LINGULIFORM BRACHIOPODS FROM THE CAMBRIAN (GUZHANGIAN) KARPINSK FORMATION OF NOVAYA ZEMLYA

by LARS E. HOLMER, LEONID E. POPOV, MANSOUREH GHOBADI POUR, INNA A. KLISHEVICH, YUE LIANG and ZHIFEI ZHANG

Abstract: A moderately diverse assemblage of micromorphic linguliform brachiopods, including Tapuritreta gribovensis sp. nov., Wahwahlingula? pankovensis sp. nov., Acrothele sp., Anabolotreta? sp., Orbithele? sp. and Stilpnotreta sp., is for the first time described from the Cambrian Karpinsk Formation (Miaolingian, Guzhangian) of the South Island of Novaya Zemlya. The morphology of the metamorphic shell in Acrothele and Wahwahlingula? suggest that both taxa had a single pair of larval setal sacs, similar to the recent discinids, but their metamorphosis was completed only at the end of the pelagic stage and shows that they did have direct development, which is characteristic of all recent lingulides. The biogeographical signature of the new Cambrian brachiopod fauna from Novaya Zemlya is discussed, and the new fauna gives new information on the poorly known Cambrian margins of the Baltica palaeocontinent.

Key words: Brachiopoda, Cambrian, Novaya Zemlya, taxonomy, ontogeny, biogeography.

The first evidence of Cambrian deposits on the South Island of Novaya Zemlya was obtained by a Norwegian expedition in 1921 (Holtedahl 1922). Subsequently the Cambrian outcrop areas along the west coast of Novaya Zemlya were revisited and sampled occasionally by Russian geologists between 1925 and 1934; they were also the subject of a small-scale geological mapping project between 1948 and 1951 (Romanovich 1970). The first systematic study of the Cambrian geology and palaeontology of the Novaya Zemlya Archipelago was carried out in 1979–1983, by research teams from the Arctic and Antarctic Research Institute, St Petersburg, in connection with an extensive survey of Cambrian outcrops along the west coast of the North and South Island. The main results were published by Solovyev (1988), including a lithostratigraphical subdivision and trilobite-based biostratigraphy.

The new assemblage of linguliform brachiopods comes from the lower part of the Karpinsk Formation, exposed on the eastern part of the Pan’kov Land peninsula (Fig. 1). It includes Acrothele sp., Anabolotreta? sp. cf. Anabolotreta? glabra Streng & Holmer, 2006, Wahwahlingula? pankovensis sp. nov., Orbithele? sp., Stilpnotreta sp. cf. Stilpnotreta minuta Holmer et al., 2001, Tapuritreta gribovensis sp. nov. and Treptotreta jucunda Henderson & MacKinnon, 1981. With the exception of Anabolotreta?, which was previously documented by Popov (1985) from the lower part of the Karpinsk Formation at the south coast of Gribovaya Bay, all other taxa were not known previously from Novaya Zemlya.

The described linguliform brachiopods were extracted from black argillaceous limestones dissolved in dilute (10%), buffered acetic acid. The brachiopod specimens were coated with gold palladium and then studied and photographed under a JEOL JCM-5000 Neoscope scanning electron microscope installed in the Department of Natural Sciences, National Museum of Wales, Cardiff.

All figured and discussed material is housed in the Department of Natural Sciences, National Museum of Wales (NMW) under the accession number NMW 2018.4G.

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GEOLOGICAL AND GEOGRAPHICAL SETTING

The Cambrian deposits exposed along the west coast of Novaya Zemlya are presently subdivided into: (1) the Astafiye Formation (unnamed Cambrian Stage 4–Wuliuan); (2) the Snezhnye Gory Formation (upper Wuliuan–lower Guzhangian); and (3) the Karpinsk Formation (upper Guzhangian–Jiangshanian; Fig. 2).

On the South Island, the Astafiye Formation (up to 150 m thick in the type section of Gribovaya Bay) comprises mainly greenish grey–dark grey siltstone and argillite intercalations with subsidiary sandstones and lenses of argillaceous limestones. Its lower contact is not exposed or faulted. On the North Island, the stratigraphical contact with the underlying metamorphosed sediments, assigned to the Mendeleev Series (unnamed Cambrian Stage 4–Wuliuan) represents a nonconformity. The stratigraphically older Lomonosov Series were dated by acritarchs as Ediacaran–basal Cambrian (Korago et al. 1984, 2004). At the section of the Gribovaya Bay south coast, the Mendeleev Series contains several species of Protagraulis, including P. priscus Matthew, 1895 in the lowermost part, suggesting Cambrian Stage 4 (Solovyev et al. 1986). The first brachiopods are known from the overlying unit (Popov 1984; fig. 2, sample 911/26), represented by Acrothrya sp. and Hadrotreta sp. Their co-occurrence with Acadoparadoxides cf. oelandicus (Sjögren, 1872) suggests a Wuliuan age.

The Snezhnye Gory Formation (Drumian–Guzhangian), up to 320 m thick, rests conformably on the Astafiye Formation. It is composed mainly of oligomict and arkosic sandstones, with a minor amount of siltstones and argillites. The age of the formation is mainly based on occurrences of the trilobites, including Paradoxides paradoxissimus (Wahlenberg, 1821) in the lower part. In the upper part of the unit at the section on the south coast of Gribovaya Bay, it yielded the brachiopods Acrothele cf. coriacea Linnarsson, 1876, Prototreta gribovensis Popov, 1985 and Diraphora simplex Popov, 1985 (Popov 1985; Solovyev et al. 1986).
The Karpinsk Formation (upper Guzhangian – Jiangshanian) is presently known only from the South Island, where it is exposed between the Bezymyannaya Bay area in the south and the Matochkin Shar Strait in the north (Solovyev et al. 1986). It rests conformably, or possibly with a slight disconformity, on the Snezhnyye Gory Formation. The Karpinsk Formation consists of black argillites and siltstones with subsidiary sandstone and limestone beds, and is a total of 220 m thick at Gribovaya Bay and more than 260 m in the east part of the Pan’kov Land peninsula. On the south coast of Gribovaya Bay, it is disconformably overlain by the Ordovician Blafyel’sk Formation. The linguliform microbrachiopod assemblage described here was recovered from limestones sampled in 1980 by I. A. Solovyev from Locality 302/3 (approximate coordinates 73°3' N, 53°29' E). The samples come from the lower part of the Karpinsk Formation located at the east side of the Pan’kov Land peninsula

