



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

Authors: Holmer, Lars E., Clausen, Sébastien, Popov, Leonid E., Pour, Mansoureh Ghobadi, Liang, Yue, et al.

Source: Journal of Paleontology, 96(6) : 1264-1284

Published By: The Paleontological Society

URL: <https://doi.org/10.1017/jpa.2022.35>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

Lars E. Holmer,^{1,2*} Sébastien Clausen,³ Leonid E. Popov,⁴ Mansoureh Ghobadi Pour,^{4,5} Yue Liang,^{1,2} Zhifei Zhang,¹ Juan José Palafox Reyes,⁶ Jesús Porfirio Sosa-Leon,⁶ and Blanca Estela Buitrón-Sánchez⁷

¹State Key Laboratory for Continental Dynamics, Shaanxi Key Laboratory of Early Life & Environments, Department of Geology, Northwest University, Xi'an 710069, China <elizf@nwu.edu.cn>

²Department of Earth Sciences, Palaeobiology, SE-752 36 Uppsala, Sweden <lars.holmer@pal.uu.se>

³Université de Lille, Centre National de la Recherche Scientifique (CNRS), UMR 8198—Evo-Eco-Paleo, F-59000 Lille, France

⁴Department of Natural Sciences, National Museum of Wales, Cathays Park, Cardiff CF10 3NP, United Kingdom <leonid.popov@museumwales.ac.uk>

⁵Department of Geology, Faculty of Sciences, Golestan University, Gorgan 49138-15739, Iran; <mghobadipour@yahoo.co.uk>

⁶Universidad de Sonora, Departamento de Geología, Boulevard Luis Encinas y Rosales, 83000, Hermosillo, Sonora, Mexico; <juan.palafox@unison.mx>, <porfirio.sosa@unison.mx>

⁷Universidad Nacional Autónoma de México, Instituto de Geología, Departamento de Paleontología, Ciudad Universitaria, Delegación Coyoacán, 04510, México D. F., Mexico; <blancab@unam.mx>

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., *Hadrotreta rara?* (Cooper), and *Linnarssonina 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, *Batenevotreta? mexicana* n. sp., *Dictyonina minutipuncta* Cooper, *Eothele* sp., *Eoobolus* sp., *Hadrotreta rara?* (Cooper), *Linnarssonina 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 biostratigraphical succession of Himalaya, where the genus makes its first appearance in the *Kaotiaia 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.

UUID: <http://zoobank.org/6598f51f-cb07-4df3-bd1f-025a13e64edf>

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

*Corresponding author.

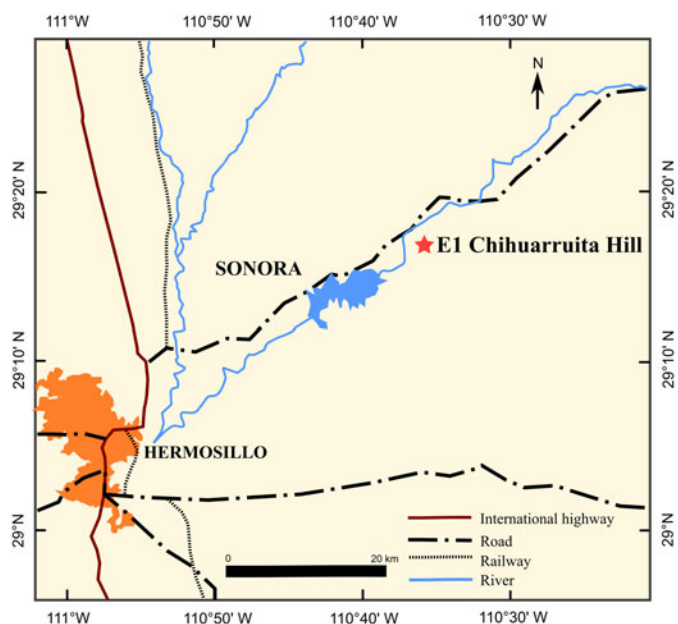


Figure 1. Geographic map of the studied area, El Chihuarruita Hill, San José de Gracia, Sonora, Mexico (modified after Cuen-Romero et al., 2022, fig.1).

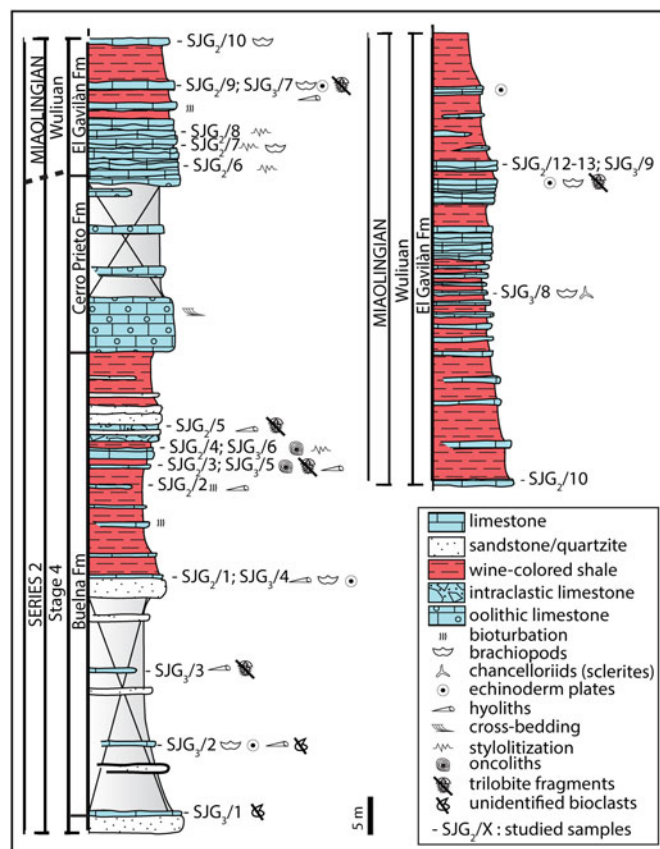


Figure 2. Stratigraphic framework and section from the El Chihuarruita Hill locality, with sampled levels.

comprehensive reports on the geological setting and stratigraphy in the general area.

The stratigraphy described in this report is based on field-work 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°34'5"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 etemini* Zone), Cape Breton Island, Canada.

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.

Formation	Buelna Formation				El Gavilán Formation					
Sample	SJG 2/2	SJG 2/3	SJG 2/6	SJG 2/7	SJG 2/9	SJG 2/12	SJG 2/13	SJG 3/7	SJG 3/8	SJG 3/9
<i>Eoobolus</i> sp.				X				X	X	
<i>Acrothele concava</i>					X		X			X
<i>Eothele</i> sp.	X						X	X		
<i>Linnarssonia arellanoi?</i>	X			X	X	X	X	X	X	X
<i>Hadrotreta rara?</i>	X		X		X	X	X	X	X	X
<i>Prototreta</i> sp.					X	X	X	X	X	X
<i>Batenevetreta? mexicana</i> n. sp.					X					
<i>Dictyonina minutipuncta</i>				X	X		X			
<i>Dictyonina</i> sp.	X									
<i>Paterina</i> sp.	X	X	X	X						
<i>Micromitra</i> sp.			X							
?Indeterminate rhynchonelliform	X	X								

Eoobolus sp.
Figure 3

Occurrence in Chihuarruita Hill outcrop.—Wuliuan 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.—USTL4031-1–4.

Remarks.—The scant available material from El Gavilán Formation (Wuliuan) 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
Figure 4

Table 2. Main dimensions and ratios of ventral and dorsal valves of *Batenevetreta? 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_a = length of ventral apical process; L_c , W_c = length and width of cardinal muscle scars; L_b = length of dorsal median buttress; L_s = length of dorsal median septum.

V	L	W	L _a	L _c	W _c	L/W	L _a /L	L _c /L	W _c /W	L _c /W _c		
N	3	3	1	1	1	2	1	1	1	1		
Mean	1145	1397	346	203	1030	82.43%	33.59%	19.71%	78.15%	19.71%		
Max	1237	1607	346	203	1030	92.18%	33.59%	19.71%	78.15%	19.71%		
Min	1030	1266	346	203	1030	76.98%	33.59%	19.71%	78.15%	19.71%		
D	L	W	L _b	L _s	L _c	W _c	L/W	L _b /L	L _s /L	L _c /L	W _c /W	L _c /W _c
N	4	4	3	3	3	3	4	3	3	3	3	3
Mean	1128	1178	339	805	232	827	94.50%	35.98%	85.81%	24.80%	90.23%	28.28%
Max	1656	1626	386	922	265	922	110.04%	41.52%	92.26%	27.27%	104.89%	33.80%
Min	770	911	265	683	210	776	81.62%	32.01%	76.45%	21.97%	65.01%	23.97%

