc. 13, Matusevich River, October Revolution Island.

FORMATION. — Golomyannyj Formation.

AGE. — Llandovery, Aeronian.

MATERIAL EXAMINED. — 19 conjoined well preserved valves from loc. 13, bed 48, Matusevich River, October Revolution Island (Männik *et al.* 2002: figs 2, 5); Golomyannyj Formation.

MEASUREMENTS (IN MM). — L = 6.8-8.4, W = 7.3-8.4, T = 5.0-5.6.

DIAGNOSIS. — Small shells, rounded in outline, biconvex in lateral profile, plicate; ventral fold and dorsal sulcus are well developed; wide dorsal sulcus limited by the flanking sinuses.

DESCRIPTION

Biconvex shells with rounded outline, plicate. Ventral beak acute, with open delthyrium, curved over the dorsal valve. Rounded ventral sinus limited laterally by rounded plicae, which originate from the anterior half of the valve. Smooth surface covered sometimes anteriorly by concentric growth lines. The internal structures consist of long, low dental plates located fairly close to the valve walls. Teeth small, deeply inserted into the dental sockets (Fig. 30). Crural bases arise from the cardinal plate and progressively curve inward to join the primary lamellae of the spiralia. Spiralia directed laterally comprising five whorls. Jugum simple, placed in the middle of the shell, comprising a pair of joined lamellae without a jugal saddle.

COMPARISON
All hyattidinids possess long, low dental plates, a simple jugum without jugal saddle and spiralia directed laterally. The specimens show some characteristics of *Hyattidina junea* (Billings, 1866) (such as the pattern of the ventral sinus and dorsal fold), illustrated by Twenhofel (1928: 223, pl. XXX, figs 4-6) from the Gun River and Jupiter formations of Anticosti Island. But the Severnaya Zemlya shells are smaller and characterized by a wider dorsal fold, limited by the flanking sinuses.

Genus *Meristina* Hall, 1867

Meristina*? *norilica
(Nikiforova *in* Nikiforova & Andreeva, 1961)
(Fig. 22I)

Meristella norilica Nikiforova *in* Nikiforova & Andreeva, 1961: 260, pl. LVI, figs 1-11.

Cryptothyrella norilica – Lopushinskaya 1976: 76, pl. XV, figs 1-5.

MATERIAL EXAMINED. — Five crushed specimens from loc. 13, bed 27, loc. 2, beds 61 and 66, Matusevich River, October Revolution Island (Männik *et al*. 2002: figs 2, 5); Srednij and Samojlovich formations.

REMARKS
Shells are characterized by rhomboidal outline, low beak, foramen, and apex pressed against dorsal valve. Thickened shelly substance borders the deep pedicle chamber. Ventral surface is smooth and convex. The features above are characteristic of *M. norilica* described from the Omnutakh Formation of the East Siberia (Nikiforova & Andreeva 1961: 260, pl. LVI, figs 1-11).

Family ATHYRIDIDAE Davidson, 1881
Genus *Greenfieldia* Grabau, 1910

Greenfieldia orbiculata n. sp.
(Figs 22E-H; 31)

HOLOTYPE. — N 62/12991, CNIGR Museum, St. Petersburg (Fig. 22E-H), conjoined valves; L = 11.0 mm, W = 11.0 mm, T = 9.0 mm.

ETYMOLOGY. — From *orbiculatus* (Latin): rounded.

TYPE LOCALITY. — Loc. 2, Matusevich River, October Revolution Island.

FORMATION. — Samojlovich Formation.

AGE. — Wenlock, Homerian-Sheinwoodian.

MATERIAL EXAMINED. — 44 well preserved conjoined valves from loc. 2, beds 61 and 66, Matusevich River, October Revolution Island (Männik *et al*. 2002: figs 2, 5); Samojlovich Formation.

MEASUREMENTS (IN MM). — L = 6.8-11.8, W = 6.8-11.0, T = 4.6-9.0.

DIAGNOSIS. — Shells small with rounded outline and strongly biconvex in lateral profile; lacking dorsal fold, anterior margin almost rectimarginate.

DESCRIPTION
Shells strongly biconvex with rounded outline. Ventral beak high and incurved, sinus weakly developed. Dorsal fold absent or restricted to narrow furrow; anterior margin almost rectimarginate or very slightly uniplicate. Interior with high, long dental plates, which are parallel and straight. Teeth deeply inserted into dental sockets (Fig. 31). Dorsal interior with perforated cardinal plate. High, vertical crura arise from outer plates and extend to the middle of the shell, becoming convex medially and merging into primary lamellae. The coils are directed laterally and comprise nine whorls. Jugal saddle directed anteriorly to the middle of the shell.