c. 10 km north-east of the Gribovaya Bay north coast and c. 8 km east of the abandoned Pan’kov military campus (Figs 1, 2). The age of the unit is based on trilobites documented by Walcott & Resser (1924) from Holtedahl’s (1922) localities 67y and 68b, and it is also based on the trilobites reported by Solovyev et al. (1986), as well as the brachiopods reported by Popov (1984, 1985). The trilobite assemblage from the locality 67y, described by Walcott & Resser (1924), contains mostly endemic species, but includes also Agnostus pisiformis (Wahlenberg, 1818) (for details of the taxon authorship, see Rushton 1978), suggesting a late Guzhangian age. It is possible that the fauna list from the locality 67y given by Walcott & Resser (1924) is composite and includes both late Guzhangian and Paibian taxa. Some species from the locality 67y assemblage were reported by Solovyev et al. (1986) and Solovyev (1988) from three lowermost informal units in the type section of the Astafiyev Formation.

The Karpinsk Formation (upper Guzhangian – Jiangshanian) is presently known only from the South Island, where it is exposed between the Bezymyannaya Bay area in the south and the Matochkin Shar Strait in the north (Solovyev et al. 1986). It rests conformably, or possibly with a slight disconformity, on the Snezhnyye Gory Formation. The Karpinsk Formation consists of black argillites and siltstones with subsidiary sandstone and limestone beds, and is a total of 220 m thick at Gribovaya Bay and more than 260 m in the east part of the Pan’kov Land peninsula. On the south coast of Gribovaya Bay, it is disconformably overlain by the Ordovician Blafyel’sk Formation. The linguliform microbrachiopod assemblage described here was recovered from limestones sampled in 1980 by I. A. Solovyev from Locality 302/3 (approximate coordinates 73°3' N, 53°29' E). The samples come from the lower part of the Karpinsk Formation located at the east side of the Pan’kov Land peninsula
Formation, exposed along the south coast of the Grivovaya Bay (Solov’yov 1988, text-fig. 2).

The trilobite assemblage from Holtedahl’s locality 68b, documented by Walcott & Resser (1924) contains Irvingella septentrionalis Walcott & Resser, 1924, which, according to Palmer (1965), is the junior synonym of Irvingella major Ulrich & Resser in Walcott, 1924. The latter occurrence suggests a Jiangshanian age for the uppermost Karpinsk Formation. The brachiopods documented by Walcott (1924) from that locality, including ‘Linguella’ cf. desiderata Walcott, 1898, Billingsella holtedahli Walcott, 1924, Huenellina triplicata Jeremejew, 1856. by Zhang et al. (2018) is followed in describing the ontogeny.

Abbreviations. W, L, T, maximum width, length and height of the shell; Lw, Ld, maximum length of ventral and dorsal valve; Iw, Il, maximum width and length of pseudointerarea; PI, PW, length and width of median groove or pedicle groove; Cw, Cl, width, length of cardinal muscle field; Sl, length of dorsal median septum; VI, length of visceral area.

Subphylum LINGULIFORMEA Williams et al., 1996
Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family ZHANATELLIDAE Koneva, 1986
Genus WAHWAHLINGULA Popov et al., 2002

Type species. By original designation Lingula antiquissima Jeremiejew, 1856.

Wahwahlingula? pankovensis sp. nov.
Figures 3, 4A–G

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Derivation of name. After the occurrence on the Pan’kov Land peninsula.

Holotype. NMW 2018.4G.3 (Fig. 3F; J; Ld = 2.64 mm, W = 1.80 mm, \( I_l = 0.48 \) mm, \( I_w = 1.67 \) mm, \( P_l = 0.32 \) mm, \( P_l = 1.77 \) mm), dorsal valve from Snezhnyye Gory Formation (Miaolingian, Guzhhangian), locality 302/3, Pan’kov Land peninsula, Novaya Zemlya, South Island.

Paratypes. Figured: NMW 2018.4G.2 (Fig. 3G; Lw = 2.84 mm, W = 2.06 mm, \( I_l = 0.54 \) mm, \( I_w = 1.32 \) mm, \( P_l = 0.34 \) mm), NMW 2018.4G.7 (Fig. 3D), ventral valves; NMW 2018.4G.1 (Figs 3K, 4E), NMW 2018.4G.4 (Fig. 4A, B), NMW 2018.4G.6 (Fig. 3C), NMW 2018.4G.9 (Figs 3L, 4D, F), NMW 2018.4G.10 (Fig. 3E, M), NMW 2018.4G.11, (Fig. 4G), NMW 2018.4G.12 (Fig. 3A), NMW 2018.4G.13 (Fig. 3H), dorsal valves. Other specimens: NMW 2018.4G.15, 16, incomplete ventral valves; NMW 2018.4G.5, 8, 14, incomplete dorsal valves. Total four ventral and 11 dorsal valves; all from locality 302/3.

Diagnosis. Shell dorsibiconvex, elongate suboval with maximum width at mid-length. Ventral pseudointerarea bisected by deep, narrow, subtriangular groove with steep lateral slopes. Ventral propareas bisected by deep flexure lines into two subequal parts. Dorsal visceral area occupies about two-thirds of sagittal valve length. Brephic and adult shell ornamented by densely packed, regular, hemispherical pits c. 1.8–2.1 µm across.

Description. Shell dorsibiconvex, elongate, suboval, with maximum width at mid-length, c. 135–150% as long as it is wide, with maximum width at about mid-length. Anterior commissure even rounded, rectimarginate. Ventral valve gently convex, subacuminate, with high subtriangular almost orthocline pseudointerarea c. 30% as wide as it is long. Pedicle groove deep, narrow subtriangular, with steep lateral slopes, c. 12% of sagittal valve length. Ventral pseudointerareas raised above the valve floor, subdivided into two almost equal parts by the deep flexure lines (Figs 3G, 4C).