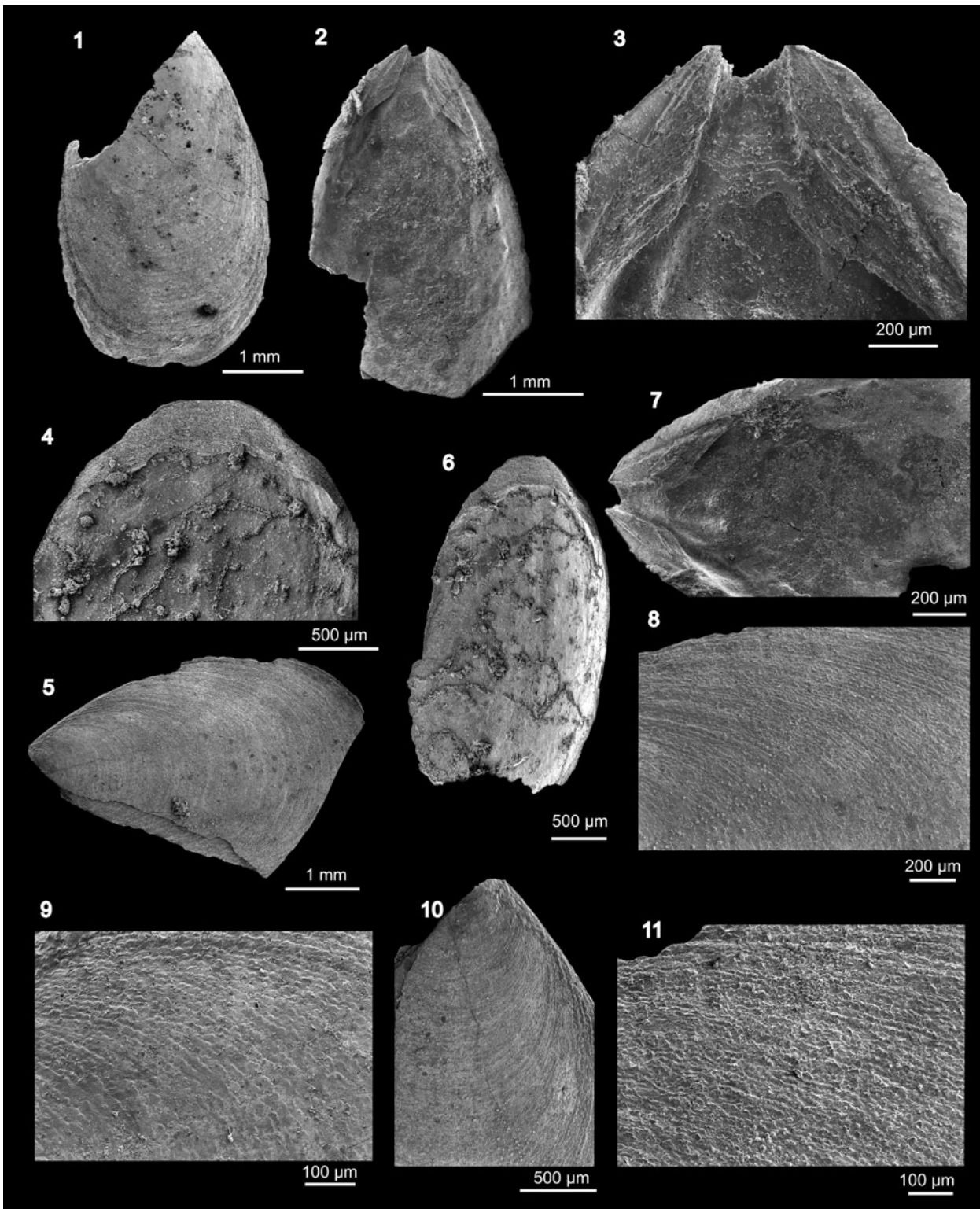


Figure 3. *Eoobolus* sp. from the El Gavilán Formation (sample SJG 3/7), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1) (USTL4031-1) Dorsal valve exterior; (2, 3, 7) (USTL4031-2) (2) ventral valve interior, (3) detail of ventral pseudointerarea, (7) oblique lateral view; (4, 6) (USTL4031-3) (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.

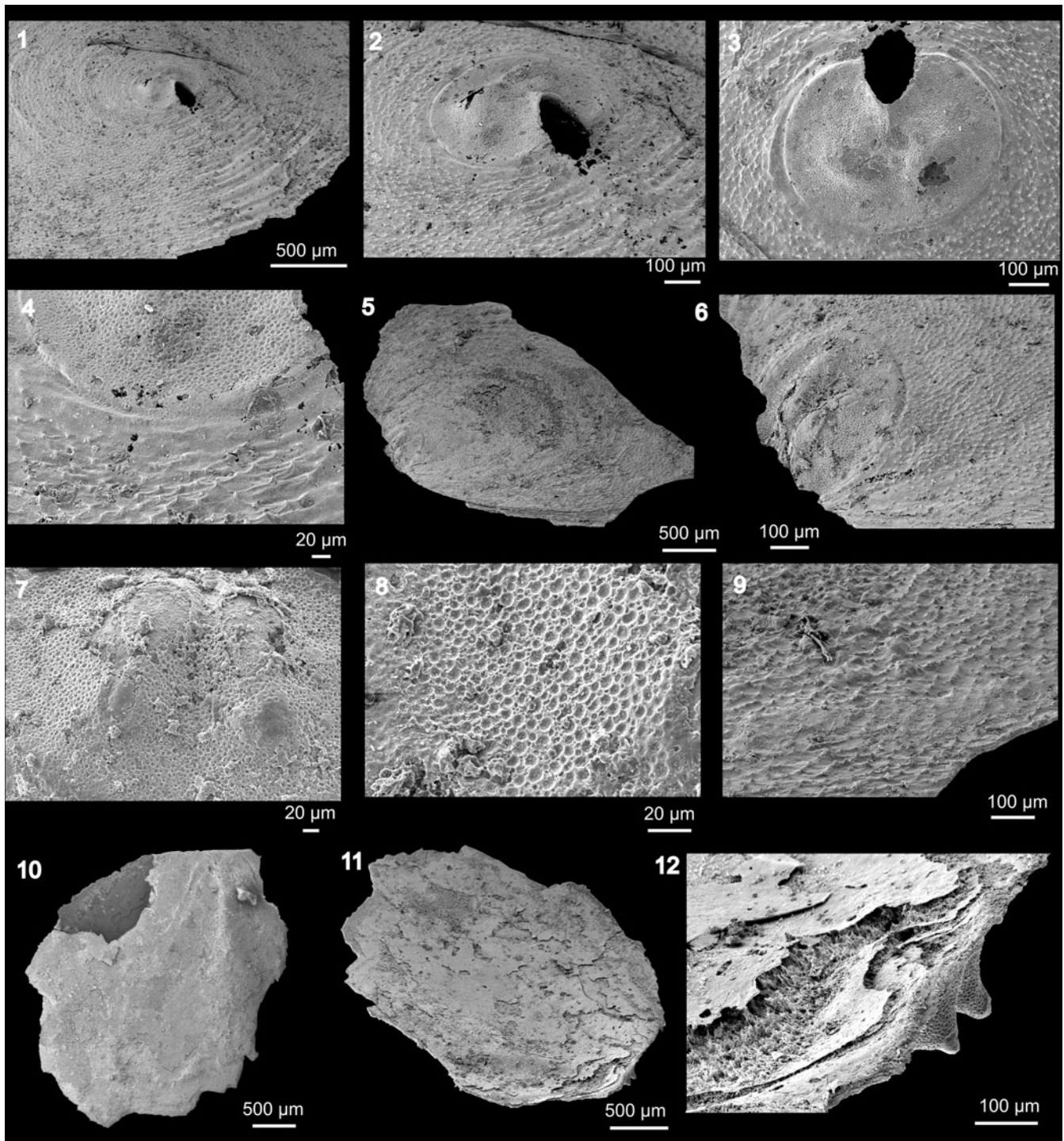


Figure 4. *Acrothele concava* Cooper in Cooper et al., 1952, from the El Gavilán Formation (sample SJG 2/9), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1–4) (USTL 4032-1) (1) Oblique posterior view of ventral valve exterior, (2) detailed view, (3) ventral metamorphic shell, (4) detail of edge of ventral metamorphic shell; (5–9) (USTL4032-2) (5) oblique lateral view of dorsal valve exterior, (6) detail of dorsal metamorphic shell, (7) detail of dorsal metamorphic shell, (8) pitted dorsal metamorphic shell, (9) pustulose adult ornamentation; (10) (USTL4032-3) dorsal valve interior; (11, 12) (USTL4032-4) (11) oblique lateral view of dorsal valve interior, (12) detail of umbo.

1952 *Acrothele concava* Cooper in Cooper et al., 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 Arjos Formation (Wuliuan), Arjos 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 fila 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 subtriangular, 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 fila 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, orthocline to apsacline; median sulcus sometimes develops 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 Guzhangian 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 also is 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 spurri* Walcott, 1908 (original designation by Rowell, 1980, p. 17); Cambrian (Series 2, *Bonnina-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 fragmented, 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. spurri* (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 Acrotretoidea Schuchert, 1893

Family Acrotretidae Schuchert, 1893

Genus *Linnarssonina* Walcott, 1885

Type species.—*Obolella transversa* Hartt in Dawson, 1868 (original designation by Walcott, 1885, p. 115); middle Cambrian of New Brunswick, Canada.

