Cambrian (Stage 4 to Wuliuan) brachiopods from Sonora, Mexico

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Abstract.—The Cambrian successions at the Chihuarruita Hill outcrop, Sonora, Mexico, have yielded two successive linguliform brachiopod assemblages that are transitional between Cambrian Stage 4 and the newly recognized global Wuliuan Stage. The lowermost assemblage includes Dictyonina sp., Paterina sp., Eothele sp., Hadroitreata rara? (Cooper), and Linnarssonia arellanoi? (Cooper), coming from the upper part of the Buelna Formation. The younger, recently named El Gavilán Formation contains a more diverse linguliform brachiopod assemblage, including Acrothele concava Cooper, Batenevrotretta mexicana n. sp., Dictyonina minutipuncta Cooper, Eothele sp., Eoobolus sp., Hadroitreata rara? (Cooper), Linnarssonia arellanoi? (Cooper), Micromitra sp., Paterina sp., and Prototreta sp. The El Gavilán Formation contains a diverse trilobite fauna suggesting Delamaran age in terms of the Laurentian regional stratigraphical scheme. The base of the global Wuliuan Stage and Miaolingian Series is defined by the first occurrence of Oryctocephalus indicus; in the absence of the index species, the base should be provisionally placed at the base of the El Gavilán Formation. The Wuliuan age of the brachiopod assemblage recovered from the El Gavilán Formation is supported by the occurrence of Acrothele in the Cambrian biostatigraphical succession of Himalaya, where the genus makes its first appearance in the Kaotata prachina Zone. In addition, the co-occurrences of Acrothele and Eothele can be taken as an indication of the Wuliuan age of the fauna. A new biogeographic analysis confirms that the Eothele Fauna first appeared at the end of Cambrian Stage 4, as a result of increased faunal migration within the southern tropical latitudes directed from Australasian Gondwana to Laurentia.

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Introduction

The Mexican state of Sonora exposes a thick Paleozoic sedimentary basin, mostly composed of carbonate platform deposits that have been studied previously (e.g., Cooper et al., 1952; Stewart et al., 1984, 2002; Cuen-Romero et al., 2016, 2018, 2019, 2020, 2022; Noriega-Ruiz et al., 2020). This study is based on the early–middle Cambrian Chihuarruita Hill section (San José de Gracia, east of Hermosillo area) in the central part of Sonora State (Figs. 1, 2). Nardin et al. (2009), and references therein) studied the fauna and stratigraphy of the Chihuarruita Hill section, which later also was studied by Cuen-Romero et al. (2016, 2018, 2019, 2020, 2022) and Noriega-Ruiz et al. (2020). The main objective of this paper is to provide the first comprehensive description of the poorly known brachiopod fauna recovered from lower-middle Cambrian limestone beds from Sonora State.

Geological setting and stratigraphy

The Mexican state of Sonora is bordered by the Gulf of California to the west, the state of Chihuahua to the east, and the south border of the United States of America (Arizona and New Mexico) to the north. The studied Chihuarruita Hill outcrop (29°17′2.10″N, 110°35′4.89″W), is located near the town of San José de Gracia, 40 km northeast of Hermosillo, the capital of Sonora (Fig. 1). Cuen-Romero et al. (2016, 2018, 2019, 2020, 2022) and Noriega-Ruiz et al. (2020) provided more detailed...
comprehensive reports on the geological setting and stratigraphy in the general area.

The stratigraphy described in this report is based on fieldwork on the lower–middle Cambrian, Chihuarruita Hill section in the San José de Gracia area, led by Sébastien Clausen and Juan José Palafox Reyes, Jesus Porfirio Sosa Leon, and Blanca Buitrón-Sánchez. The studied section extends approximately from 29°17'02"N, 110°35'00"W to 29°17'00"N, 110°34'55"W. The same area was studied previously by Nardin et al. (2009), and more recently by Cuen-Romero et al. (2016, 2019, 2020, 2022) and Noriega-Ruiz et al. (2020). Brachiopods were recovered from the Buelna and El Gavilán formations in the Chihuarruita Hill section (Figs. 1, 2; Table 1).

The Buelna Formation contains various limestones, dolomites, siliciclastic limestone, siliciclastic dolomite, and a few siltstones and sandstones mostly found in its basal part. The few productive samples (samples SJG2/2 and 2/3; Fig. 2, Table 1) come from limestone beds that are overlaid by alternating sandstones and shales towards the top of the formation. The whole Buelna Formation is ~60 m thick. The overlying Cerro Prieto Formation consists of 22.5 m of oolitic beds, sometimes interrupted by centimetric layers of micritic mudstones, but did not yield any brachiopods.

The richly fossiliferous El Gavilán Formation (samples SJG 2/6, 2/7, 2/9, 2/12, 2/13, 3/7, 3/8, 3/9; Fig. 2; Table 1) contains various lithologies, and consists of thinly bedded limestones, siliciclastic limestones, limy siltstone, and siltstone. Its thickness in Chihuarruita Hill section is ~200 m, and the formation is unconformably overlain by Tertiary volcanic deposits.

Materials and methods

Limestone samples (average weight of 1.2 kg) were collected directly from the lower–middle Cambrian limestone beds from the Chihuarruita Hill section (Figs. 1, 2; Table 1). They were broken into fragments and dissolved, either with ~10% acetic acid when dealing with limestone or with ~8% formic acid for the slightly dolomitic limestone. The acid-resistant residues were sifted (>50 μm), dried, and the microfossils were picked from the residues under a stereomicroscope. The brachiopods were coated with palladium and observed and imaged with a Scanning Electron Microscope at the University of Lille, France, and at the Evolutionary Biology Center, University of Uppsala, Sweden.

Repositories and institutional abbreviations.—The described and figured new material is housed in the collections of University of Lille (USTL = Université des Sciences et Technologies de Lille) following the recommendation of the International Commission on Zoological Nomenclature. Other type material referred to is housed in the Smithsonian National Museum of Natural History, Washington DC (USNM).

Systematic paleontology

Subphylum Linguliformea Williams et al., 1996
Class Lingulata Gorjansky and Popov, 1985
Superfamily Linguloidea Menke, 1828
Family Eoobolidae Holmer, Popov, and Wrona, 1996
Genus Eoobolus Matthew, 1902

Type species.—Obolus triparilis Matthew, 1902 (subsequent designation by Rowell, 1965, p. H263); Drumian (Eccaparadoxides eteminicus Zone), Cape Breton Island, Canada.
Eoobolus sp.

**Occurrence in Chihuarruita Hill outcrop.**—Wuluan El Gavilán Formation (samples SJG 2/7, 3/7, 3/8).

**Description.**—Shell equibiconvex elongate, subtriangular. Ventral valve acuminate with triangular pseudointerarea bisected by narrow and deep pedicle groove. Propareas elevated above the valve floor, bisected by flexure lines running close to the smooth outer margins of proparea. Dorsal valve elongate, suboval. Dorsal interarea mainly occupied by shallow concave median grove. External surface of post-metamorphic shell finely and densely pustulose. Ventral interior with weakly impressed visceral area. Posterolateral muscle scars well defined, emerging from under raised propareas. Ventral *vascula lateralia* almost straight, narrowly divergent. Dorsal interior with long median ridge. Posterolateral muscle scars well defined, emerging from under raised propareas.