VARIATION
Young specimens have a flattened anterior margin. Outline varies from rounded to oval, ventral sinus and dorsal furrow are absent or weakly developed.

COMPARISON
In development of a ventral sinus and lack of a dorsal fold the specimens from Severnaya Zemlya are most similar to *Greenfieldia uberis tanta* Modzalevskaya, 1980 described from the Dolgij Formation on Dolgij Island (Modzalevskaya 1980: 92, pl. II, figs 4, 5). The main differences are the smaller size and more rounded outline of the Severnaya Zemlya specimens.

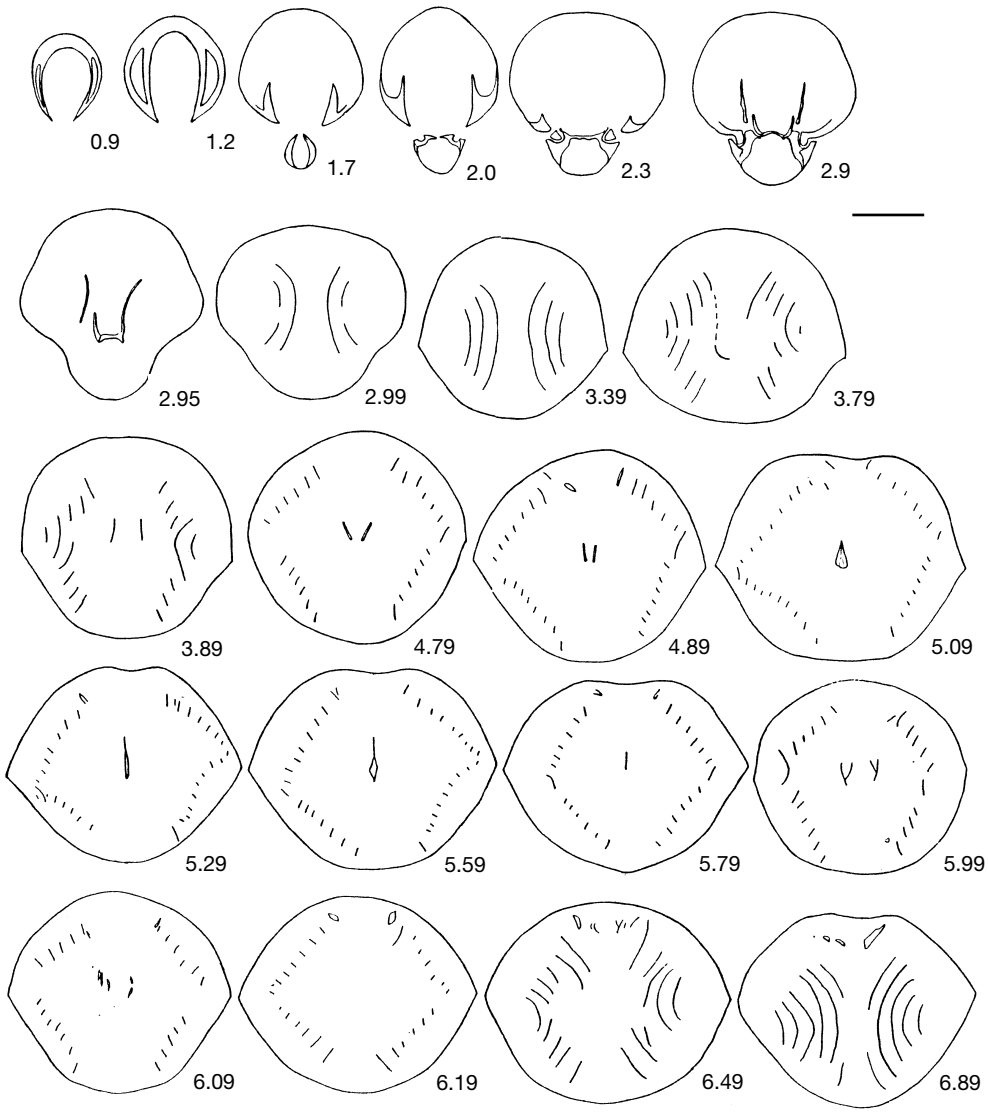

FIG. 31. — Selected transverse serial sections, illustrating the development of internal structures in *Greenfieldia orbiculata* n. sp. (N 63/12991). Measurements: length 10.9 mm, width 9.1 mm, thickness 9.2 mm; loc. 2, bed 66, Samojlovich Formation. Numerical designations are the same as on Fig. 11. Scale bar: 2.7 mm.