Dorsal valve evenly convex in sagittal profile with maximum height at about mid-length. Dorsal anterior margin even rounded. Dorsal pseudointerarea c. 30% as long as it is wide mainly occupied by broad median groove lying along the valve floor. Dorsal propareas rudimentary, lacking flexure lines. Shell surface smooth with faint growth lines and micro-ornament of faint, closely packed, regular, hemispherical pits c. 1.8–2.1 µm in diameter, which cover all the shell surface, including the brephic shell (Fig. 3B).

Ventral valve visceral area, muscle scars and mantle canals are not clearly expressed except for paired umbonal muscle scars located in weakly defined impressions anterolateral of the anterior termination of the pedicle groove. Dorsal visceral area weakly impressed, extended anteriorly as a pronounced median tongue and terminated at about two-thirds sagittal valve length from the umbo. The latter occupied by a pair of elongate outside lateral muscle scars (Fig. 3F, ol). A pair of weakly defined central muscle scars (Fig. 3F, ol) is situated at the anterior end of indistinct muscle tracks in the centre of the valve. Posterolateral muscle fields (Fig. 3F, plm) representing combined scars of the outside lateral, middle lateral and transmedian muscles located at the outer margins of the visceral area in front of the
FIG. 3. *Wahwahlingula?* pankovensis sp. nov.; Snezhnyye Gory Formation (Miaolingian, Guzhangian), locality 302/3, Pan’kov Land peninsula, Novaya Zemlya, South Island. A, NMW 2018.4G.12, incomplete dorsal valve exterior. B, I, NMW 2018.4G.8, dorsal valve exterior, dorsal and oblique lateral views. C, NMW 2018.4G.6, dorsal valve umbonal area. D, NMW 2018.4G.7, incomplete ventral valve exterior. E, M, NMW 2018.4G.10, dorsal valve interior, oblique side view of interior. F, J, NMW 2018.4G.3, holotype, dorsal valve interior, oblique side view of interior. G, NMW 2018.4G.2, ventral valve interior. H, NMW 2018.4G.13, incomplete dorsal valve interior. K, NMW 2018.4G.1, incomplete dorsal valve exterior. L, NMW 2018.4G.9, incomplete dorsal valve exterior. Abbreviations: cm, central muscle scars; fl, flexure lines; ol, outside lateral muscle scars; plm, posterolateral muscle fields. Scale bars represent: 100 μm (A–E, H, K–M); 200 μm (F, G, I, J).
Remarks on the ontogeny. No protogulum is recognizable at the umbonal area of both valves. The dorsal brephic shell, c. 160 μm wide, is recognized as a slightly swollen area bisected by a shallow medial cleft (Figs 3C, 4A, F). A pair of lateral swellings on both sides of the cleft probably represent impressions of larval setal sacs. The dorsal brephic shell of Wahwahlingula? pankovenensis is very similar to the brephic shell of Diencobolus as described by Ghobadi Pour et al. (2011), and both taxa have a pair of lateral swellings, which are interpreted as impressions of larval setal sacs. The closest recent analogy can be found in Discinisca, which also retains a pair of larval setal sacs that disappear shortly after hatching (Lüter 2001; Zhang et al. 2018, fig. 8), but the metamorphosis in Wahwahlingula? pankovenensis was completed somewhat later during a free swimming stage.

Remarks. Wahwahlingula? pankovenensis is the oldest yet recorded species of the genus and the only Miaolingenian species of the genus yet known. In size, general shell shape and proportions it most resembles Wahwahlingula severensis Popov et al., 2002 from the House Limestone (Barn Canyon and Red Canyon members) and the lower part of Fillmore Formation (Tremadocian) of the Ibex area, Utah, USA, but it can be distinguished from the latter taxon by a slightly more elongate shell, ventral preparaeas distinctly raised above the valve floor and subdivided into two almost equal parts by deep flexure lines, shorter dorsal visceral area not exceeding two-thirds valve length and the invariable absence of the dorsal median ridge. In Wahwahlingula? pankovenensis faint regular hemispherical pits cover the whole shell surface, while in Wahwahlingula severensis the brephic shell is covered by flat-bottomed and cross-cutting pits. Unlike Wahwahlingula kharbashi Ghobadi Pour et al., 2011, from the Tremadocian (Paltodus deltifer Biozone) of the eastern Alborz Mountains, Iran, and Wahwahlingula? emanuelensis Brock & Holmer, 2004, from the Emanuel Formation (Floian) of Western Australia, Wahwahlingula? pankovenensis has a pitted brephic shell, and an elongate suboval shell with maximum width at mid-length. In addition it completely lacks a dorsal median ridge, unlike Wahwahlingula kharbashi.

In comparison with Wahwahlingula antiquissima (Jeremejew, 1856), from the lower part of the Tosna Formation (Cordylodus lindstromi Biozone), Wahwahlingula? pankovenensis is characterized by a much smaller size, a strongly elongate, suboval, rather than a subtriangular shell outline and the lack of a dorsal median ridge. Micro-ornamentation on the brephic shell of Wahwahlingula antiquissima is yet to be observed.
present in front of the pedicle foramen, there is no sign of tubercles or spines in the metamorphic shell (Fig. 5F, G). Instead a pair of inflated lobes diverges from the outer margin of the pedicle foramen towards the anterior margin of the ventral metamorphic shell. Only a single pair of spines is present in front of the posterior margin of the dorsal metamorphic shell (Fig. 6E–H). The spine bases continue anteriorly as a pair of divergent, anteriorly inflated lobes terminated close to the anterior margin of the metamorphic shell, but no distinct anterior pair of tubercles is present (Fig. 6F, G). These dorsal lobes are considered here as impressions of a single pair of larval setal sacks, by analogy with recent discinids (e.g. Lütter 2001; Zhang et al. 2018, fig. 8); however, unlike recent lingulides, the presence of a large metamorphic shell suggests that metamorphosis in the Acrothelidae was completed at the end of the prolonged pelagic stage; this shows that indirect development was still characteristic of the life cycle of these lingulides.