**Figured material.**—USTL4031–4.

**Remarks.**—The scant available material from El Gavilán Formation (Wuluan) is fragmentary, making detailed description and taxonomic discrimination difficult. The species exhibits characteristic features of *Eoobolus*, including an elevated ventral pseudointerarea with both a deep pedicle groove and well-developed flexure lines (Fig. 3.2, 3.3, 3.7), as well as a divided and raised dorsal pseudointerarea (Fig. 3.4, 3.6), and, most importantly, a finely pustulose postmetamorphic shell (Fig. 3.1, 3.5, 3.8–3.11). The poorly known *Lingulella proveedorensis* Cooper in Cooper et al., 1952, and *Lingulella* sp., reported by McMenamin (1984) from the somewhat older Puerto Blanco Formation (Cambrian Age 3 to 4), appear to be similar in ornamentation and outline and probably represent *Eoobolus*, but cannot be compared in detail based on existing information. Devaere et al. (2019, figs. 13–16) more recently described material of *Eoobolus* sp. from the Puerto Blanco Formation; the ventral valve and ornamentation is closely similar to the younger *Eoobolus* sp. and may be conspecific.

Specimens referred to *Lingulella proveedorensis* Cooper and *Lingulella* sp. (probably also representing species of *Eoobolus*) have been briefly listed and illustrated by Cuen-Romero et al. (2018, 2019, 2020), Ramírez-Valenzuela (2019), and Noriega-Ruiz et al. (2020), but remain poorly understood.

**Superfamily Acrotheloidea Walcott and Schuchert in Walcott, 1908**

**Family Acrothelidae Walcott and Schuchert in Walcott, 1908**

**Subfamily Acrothelinae Walcott and Schuchert in Walcott, 1908**

**Genus Acrothele** Linnarsson, 1876

**Type species.**—*Acrothele coriacea* Linnarsson, 1876 (subsequent designation by Oehlert, 1887, p. 1279); Cambrian (Miaolingian), Sweden.

**Acrothele concava** Cooper in Cooper et al., 1952

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**Table 1.** Distribution of brachiopods in the sampled levels (see Fig. 2) from the Buelna and El Gavilán formations at the Chihuarruita Hill outcrop, northwest Sonora State, Mexico.

<table>
<thead>
<tr>
<th>Formation</th>
<th>Buelna Formation</th>
<th>El Gavilán Formation</th>
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</thead>
<tbody>
<tr>
<td>Sample</td>
<td>SJG 2/2</td>
<td>SJG 2/3</td>
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<tr>
<td>Eoobolus sp.</td>
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<tr>
<td>Acrothele concava</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Eothele sp.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Linnarssonia arellanoi?</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Hadrotreta rara?</td>
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<td></td>
</tr>
<tr>
<td>Prototrema sp.</td>
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<td></td>
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<tr>
<td>Batenevettea? mexicana n. sp.</td>
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<td></td>
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<tr>
<td>Dictyonina minutipuncta</td>
<td>X</td>
<td></td>
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<tr>
<td>Dictyonina sp.</td>
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<tr>
<td>Paternia sp.</td>
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<td></td>
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<tr>
<td>Micromitra sp.</td>
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<td></td>
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<tr>
<td>?Indeterminate rhynchonelliform</td>
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<td></td>
</tr>
</tbody>
</table>

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**Table 2.** Main dimensions and ratios of ventral and dorsal valves of *Batenevettea? mexicana* n. sp. from the El Gavilán Formation (sample SJG 2/9). Measurements (in μm) have been made as follows: *V* = ventral valve, *D* = dorsal valve, *L* = sagittal length of shell, *W* = maximum width of shell, *L*<sub>c</sub>, *W*<sub>c</sub> = length and width of cardinal muscle scars; *L*<sub>d</sub> = length of dorsal median buttress; *L*<sub>s</sub> = length of dorsal median septum.

<table>
<thead>
<tr>
<th>V</th>
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<tr>
<td>Mean</td>
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<td>1397</td>
<td>346</td>
<td>203</td>
<td>1030</td>
<td>82.43%</td>
<td>33.59%</td>
<td>19.71%</td>
<td>78.15%</td>
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<tr>
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<td>1607</td>
<td>346</td>
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<td>1030</td>
<td>92.18%</td>
<td>33.59%</td>
<td>19.71%</td>
<td>78.15%</td>
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<tr>
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<td>1030</td>
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<td>203</td>
<td>1030</td>
<td>76.98%</td>
<td>33.59%</td>
<td>19.71%</td>
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<table>
<thead>
<tr>
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<th>L&lt;sub&gt;c&lt;/sub&gt;/L</th>
<th>L&lt;sub&gt;d&lt;/sub&gt;/L</th>
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<td>4</td>
</tr>
<tr>
<td>Mean</td>
<td>1128</td>
<td>1178</td>
<td>339</td>
<td>805</td>
<td>232</td>
<td>82.7</td>
<td>35.98%</td>
<td>24.80%</td>
<td>90.23%</td>
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<tr>
<td>Max</td>
<td>1656</td>
<td>1626</td>
<td>386</td>
<td>922</td>
<td>265</td>
<td>922</td>
<td>110.04%</td>
<td>41.52%</td>
<td>92.26%</td>
</tr>
<tr>
<td>Min</td>
<td>770</td>
<td>911</td>
<td>265</td>
<td>682</td>
<td>210</td>
<td>776</td>
<td>81.62%</td>
<td>32.01%</td>
<td>76.45%</td>
</tr>
</tbody>
</table>
Figure 3. *Eoobolus* sp. from the El Gavilán Formation (sample SJG 3/7), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1) (USTL4031-1) Dorsal valve exterior; (2, 3, 7) (USTL4031-2) (2) ventral valve interior, (3) detail of ventral pseudointerarea, (7) oblique lateral view; (4, 6) (USTL4031-3) (4) detail of dorsal pseudointerarea, (6) dorsal valve interior; (5, 8–11) (USTL4031-4) (5) ventral valve exterior, (8) detail of ornamentation, (9) detail of weak pustulose ornamentation on juvenile part, (10) detail of umbo, (11) detail of adult pustulose ornamentation.
1952 *Acrothele concava* Cooper in Cooper et al., 1952, p. 44, pl. 12A, figs. 1–6.

*Holotype.*—USNM116035d, a dorsal valve (Cooper in Cooper et al., 1952, pl. 12A, fig. 6) from the uppermost Arrojos Formation (Wuliuan), Arrojos Hills, Sonora.

*Diagnosis.*—See Cooper in Cooper et al. (1952, p. 44).

*Occurrence in Chihuarruita Hill outcrop.*—Wuliuan El Gavilán Formation (samples SJG 2/9, 2/13, 3/8).