BIOSTRATIGRAPHY AND PALAEOGEOGRAPHICAL AFFINITIES

Brachiopods are dominating in the benthic faunas of the studied region. Quite often they form lenses or continuous shell beds. Brachiopod associations are mainly reported from the Silurian formations. In spite of the great number of specimens brachiopod beds are often monotaxic, and are mainly represented by endemic taxa.

On the basis of the brachiopods studied the Silurian rocks on Severnaya Zemlya were correlated with those on the Novaya Zemlya-Urals region and Siberian Platform. The age of the beds with brachiopods can be dated rather accurately on the basis of conodonts (Männik

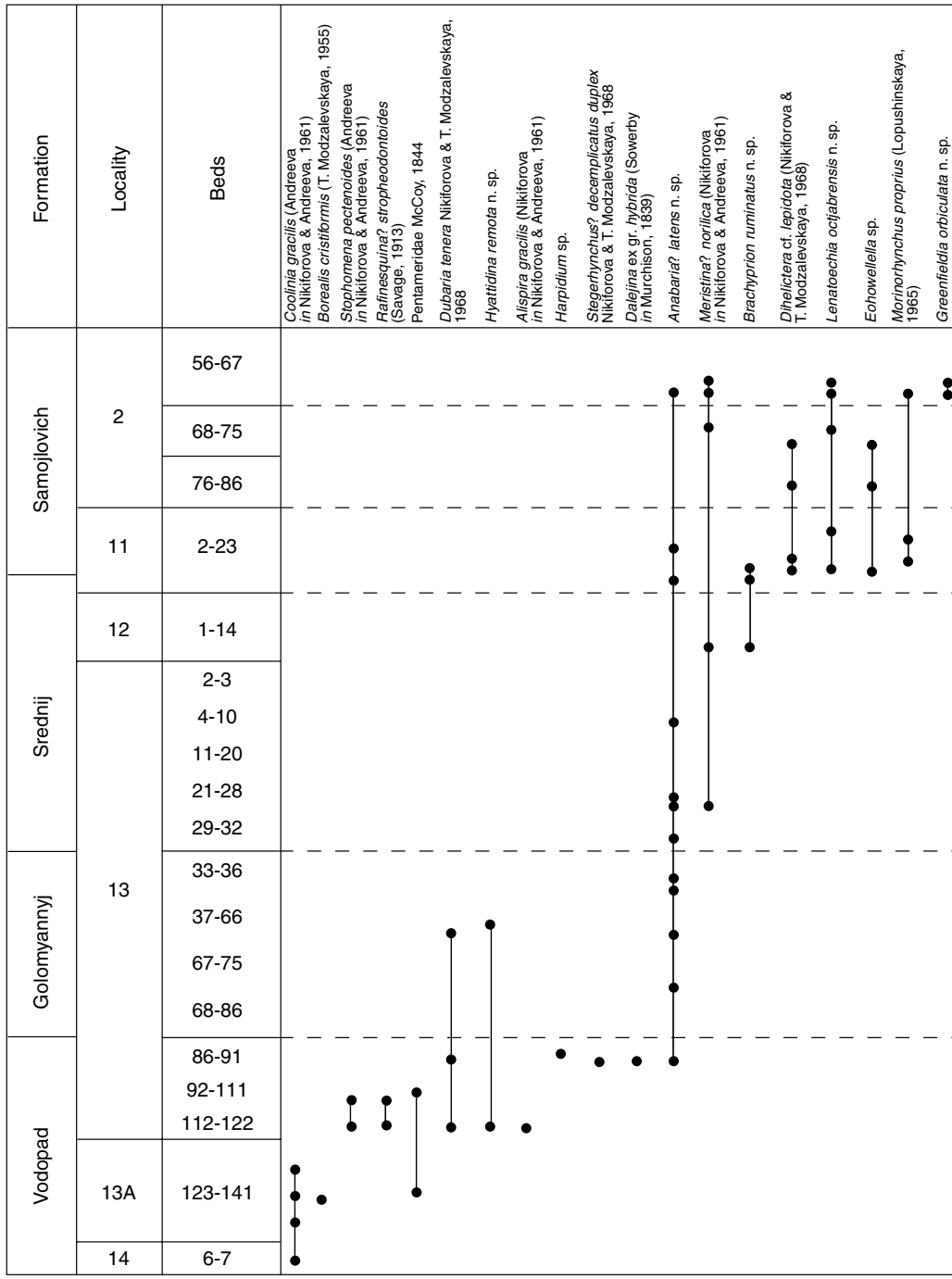

FIG. 32. — Range chart of brachiopods of the Vodopad, Golomyannyj, Srednij, Samojlovich formations of the key section in Matusevich River (October Revolution Island, Severnaya Zemlya Archipelago). Stratigraphic positions of species are estimated by the level of the beds within each formation.