In contrast, other species of Acrothele are characterized by well-ordered, flat-based imprints varying in diameter from 3.2 to 9.5 μm, forming relatively open hexagonal arrays and separated by narrow, rounded walls (Williams 2003). Other characteristic features of Acrothele are the presence of four short spines on the dorsal metamorphic shell and a pair of prominent tubercles or short spines anterolateral of the pedicle.
foramen in the ventral valve. This type of metamorphic shell morphology is characteristic, in particular, of *Acrothele coriacea* from the Miaolingian of Baltoscandia (Holmer & Popov 2000; fig. 46.1), the type species of the genus; and of *Acrothele vertex* Reed, 1910 from the Parahio Formation (Wulian, Oryctocephalus salteri Biozone) of the Indian Himalayas (Popov et al. 2015; fig. 15D, I, L–P), which is probably the earliest formally designated species of the genus.

While these acrothelid shells from Novaya Zemlya definitely represent a new, as yet unnamed taxon, a formal taxonomic designation is postponed due to insufficient material presently available; however, very similar and most probably conspecific shells were described as unnamed species of *Acrothele* by Gonzalez-Gomez (2005), from the Val d’Homs Formation (Guzhangian) of Montagne Noire at southern France. These shells have a distinct similarity to the specimens from Novaya Zemlya in having a small pedicle foramen mainly within the metamorphic shell, a lobate ventral metamorphic shell lacking spines, and a dorsal metamorphic shell with a single pair of spines, while the pitted micro-ornament looks almost identical.
Genus *Orbithele* Sdzuy, 1955

Type species. By original designation *Discina contraria* Barrande, 1868.

*Orbithele*? sp.

**Material.** Figured: NMW 2018.4G.23 (Fig. 4H, L), NMW 2018.4G.24 (Fig. 4I), NMW 2018.4G.25 (Fig. 4K), NMW 2018.4G.26 (Fig. 4L), ventral valves; NMW 2018.4G.28 (Fig. 6C); NMW 2018.4G.29 (Fig. 6A, B, D) dorsal valves. Other specimens: NMW 2018.4G.27, 30–34, ventral valves. Total 10 ventral and two dorsal valves; all from locality 302/3.

**Remarks.** All available specimens represent incomplete ventral and dorsal valves. Nevertheless, they show a number of distinctive morphological features, including a low conical ventral valve with subcentral apex, a strongly elongate pedicle foramen crossing the outer boundary of the metamorphic shell bearing a pair of low umbonal spines, and finely pustulose ornament on the postmetamorphic shell. These features can also be observed in a number of late Miaolingian acrothelides provisionally assigned to *Orbithele* (e.g. Zell & Rowell 1988; Percival & Kruse 2014), but there is no evidence of marginal spines characteristic of the Early Ordovician species of the genus including the type species. The ventral interior has a pedicle tube on the posterior slope of the valve, supported anteriorly by a short, blade-like median septum with a short rod in front of the internal foramen, which are among the most distinctive features of *Orbithele* (Popov & Holmer 1994). The dorsal valve is characterized by having a marginal umbo and a low dorsal median ridge bisecting the visceral area (Fig. 6C). The metamorphic shell of *Orbithele*? sp. shows typical features first described by Henderson (1974). It has a median tubercle in front of the pedicle foramen and a pair of short spines on the ventral valve (Fig. 4I, L). The dorsal metamorphic shell (preserved on a single specimen), is poorly preserved, but the presence of two pairs of short spines is evident. The pitted ornament of the metamorphic shell is identical to that described by Williams (2003) and is characterized by densely packed, irregular, flat-based imprints strongly variable in size (3.2–11 μm), separated by narrow, convex walls bearing occasional small hemispherical pits less than 1 μm across. Due to the poor preservation of the shells from Novaya Zemlya the material is kept under open nomenclature.

**Order ACROTRETIDA Kuhn, 1949**

**Superfamily ACROTRETOIDEA Schuchert, 1893**

**Family ACROTRETIDAE Schuchert, 1893**

*Anabolotreta* Rowell & Henderson, 1978

Type species. By original designation, *Anabolotreta tegula* Rowell & Henderson, 1978.

*Anabolotreta*? sp. cf. *Anabolotreta glabra* Streng & Holmer, 2006

**Figure 7**

1985 *Anabolotreta* sp.; Popov, p. 25; pl. 2, fig. 15.

**Material.** NMW 2018.4G.35, 36, ventral valves, and NMW 2018.4G.37 dorsal valve.

**Description.** Shell slightly ventribiconvex, slightly transverse, sub-oval to almost subcircular. Anterior commissure broadly rounded, rectimarginate. Posterior commissure almost straight, c. 55% as wide as maximum shell width. Ventral valve low, moderately convex, with evenly convex sagittal profile anterior to the apex. Ventral pseudointerarea procline, bisected by a weakly defined, shallow intertrough and indistinctly separated from the lateral sides of the valve. Pedicle foramen posteroventrally directed, small, subcircular, within the metamorphic shell. Dorsal valve sagittal profile gently and evenly convex. Dorsal pseudointerarea low, occupied mainly by the broad, gently concave median groove, proareas rudimentary. Shell surface ornamented with faint, crowded growth lines and up to three strong growth lamellae in the anterior half of the valves.

Ventral interior with a strong, boss-like, posteriorly grooved apical process with undercut anterior slope and steep, subparallel lateral slopes, situated anterior to the internal foramen. Two small circular umbonal muscle scars (apical pits) located anterolaterally to the internal foramen and surrounded by faint ridges. Cardinal muscle fields slightly thickened, clearly defined, posterolaterally located. Mantle canals not clearly impressed. Dorsal interior with short, rounded, subtriangular, posterolaterally located cardinal muscle fields, and vestigial faint median ridge recognizable only in central part of the valve. No median buttress.