*Description.*—Shell ventribiconvex, transversely oval.
Ventral valve convex; subconical in lateral view with rounded margin, and with umbo at maximum height; well-defined sulcus on adult shell (Fig. 4.5). Ornamentation of fine concentric filla and knob-shaped pustules (Fig. 4.1–4.9). Ventral metamorphic shell (400–535 μm wide), oval with pitted ornamentation, and two low lobes, close to the center and extending to margin (Fig. 4.1–4.4). Oval pedicle foramen (120–170 μm long) not enclosed within metamorphic shell (Fig. 4.1–4.3). Median tubercle in front of pedicle foramen very poorly developed to absent (Fig. 4.1–4.3). Pseudointerarea procline and sub-triangular, mostly defined by the absence of pustule-like ornamentation, and lacking well-defined intertrough.

Ventral interior poorly preserved, with somewhat thickened area around foramen, and poorly defined *vascula lateralia* diverging anteriorly.

Dorsal valve flattened to slightly convex in lateral view, with subcircular margin and very shallow sulcus; fine concentric filla and pustule-like ornamentation (Fig. 4.5). Dorsal metamorphic shell marginal, oval (625–350 μm wide), with pitted ornamentation; single pair of spines at posterior margin of metamorphic shell (Fig. 4.5–4.7, 4.12). Pair of divergent, anteriorly inflated lobes terminated close to anterior margin of metamorphic shell (Fig. 4.5–4.8). Dorsal pseudointerarea poorly developed, orthoclone to apsacrine; median sulcus sometimes developed at edge of metamorphic shell (Fig. 4.10–4.12).

Dorsal interior poorly preserved, but with low median ridge (Fig. 4.10–4.12).

**Figured material.**—USTL4032-1–4.

**Remarks.**—The most distinguishing character of *A. concava* from the El Gavilán Formation (Wuliuan) is the unusual morphology of the metamorphic shell morphology (Fig. 4.1–4.8). Most well-known species of *Acrothele* have a distinctive low median tubercle in front of the pedicle foramen (e.g., *Acrothele vertex* Reed, 1910; Popov et al., 2015, fig. 13C, D), but here it is very poorly developed to absent (Fig. 4.1–4.3); the ventral metamorphic shell of the Mexican species lacks the characteristic *Acrothele* spines, and only has two low raised lobes, close to the center and extending to margin (Fig. 4.1–4.3). Moreover, the dorsal metamorphic shell of *A. concava* only has a single pair of low spines in front of the posterior margin, and anterior to the spines, a pair of divergent raised and inflated lobes are present (Fig. 4.7, 4.12). This type of dorsal metamorphic shell is similar to that described from an unnamed problematic species of *Acrothele* from the Gzuhangian of Novaya Zemlya (Holmer et al., 2020, fig. 6E–H); in both these species, the dorsal lobes are considered to represent impressions from a single pair of metamorphic setal sacks (see also Zhang et al., 2018, fig. 8). In the type species, *A. coriacea*, the dorsal metamorphic shell has two pairs of well-developed spines (e.g., Rowell, 1980, pl. 2:6; Holmer and Popov, 2000, fig. 46.1). The species from Novaya Zemlya also lacks the paired ventral metamorphic spines, and has two inflated lobes. Most well-known species of *Acrothele* have a well-developed internal pedicle tube (e.g., *Acrothele vertex* Reed; Popov et al., 2015, fig. 13G, K), but this is absent in *A. concava*, where there is only a slightly thickened interior area around the foramen; a very similar morphology is also found in *Acrothele*? sp. from Novaya Zemlya (Holmer et al., 2020, fig. 5A, C). However, the pustulose adult ornamentation and pitted ornamentation on the metamorphic shell of *A. concava* is unlike the species from Novaya Zemlya, and closely similar to that of other *Acrothele* species (Fig. 4.8, 4.9).

Cooper in Cooper et al. (1952, p. 45) provided a short comparative discussion of his species with *A. colleni* Walcott, 1912, from the middle Cambrian of Montana. Specimens possibly referable to *Acrothele concava* and *Acrothele* sp. also have been listed and illustrated from the Cambrian of the region by Cuen-Romero et al. (2018, 2019, 2020) and Noriega-Ruiz et al. (2020).

**Genus Eothele** Rowell, 1980

**Type species.**—*Acrothele spuri Walcott, 1908* (original designation by Rowell, 1980, p. 17); Cambrian (Series 2, *Bonnia-Olenellus* Zone), Nevada.

**Eothele* sp.

**Figure 5**

**Occurrence in Chihuarruita Hill outcrop.**—Cambrian Stage 4 Buelna Formation (sample SJG 2/2), and Wuliuan El Gavilán Formation (samples 2/13, 3/7).

**Description.**—All specimens represent incomplete ventral valves, showing only a part of the shell around the metamorphic shell and the foramen opening.

Ventral valve strongly conical. Pedicle opening (330–400 μm long, 160–240 μm wide) not enclosed within metamorphic shell; well-developed media tubercle bounding anterior margin of oval foramen opening; pitted metamorphic shell with two symmetrical tubercles anterior to apex (Fig. 5). Pedicle foramen opening strongly elongate oval, almost two times longer than wide, and continuing internally as a collar-like tube; pseudointerarea procline, poorly defined, lacking intertrough (Fig. 5). Pustulose adult ornamentation. Ventral interior with short pedicle tube (Fig. 5.8).

**Figured material.**—USTL4033-1–3.

**Remarks.**—Although the material from the Buelna Formation (Stage 4) is fragmentated, the large elongate pedicle foramen (Fig. 5.1–5.5, 5.7, 5.8), and the ventral metamorphic shell with the strong median tubercle (Fig. 5.9) and pedicle tube (Fig. 5.6) show some similarities with the type species *E. spuri* (Walcott, 1908) from Nevada. However, due to the lack of a definite dorsal valve and the poor preservation of the ventral, it is kept under open nomenclature.

Order Acrotretida Kuhn, 1949
Superfamily Acrotretoida Schuchert, 1893
Family Acrotretidae Schuchert, 1893
Genus *Linarossonia* Walcott, 1885

**Type species.**—*Obolella transversa* Hartt in Dawson, 1868 (original designation by Walcott, 1885, p. 115); middle Cambrian of New Brunswick, Canada.
**Linnumsonia arellanoi**? (Cooper in Cooper et al., 1952)  
**Figure 6**

1952 *Pegmatreta arellanoi* Cooper in Cooper et al., p. 43, pl. 13C, figs. 7–12.

**Holotype.**—USNM116057d, a ventral valve (Cooper in Cooper et al., 1952, pl. 13C, fig. 7) from the El Tren Formation (Wuliuan), Arrojos Hills, Sonora.

**Diagnosis.**—See Cooper in Cooper et al. (1952, p. 44).

**Occurrence in Chihuarruita Hill outcrop.**—Cambrian Stage 4 Buelna Formation (sample SJG 2/2) and Wuliuan El Gavilán Formation (samples SJG 2/7, 2/9, 2/13, 3/7, 3/8, 3/9).