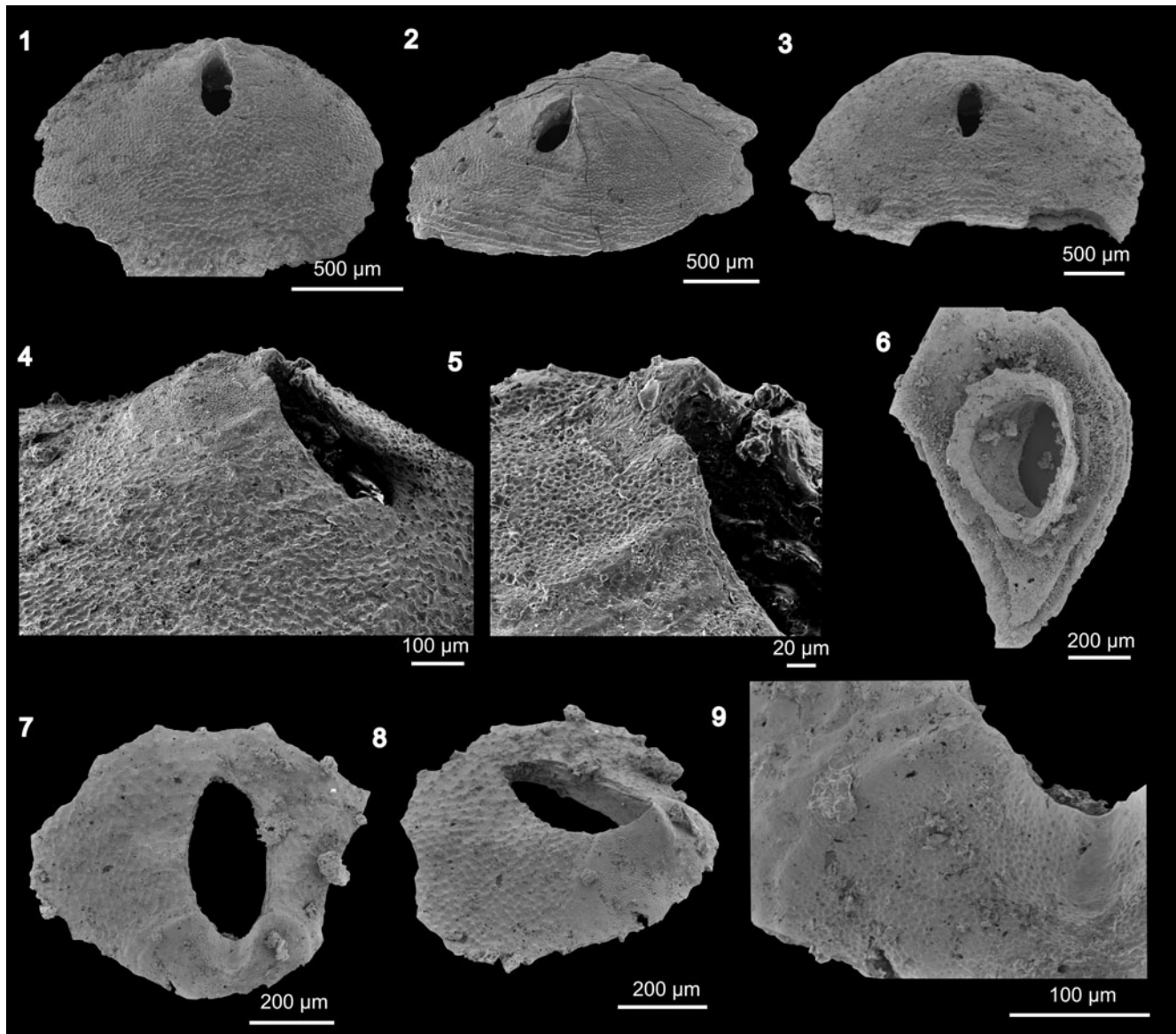


Figure 5. *Eothele* sp. from the Buelna Formation (Cambrian Stage 4; sample SJG 2/2), Chihuarruita Hill outcrop, Mexico. (1, 4, 5) (USTL4033-1) (1) Oblique posterior view of ventral valve exterior, (4) oblique lateral view of ventral apex, (5) detail of ventral metamorphic shell; (2) (USTL4033-2) oblique 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.

Linnarssonina 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 ventribiconvex 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).

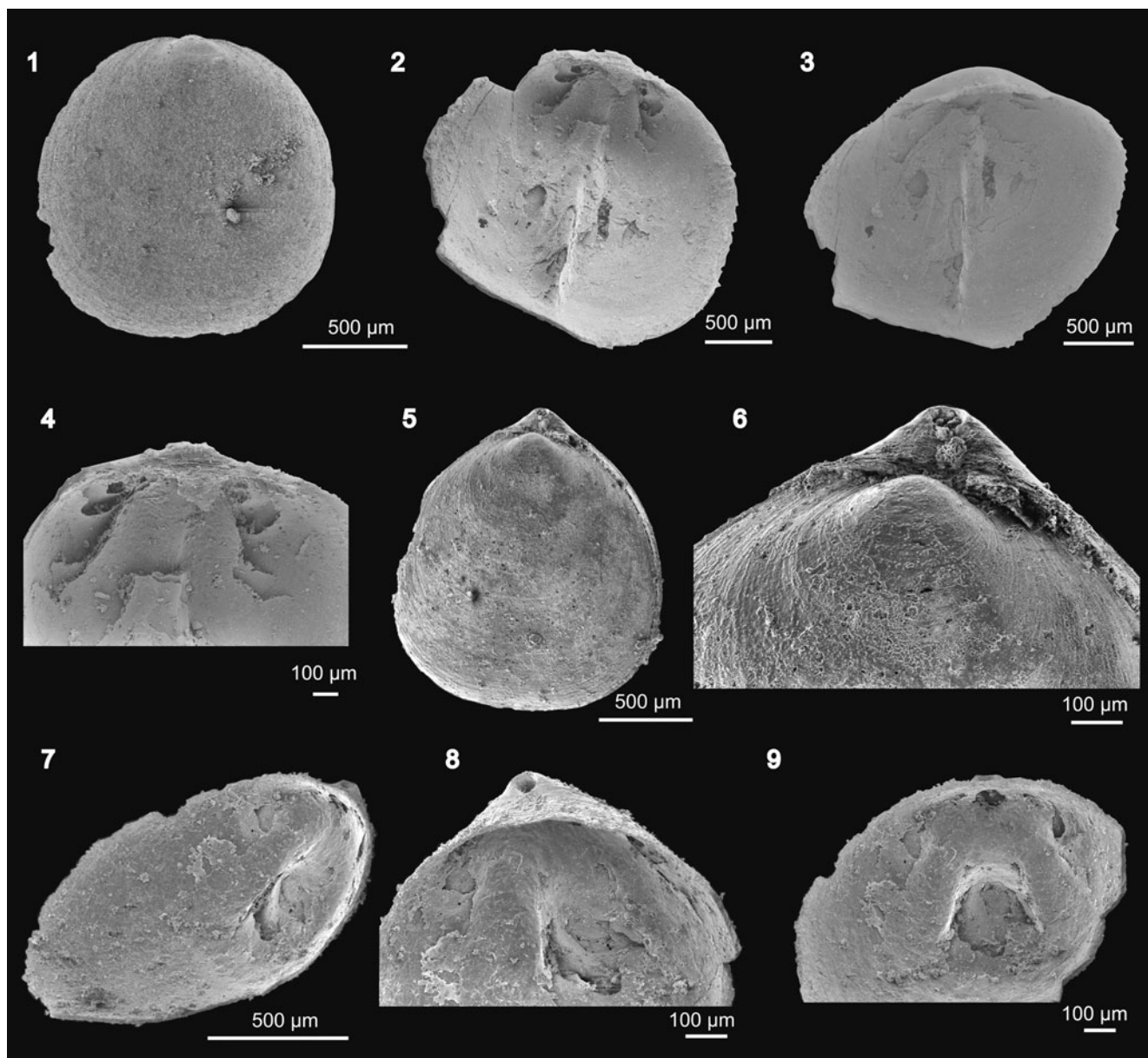


Figure 6. *Linnarssonina arellanoi*? (Cooper in Cooper et al., 1952) from the El Gavilán Formation: (1) sample SJG 2/9; (2–4), sample SJG 2/13; (5, 6), sample SJG 3/8; (7–9), sample SJG 2/7), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1) (USTL4035-1) Dorsal valve exterior; (2, 4) (USTL4036-1) (2) dorsal valve interior, (4) detail of pseudointerarea and cardinal muscle scars; (3) (USTL4036-2) dorsal valve interior; (5, 6) (USTL4036-3) (5) dorsal view of complete articulated shell, (6) detail of umbo; (7–9) (USTL4037-1) (7) oblique lateral view of ventral valve interior, (8) detail of posterior interior and pedicle foramen, (9) detail of apical process, cardinal muscle scar.

Dorsal valve with short median groove and orthocline pro-
 preas. Median groove almost four times longer 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.—*Linnarssonina* 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 *Linnarssonina*,
 and this is followed here. *Linnarssonina 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.

Linnarssonella arellanoi is similar in most characters to the somewhat younger *L. ophirensis* (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 primaeva* 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) Figure 7

?1952 *Hadrotreta rara* Cooper in Cooper et al., p. 42, pl. 12C, figs. 10–19.

Holotype.—USNM116057d, a dorsal valve (Cooper in Cooper et al., 1952, pl. 12C, fig. 18) from the uppermost Arrojos Formation (Wuliuan), Arrojos Hills, Sonora.

Diagnosis.—See Cooper in Cooper et al. (1952, p. 42).

Occurrence in Chihuarruita Hill outcrop.—Cambrian Stage 4 Buelna Formation (samples SJG 2/2) and Wuliuan El Gavilán Formation (samples SJG 2/6, 2/9, 2/13, 3/7, 3/8, 3/9.).

Description.—Shell ventribiconvex, subcircular in outline.

Ventral valve cone-shaped with rounded to subrectangular outline (length 863 μ m–1.8 mm, width 858 μ m–1.9 mm), ~71–102% as long as wide; maximum width about mid-valve (Fig. 7.3, 7.6). Ventral pseudointerarea poorly defined, subtriangular, and procline to apsacline, but with well-developed narrow intertrough that runs from the margin to the pedicle opening. Ventral metamorphic shell convex and circular. Oval pedicle foramen situated outside the metamorphic shell (Fig. 7.7–7.9). Ventral interior poorly preserved in most specimens, with well-defined pedicle tube, a pair of cardinal muscle scars, and well-developed apical process anterior to the foramen. Apical pits placed directly lateral to pedicle foramen (Fig. 7.11).