1997). The vertical distribution of brachiopods was evaluated with respect to the corresponding lithostratigraphical units (formations) in the Matusevich River section. The lowermost Silurian strata in this section correspond to the Vodopad Formation (outcrop 13, beds 87-122, outcrops 13a and 14; Männik *et al*. 2002: figs 2, 5) (Fig. 32). This formation is represented by highly variable lithologies formed in open-shelf conditions during early Silurian transgression. Many different groups of brachiopods, such as strophomenids, atrypids and early athyrids, occur in the Vodopad Formation. Characteristic of the Vodopad Formation is very abundant occurrence of pentamerids in the lower and uppermost strata of the formation. Some of the shells are still articulated and all are largely infragmented (BA-3, bank environment). Such kind of burial conditions are interpreted to have been occurred on the seafloor at depth affected by storms (Johnson 1989). Scattered and fragmented shells accumulated in the coastal side of these formations. The sequence of pentamerids composes of two genera among which *Borealis* is the earliest one in the Severnaya Zemlya region as well as in Novaya Zemlya. It is also one of the most distinctive taxon of the Early Silurian brachiopod assemblage in Baltoscandia. On Novaya Zemlya, *Borealis cristiformis* appears in the *Virgiana* Biozone, which probably correlates with the *acuminatus-convolutus* graptolite zones, Rhuddanian. Abundant pentamerids also occur within the Vodopad (Snezhinka) Formation on the Komsomolets Island. These brachiopods are often found in growth position allowing their confident assignment to the BA-3. Immigration and wide distribution of *Borealis samojedicus*, characteristic of the Timan-Pechora region, perhaps, caused their appearance. According to Mørk (1981), in Norway, *Borealis* always occupied a lower stratigraphical level in comparison with *Pentamerus*. In deeper facies (loc. 13, beds 122-111, Fig. 32) small smooth atrypids (*Dubaria*), and athyrids (*Hyattidina*) are locally abundant (BA-4). The composition of the brachiopod associations is similar to that from the Siberian Platform, but on Severnaya Zemlya brachiopods are less numerous than in the last region. The really significant taxonomic change was recognized in the uppermost Vodopad Formation (loc. 13, beds 87-89). The highest pentamerid coquina in the Vodopad Formation is represented by *Harpidium*, which is rare in the northern Baltic. In many regions in the North-Atlantic palaeogeographical area the oldest *Harpidium* is found in the lowermost part of the upper Llandovery strata.

No new brachiopods appear in the Golomyannyj Formation which was formed in the conditions of a major marine regression. Some genera (*Dubaria*, *Hyattidina* and *Anabaria*?) often cross the boundary between the Vodopad and Golomyannyj formations (loc. 13; beds 86-33, Fig. 32).

Brachiopods are less abundant in the Srednij Formation (loc. 13, beds 2-32; loc. 12, beds 1-14; loc. 11, beds 22-23; Fig. 32). This formation is characterized by wide variety of facies ranging from normal marine to lagoonal and shoal environments with coral-stromatoporoid biostromes and bioherms. There are no key species in this assemblage except, probably, *Trimerella* which is the most abundant taxon in the same formation on Srednij Island. The typical species of the Srednij Formation is *Dihelictera lepidota* – a form generally found on Pioneer Island. *Dihelicterа*-fauna (BA-2) is found in inter-reefal carbonates as well as within patch reef facies in Anticosti Island (Copper 1995), and in Agidyj and Khakom stages of the Siberian Platform (Telychian-Homerian?).