**Description.**—Shell ventribconvex and elongate oval in adults, ~80–112% as long as wide (Fig. 6.5).

Ventral valve (length 1.2–2.3 mm, width 1.2–2.3 mm) evenly convex in lateral view. Pseudointerarea apsacline, poorly defined. Intertrough short and well defined (Fig. 6.5–6.8). Pedicle opening oval and not enclosed within metamorphic shell.

Ventral interior with prominent boss-like apical process, extending anteriorly for ~36–40% of the total length of valve; process laterally bounded by apical pits and a pair of diverging *vascula lateralia*. The apical process is triangular in anterior view. Prominent oval cardinal muscle scars placed laterally, located close to the internal foramen (Fig. 6.7–6.9).

Dorsal valve (length 1.7–2.3 mm, width 1.8–2.5 mm) convex. Dorsal metamorphic shell located near posterior edge of shell (Fig. 6.6).

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**Figure 5.** *Eothele* sp. from the Buelna Formation (Cambrian Stage 4; sample SJG 2/2), Chihuarruita Hill outcrop, Mexico. (1, 4, 5) (USTL4033-1) (1) Oblique posterior view of ventral valve exterior; (4) oblique lateral view of ventral apex; (5) detail of ventral metamorphic shell; (2) (USTL4033-2) oblique posterior view of ventral valve exterior; (3) (USTL4034-1) oblique posterior view of ventral valve exterior; (6) (USTL4034-2) ventral valve interior with pedicle tube; (7–9) (USTL4034-3) (7) ventral pedicle foramen, (8) oblique lateral view, (9) detail of metamorphic shell.

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Dorsal valve with short median groove and orthocline propareas. Median groove almost four times wider than long. Well-developed median ridge extending anteriorly for ∼64–83% of total valve length; well-developed median buttress fused with median ridge. Prominent cardinal and anterocentral muscle scars (Fig. 6.2–5.4).

Figured material.—USTL4035-1, 4036-1–3, 4037-1.

Remarks.—Linnarssonia and similar taxa (e.g., Pegmatreta and Hadrotreta) are known to be taxonomically complex genera because of the great morphological variation and general lack of detailed studies (see Holmer et al., 2001); recent discussions on this and related problematic genera can be found in Peel et al. (2016) and Ushatinskaya and Korovnikov (2019). Holmer and Popov (2000) and Ushatinskaya and Korovnikov (2019) included Pegmatreta within Linnarssonia, and this is followed here. Linnarssonia arellanoi (Cooper in Cooper et al., 1952) is a particularly poorly known species that has only ever been recorded from the type horizon in the slightly younger El Tren Formation. It has never been re-studied, but the illustrations and description by Cooper in Cooper et al. (1952, pl. 13C, figs. 7–12) are very similar in all morphological details—including the elongate oval shape of the shell, prominent boss-like apical process, and long dorsal median septum—to the slightly older material described here (Fig. 6).
Pending re-study of the type material, they are questionably referred to the same species.

Linnarssonia arellanoi is similar in most characters to the somewhat younger L. ophiirensis (Walcott, 1902) from the Drumian of Utah (Rowell, 1966), and pending further studies it is possible that they are conspecific.

Genus Hadrotreta Rowell, 1966

Type species.—Acrotreta primaea Walcott, 1902 (original designation by Rowell, 1966, p. 12); lower to middle Cambrian (Stage 4 to Wuliuan) Pioche Shale, Nevada, USA.

Hadrotreta rara? (Cooper in Cooper et al., 1952)

Type species?—? appears to be most similar to the type species (see Liang et al., 2022), but has a longer dorsal median ridge, although most dorsal valves are fragmented anteriorly, and moreover, the “forked” septum with the dorsal anterior lateral scars (Fig. 7.2, 7.4, 7.5) are not as well developed as in other species of the genus.

Poorly known specimens referred to Pegmatreta rara also have been listed and illustrated from the Cambrian of the region by Cuen-Romero et al. (2018, 2019, 2020) and Noriega-Ruiz et al. (2020).

Genus Prototreta Bell, 1938

Type species.—Prototreta trapeza Bell, 1938 (original designation by Bell, 1938, p. 405); middle Cambrian (Bathyuriscus Zone), Montana, USA.

Prototreta sp.


Description.—Shell ventribiconvex, with a plano-convex dorsal valve and a highly conical ventral valve, ~25–33% as high as wide. Ornamentation with fine rugae.

Ventral valve conical, with a plano-convex dorsal valve and a highly conical ventral valve, ~25–33% as high as wide. Ornamentation with fine rugae.

Ventral valve conical (length 1.2–2.8 mm, width 1.3–3.2 mm), ~87–97% as long as wide. Pedicle foramen not enclosed within metamorphic shell. Pseudointerarea strongly procline, with well-defined intertrough (Fig. 8.1–8.3). Ventral interior with apical process forming ridge along posterior wall of shell. Pedicle tube penetrating apical process, which is often broken in the available specimens. Pair of apical pits located postero-laterally to internal pedicle opening. Parallel ventral vascula lateralia extending from apical pits, continuing alongside apical process, before diverging anteriorly. Well-developed oval cardinal muscle scars located postero-laterally to pedicle opening (Fig. 8.11, 8.12).

Dorsal valve circular in outline and almost planar in lateral view (length 1.7–2.9 mm, width 1.6–3.4 mm), ~83–104% as long as wide. Ornamentation of fine concentric growth lines. Metamorphic shell circular, with two parallel small ridges (Fig. 8.4–8.6).

Dorsal pseudointerarea well developed, long, and wide, occupying ~18–20% and 83–100% of total length and width of valve,
respectively; anacline to orthocline, with triangular wide dorsal median groove and small propareas. Dorsal cardinal muscle scars located just anterior to propareas and median groove. Moderately high median ridge, extending for \( \sim 56-60\% \) of the length of valve; triangular in lateral view with a blade-like structure on the posterior part of the crest (Fig. 8.7–8.10).
Figure 8. Prototreta sp. from the El Gavilán Formation (sample SJG 2/13), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1–3) (USTL4039-1) (1) ventral valve exterior, (2) oblique posterolateral view, (3) detail of umbo, (4–6) (USTL4039-2) (4) oblique lateral view dorsal valve exterior, (5) oblique lateral view of umbo, (6) oblique lateral view of dorsal metamorphic shell, (7) (USTL4039-3) dorsal valve exterior, (8–10) (USTL4039-4) (8) dorsal valve exterior, (9) oblique lateral view, (10) oblique lateral view of dorsal pseudointerarea, (11, 12) (USTL4039-5) (11) oblique anterolateral view of ventral valve interior, (12) oblique anterolateral view of apical process and muscle scars.
Figured material.—USTL4039-1–5.