Dorsal valve convex, subcircular in outline (length 1.1–1.8 mm, width 1.2–2.1 mm), ~83–88% as long as wide, width with flat posterior part. Dorsal metamorphic shell with shallow median sulcus extending from metamorphic shell to anterior margin (Fig. 7.1, 7.10).

Dorsal pseudointerarea anacline, median groove occupying total width of posterior margin, but shortly developed along posterior-anterior axis. Median groove, wide, triangular, supported by median buttress, which is fused with a median septum. Triangular median septum extending for ~65–75% of the total valve length. Dorsal cardinal muscle scars bean-shaped, located directly anterior to propleas (Fig. 7.2, 7.4, 7.5).

Figured material.—USTL4038-1–6.

Remarks.—As discussed above, *Hadrotreta* can be difficult to distinguish from *Linnarssonella* (= *Pegmatreta* Bell, 1941;

Holmer and Popov, 2000). *Pegmatreta rara* Cooper in Cooper et al., 1952, has never been re-studied, but the illustrations and description (Cooper in Cooper et al., 1952, pl. 12C, figs. 10–19) appear to be very similar in all morphological details—including the shape of the shell, dorsal pseudointerarea, and dorsal median septum (Fig. 7.1–7.6). The new Sonoran material is tentatively considered to be conspecific, pending restudy, and it is placed within *Hadrotreta* based on the presence of an oval pedicle foramen situated outside the metamorphic shell (Fig. 7.9), widely spaced dorsal cardinal scars (Fig. 7.2, 7.4, 7.5), and deep apical pits directly lateral to the internal pedicle tube (Fig. 7.11), as well as having a low dorsal median ridge (Fig. 7.4, 7.5). However, the ventral interior is comparatively poorly preserved in the available specimens and the characteristic boss-like apical process is not well seen (Fig. 7.11). *Hadrotreta rara*? 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 (*Bathyriscus* Zone), Montana, USA.

Prototreta sp. Figure 8

Occurrence in Chihuarruita Hill outcrop.—Wuliuan El Gavilán Formation (samples SJG 2/9, 2/13, 3/7, 3/8, 3/9).

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 (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,

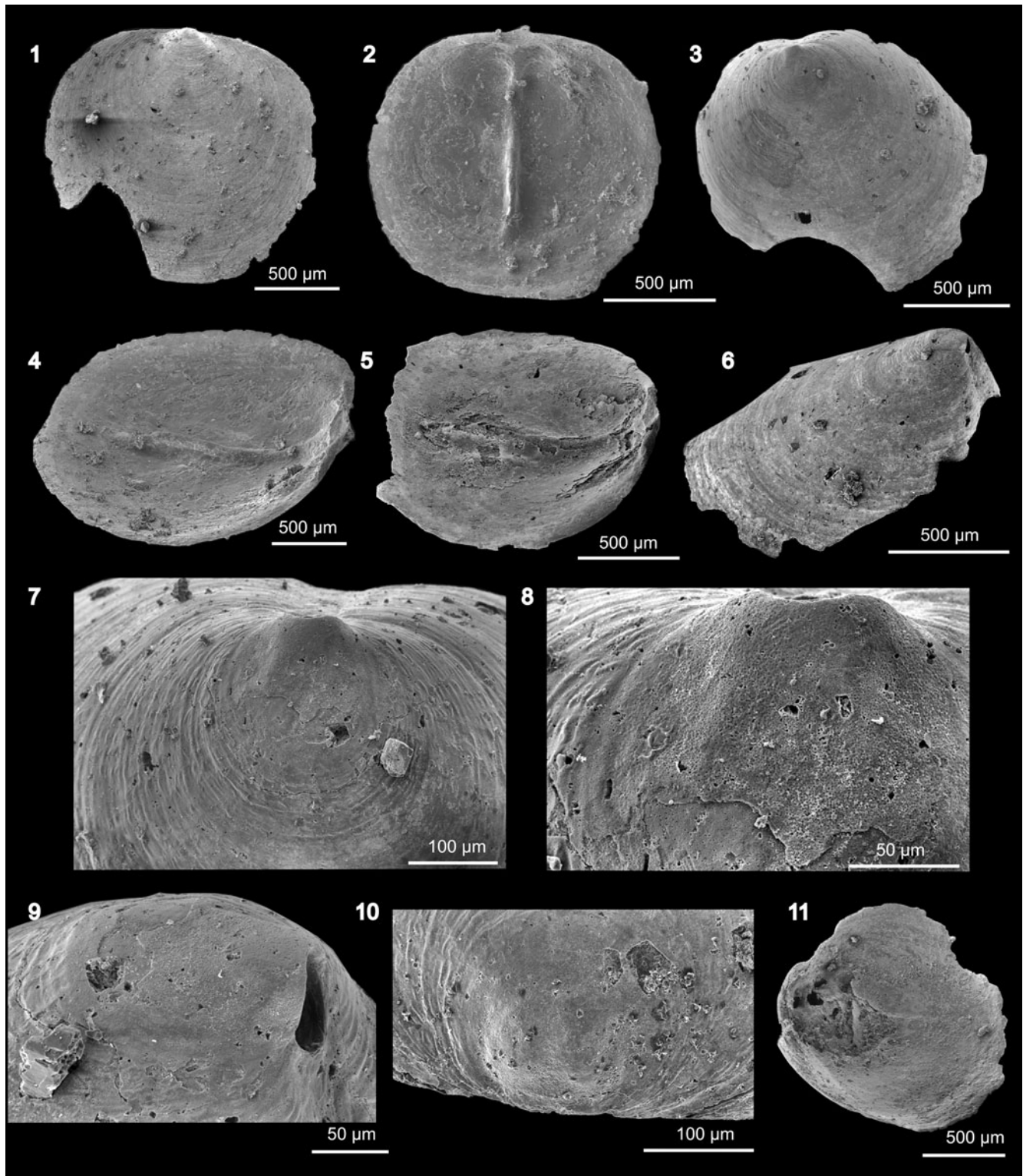


Figure 7. *Hadrotreta rara?* (Cooper in Cooper et al., 1952) from the Buelna Formation (Cambrian Stage 4; sample SJG 2/2), Chihuarruita Hill outcrop, Mexico. (1, 10) (USTL4038-1) (1) Dorsal valve exterior, (10) oblique posterior view of dorsal metamorphic shell; (2, 4) (USTL4038-2) (2) dorsal valve interior, (4) oblique lateral view; (3) (USTL4038-3) ventral valve exterior; (5) (USTL4038-4) oblique lateral view of dorsal valve interior; (6–9) (USTL4038-5) (6) oblique lateral view of ventral valve exterior, (7) detail of umbo, (8) detail of ventral metamorphic shell, (9) oblique lateral view of umbo; (11) (USTL4038-6) oblique lateral view of ventral valve interior.

respectively; anacoline 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 ~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).