**Remarks.** In spite of the limited material available for study, the affinity of these shells to *Anabolotreta*? sp. cf. *A. glabra* is evident, because they are characterized by a pedicle foramen enclosed within the metamorphic shell, evenly convex anterior slope of the ventral valve, concentric ornament with a few growth lamellae in the anterior part of the shell, a prominent, medially grooved apical process, and a broad and short dorsal median groove. However, unlike the types from the lowermost Dunderberg Formation (Guzhangian, *Celaria–Crepicephalus* trilobite Zone) of Nevada and the specimens from the Huaqiao Formation (Drumian–Guzhangian, *Psychagnostus atavus–Linguagnostus reconditus* trilobite zones) of Paibí section, in Hunan Province, South China, the shells from Novaya Zemlya have a vestigial dorsal median ridge clearly expressed only in the central part of the valve and a pair of well-defined umbonal muscle scars (apical pits) anterolateral to the internal foramen. Therefore, their species attribution is considered here as provisional. In poor development of concentric growth lamellae, the specimens from Novaya Zemlya are similar to *Anabolotreta groenlandica* Zell & Rowell, 1988, from the Guzhangian part of the Holm Dal Formation of central North
Greenland, but can be readily distinguished in having a pedicle foramen enclosed within the metamorphic shell, an evenly convex (not concave) anterior slope of the ventral valve, a prominent, boss-like apical process with steep, subparallel lateral margins, small, as well as well-defined apical pits surrounded by ridges, and a dorsal vestigial median ridge. A single dorsal valve briefly described and illustrated by Popov (1985) from the Karpinsk Formation of the Gribovaya Bay southern coast is closely similar and considered here as conspecific to the shells from the Pan’kov Land peninsula.

Genus TAPURITRETA Popov et al., 2009

Type species. By original designation Tapuritreta angusta Popov et al., 2009.

Tapuritreta gribovensis sp. nov.

Figures 8, 9

LSID. urn:lsid:zoobank.org:act:6227614F-1EC5-4726-BBF3-F19A5E6AA148

Derivation of name. After Gribovaya Bay south of the type locality.

Holotype. NMW 2018.4G.43 (Lv = 1.30 mm, W = 1.47 mm, T = 0.64 mm; Fig. 8E–G), ventral valve from Snezhnyye Gory Formation (Miaolingian, Guzhangian), locality 302/3, Pan’kov Land peninsula, Novaya Zemlya, South Island.

Paratypes. Figured: NMW 2018.4G.41 (Fig. 8K, L), NMW 2018.4G.42 (Fig. 8I, J), NMW 2018.4G.44 (L = 1.53, T = 0.80; Fig. 8B), NMW 2018.4G.45 (Fig. 8M), NMW 2018.4G.46 (Fig. 8H), ventral valves and NMW 2018.4G.47 (Fig. 9H, K), NMW 2018.4G.50 (Ld = 1.47 mm, W = 1.80; Fig. 9B, F, I), NMW 2018.4G.52 (Ld = 2.02 mm, W = 1.81 mm, lw = 1.00 mm, Pw = 0.47 mm, Sl = 1.23 mm; Cl = 0.53 mm, Cw = 82 mm; Fig. 9G, J); NMW 2018.4G.53 (Ld = 2.05 mm, W = 2.10 mm, lw = 1.07 mm, Pw = 0.53 mm, Sl = 1.33 mm; Cl = 0.61 mm, Cw = 1.02 mm; Fig. 9A, C, D). Other material: NMW 2018.4G.54.1–4, ventral valves; NMW 2018.4G.48, 49, 51, 54.5–15 dorsal valves. Total 10 ventral and 17 dorsal valves from locality 302/3.

Diagnosis. Ventral valve between one half and two-thirds as high as long, with procline deltoid pseudointerarea, almost straight in sagittal profile and bisected by vestigial intertrough. Dorsal pseudointerarea slightly exceeding half of maximum shell width. Dorsal cardinal muscle scars gently impressed less than one-third as long as the valve.

Description. Shell strongly dorsibiconvex, subcircular, almost as long as wide, with maximum width at mid-length. Ventral valve conical, about two-thirds as high as long with a strongly flattened, distinctly procline deltoid interarea almost straight in sagittal profile (Fig. 8F). Intertrough very weakly defined mainly by slight deflections of growth lines (Fig. 8G, I). Pedicle foramen small, circular,
FIG. 8. *Tapuritreta gribovensis* sp. nov.; Snezhnyye Gory Formation (Miaolingian, Guzhangian), locality 302/3, Pan’kov Land peninsula, Novaya Zemlya, South Island. A, L, NMW 2018.4G.45, ventral valve: lateral view of exterior, oblique posterior view of interior showing apical process and internal pedicle tube attached to the inner side of the posterior slope of the valve. B, NMW 2018.4G.44, oblique posterior view of interior showing internal foramen and apical process. C, G, NMW 2018.4G.46, oblique posterior views of ventral valve exterior, enlarged metamorphic shell. H, I, NMW 2018.4G.42, oblique posterior view of ventral valve exterior, enlarged metamorphic shell. D–F, NMW 2018.4G.43, holotype, ventral valve exterior: ventral, oblique lateral and posterior views. J–K, NMW 2018.4G.41, incomplete ventral valve interior, oblique lateral view of interior showing high, septiform apical process. Abbreviations: ap, apical process; ipt, internal pedicle tube; um, umbonal muscle scar. Scale bars represent: 200 μm (A, G, H, L); 500 μm (B, D–F, J, K); 50 μm (C, I).
FIG. 9. *Tapuritreta gribovensis* sp. nov.; Snezhnyye Gory Formation (Miaolingian, Guzhangian), locality 302/3, Pan’kov Land peninsula, Novaya Zemlya, South Island. A, C, D, NMW 2018.4G.53, enlarged view of dorsal metamorphic shell, dorsal valve exterior, dorsal valve interior. B, F, I, NMW 2018.4G.50, enlarged view of dorsal metamorphic shell, dorsal valve exterior, oblique posterior view of exterior. E, NMW 2018.4G.52, dorsal valve interior. G, J, NMW 2018.4G.49, dorsal valve interior, oblique lateral view of interior. H, K, NMW 2018.4G.47, dorsal valve interior, oblique lateral view of interior of juvenile individual. Scale bars represent: 50 μm (A, B); 500 μm (C–G, I, J); 200 μm (H, K).
c. 50 μm in diameter, facing posteroventrally, enclosed within the metamorphic shell (Fig. 8f). Anterior slope of the ventral valve very gently convex to almost straight in sagittal profile. Dorsal valve sagittal profile very gently convex with maximum height between the umbo and mid-length. Dorsal interarea orthocline, c. 50–55% as wide as the valve, with a broad shallow median groove almost half as wide as the pseudointerarea. Dorsal sulcus very shallow, originating at the umbo, strongly widening towards the anterior margin. Postmetamorphic shell smooth, with faint growth lines. Metamorphic shell, c. 180–200 μm wide, ornamented with faint, densely packed, slightly irregular, hemispherical pits, c. 1–3 μm in diameter (Fig. 9A, B).