Remarks.—Brock and Percival (2006) recently discussed and reviewed Prototreta, which is clearly in need of revision. Pending such revision, it is difficult to make a detailed comparison with other species of the genus, therefore the material is kept under open nomenclature. The dorsal median septum of the Sonoran Prototreta sp. is not very high and digitate, as compared with P. trapeza Bell, 1938, and P. flabellium Bell, 1941, but more similar to P. interrupta Bell, 1941, and P. minica Bell, 1941, all from the Cambrian of Montana, in having a lower septum with an upper rod (Fig. 8.7–8.9).

Specimens referred to Prototreta sp. also have been listed and illustrated from the Cambrian of the region by Cuen-Romero et al. (2018, 2019, 2020) and Noriega-Ruiz et al. (2020).

?Family Scaphelasmatidae Rowell, 1965
?Genus Batenevotreta Ushatinskaya, 1992

Type species.—Batenevotreta formosa Ushatinskaya, 1992 (original designation by Ushatinskaya, 1992, p. 87); middle Cambrian (Amgian), Altay, Russia.

Batenevotreta? mexicana new species

Figure 9

Holotype.—USTL4040-6, a ventral valve (Figure 9.8, 9.11, 9.12) from Wuliuan El Gavilán Formation (sample SJJ 2/9).

Diagnosis.—Shell transversely oval with strong, irregularly spaced rugae; ventral valve low conical; ventral pseudointerarea procline to catacline, poorly defined laterally, with shallow, poorly defined intertrough; foramen circular, not enclosed within metamorphic shell; apical process high, broad, boss-like, directly anterior to short pedicle tube; dorsal valve moderately convex; dorsal pseudointerarea poorly defined, very short, raised high above valve floor, with shallow very poorly defined median groove; dorsal interior with small, poorly developed median buttress and low median ridge; dorsal cardinal muscle fields large, transversely oval, thickened.

Occurrence in Chihuauvuita Hill outcrop.—Wuliuan El Gavilán Formation (sample SJJ 2/9).

Description.—Shell unequally biconvex, rounded, transversely oval, with strong, irregularly spaced rugae (Fig. 9.1, 9.3, 9.4).

Ventral valve low conical (length 1.0–1.2 mm, width 1.3–1.6 mm), ~76–92% as long as wide (Fig. 9.8–9.10). Maximum width in middle of shell length. Ventral pseudointerarea poorly defined laterally, procline to catacline; intertrough, shallow, poorly defined (Fig. 9.8). Ventral metamorphic shell well defined (~150–170 μm wide); pitted ornamentation poorly preserved (Fig. 9.11, 9.12). Foramen circular (~60 μm wide and long), not entirely enclosed within metamorphic shell (Fig. 9.11). Ventral interior with short pedicle tube, directly posterior to well-developed, high, boss-like apical process, extending for around one-third of the total valve length (Fig. 9.6, 9.10). Ventral cardinal muscle scars thickened and raised, short and wide extending for ~20% and 78% of total valve length and width, respectively (Fig. 9.6, 9.10). Apical pits small, located near posterior margin. Ventral vascula lateralia starting lateral to apical pits and diverging widely up to the mid-length of the valve (Fig. 9.6, 9.10).

Dorsal valve moderately convex (length 770 μm–1.66 mm, width 911 μm–1.62 mm), ~82–110% as long as wide (Fig. 9.4). Dorsal pseudointerarea very poorly defined, very short, raised high above valve floor, with shallow, very poorly defined median groove (Fig. 9.2, 9.5, 9.7).

Dorsal interior with small, poorly developed median buttress and low median ridge; dorsal cardinal muscle fields large, transversely oval, thickened. Foramen circular (~75 μm wide and ~120 μm long), not entirely enclosed within metamorphic shell (Fig. 9.10). Apical pits poorly preserved, located near apical margins. Ventral vascula lateralia starting lateral to apical pits and diverging widely up to the mid-length of the valve (Fig. 9.6, 9.10).

Remarks.—Prototreta is a rare and early member of the Scaphelasmatidae, which was originally described from the middle Cambrian of Altay, Russia, by Ushatinskaya (1992), and later recorded from the late Cambrian of Kazakhstan by Koneva and Ushatinskaya (2010). Unfortunately, the type species, B. formosa Ushatinskaya, 1992, is not well known (Holmer and Popov, 2000). Percival and Kruse (2014) most recently illustrated a questionable record from the mid-Cambrian of central Australia (southern Georgia Basin). In the species from Kazakhstan (Koneva and Ushatinskaya, 2010), B. variabilis Koneva and Ushatinskaya, 2010, and B. ivshini Koneva and Ushatinskaya, 2010, the adults have a very large pedicle foramen, which is oval to slit-like, as in other members of the Scaphelasmatidae, and the metamorphic shells have a characteristic pitting with two distinctive sizes of pits. In contrast, the pedicle foramen of B.? mexicana n. sp. is circular and comparatively small, and moreover, the pitting of the metamorphic shells is not well preserved (Fig. 9.11, 9.12). The new Sonoran material is most similar in most other characters to the species from Kazakhstan and Russia, but assignation to the genus is kept questionable due to the differences in pedicle foramen and lack of information on metamorphic pitting.

Etymology.—From the occurrence in Mexico.

Figured material.—USTL4040-1–6, from sample SJJ 2/9.

Remarks.—Batenevotreta is a rare and early member of the Scaphelasmatidae, which was originally described from the middle Cambrian of Altay, Russia, by Ushatinskaya (1992), and later recorded from the late Cambrian of Kazakhstan by Koneva and Ushatinskaya (2010). Unfortunately, the type species, B. formosa Ushatinskaya, 1992, is not well known (Holmer and Popov, 2000). Percival and Kruse (2014) most recently illustrated a questionable record from the mid-Cambrian of central Australia (southern Georgia Basin). In the species from Kazakhstan (Koneva and Ushatinskaya, 2010), B. variabilis Koneva and Ushatinskaya, 2010, and B. ivshini Koneva and Ushatinskaya, 2010, the adults have a very large pedicle foramen, which is oval to slit-like, as in other members of the Scaphelasmatidae, and the metamorphic shells have a characteristic pitting with two distinctive sizes of pits. In contrast, the pedicle foramen of B.? mexicana n. sp. is circular and comparatively small, and moreover, the pitting of the metamorphic shells is not well preserved (Fig. 9.11, 9.12). The new Sonoran material is most similar in most other characters to the species from Kazakhstan and Russia, but assignation to the genus is kept questionable due to the differences in pedicle foramen and lack of information on metamorphic pitting.

Class Paterinata Williams et al., 1996
Order Paterinida Rowell, 1965
Superfamily Paterinioidea Schuchert, 1893
Family Paterinidae Schuchert, 1893

Remarks.—The studied material includes very fragmentary specimens of Dictyonina sp., Micromitra sp., and Paterina sp. that are too poorly preserved to allow closer taxonomic discrimination (Fig. 10.10–10.12). A poorly preserved ventral valve, lacking preserved ornamentation, may also represent an unidentified Paterinidae (Fig. 10.13–10.15). Sonoran specimens of Micromitra sp. and Paterina sp. were described by Cooper in Cooper et al. (1952, p. 38–39, pl. 11B, figs. 7, 8, pl. 13A, figs. 1–3), as well as listed and illustrated by Cuen-Romero et al. (2018, 2019, 2020) and Noriega-Ruiz et al. (2020).
Genus *Dictyonina* Cooper, 1942

*Type species.*—*Trematis pannulus* White, 1874 (original designation by Cooper, 1942, p. 228); Cambrian (Stage 4–Wuliuan) Pioche Shale, Nevada, USA.