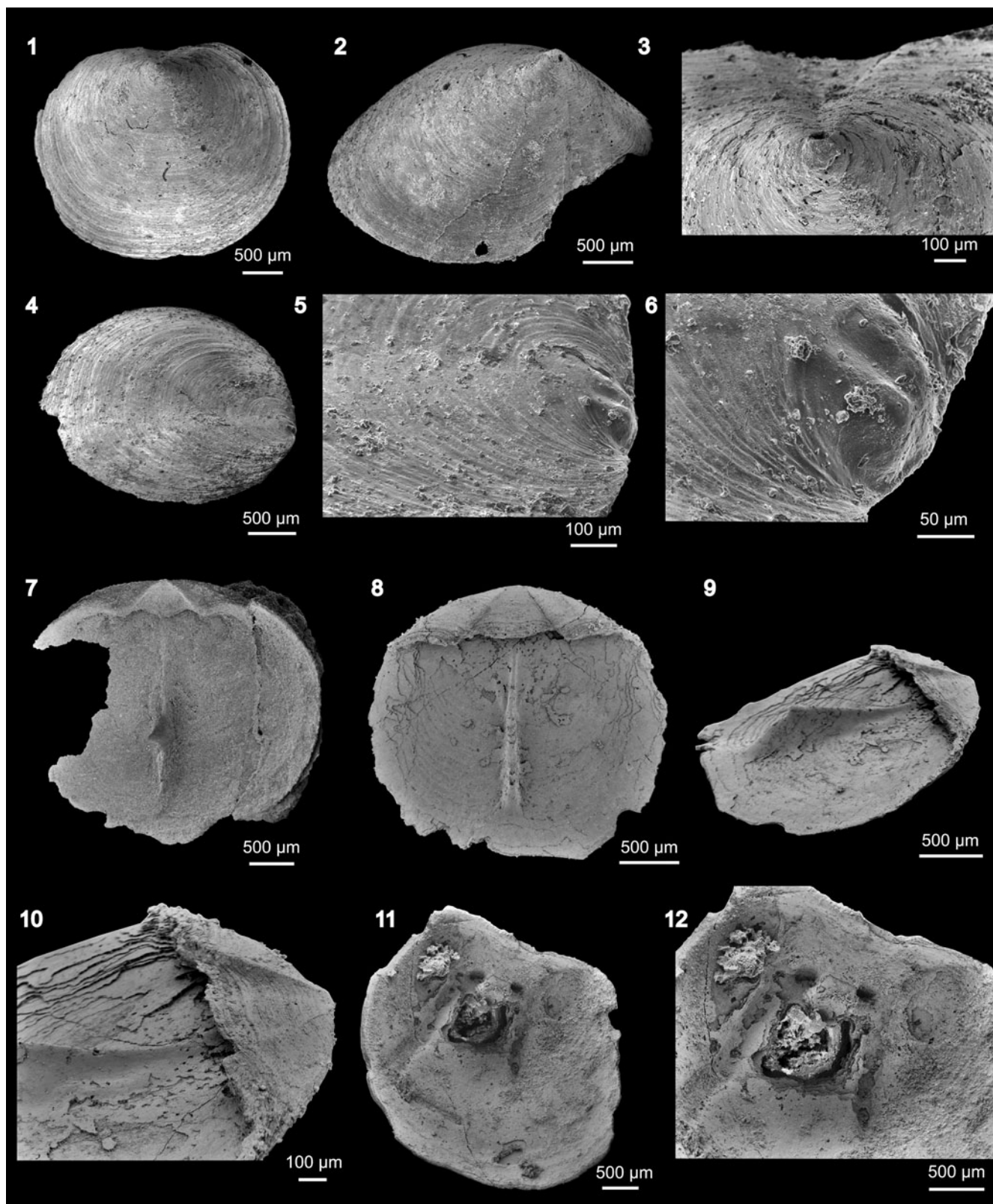


Figure 8. *Prototreta* sp. from the El Gavilán Formation (sample SJG 2/13), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1–3) (USTL4039-1) (1) ventral valve exterior, (2) oblique posterolateral view, (3) detail of umbo, (4–6) (USTL4039-2) (4) oblique lateral view dorsal valve exterior, (5) 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. flabellum* Bell, 1941, but more similar to *P. interrupta* Bell, 1941, and *P. mimica* 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 Scaphelasmataidae 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 SJG 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 Chihuarruita Hill outcrop.—Wuliuan El Gavilán Formation (sample SJG 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 μ m wide); pitted ornamentation poorly preserved (Fig. 9.11, 9.12). Foramen circular (~60 μ m 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 μ m–1.66 mm, width 911 μ m–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, extending for ~25% and 90% of total valve length and width, respectively (Fig. 9.2, 9.5, 9.7). Dorsal median ridge low and long, extending for ~86% of total valve length. Dorsal anterolateral muscle scars located directly lateral to the median ridge (Fig. 9.2, 9.5, 9.7).

Etymology.—From the occurrence in Mexico.

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

Remarks.—*Batenevotreta* is a rare and early member of the Scaphelasmataidae, 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 Georgina 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 Scaphelasmataidae, 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 Paterinoidea 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).

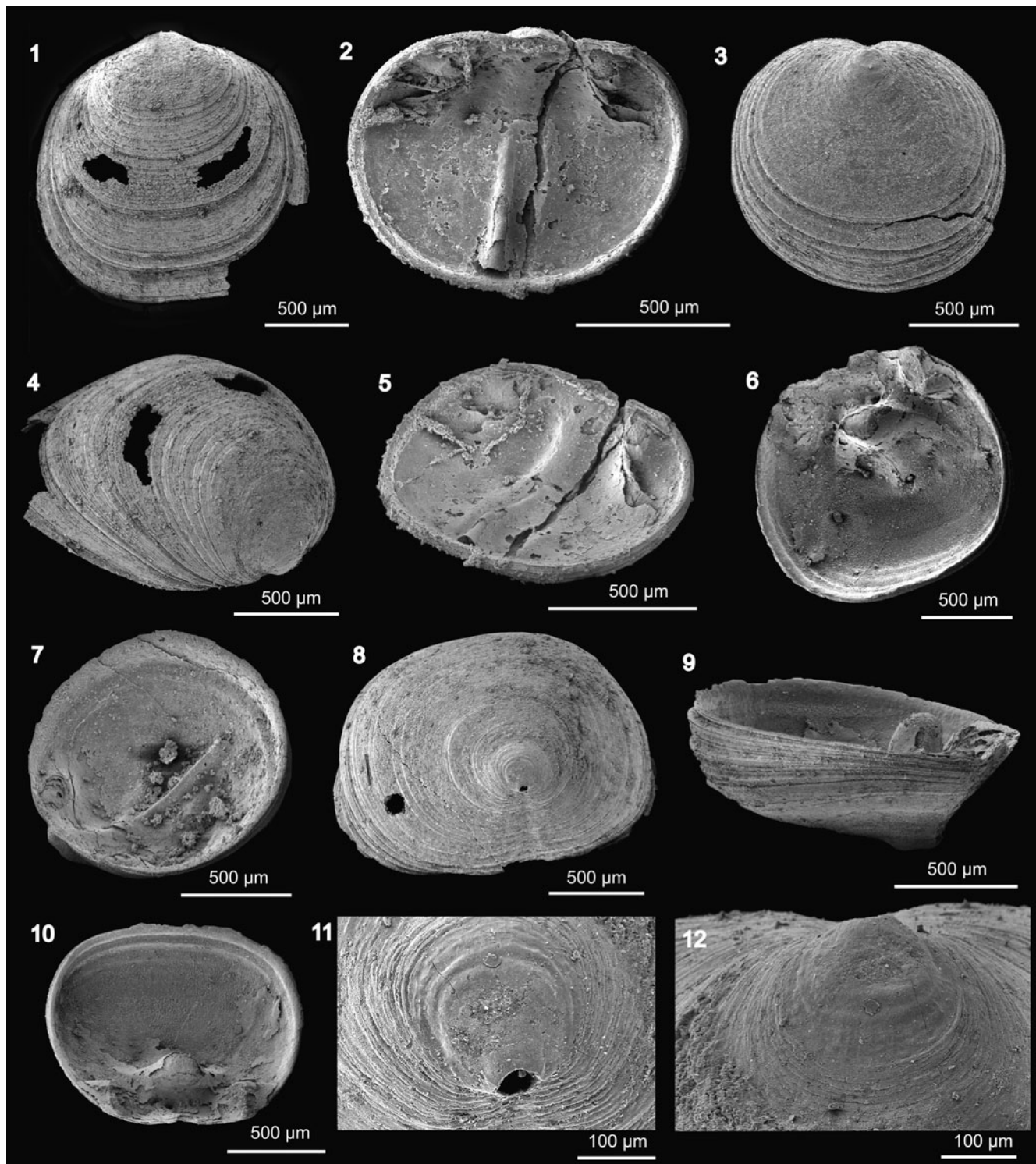


Figure 9. *Batenevotrete? mexicana* n. sp., from the El Gavilán Formation (sample SJG 2/9), Cambrian (Wuliuan), Chihuarruita Hill outcrop, Mexico. (1, 4) (USTL4040-1) (1) Dorsal valve exterior, (4) oblique posterolateral view; (2, 5) (USTL4040-2) (2) dorsal valve interior; (3) (USTL4040-3) ventral valve exterior, (5), oblique anterolateral view; (6, 9, 10) (USTL4040-4) ventral valve interior, (9) oblique lateral view, (10) oblique posterior view; (7) (USTL4040-5) oblique lateral view of dorsal valve interior; (8, 11, 12) (USTL4040-6) holotype, oblique posterolateral view of ventral valve exterior, (11) oblique posterolateral view of ventral metamorphic shell, (12) detail of umbo.

Genus *Dictyonina* Cooper, 1942

Dictyonina minutipuncta Cooper in Cooper et al., 1952
Figure 10.1–10.9

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

1952 *Dictyonina minutipuncta* Cooper in Cooper et al., p. 40, pl. 11A, figs. 1–6.