The sedimentological features of the Samojlovich Formation (loc. 11, beds 2-21; loc. 2, beds 56-86, Fig. 32) indicate that these strata were formed in shallow-water rimmed-shelf environments in conditions of continuing shallowing of the basin. *Dichelictera* (BA-2) is still common in the fore-shoal facies of the Samojlovich Formation. Other taxa in the brachiopod association of this formation include *Eohowellella* and *Morinorhynchus* which are similar to brachiopod fauna known from Siberia. An earliest spiriferid, *Eohowellella*, is the commonest in the *Hyattidina*-

Eohowellella community. *Eohowellella* is also well known from the Agidyj and Khakom stages from many regions of East Siberia. A globose species of *Greenfieldia* is found at some levels near the top of the Samojlovich Formation. Locally, this species is bed forming. The ancestor of *Greenfieldia* is unknown. In the Urals-Novaya Zemlya Region, this genus appears in the earliest Gerd"yu time. According to the indirect correlation, the level of appearance of *Greenfieldia* probably corresponds to the Wenlock-Ludlow boundary in this region.

On the basis of the analysis of the taxonomic structure of successive brachiopod associations, palaeogeographical connections of the Severnaya Zemlya Silurian basin can be reconstructed. At the beginning of the Silurian transgression, normal marine shallow-water conditions, favorable for the brachiopod evolution, appeared in the Severnaya Zemlya region. In the early Silurian associations of brachiopods the Novaya Zemlya-Siberian taxa are prevailing, but also Euro-American ones are common. Abundant occurrence on Severnaya Zemlya (on Komsomolets Island) of Timan pentamerids indicates well established connections between the Severnaya Zemlya and Novaya Zemlya-Urals basin. However, the existence of endemic species (*Hyattidina remota* n. sp., *Anabaria*? *latens*) in the Silurian of Severnaya Zemlya indicates the appearance of ecological niches, isolated from the main migration ways. At the beginning of the Samojlovich time, diverse Siberian taxa (*Meristina*, *Morinorhynchus*, *Dihelictera*, *Eohowellella*) were developed. Among them, *D. lepidota* is widely distributed in the eastern and southwestern parts of the Severnaya Zemlya basin. The increasing number of endemic species of the genera *Brachyprion*, *Lenatoechia*, *Anabaria*, and the appearance of *Greenfieldia*, is observed at the end of the Samojlovich time. This fact suggests a gradual reduction of the basin to the south of the Severnaya Zemlya Archipelago and an expanded connection with the Novaya Zemlya-Urals basin, and with the basins of North-East Asia and Canadian Arctic Archipelago during the Late Silurian-Early Devonian.

Acknowledgements

This work was made possible through a Russian Foundation for Fundamental Investigations (Grant 96-05-65762) and under the IGCP Project 406 "Circum Arctic Palaeozoic Vertebrates". I thank all people mentioned in the introduction for presenting the brachiopod collections from Severnaya Zemlya Archipelago. I would like to thank S. V. Cherkesova and L. E. Popov for consultations on brachiopods. My thanks are due to Dr. N. Savage (University of Oregon) for improving my English text, and for very helpful comments on the fauna and revising the paper. I also thank Dr. P. Racheboeuf, N. Norman, and an anonymous reviewer for useful comments on the manuscript.

REFERENCES

ALEKSEEVA R. E. 1966. — [*Sibiritoechia*, a new genus of Order Rhynchonellida]. *Doklady Akademii Nauk SSSR* 167, attributed 5: 1147-1149 (in Russian).

ALEKSEEVA R. E. 1967. — [*Lower Devonian Brachiopods and Stratigraphy of North-East of USSR*]. Nauka, Moskva, 144 p. (in Russian).

ALEKSEEVA R. E., GRATSIANOVA R. T., ELKIN E. A. & KUL'KOV N. P. 1970. — [*Lower Devonian Stratigraphy and Brachiopods of North-Eastern Salair*]. Nauka, Moskva, 188 p. (in Russian).

ALEKSEEVA R. E, SIDIACHENKO A. I., BARANOV V. V., AFANAS'EVA G. A., GRUNT T. A., KOMAROV V. N., LAZAREV S. S. & MANANKOV I. N. 1996. — [*Atlas of the Devonian Brachiopods of the North-East of Russia*]. Nauka, Moskva, 227 p. (in Russian).

AMSDEN TH. 1951. — Brachiopods of the Henryhouse Formation (Silurian) of Oklahoma. *Journal of Paleontology* 25 (1): 69-96.

AMSDEN TH. 1974. — Late Ordovician and Early Silurian Articulate Brachiopods from Oklahoma Southwestern Illinois and Eastern Missouri. *Oklahoma Geological Survey*, *Bulletin* 119, 154 p.

BASSETT M. G. & COCKS L. R. M. 1974. — A review of Silurian brachiopods from Gotland. *Fossils and Strata* 3: 1-56.

BOUCOT A. J. & JOHNSON J. G. 1979. — Pentamerinae (Silurian brachiopoda). *Palaeontographica* 163 A, 4-6: 87-129.