*Dictyonina minutipuncta* Cooper in Cooper et al., 1952

*Figure 10.1–10.9*
Figure 10. *Dictyonina minutipuncta* (1–9) Cooper in Cooper et al., 1952, from the Cambrian (Wuliuan) El Gavilán Formation: (1–6) sample SJG 2/9, (7–9) sample SJG 2/7; *Paterina* sp. (10–12) and an unidentified *Paterinidae* (13–15) from the Cambrian Stage 4 Buena Formation (sample SJG 2/2), Chihuarruita Hill outcrop, Mexico. (1–6) (USTL4041-1) (1) Ventral valve exterior, (2) oblique posterolateral view, (3) oblique posterolateral view of umbo, (4) detail of umbo, (5) detail of ventral metamorphic shell, (6) detail of adult ornamentation; (7–9) (USTL4042-1) oblique lateral view of ventral valve exterior, (8) detail of umbo, (9) detail of adult ornamentation; (10–12) (USTL4043-1) (10) oblique lateral view of ventral valve exterior, (11) detail of adult ornamentation, (12) detail of adult ornamentation; (13–15) (USTL4043-2) (13) ventral valve exterior, (14) oblique posterolateral view, (15) detail of umbo.
Holotype.—USNM116054a, a ventral valve (Cooper in Cooper et al., 1952, pl. 11A, fig. 5, 6) from the uppermost Arrojos Formation (Wuliuan), Arrojos Hills, Sonora.

Diagnosis.—See Cooper in Cooper et al. (1952, p. 40).

Occurrence in Chihuarruia Hill outcrop.—Wuliuan El Gavilán Formation (samples SJG 2/7, 2/9, 2/13).

Description.—Ventral valve strongly convex with prominent beak and short homeodeltidium (Fig. 10.1–10.9). Ornamentation of radiating rows of subhexagonal pits, increasing in size distally (Fig. 10.1–10.9). Metamorphic shell bi-lobate, with fine pustulose ornamentation (Fig. 10.5). Ventral pseudointerarea well developed, lacking pitted ornamentation. Interior ventral valve poorly preserved.

Figured material.—USTL4041-1, 4042-1, 4043-1, 2.

Remarks.—The pitted ornamentation (Fig. 10.1–10.9) and shape of the ventral valve are closely similar to the material described by Cooper in Cooper et al. (1952, pl. 11A, fig. 5, 6) from the Arrojos Formation, and they are considered to be conspecific. The Sonoran species is also similar to Dictyonina panula (White, 1874) (see Liang et al., 2022). Specimens also have been listed and illustrated by Cuen-Romero et al. (2018, 2019, 2020) and Noriega-Ruiz et al. (2020).

Biographical affinities

During the Cambrian, the Sonora Region formed a part of the Caborca Terrain, which was an integral part of the southern margin of Laurentia, facing the South American sector of Gondwana (Torsvik and Cocks, 2017; Fig. 12.3).

Two successive linguliform brachiopod assemblages have been recognized in the Sonoran deposits in the time interval between Cambrian Series 4 and the newly recognized Wuliuan Stage. The lowermost assemblage, which includes Dictyonina sp., Paterina sp., Eothele sp., Hadrotreta rara?, Linnarssonia arellanoi?, comes from the upper part of the Buelna Formation (Fig. 2; Table 1). Trilobite-based correlation (e.g., Cuen-Romero et al., 2016, 2018, 2019, 2020, 2022, and references herein) supports assignment of the unit to Cambrian Series 4. The younger El Gavilán Formation contains a more diverse linguliform brachiopod assemblage, including Acrothele concava, Batenetrotre? mexicana n. sp., Dictyonina minutipuncta, Eothele sp., Eoebolus sp., Hadrotreta rara?, Linnarssonia arellanoi?, Micromitra sp., Paterina sp., and Prototreta sp. (Fig. 2; Table 1). The El Gavilán Formation also contains a diverse trilobite fauna that suggests a Delamaran age (in terms of the Laurentian regional stratigraphical scheme). Although, the index fossil for the base of the global Wuliuan Stage and Miaolingian Series–Ortycocephalus indicus—is absent, Cuen-Romero et al. (2018) suggested that it should be provisionally placed in the lower part of the El Gavilán Formation. The Wuliuan or younger age of the linguliform brachiopod assemblage recovered the El Gavilán Formation is also supported by the occurrence of Acrothele. In the Cambrian succession of Himalayas, Acrothele makes it first appearance in the Kaotaiia prachina Zone, which is definitely above the estimated position of the Wuliuan Stage base (Popov et al., 2015). The co-occurrence of Acrothele and Eothele also can be taken as indication of the Wuliuan age of the fauna.

To investigate biogeographical relations of the newly recovered Cambrian linguliform brachiopod faunas from the Caborca Terrain, a cluster analysis (Raup-Crick similarity) was performed using the computer program PAST (version 3.06; Hammer et al., 2001; Fig. 12.1, 12.2). The data set (Appendix) used in analysis is modified from Popov et al. (2015), with addition of the newly recovered faunas from Sonora and new data for the Wuliuan faunas from Siberia reported by Ushatinskaya and Korovnikov (2019). In spite of restrictions caused by the low generic richness of the faunas, as well as the heterogenous character of available data (already discussed by Popov et al., 2015), it was possible to recover general patterns of biogeographical differentiation and biotic changes caused by increased migration and major biodiversification of linguliform faunas close to the base of the Wuliuan Stage (Fig. 12).

The first analysis is based on a data matrix including generic composition of 19 individual faunas (A1–A11 and B1–B8) from Cambrian Stage 4 (Fig. 12.1). The core of the analyzed matrix is derived from faunal lists, including 31 total genera, as presented by Popov et al. (2015), with addition of the faunal assemblage from the Caborca Terrane (Sonora, Buelna Formation; Appendix). The resulting cladogram mainly preserves general patterns shown by Popov et al. (2015; Fig. 12.1); however, there are also some important differences, which require consideration.

Excluding the highly endemic fauna of Anti-Atlas, Morocco (B5; located on the margin of the North African sector of Gondwana), two major clusters (Cluster A and B) can be recognized (Fig. 12.1). Cluster A includes two second-order subclusters. The first cluster is formed by the Siberian faunas (B2 and A6) plus the faunal assemblage of the peri-Gondwanan Karatau-Naryn microplate (A2). The second cluster includes most, but not all, of the faunas grouped in previous analyses by Popov et al. (2015) within the Schizopholis-Botsfordia Fauna, which is confined to tropical Gondwana, plus a single Laurentian faunal assemblage from Greenland (Fauna A4; Fig. 12.1). The latter abnormality probably was caused by the fact that Laurentian faunas from the lower to middle part of Cambrian Stage 4 are poorly known and strongly underrepresented, both in terms of geographical distribution and generic richness.