Ventral interior with weakly impressed cardinal muscle fields and high, septiform apical process undercut anteriorly (Fig. 8B) and enclosing the internal pedicle tube situated on the posterior slope of the valve (Fig. 8L). Ventral umbonal muscle scars gently impressed as a pair of small hemispherical pits, posterolateral of the internal foramen (Fig. 8B). Ventral mantle canals not impressed. Dorsal interior with weakly impressed, suboval cardinal muscle fields divergent anterolaterally, terminated anteriorly at c. 27–29% valve length from the umbo. Dorsal medium septum moderately high, blade-like, triangular, terminated at c. 63–81% anterior from the umbo, and with the highest point at mid-length. Median buttress narrow, poorly defined, widening posteriorly towards dorsal pseudointerarea.

Remarks. *Tapuritreta gribovensis* differs from the type species *Tapuritreta angusta* in having a distinctly procline deltoid pseudointerarea bisected by a vestigial intertrough and shallow dorsal sulcus.

*Tapuritreta gribovensis* differs from *Tapuritreta reclinata* Sten et al., 2011 from the Yudacha Member (Cambrian, Furongian) of the Oaxaquia Terrane, Mexico, in having a less convex ventral valve with an almost straight (not convex) lateral profile of ventral pseudointerarea, a distinct dorsal median sulcus, less prominent median buttress and dorsal median septum, and smaller and weakly impressed cardinal muscle scars not exceeding one-third valve length.

**Stilpnotreta** Henderson & MacKinnon, 1981

*Type species.* *Stilpnotreta magna* Henderson & MacKinnon, 1981.

*Stilpnotreta sp. cf. Stilpnotreta minuta* Holmer et al., 2001

**Figure 10A-D**

**Material.** NMW 2018.4G.38 (Fig. 10C), dorsal valve; NMW 2018.4G.39 (L = 0.51 mm, W = 0.51 mm; Fig. 10A), NMW 2018.4G.40 (L = 0.56 mm, W = 0.62 mm; Fig. 10B, D), ventral valves; all from locality 302/3.

Remarks. These shells are most similar to *Stilpnotreta minuta* Holmer et al., 2001 from the Sarykumy Formation (Miaolingian, Guzhangian) in their small size and in having a subcircular, slightly ventribiconvex shell with a vestigial deltoid pseudointerarea, low apical process in front of the internal opening of the pedicle foramen, extending to the mid-valve, as well as in the absence of distinct denticulation of a ventral valve posterior margin and a median buttress. However, the new material differs in the complete absence of a dorsal median ridge. All listed characters, except the shape of the apical process, clearly discriminate the Novaya Zemlya specimens from *Stilpnotreta magna*. Nevertheless, their species affiliation remains provisional because of insufficient material available for study.

**Treptotreta** Henderson & MacKinnon, 1981

*Type species.* *Treptotreta jucunda* Henderson & MacKinnon, 1981; middle Cambrian (*Goniagnostus nathorsti* Biozone), Maimchange Limestone, western Queensland, Australia.

**Treptotreta jucunda** Henderson & MacKinnon, 1981

**Figures 10E–M, 11**

1981 *Treptotreta jucunda*; Henderson & MacKinnon, p. 296, fig. 5A–1, text-figs 3–4.
2014 *Treptotreta jucunda* Henderson & MacKinnon; Percival & Kruse, p. 389, fig. 22 (full synonymy).
1985 *Angularotreta postapicalis* Palmer; Popov, p. 21; pl. 2, figs 5–14; text-fig. 3.

**Holotype.** JCF 10714 (housed in James Cook University, Townsville), ventral valve from Maimchange Limestone, Drumian, Western Queensland.

**Material.** NMW 2018.4G.55–58, 63, 78 ventral valves; 59–62, 65–66, dorsal valves plus NMW 2018.4G.67.1–3 ventral valves; NMW 2018.4G.77.4–10 dorsal valves.

Remarks. The specimens from the Guzhangian of Novaya Zemlya are assigned to *Treptotreta jucunda* because they exhibit a number of diagnostic characters of the taxon as revised by Percival & Kruse (2014); they are similar in having the following characters: a moderately high, conical ventral valve with a procline deltoid pseudointerarea divided by an indistinct intertrough defined by deflection of growth lines (Fig. 9, K); small, circular pedicle foramen, completely enclosed into metamorphic shell (Fig. 9M); a strong ridge-like, apical process widening anteriorly and perforated by the internal foramen at the anterior termination (Fig. 9C, L); a narrow dorsal pseudointerarea occupying less than half maximum valve width; and a high, blade-like, triangular dorsal median septum with a rod-like projection at the tip (Fig. 11D–F).