COCKS L. R. M. 1968. — Some strophomenacean brachiopods from the British Lower Silurian. *Bulletin of British Museum (Natural History)*, *Geology* 15, 6: 1-324.

COCKS L. R. M. 1978. — A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's monograph. *Palaeontological Society* 131, 549: 1-256.

COPPER P. 1991. — Evolution of the atrypid brachiopods, *in* MACKINNON D. I., LEE D. E. & CAMPBELL J. D. (eds), *Brachiopods through Time*. A. A. Balkema, Rotterdam; Brookfield: 35-40.

COPPER P. 1995. — Five new genera of Late Ordovician-Early Silurian brachiopods from Anticosti Island, Eastern Canada. *Journal of Paleontology* 69 (5): 846-862.

EGIAZAROV B. KH. 1959. — [Geological structure of the Severnaya Zemlya Archipelago]. *Trudy NIIGA* 94: 1-138 (in Russian).

GORJANSKY V. YU. 1972. — [New Ordovician and Silurian Inarticulate Brachiopods of Kazakhstan], *in* ZANINA I. E. (ed.), *New Species of Fossil Plants and Invertebrates*. Nauka, Moskva: 169-174 (in Russian).

HAVLIČEK VL. 1987. — Lower Devonian and Eifelian Atrypacea (Brachiopoda) in Central Bohemia. *Sbornik geologickych ved. Paleontologie* 28: 61-115.

HOU H. F. & XIAN S. Y. 1975. — [The Lower and Middle Devonian Brachiopods from Kwangsi and Rueichow]. *Professional Paper*, *Stratigraphy & Palaeontology* 1: 314 (in Chinese).

IVANOVSKY A. B. & KUL'KOV N. P. 1974. — [*Silurian Rugose Coral, Brachiopods and Stratigraphy of Altai-Sayan Folded Area*]. Nauka, Moskva, 96 p. (in Russian).

JOHNSON J. G. 1975. — Devonian brachiopods from the Quadrithyris Zone (Upper Lochkovian). *Contributions to Canadian Paleontology* 235: 5-56.

JOHNSON MARKES E. 1989. — Tempestites recorded as variable Pentamerus layers in the Lower Silurian of Southern Norway. *Journal of Paleontology* 63, 2: 195-205.

KEYSERLING A. 1846. — Geostische Beobachtungen in Wissenschaftlichen Beobachtungen auf einer Reise in das Petshora-Land im Jahre-1843. I. *Palaeontologische Bemerkungen II Geognostische Reise*: 151-406.

KOZLOWSKI R. 1929. — Brachiopodes gothlandiens de la Podolie polonaise. *Palaeontologia Polonica* I, 254 p.

KURIK E. YU., KURSHS V. M., MARKOVSKY V. A., MATUKHIN R. G., MENNER V. VL., MODZALEVSKAYA T. L., PATRUNOV D. K., SAMOILOVICH YU. G., SMIRNOVA M. A., TALIMAA V. N., KHAPILIN A. F., CHERKESOVA S. V. & ABUSHIK A. F. 1982. — [On Silurian and Devonian stratigraphy of Severnaya Zemlya], *in* YUFEREV O. V. (ed.), *Devonian and Carboniferous Stratigraphy and Paleontology*. Moskva, Nauka 483: 65-73 (in Russian).

LEBEDEV N. 1892. — [Upper Silurian fauna of Timan]. *Trudy Geologicheskogo Komiteta* XII, 2: 1-135 (in Russian).

LENZ A. C. & JOHNSON B. D. 1985. — Brachiopods of the Garra Formation (Lower Devonian), Wellington Area, New South Wales, Australia: Rhynchonellida, Spiriferida, Terebratulida. *Palaeontographica* A, 188, 4-6: 71-104.

LOPUSHINSKAYA T. V. 1965. — [On new brachiopods from Silurian deposits of Siberian Platform], *in* KHALFIN L. L. (ed.), Materialy po geologii, geofizike i poleznym iskopaemym Sibiri. *Trudy SNIIGGiMS'a* 34: 23-34 (in Russian).

LOPUSHINSKAYA T. V. 1967. — [Silurian strophomenids of Siberian Platform], *in* IVANOVSKY A. B. & SOKOLOV B. S. (eds), *Novye dannye po biostratigrafii nizhnego paleozoya Sibirskoj platformy*. Nauka, Moskva: 86-97 (in Russian).