Cluster B includes faunal assemblages of the so-called Eothele Fauna (Fig. 12.1; Popov et al., 2015) as a separate Subcluster B2. Cluster B is composed of the individual faunas from
the Australasian sector of Gondwana and Laurentian faunas. The latter form a distinct third-order subcluster, which also includes the faunal assemblage from Sonora (B8), clearly showing the Laurentian biogeographical signature. Subcluster B1 includes two individual faunas (A3 and A10; Fig. 12.1) from the Australian Sector of Gondwana, which in the previous analysis by Popov et al. (2015) was included within the Schizopholis-Botsfordia Fauna. It is possible that these Australian faunas are among the precursors of the Eothele Fauna. The new biogeographic analysis confirms the earlier suggestion by Popov et al.

Figure 11. ?Indeterminate rhynchoelliform, from the Buelna Formation (Cambrian Stage 4; sample SIG 2/2), Chihuarruita Hill outcrop, Mexico. (1–5) (USTL4043-3) (1) Internal mold of ventral valve, (2) detail of umbo, (3) detail of umbo, (4) oblique lateral view of umbo, (5) posterior view of umbo; (6, 7, 10, 11) (USTL4043-4) (6) internal mold of ventral valve, (7) detail of umbo, (10) oblique posterolateral view, (11), oblique posterior view; (8, 9) (USTL4043-5) (8) detail of umbo of internal mold of ventral valve, (9) posterior view.
that the *Eothele* Fauna evolved late in Cambrian Stage 4 due to increased faunal migration within the southern tropical latitudes directed from Australasian Gondwana to Laurentia. Remarkably, the contemporaneous faunas of Siberia (A6), which formed an isolated continent mainly in the northern tropical latitudes, and North African sector of Gondwana (Fig. 12.1: B1, located in temperate southern latitudes) retained their individuality. Yet both contain *Eothele*, which was a short-lived taxon that proliferated close to the end of Cambrian Stage 4.

The second cluster analysis, which only comprises the Wuliuan Stage (Fig. 12.2), includes 41 genera representing 16 individual faunas mainly based on data published by Popov et al. (2015), with addition of new data on the linguliform faunas from Sonora and Siberia (Appendix). The results of the analysis also mainly preserved the general pattern that was found in the analysis published earlier by Popov et al. (2015); however, there are notable differences addressed below.
As in the earlier biogeographical analysis by Popov et al. (2015), two major clusters (A and B) are recognized (Fig. 12.2). Cluster A includes diverse and highly endemic faunas of Kazakh terranes (C1 and C2), which are characterized by diverse micromorphic brachiopod taxa, predominantly acrotretoids. However, the Baltic fauna (C8; Fig. 12.2) surprisingly appears within this cluster—a possible explanation could be that, unlike the Kazakh faunas, which represent genuine faunal associations, the Baltic fauna is based on a composite list, while characters of individual Baltoscandian faunal associations and their biofacies differentiation remain inadequately known. Thus, the observed grouping reflects heterogeneity of the original data set used in the analysis. Nevertheless, this clustering also suggests a relative isolation of linguliform brachiopod faunal assemblages that inhabited the Kazakh terranes and Baltic continent in relation to other contemporaneous faunas.

Other Wuliuan faunas form Cluster B, which is subdivided into two second-order subclusters (Fig. 12.2; B1 and B2). The Wuliuan linguliform faunal assemblage from Sonora, Caborca Terrain (C16) appears within the large third-order Subcluster B1a, together with numerous faunas from tropical Gondwana and associated volcanic arcs and microcontinents; this subcluster also includes the Siberian fauna (C10; Fig. 12.2). The faunal assemblage from Sonora shows closest similarity to the fauna of the Alai peri-Gondwana terrane.

The only other Wuliuan fauna from Laurentia, from the Pioche Shale of Utah (C5), occurs within the third-order Subcluster B1b of the peri-Iapetus faunas together with faunal assemblages Novaya Zemlya (C4; considered as part of Baltica continent) and New Brunswick (Avalonia), which was attached as in the earlier biogeographical analysis by Popov et al. (2015), but that also included the Wuliuan fauna of Spain (C7), which was attached to the North African sector of Gondwana. In the new analysis, the latter fauna appears at the base of second-order Subcluster B (Fig. 12.3).

The biogeographical affinities of Laurentian faunas of Wuliuan age remain poorly resolved because of our insufficient knowledge. Further progress in biogeographical studies of the Cambrian faunas is not possible without proper documentation of individual faunas from Laurentia and Siberia, two major Cambrian continents that were distinctly isolated from the Gondwana supercontinent. A better understanding of biofacies differentiation of the Cambrian linguliform brachiopod faunas also should be taken in consideration in future analyses of their biogeographical affinities.

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### Appendix: Faunal lists for cluster analysis

Faunal lists for cluster analysis (Raup–Crick similarity) using the computer program PAST (version 3.06; Hammer et al., 2001). The data set used in analysis is modified from Popov et al. (2015) with addition of the newly recovered faunas from Sonora (Caborca: B8 and C15) and new data for the Wuliuan faunas from Siberia presented by Ushatinskaya and Korovnikov (2019).

**Cambrian Stage 4, ‘Botsfordia-Schizopholis faunas’.—**

A1.—Gondwana; Antarctica, King George Island (South Shetland Islands), glacial erratics in the Early Miocene Cape Melville Formation (Holmer et al., 1996); *Eoobolus, Schizopholis, Vandalotreta*.

A2.—Karatau-Naryn microplate; Malyi Karatau Range, *Redlichia chinensis* - Kootenia gimmelfarbi Biozone (Holmer et al., 2001); *Botsfordia, Lingulellotreta, Linnarssonia, Palaeeobolus*.

A3.—Australasian segment of Gondwana; Northern Territories, composite list (Wiso, Georgina and Daly Basin) (Kruse, 1990, 1991, 1998); *Westonia, Schizopholis, Kyshabaktella, Vandalotreta, Micromitra?*.

A4.—Laurentia, North-East Greenland, Bastion and Ella Island formations (Skovsted and Holmer, 2005); *Botsfordia, Eooobolus, Micromitra, Vandalotreta*.

A5.—South China, Shaanxi Province, Guojiaba and Xiannudong formations (Li and Holmer, 2004); *Eoohadrotreta, Eooobolus, Kyshabaktella, Palaeobolus, Lingulellotreta*.

A6.—Siberia, Toyon Regional Stage (Pelman, 1977; Ushatinskaya and Malakhovskaya, 2001); *Botsfordia, Eooobolus, Kyshabaktella, Linnarssonia, Paterina*.

A7.—Australasian segment of Gondwana; South Australia, Parara and Ramsey limestone formations (Ushatinskaya and Holmer, 2001); *Eooobolus, Kyshabaktella, Schizopholis, Vandalotreta*.