Compared with the Baltoscandian material of the species, described by Topper et al. (2013a, b) from The Alum Shale Formation (Furongian, Jiangshanian, *Parabolina brevispina* Zone) of Västergötland, Sweden, the shells from Novaya Zemlya differ by
FIG. 10. Specimens from Snezhnyye Gory Formation (Miaolingian, Guzhangian), locality 302/3, Pan’kov Land peninsula, Novaya Zemlya, South Island. A–D, Stilpnotreta sp.: A, NMW 2018.4G.40, ventral valve exterior; B, D, NMW 2018.4G.39, ventral valve interior, oblique lateral view of exterior; C, NMW 2018.4G.38, dorsal valve interior. E–M, Treptotreta jucunda Henderson & MacKinnon, 1981: E–F, H–I, NMW 2018.4G.58, ventral valve exterior, ventral, oblique lateral and oblique posterior views, enlarged pitted micro-ornament of metamorphic shell; G, NMW 2018.4G.57, ventral valve interior; J, M, NMW 2018.4G.78, ventral valve posterior view, enlarge posterior view of the umbonal area showing pedicle foramen; K, NMW 2018.4G.73, ventral valve posterior view; L, NMW 2018.4G.55, oblique anterior view of ventral valve interior. Abbreviations: ap, apical process; cmf, cardinal muscle field; um, umbonal muscle scar. Scale bars represent: 200 μm (A–D, J–L); 500 μm (E–H); 5 μm (I); 20 μm (M).
having a posteriorly inclined umboval area of the ventral valve, a straight to gently convex (not concave) ventral valve sagittal profile, and a less prominent rod on the tip of the dorsal median septum. The shells from the Karpinsk Formation on the southern coast of Gribovaya Bay, described and illustrated by Popov (1985) as Angulotreta postapicalis, are morphologically very close to the specimens from the Pan’kov Land peninsula and are here reassigned to Treptotrema jucunda.

**SIGNIFICANCE OF THE FAUNA**

Cambrian (Miaolingian–Furongian) deposits of the epeiric Baltoscandian Basin preserve an extensive record of successive brachiopod faunas (Walcott 1912; Martinsson 1968; Popov et al. 1989; Holmer & Popov 1990; Puura & Holmer 1993; Topper et al. 2013a, b, etc.). However, the existing information on the brachiopod faunas that inhabited the Cambrian margins of the Baltic palaeocontinent is very poor, because the Palaeozoic continental shelves of Baltic were mainly destroyed by the subsequent continental collisions later in the Palaeozoic (Cocks & Torsvik 2005; Torsvik & Cocks 2017). The only possible preserved information from the marginal faunas derives from the Holy Cross Mountains, Poland and the Novaya Zemlya Archipelago. The published documentation on the Cambrian brachiopods of the Holy Cross Mountains is inadequate, while its position at the continental margin of Baltica during the Cambrian times is somewhat controversial (Cocks & Torsvik 2005; Źylińska 2013; Torsvik & Cocks 2017). The Novaya Zemlya Archipelago is widely considered as the outer part of the Taimiad Orogen, which represents a terrane assemblage that was accreted along the active Baltica continental margin sometime in the Infra-Cambrian (Torsvik & Cocks 2017). During the Cambrian – Middle Ordovician the whole Baltic continent underwent a large scale rotation of $\theta \approx 120^\circ$, which probably occurred mainly during the Furongian – Early Ordovician (Torsvik & Rehnström 2001; Cocks & Torsvik 2005). Thus, during Guzhangian time, the Novaya Zemlya sector was located at the easternmost corner of Baltica, being separated from the North African sector of Gondwana by a narrow oceanic space (Torsvik & Cocks 2017; fig. 5.1). It is not surprising that the most recent analysis of Cambrian trilobite biogeography by Álvaro et al. (2013, fig. 19.5), shows that the Cambrian (Miaolingian) trilobite faunas of Novaya Zemlya appear within the distinct cluster, uniting the Miaolingian faunas from Avalonia, Bohemia, Holy Cross Mountains, Morocco, Sweden/Norway, Turkey and the Armorican cluster of terranes. The published information on Cambrian (Wulian–Jiangshanian) brachiopod faunas from Novaya Zemlya has mainly been published in Russian and is not accessible (Walcott 1924; Popov 1984). The previously described faunas are characterized by a low richness, which makes it difficult to use them for a detailed biogeographical assessment. Nevertheless, as discussed below, five succeeding brachiopod assemblages can be recognized in the Cambrian sedimentary succession of Novaya Zemlya.

The earliest brachiopod assemblage yet documented from Novaya Zemlya, is recovered from the lower part of Astafieyev Formation and is Wulian in age (Fig. 2). This is a low richness micromorphic linguliform brachiopod association including unnamed species assigned to Acrothyra and Hadrotreta, and early representatives of Acrothele (Popov 1985), which was a cosmopolitan genus. Acrothyra is otherwise confined to Laurentia (Rowell 1980; Skovsted et al. 2017), while the poorly known type species Acrothyra proavia (Matthew, 1899), probably originated from the West Avalonia location at Cape Breton, suggesting that it was dispersed across the Iapetus Ocean during Miaolingian time. This is supported also by its Baltic (Novaya Zemlya) occurrence. The data presented by Skovsted et al. (2017) show a close association of Acrothyra and Hadrotreta with outer shelf settings, which is consistent with the distribution of these taxa in the Wulian deposits of Novaya Zemlya, where they occur in limestone nodules within laminated, grey shale as well as co-occurring with the trilobite Ellipscephalus (Solovyev et al. 1986). Remarkably, there is no record of these acroretidites from the Baltoscandian Basin. Hadrotreta is a widespread taxon that achieved an almost cosmopolitan distribution at low latitudes during Miaolingian time (Popov et al. 2015), but it is yet unknown from temperate to high-latitude Gondwana including North Africa, Central Iran and Mediterranean peri-Gondwana, as well as from the Baltoscandian Basin. The geographically closest Hadrotreta occurrence to Novaya Zemlya was probably documented from the Parahio Formation.
biogeographical distribution suggests that the dispersal of Diraphora originated from Gondwana locations, where it probably first appeared.