LOPUSHINSKAYA T. V. 1976. — [Silurian brachiopods and stratigraphy of the North of Siberian Platform]. *Trudy SNIIGGiMS'a* 199, 104 p. (in Russian).

LOPUSHINSKAYA T. V. 1991. — [New Lower Silurian brachiopods of Siberian Platform], *in* KRASNOV V. I. & YADRENKINA A. G. (eds), *Stratigrafiya i glavnejshie sobytiya v istorii Sibiri. Sbornik nauchnykh trudov*. SNIIGGiMS, Novosibirsk: 51-59 (in Russian).

LOPUSHINSKAYA T. V. & DOROSHENKO L. D. 1991. — [Brachiopod associations and sedimentation stages in the Silurian of the Siberian Platform], *in* KRASNOV V. I. & YADRENKINA A. G. (eds), *Stratigrafia i glavnejshie sobytiya v istorii Sibiri. Sbornik nauchnykh trudov*. SNIIGGiMS, Novosibirsk: 110-121 (in Russian).

LOPUSHINSKAYA T. V. & YADRENKINA A. G. 1987. — [Silurian brachiopods], *in* ZHURAVLEVA I. T. (ed.), *Nizhnij paleozoj yugo-zapadnogo sklona Anabarskoj anteklizy po materialam bureniya*. Nauka, Novosibirsk: 114-121 (in Russian).

MÄNNIK P. 1997. — Silurian conodonts from Severnaya Zemlya, *in* IVANOV A., WILSON M. V. H. & ZHURAVLEV A. (eds), Palaeozoic Strata and Fossils of the Eurasian Arctic. *Ichthyolith Issues Special Publication* 3: 25, 26.

MÄNNIK P., MENNER V. V., MATUKHIN R. G. & KURŠS V. 2002. — Silurian and Devonian strata on the Severnaya Zemlya and Sedov archipelagos (Russia). *Geodiversitas* 24 (1): 99-122.

MARKOVSKIJ V. A. & SMIRNOVA M. A. 1982. — [Silurian deposits of Severnaya Zemlya Archipelago], *in* KABAN'KOV V. YA. & LAZARENKO N. P. (eds), *Geologiya arkhipelaga Severnaya Zemlya*. PGO "Sevmorgeo", Leningrad: 39-60 (in Russian).

MATUKHIN R. G., MENNER V. VL., ABUSHIK A. F., AFANASIEVA O. B., BLIECK A., VALIUKYAVICHIUS JU., VAITEKUNENE G., EVDOKIMOVA I. O., KARATAJŪTĖ-TALIMAA V. N., KURSHS V., LUKSHEVICH E., MARK-KURIK E., MODZALEVSAYA T. L., MÄNNIK P., MÄRSS T., NEKHOROSHEVA L. V., SMIRNOVA M. A., SOBOLEV N. N., STUKALINA G. A., SYTOVA V. A. & SHURYGINA M. V. 1999. — *Silurian*

and Devonian Stratigraphy of the Severnaya Zemlya Archipelagos. Novosibirsk, SNIIGGiMS (Siberian Scientific Research Institute of Geology, Geophysics and Mineral products), 174 p. (in Russian).

MODZALEVSKAYA T. L. 1980. — [Silurian and Lower Devonian brachiopods of Dolgii Island and its stratigraphical significance], *in* SAPEL'NIKOV V. P. (ed.), Silur i nizhnij devon ostrova Dolgij (Pechorskoe more). *Sverdlovsk*. *Trudy instituta geologii i geokhimii UNC AN SSSR* 157: 82-106 (in Russian).

MODZALEVSKAYA T. L. 1985. — [Early Silurian brachiopods from Southern Island of Novaya Zemlya], *in* BONDAREV V. I. (ed.), *Stratigrafiya i fauna paleozoya Novoj Zemli*. PGO "Sevmorgeo". Leningrad: 57-77 (in Russian).

MODZALEVSKAYA T. L. & CHERKESOVA S. V. 1994. — [Brachiopods], *in* CHERKESOVA S. V., KARATAJŪTĖ-TALIMAA V. N. & MATUKHIN R. G. (eds), *Stratigrafiya i fauna nizhnedevonskikh otlozhenji Tarejskogo opornogo razreza (Tajmyr)*. Nedra, St. Petersburg: 33-90 (in Russian).

MODZALEVSKAYA T. & RUBEL M. 2000. — Revision of the Silurian brachiopod *Pentamerus samojedicus* Keyserling, 1846 from the Timan Ridge, Russia. *Proceedings of the Estonian Academy of Sciences* 49, 2: 147-156.