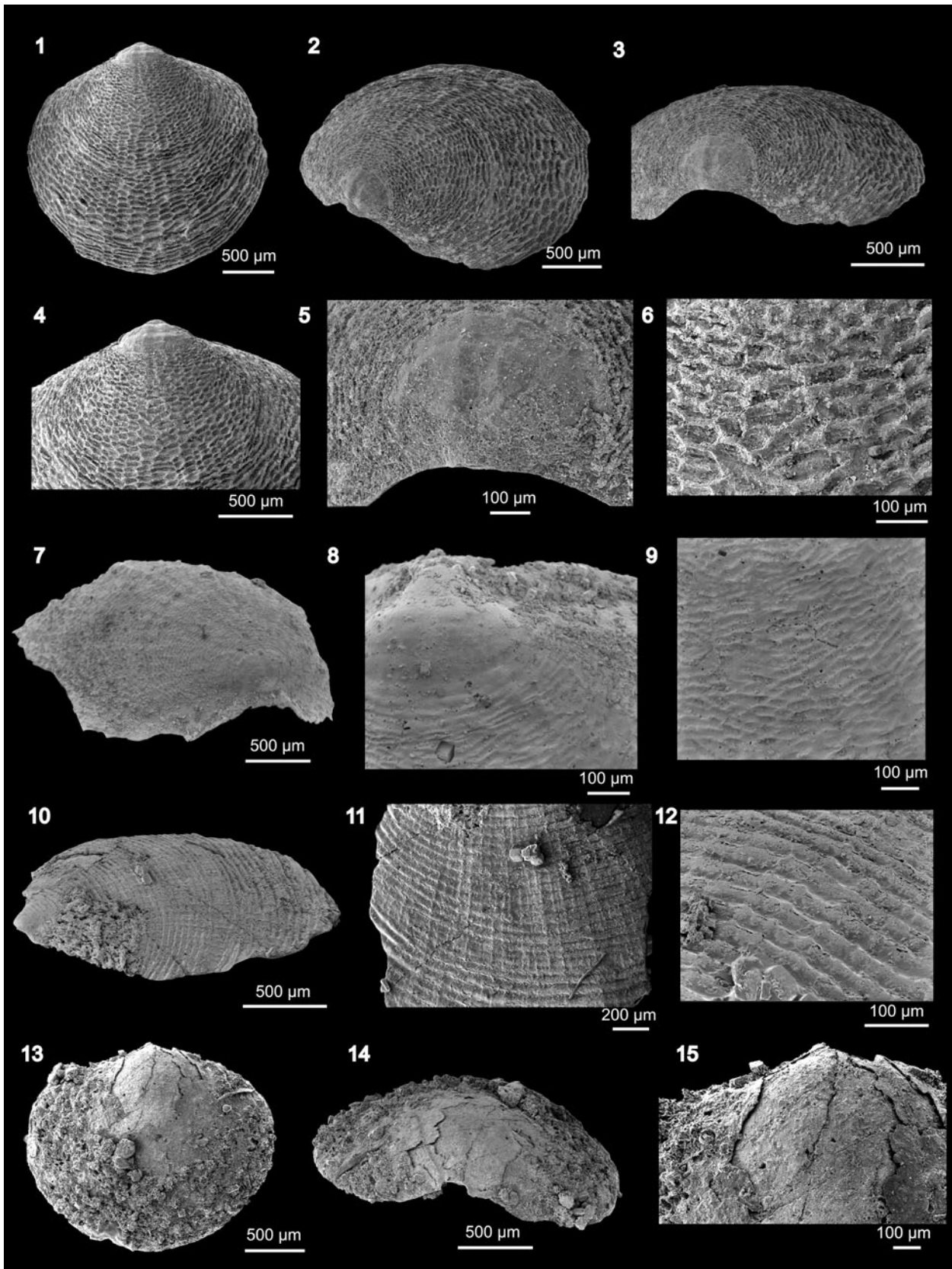


Figure 10. *Dictyonina minutipuncta* (1–9) Cooper in Cooper et al., 1952, from the Cambrian (Wuliuan) El Gavilán Formation: (1–6) sample SJG 2/9, (7–9) sample SJG 2/7); *Paterina* sp. (10–12) and an unidentified Paterinidae (13–15) from the Cambrian Stage 4 Buelna Formation (sample SJG 2/2), Chihuarruita 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) (7) 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 Chihuarruita 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 pannula* (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).

?Subphylum Rhynchonelliformea Williams et al., 1996

?Indeterminate rhynchonelliform

Figure 11

Remarks.—The studied material also includes possible rhynchonelliform brachiopods represented by internal molds that are too poorly preserved for closer taxonomic discrimination (Fig. 11).

Biogeographical 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*?, *Linnarssonina 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*, *Batenevotreta? mexicana* n. sp., *Dictyonina minutipuncta*, *Eothele* sp., *Eoobolus* sp., *Hadrotreta rara*?, *Linnarssonina 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—*Oryctocephalus 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 its first appearance in the *Kaotaia 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 heterogeneous 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 Sub-cluster B₂. Cluster B is composed of the individual faunas from

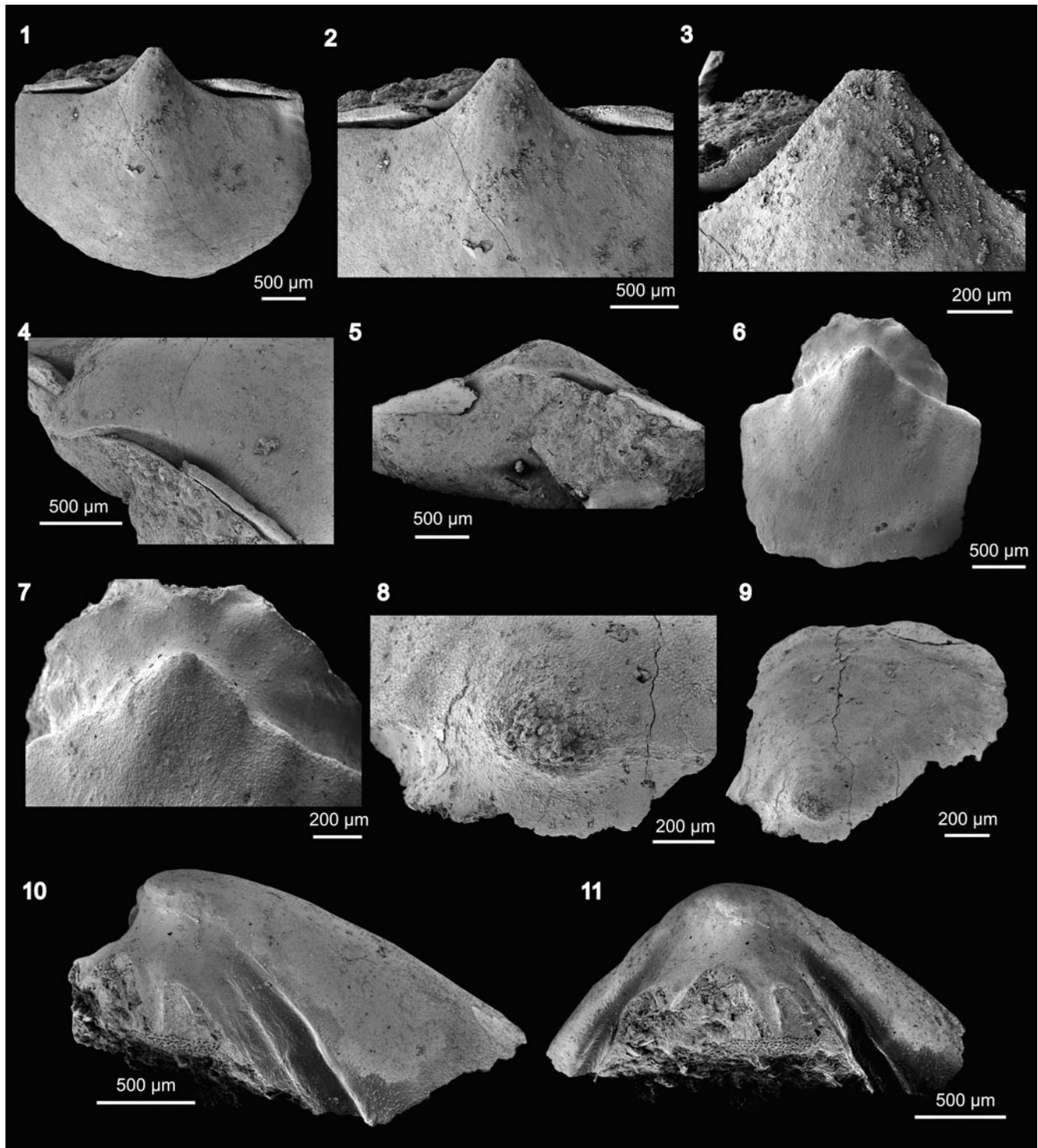


Figure 11. ?Indeterminate rhynchonelliform, from the Buelna Formation (Cambrian Stage 4; sample SJG 2/2), Chihuarruita Hill outcrop, Mexico. (1–5) (USTL4043-3) (1) Internal mold of ventral valve, (2) detail of umbo, (3) detail of umbo, (4) oblique lateral view of umbo, (5) posterior view of umbo; (6, 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.

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.