A8.—Sub-Himalaya; *Botsfordia, Eooobolus, Neobolus, Schizopholis, Wynnia*.

A9.—Spiti, Tethyan Himalaya; Parahio Formation, *Haydenopsis pararyana Level*; *Aksarinaia, Eohadrotreta, Eooobolus, Paterina, Schizopholis*.

A10.—Australasian segment of Gondwana, central Australia, southern Georgina Basin, Thorntonia Limestone (Percival and Kruse, 2014); *Aksarinaia, Dictyonyina, Hadrotreta, Kostjubella, Kyshabaktella, Micromitra, Schizopholis, Vandalotreta, Westonia, Wynnia?*.

A11.—South China, Yunnan Province, Wulongqi Formation, Guanshan Fauna (Zhao et al., 2011): *Acanthoretellota, Diandongia, Eooobolus, Lingulellotreta, Palaeobolus*.

**Transitional ‘Eothele faunas’.—**

B1.—Laurentia, Canada, Mackenzie Mountains (Voronova et al., 1987) Lars, could you please supply list of the brachiopod genera for the “Toyonian” and if it is possible for basal Middle Cambrian as well. Dyean Mackenzie Mountain (*Bomaia-Olenellus zone*) Laurentia (Voronova et al., 1987); *Palaeeochmidites, Linnarssonia, Eothele, Micromitra, Paterina*.

B2.—Peri-Siberia, Altai-Sayany Region, ‘Toyon Stage’, composite list (Ushatinskaya and Malakhovskaya, 2001; *Botsfordia, Chakassilingula, Eothele, Kyshabaktella, Linnarssonia, Oeepikites*).

B3.—Australasian segment of Gondwana; western New South Wales, Coonigan Formation (Roberts and Jell, 1990); *Eothele, Hadrotreta, Kleithriatreta, Dictyonyina, Micromitra, Eoobolus (=Palaeeochmidites), Oeepikites(?) (=Lingulella), Westonia*.

B4.—Australasian segment of Gondwana; north-western New South Wales, Wydjah Formation (Pimpira Member) (Brock and Percival, 2006); *Dictyonyina, Eothele, Eooobolus, Micromitra, Protrotreta*.

B5.—North African Sector of Gondwana; Morocco, composite list (Mergl, 1988; Streng, 1999; Alvaro et al., 2008), *Acanthoretella, Almohadelia, Botsfordia, Eothele, Monophtalma, Vandalotreta*.

B6.—Laurentia, late Dyean – early Delamaran, Nevada, Pioche Shale (Rowell, 1980), and Harkless Formation (Skovsted and Holmer, 2006); *Dictyonyina, Eothele, Hadrotreta*.

B7.—Laurentia, Nevada, Harkless Formation (Skovsted and Holmer, 2006); *Eothele, Kyshabaktella, Hadrotreta*.

B8.—Caborca Terrane, Sonora, Cerro Prieto Formation; *Dictyonyina, Eothele, Hadrotreta, Linnarssonia, Paterina*.

**Cambrian Stage 5, Acrrothele Fauna**

C1.—Karatau-Naryn microplate; Malyi Karatau Range, *Pernopsis ultimus and Psychagnostus intermedius* biozones (Holmer et al., 2001); *Aksarinaia, Akmolina?, Canallilatus,
Kotylotreta, Kyshabaktella, Linnarssonia, Prototreta, Schizopolis, Stilpnotreta.

C2.—North Tien- Shan microplate, Kargajly Formation (Holmer et al., 2001); Anabolotreta?, Canalilatus, Conthylotreta, Kleithriatreta, Kotylotreta, Kyshabaktella, Neotreta, Paterina.

C3.—Chingiz-Tarbagatai island arcs; Tarbagatai Range, ‘Anga’ Stage (Popov et al., 1996), Acrothele, Kleithriatreta, Kostjubella, Prototreta.

C4.—Novaya Zemlya; Southern Island, Astafiev Formation (Popov, 1985); Acrothele, Acrothyra, Hadrotreta.

C5.—Laurentia; Utah, Pioche Shale (Rowell, 1980); Acrothele, Acrothyra, Amictocracens, Dictyonina, Micromitra.

C6.—Avalonia; New Brunswick (Walcott, 1912); Acrothele, Acrothyra, Botsfordia, Eoobolus, Eohadrotreta, Eothele, Micromitra, Paterina.

C7.—Western Mediterranean peri-Gondwana; Spain, Láncara Formation (Wotte and Mergl, 2007); Muerero Formation (Liñán and Mergl, 1982); Acrothele, Dictyonina, Genetreta, Iberotreta, Luhotreta, Micromitra.

C8.—Baltica, Sweden, Forsemølla Limestone Bed and erratic boulders (Streng, 1999; Streng et al., 2007), and Sablinka Formation (Gertovo Member) (Khazanovich et al., 1984); Acrothele, Canalilatus, Eoobolus, Kotylotreta, Linnarssonia, Monophthalma, Obolus, Oepikites, Vandalotreta.

C9.—Alai terrane; Kyrgyzstan, Alai Range, Pseudoanomocarina Beds (Aksarina, 1975); Acrothele, Dictyonina, Hadrotreta, Kleithriatreta, Linnarssonia, Micromitra, Paterina.

C10.—Siberia, Amga Regional Stage, composite list (Pelman, 1977; Pelman and Pereladov, 1986; Korovnikov, 1998); Acrothele, Botsfordia, Eoobolus, Eothele, Erbrotreta, Kotylotreta, Kyshabaktella, Linnarssonia, Paterina, Prototreta.

C11.—Spity, Tethyan Himalaya; Parahio Formation, Cambrian Stage 5; Acrothele, Amictocracens, Aphelotretta, Eohadrotreta, Hadrotreta, Linnarssonia, Oepikites, Paterina, Prototreta.

C12.—Central Bohemia, Czech Republic, Jince Formation (Mergl and Šlehoferová, 1990; Mergl and Kordule, 2008); Acrothele, Almohadella, Botsfordia, Hadrotreta, Lindinella, Luhotreta, Treptotreta?, Vandalotreta, Westonia.

C13.—West Antarctica, Shackleton and Argentina ranges, Unnamed Cambrian Stage 5 (Popov and Solovyev, 1981); Acrothele, Linnarssonia, Notiobolus.


C15.—South China Guizhou Province, Kaili Formation, Unnamed Cambrian Stage 5 (Zhao et al., 2011), Acrothele, Dictyonina?, Linnarssonia?, Palaeobolus (=Lingulepis), may also belong to Notiobolus Paterina? (=Micromitra). Generic assignation of so-called ‘Lingulella’ and ‘Paterina’ cannot be proved from provided descriptions and illustrations.

C16.—Caborca Terrane, Sonora, Arrojos Formation; Acrothele, Batenevotreta?, Dictyonina, Eothele, Eoobolus, Hadrotreta, Linnarssonia, Micromitra, Paterina, Prototreta.

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