MØRK A. 1981. — A reappraisal of the Lower Silurian brachiopods *Borealis* and *Pentamerus*. *Palaeontology* 24, 3: 537-553.

MURCHISON R. I. 1839. — *The Silurian System, founded on Geological Researches in the Counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcestor, and Stafford; with Descriptions of the Coalfields and overlying Formations*. London, i-xxxii + 768 p.

NIKIFOROVA O. I. & ANDREEVA O. N. 1961. — [Ordovician and Silurian stratigraphy of Siberian Platform and its paleontological grounds (Brachiopods)]. *Biostratigrafiya paleozoya Sibirskoj platformy*. *Trudy VSEGEI, novaya seriya* 56, 1, 412 p. (in Russian).

NIKIFOROVA O. I. & MODZALEVSKAYA T. L. 1968. — [Some Llandovery and Wenlock brachiopods of NorthEastern Siberian Platform]. *Uchenye zapiski NIIGA*. *Paleontologiya i stratigrafiya* 21: 50-81 (in Russian).

NIKIFOROVA O. I. MODZALEVSKAYA T. L. & BASSETT M. G. 1985. — Review of the Upper Silurian and Lower Devonian articulate brachiopods of Podolia. *Special Paper of Palaeontology* 34, 66 p.

PERRY D. G. 1984. — Brachiopoda and biostratigraphy of the Silurian-Devonian Delorme Formation in the District of Mackenzie, the Yukon. *Life sciences, Contributions* 138, 243 p.

POPOV L. E., BASSETT M. G., HOLMER L. E. & LAURIE J. 1993. — Phylogenetic analysis of higher taxa of Brachiopods. *Lethaia* 26: 1-5.

POULSEN CHR. 1934. — The silurian faunas of North Greenland. I: The fauna of the Cape Schuchert Formation. *Meddelelser om Gronland* 72 (1), 46 p.

POULSEN CHR. 1943. — The Silurian faunas of North Greenland. II: The fauna of the Offley Island Formation. Part II. Brachiopoda. *Meddelelser om Gronland udgivne af Komissionenfor viden skabelige undersogelser i Gronland* 72 (3), 59 p.

RACHEBOEUF P. R. 1987. — Upper Lower and Lower Middle Devonian Chonetacean brachiopods from Buthurst, Devon and Ellesmere Islands, Canadian Arctic Archipelago. *Geological Survey of Canada* 375, 29 p.

RUBEL M. 1970. — *Brachiopods Pentamerida and Spiriferida of the Silurian of Estonia*. Valgus, Tallin, 75 p.

SAPEL'NIKOV V. P. 1985. — [*System and Stratigraphical Significance of the Brachiopods of Suborder Pentameridina*]. Nauka, Moskva, 206 p.

SAPEL'NIKOV V. P. & BESNOSOVA T. M. 1980. — [Some key forms of Ashgillian and Silurian pentamerids of Pechora Urals], *in* MALAKHOVA N. P. (ed.), *Novye materialy po pentameridam Urala*. *Preprint*. UNC AN SSSR, Sverdlovsk: 3-17 (in Russian).

SAVAGE T. E. 1913. — Alexandrian series in Missouri and Illinois. *Geological Society of America* 24: 351-376.

SMITH R. E. 1980. — Lower Devonian (Lochkovian) biostratigraphy and brachiopod faunas, Canadian Arctic Islands. *Geological Survey of Canada* 308, 156 p.

TWENHOFEL W. H. 1928. — Geology of Anticosti Island. *Geological Survey* 154, 135, 351 p.

WAITE R. H. 1956. — Upper Silurian brachiopoda from the Great Basin. *Journal of Paleontology* 30, 1: 15-18.

WILLIAMS A., CARLOSON S. J., BRUNTON C. H. C., HOLMER L. E. & POPOV L. E. 1996. — A suprаordinal classification of the Brachiopoda. *Philosophical Transactions of Royal Society of London* B 351: 1171-1193.

WILLIAMS A. & BRUNTON C. H. C. 1997. — Morphological and anatomical term applied to brachiopods, *in* KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*. Part H: *Brachiopoda, revised*. Geological Society of America and University of Kansas, Lawrence: 423-440.

ZHIZHINA M. S. 1965. — Severnaya Zemlya, *in* NIKIFOROVA O. I. & OBUT A. M. (eds), *Silurian System*. *Stratigraphy of USSR*. Nedra, Moskva: 378-381 (in Russian).

Submitted on 28 April 1998;
accepted on 5 March 2000.