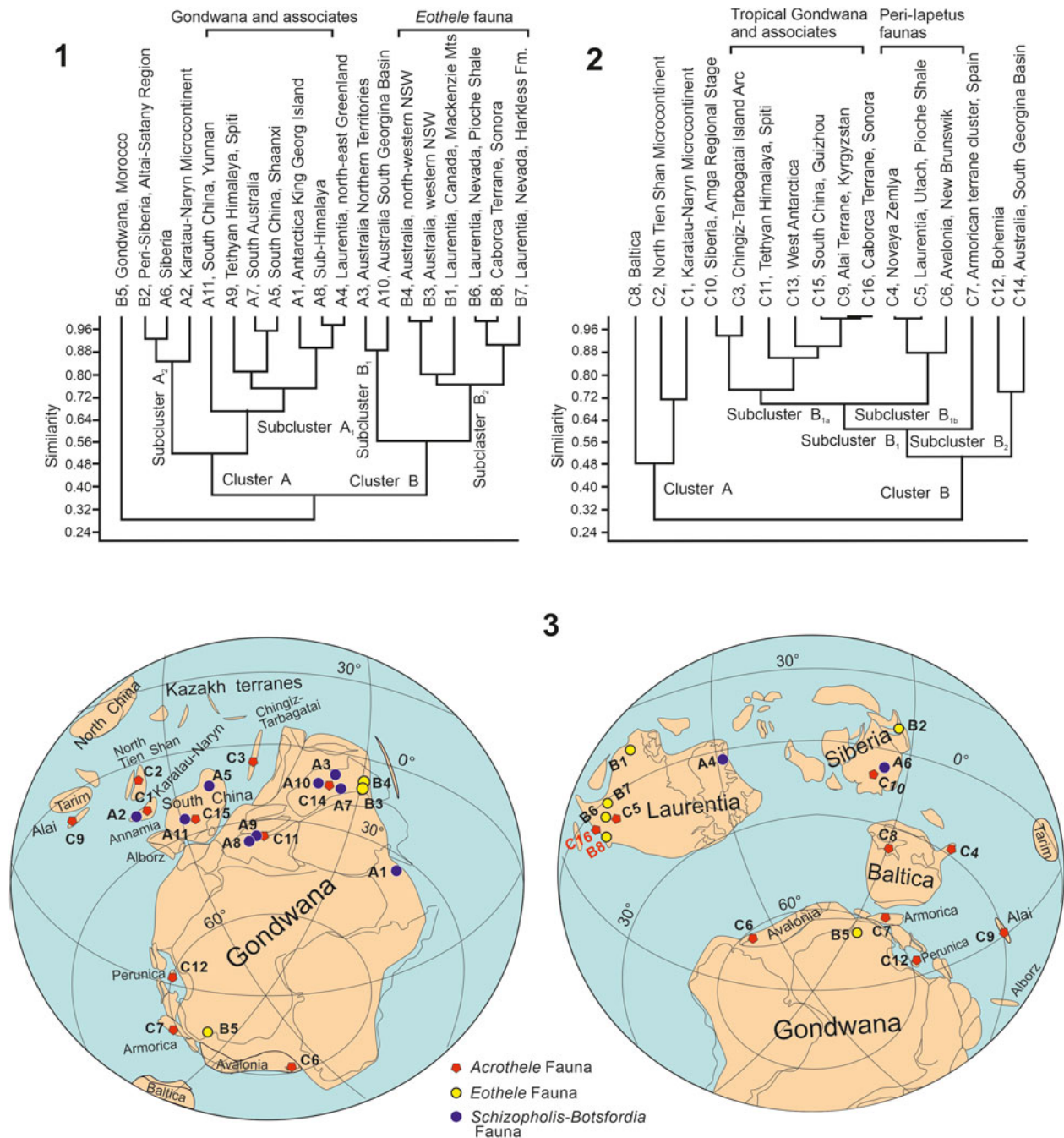


Figure 12. Results of the pair-group cluster analysis for presence-absence data (Raup-Crick similarity) for the Cambrian linguliform genera (Cambrian Stages 4 and Wuliuan) from 26 localities (for details see Appendix; see also Popov et al., 2015). (1) Cambrian Stage 4 and *Eothele* Fauna; (2) Cambrian Wuliuan. (3) Paleogeographical reconstruction for Cambrian Stage 4 showing geographical distribution of the localities used in cluster analysis. Relative position of major early Paleozoic continents (Laurentia, Baltica, Gondwana, and Siberia) mainly after Cocks and Torsvik (2002), with significant emendations for Australasian peri-Gondwana.

(2015) 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 acrotretides. 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 to the North African sector of Gondwana through the Cambrian (Cocks and Torsvik, 2002; Fig. 12.3). A cluster of the Wuliuan peri-Iapetus faunas also was recognized earlier 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.

Acknowledgments

LD benefited from funding from the Alexander von Humboldt Foundation and SC from a grant from Spanish Ministry of Economics, Finance and Competitiveness CGL2017-87631-P. The study was supported by projects UNAM-DGAPA-PAPIIT No. IN105012, CONACyT No. 165826, and ECOS-France-Mexico No. M13U01, and by the National Natural Science Foundation of China (NSFC 41720104002, 41890844, 41425008, and 41621003), by Strategic Priority Research Program of Chinese Academy of Sciences (Grant XDB26000000), by Program of

Introducing Talents of Discipline to Universities (the 111 Project D17013). The research of LEH was supported by the Swedish Research Council (VR Project no. 2018-03390) and by a Zhongjian Yang Scholarship from the Department of Geology, Northwest University, Xi'an. Many thanks to the editor S. Zamora, as well as the reviewers M. Mergl and R. Freeman for valuable comments that greatly improved the manuscript.

References

- Aksarina, N.A., 1975. Brakhiopody [Brachiopods], in Repina, L.N., Yaskovich, B.V., Aksarina, N.A., Petrunina, Z.E., Ponilenko, I.A., Rubanov, D.A., Bologova, G.V., Golikov, A.N., Hajrullina, T.I., and Posochova, M.M., *Stratigrafiya i fauna nizhnego paleozoya severnykh predgoriy Turkestanskogo i Alayskogo khrebtov (yuzhnyy Tyan'-Shan')* [Stratigraphy and fauna of the lower Paleozoic of the northern submontane belt of Turkestan and Alai ridges (southern Tyan-Shan)]: Akademiya Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki, v. 278, p. 91–100. [in Russian]
- Álvarez, J.J., Ezzouhairi, H., Ayad, N.A., Charif, A., Popov, L.E., and Ribeiro, M.L., 2008. Short-term episodes of carbonate productivity in a Cambrian uplifted rift shoulder of the Coastal Meseta, Morocco: Gondwana Research, v. 14, p. 410–428.
- Bell, W., 1938. *Prototreta*, a new genus of brachiopod from the middle Cambrian of Montana: Papers of the Michigan Academy of Science, Arts and Letters, v. 23, p. 403–408.
- Bell, W., 1941. Cambrian Brachiopoda from Montana: Journal of Paleontology, v. 15, p. 193–255.
- Brock, G.A., and Percival, I.G., 2006. Cambrian stratigraphy and faunas at Mount Arrowsmith, northwestern New South Wales: Memoirs of the Association of Australasian Palaeontologists, v. 32, p. 75–101.
- Cocks, L.R.M. and Torsvik, T.H., 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review: Journal of the Geological Society (London), v. 159, p. 631–644.
- Cooper, G.A., 1942. New genera of North American brachiopods: Journal of the Washington Academy of Sciences, v. 32, p. 228–235.
- Cooper, G.A., Arellano, A.R.V., Johnson, J.H., Okulitch, V.J., Stoyanow, A., and Lochman, C., 1952. Cambrian stratigraphy and paleontology near Caborca, Northwestern Sonora, Mexico: Smithsonian Miscellaneous Collections, v. 119, p. 1–184.
- Cuen-Romero, F.J., Valdez, J.E., Buitrón, B.E., Monreal, R., Sundberg, F., Montijo-González, A., and Minjarez-Sosa, I., 2016. Cambrian stratigraphy of San José de Gracia, Sonora, México: El Gavilán Formation, a new middle Cambrian lithostratigraphic unit of open shelf environment: Boletín de la Sociedad Geológica Mexicana, v. 68, p. 429–441.
- Cuen-Romero, F.J., Valdez-Holguín, J.E., Buitrón-Sánchez, B.E., Monreal, R., Enríquez-Ocaña, L.F., Aguirre-Hinojosa, E., Ochoa-Granillo, J.A., and Palafox-Reyes, J.J., 2018. Trilobite-based biostratigraphy (Arthropoda-Trilobita) and related faunas of the Cambrian from Sonora, Mexico: Journal of South American Earth Sciences, v. 83, p. 227–236.
- Cuen-Romero, F.J., Valdez-Holguín, J.E., Buitrón-Sánchez, B.E., Monreal, R., Enríquez-Ocaña, L.F., Hinojosa, E.A., Ochoa-Granillo, J.A., Grijalva-Noriega, F.J., and Palafox Reyes, J.J., 2019. Paleocology of Cambrian communities of central Sonora, Mexico: paleoenvironmental and biostratigraphic considerations: Journal of South American Earth Sciences, v. 92, p. 631–645.
- Cuen-Romero, F.J., Reyes-Montoya, D.R., and Noriega-Ruiz, H.A., 2020. El Paleozoico inferior de Sonora, México: 120 años de investigación paleontológica: Paleontología Mexicana, v. 9, p. 21–35.
- Cuen-Romero, F.J., Reyes-Montoya, D.R., and Noriega-Ruiz, H.A., 2022. Cambrian (Series 2 to Miaolingian) platform facies from central Sonora, Mexico and the regional correlation: Palaeoworld, v. 31, p. 41–57.
- Dawson, J.W., 1868. Acadian Geology; the geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick, and Prince Edward Island: London, Macmillan, 694 p.
- Devaere, L., Clausen, S., Sosa-Leon, J.P., Palafox-Reyes, J.J., Buitrón-Sánchez, B.E., and Vachard, D., 2019. Early Cambrian small shelly fossils from northwestern Mexico: biostratigraphic implications for Laurentia: Palaeontologica Electronica, v. 22.2.41A, p. 1–60. <https://doi.org/10.26879/880>.
- Gorjansky, V.Y., and Popov, L.E., 1985. [The morphology, systematic position and origin of inarticulate brachiopods with calcareous shells]: Palaeontologicheskij Zhurnal, v. 3, p. 3–14. [in Russian]
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis: Palaeontologica Electronica, v. 4.1.4, p. 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