The late Guzhangian linguliform microbrachiopod fauna is derived from the lower part of the Karpinsk Formation (Koldiniella mittella – Modocia arctica local trilobite Zone), which by occasional occurrences of the eponymous species can be correlated with the Agnostus pisiformis Zone of Baltoscandia (Solovyev 1986). The full brachiopod assemblage (Fig. 2) includes species of Acrothele, Anabolotreta?, Orbithele?, Stilpnotreta, Tapuritreta, Treptotreta and Wahwahlingula, described here, plus Dictyonina, which was briefly discussed and illustrated by Popov (1985).

The acrotheloids Acrothele and Orbithele? and the paterinide Dictyonina are relatively common and cosmopolitan components in Drumian–Guzhangian linguliform brachiopod faunas, while the presence of Tapuritreta and Wahwahlingula is somewhat unusual, because these are their only documented Miaolingian occurrences to date. The Furongian occurrences of Tapuritreta are confined to Alborz (Popov et al. 2009) and Oaxaquia (Streng et al. 2011) terranes, where both are associated with temperate latitude Peri-Gondwana. The proliferation of Wahwahlingula occurred only near the Cambrian–Ordovician boundary, when species of the genus dispersed across Baltica (Popov et al. 1989),

![FIG. 12. Palaeogeographical reconstruction for Cambrian, Guzhangian age showing the position of Novaya Zemlya on the eastern margin of the Baltica continent, and the geographical distribution of selected brachiopod taxa documented from the Cambrian of Novaya Zemlya. Relative position of major early Palaeozoic continents (e.g. Laurentia, Baltica, Gondwana and Siberia) mainly after Torsvik & Cocks (2017) with significant emendations for tropical peri-Gondwana, related to the position of the North China Palaeocontinent and terranes associated with Kazakh Archipelago (for further discussion see Popov & Cocks 2017). Colour online.](image-url)
Laurentia (Popov et al. 2002; Holmer et al. 2005) and Alborz (Ghobadi Pour et al. 2011), and has little relevance to the brachiopod biogeography in Guzhangian time. *Anabolotreta? glabra* is a distinct species, which occurs in Laurentia (Streng & Holmer 2006) and South China (Engelbreten & Peng 2007).

*Treptotreta jucunda* has a long stratigraphical range (from Drumian to Jiangshanian) and a wide geographical distribution, including the Australian sector of Gondwana (Percival & Kruse 2014), New Zealand (Henderson & MacKinnon 1981), South China (Engelbreten & Peng 2007), and probably the Atasu–Zhamshi Terrane of Kazakhstan (Holmer et al. 2001), but it is remarkably absent from Laurentia (Fig. 12). Its appearance in Baltoscandia (Topper et al. 2013a, b) was delayed until the Paibian. *Stilpnotreta* has a pantropical distribution (Fig. 12), but its reported occurrence in the Furongian of Baltoscandia (Puura & Holmer 1993) is questionable.

The Furongian brachiopod faunas at Novaya Zemlya are characterized by a proliferation of rhyonchelliform brachiopods, which is not found in Baltoscandia, and they are represented by different taxa in these areas. The Paibian assemblage includes *Billingsella holtedahli* and *Ocnerorthis opius* (see Walcott 1924). Both belong to genera that are known from Laurentia (Freeman & Stitt 1996), where they make a later appearance in the Jiangshanian (*Elvinia Zone*). The only other *Billingsella* species reported from Baltic is *Billingsella? lindstromi* (Linnarsson, 1876) from the Guzhangian (*Paradoxides forchhammeri Zone*) of Sweden. This species remains very poorly known. It was originally considered as an orthide (Linnarsson 1876), and subsequently re-assigned to *Billingsella* by Walcott (1912), but this record is still uncertain. Rhyonchelliform brachiopods are common in the peri-Gondwanan teranes of Iran, and, in particular, from Alborz (Popov et al. 2013), where billingsellids and synthrophoids form extensive shell beds in the Mila Formation Member 3 (Paibian–Jiangshanian). The record of rhyonchelliform brachiopods from North Africa and Mediterranean Gondwana is relatively poor. It includes only reports on the occasional occurrence of *Billingsella* and *Saccogonum* species in Morocco and Spain (Havlíček & Josopait 1972; Mergl et al. 1990; Álvaro et al. 2007). Mergl (1983) described *Billingsella destombesi* from the ‘middle’ Cambrian of Anti-Atlas, Morocco and if the Guzhangian age of this taxon is confirmed, it could be the earliest species of the genus yet recorded.

The youngest Cambrian (Furongian) brachiopod association from the uppermost Karpinsk Formation has a Jiangshanian age. It includes ‘*Lingulella*’ cf. *desiderata*, *Billingsella holtedahli*, *Eoorthis sabus*, *Huenellina triplicata* and *Ocnerorthis* sp. cf. *O. opius* documented by Walcott (1924) from Holtedahl’s locality 6Bb. This fauna has unfortunately never been re-studied and the linguliform requires further study; the recorded rhyonchelliform brachiopod species are local endemics, and two of them, *Eoorthis sabus* and *Huenellina triplicata*, first appear in Jiangshanian. The genus *Eoorthis* is a cosmopolitan taxon, which appears in Laurentia at about the same time as in Novaya Zemlya, while *Huenellina* is unknown outside Novaya Zemlya. As for the family Huenellidae, it exhibits pantropical distribution throughout the Furongian Epoch (Carlson 2002), being documented from Laurentia, Siberia and Kazakh terranes.

In general, the Miaolingian–Furongian brachiopod faunas of Novaya Zemlya are characterized by low richness and show little overlap with contemporaneous faunas of the Baltoscandian Basin in their generic composition. The Guzhangian brachiopod assemblage shows mixed biogeographical signals suggesting faunal exchange with temperate latitude (*Tapuritreta, Diraphora*) and tropical (*Stilpnotreta, Treptotreta*) peri-Gondwana. This was probably facilitated by the geographical position of the region on the east margin of Baltic, as well as favourable oceanic currents (Fig. 12). The Furongian (Paibian–Jiangshanian) is associated with a proliferation of rhyonchelliform brachiopods, which is unknown from Baltoscandia, while the appearance of *Billingsella* and *Ocnerorthis* at Novaya Zemlya pre-dates their appearance in Laurentia.

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