- Holmer, L.E., and Popov, L.E., 2000, Class Lingulata, in Williams, A., Brunton, C.H.C., and Carlson, S.J., eds., Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised), Volume 2: Boulder, Colorado and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. H20–H146.
- Holmer, L.E., Popov, L.E., and Wrona, R., 1996, Early Cambrian lingulate brachiopods from glacial erratics of King George Island (South Shetland Islands), Antarctica: *Palaeontologia Polonica*, v. 55, p. 37–50.
- Holmer, L.E., Popov, L.E., Koneva, S.P., and Bassett, M.G., 2001, Cambrian–Early Ordovician brachiopods from Malý Karatau, the western Balkash region, and Tien Shan, central Asia: The Palaeontological Association, Special Papers in Palaeontology, v. 65, p. 1–180.
- Holmer, L.E., Popov, L.E., Ghobadi Pour, M., Klishevich, L.A., Liang, Y., and Zhang, Z., 2020, Linguliform brachiopods from the Cambrian (Guzhangan) Karpinsk Formation of Novaya Zemlya: *Papers in Palaeontology*, v. 6, p. 571–592.
- Khazanovitch, N.K., Popov, L.E., and Melnikova, L.M., 1984, [Inarticulate brachiopods, ostracods (Bradoriida), and hyolithelminthes from the Sablino Suite of Leningrad District]: *Paleontologicheskii Zhurnal*, v. 4, p. 33–47. [in Russian]
- Koneva, S.P. and Ushatinskaya, G.T., 2010, New brachiopod species from the Order Acrotretida from the Cambrian of central Kazakhstan: *Paleontological Journal*, v. 44, p. 632–643.
- Korovnikov, I.V., 1998, [Phylogeny of early and middle Cambrian acrotelid brachiopods]: *Geologiya i Geofizika*, v. 39, p. 158–170. [in Russian]
- Kruse, P.D., 1990, Cambrian palaeontology of the Daly Basin: Northern Territory Geological Survey, v. 7, 58 p.
- Kruse, P.D., 1991, Cambrian fauna of the Top Springs Limestone, Georgina Basin: The Beagle, Records of the Northern Territory Museum of Arts and Sciences, v. 8, p. 169–188.
- Kruse, P.D., 1998, Cambrian palaeontology of the eastern Wiso and western Georgina basins: Northern Territory Geological Survey, Report, v. 9, p. 1–68.
- Kuhn, O., 1949, *Lehrbuch der Paläozoologie*: Stuttgart, Schweizerbart, 326 p.
- Li, G., and Holmer, L.E., 2004, Early Cambrian lingulate brachiopods from the Shaanxi Province, China: *GFF*, v. 126, p. 193–211.
- Liang, Y., Holmer, L.E., Duan, Xiaolin, D., and Zhang, Z., 2022, Brachiopods from the Latham Shale Lagerstätte (Cambrian Series 2, Stage 4) and Cadiz Formation (Miaolingian, Wuliuan), California: *Journal of Paleontology*, v. 96, p. 61–80.
- Liñán, E., and Mergl, M., 1982, Lower Cambrian brachiopods of Sierra Morena, SW Spain: *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica*, v. 80, p. 207–220.
- Linnarsson, J.G.O., 1876, On the Brachiopoda of the *Paradoxides* Beds of Sweden: Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar, v. 3, p. 1–34.
- Matthew, G.F., 1902, Ostracoda of the basal Cambrian rocks in Cape Breton: *Canadian Record of Science*, v. 8, p. 437–470.
- McMenamin, M.A.S., 1984, Paleontology and stratigraphy of lower Cambrian and upper Proterozoic sediments, Caborca Region Northwestern Sonora, Mexico [PhD thesis]: Santa Barbara, California, University of California, Santa Barbara, 218 p.
- Menke, C. T., 1828, *Synopsis Methodica Molluscorum Generum Omnium et Specierum Earum, quae in Museo Menkeano Adservantur*: Pyramonti, G. Uslar, 91 p.
- Mergl, M., 1988, Inarticulate brachiopods of early middle Cambrian age from the High Atlas, Morocco: *Věstník Ústředního Ústavu Geologického*, v. 63, p. 291–295.
- Mergl, M., and Kordule, V., 2008, New middle Cambrian lingulate brachiopods from the Skryje-Týřovice area (central Bohemia, Czech Republic): *Bulletin of Geosciences*, v. 83, p. 11–22.
- Mergl, M., and Šlechťerová, P., 1990, Middle Cambrian inarticulate brachiopods from central Bohemia: *Sborník Geologických Věd. Paleontologie*, v. 31, p. 67–104.
- Nardin, E., Almazán-Vázquez, E., and Buitrón-Sánchez, B.E., 2009, First report of *Gogia* from the early–middle Cambrian of Sonora, with biostratigraphical and palaeoecological comments: *Geobios*, v. 42, p. 233–242.
- Noriega-Ruiz, H.A., Cuen-Romero, F.J., Enríquez-Ocaña, L.F., Sundberg, F.A., Monreal, R., Varela-Romero, A., Palafox-Reyes, J.J., Grijalva-Noriega, F.J., 2020, Cambrian stratigraphy (Series 2 to Miaolingian) of the El Sahuaral area in central Sonora, Mexico: biostratigraphic implications: *Journal of South American Earth Sciences*, v. 103, 1027987. <https://doi.org/10.1016/j.jsames.2020.102797>.
- Oehlert, D.P., 1887, Brachiopodes, in Fischer, P., ed., *Manuel de Conchyliologie et de Paleontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles*: Paris, F. Savy, p. 1189–1334.
- Peel, J.S., Streng, M., Geyer, G., Kouchinsky, A., and Skovsted, C.B., 2016, *Ovatortyocara granulata* assemblage (Cambrian Series 2-Series 3 boundary) of Løndal, North Greenland: *Memoir of the Association of Australasian Palaeontologists*, v. 49, p. 241–282.
- Pelman, Y.L., 1977, [Early and middle Cambrian inarticulate brachiopods of the Siberian Platform]: *Trudy Instituta Geologii i Geofiziki Akademii Nauk SSSR, Sibirskoe Otdelenie*, v. 316, p. 1–168. [in Russian]
- Pelman, Y.L., and Pereladov, V.S., 1986, [The lower to middle Cambrian stratigraphy and brachiopods of the Arga-Sala River (Southern Trans-Anabar Region)]: *Trudy Instituta Geologii i Geofiziki Sibirskoi Otdeleny Akademii Nauk SSSR*, v. 669, p. 119–154. [in Russian]
- Percival, I.G., and Kruse, P.D., 2014, Middle Cambrian brachiopods from the southern Georgina Basin of central Australia: *Memoirs of the Association of Australasian Palaeontologists*, v. 45, p. 349–402.
- Popov, L.E., 1985, [Cambrian inarticulate brachiopods from northwestern part of Southern Island of Novaya Zemlya archipelago], in Bondarev, V.E., ed., *Stratigraphy and Fauna of the Palaeozoic of Novaya Zemlya: Sevmorgeologiya*, Leningrad, p. 17–30. [in Russian]
- Popov, L.E., and Solovyev, I.A., 1981, [Middle Cambrian inarticulate brachiopods, cancelloriids, hyolithids, and trilobites from West Antarctica (Shackleton and Argentina ranges)]: *Antarktika*, v. 20, p. 64–72. [in Russian]
- Popov, L.E., Holmer, L.E., and Gorjansky, V.J., 1996, Middle Cambrian lingulate brachiopods from the Tarbagatay Range, Kazakhstan: *Acta Palaeontologica Polonica*, v. 41, p. 299–317.
- Popov, L.E., Holmer, L.E., Hughes, N.C., Ghobadi Pour, M., and Myrow, P.M., 2015, Himalayan Cambrian brachiopods: *Papers in Palaeontology*, v. 1, p. 345–399.
- Ramírez-Valenzuela, I., 2019, Braquiopodos (Acrotretida-Paterinida) del Cámbrico medio del Cerro El Sahuaral, Sonora, México [Bachelor thesis]: Hermosillo, Mexico, Universidad de Sonora, 51 p.
- Reed, F.R.C., 1910, The Cambrian fossils of Spiti: *Palaeontologia Indica*, ser. 15, v. 7, p. 1–70.
- Roberts, J., and Jell, P.A., 1990, Early middle Cambrian (Ordian) brachiopods of the Coonigan Formation, western New South Wales: *Alcheringa*, v. 14, p. 257–309.
- Rowell, A.J., 1965, Inarticulata, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology, Part H. Brachiopoda, Volume 1: Boulder, Colorado and Lawrence, Kansas, Geological Society of America and University of Kansas Press*, p. H260–H296.
- Rowell, A.J., 1966, Revision of some Cambrian and Ordovician inarticulate brachiopods: *University of Kansas Paleontological Contributions*, v. 7, p. 1–36.
- Rowell, A.J., 1980, Inarticulate brachiopods of the lower and middle Cambrian Pioche Shale of the Pioche District, Nevada: *University of Kansas Paleontological Contributions*, v. 98, p. 1–26.
- Schuchert, C., 1893, A classification of the Brachiopoda: *The American Geologist*, v. 11, p. 141–167.
- Skovsted, C.B., and Holmer, L.E., 2005, Early Cambrian brachiopods from north-east Greenland: *Palaeontology*, v. 48, p. 325–345.
- Skovsted, C.B., and Holmer, L.E., 2006, The lower Cambrian brachiopod *Kyrshabaktella* and associated shelly fossils from the Harkless Formation, southern Nevada: *GFF*, v. 128, p. 327–337.
- Stewart, J.H., McMenamin, M.A.S., and Morales-Ramírez, J.M., 1984, Upper Proterozoic and Cambrian rocks in the Carborca region, Sonora, Mexico —physical stratigraphy, biostratigraphy, paleocurrent studies, and regional relations: *US Geological Survey Professional Paper*, v. 1309, p. 1–41.
- Stewart, J.H., Amaya-Martínez, R., and Palmer, A.R., 2002, Neoproterozoic and Cambrian strata of Sonora, Mexico: Rodinian supercontinent to Laurentian Cordilleran margin, in Barth, A., ed., *Crustal Evolution in the Southwest USA: Geological Society of America Special Paper*, v. 365, p. 5–48.
- Streng, M., 1999, Early middle Cambrian representatives of the superfamily Acrotretoidea (Brachiopoda) from Morocco: *Zeitschrift der Deutschen Geologischen Gesellschaft*, v. 150, p. 27–87.
- Streng, M., Holmer, L.E., Popov, L.E., and Budd, G.E., 2007, Columnar shell structures in early linguloid brachiopods—new data from the middle Cambrian of Sweden: *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, v. 98, p. 221–232.
- Torsvik, T.H., and Cocks, L.R.M., 2017, *Earth History and Palaeogeography*: Cambridge, Cambridge University Press, 317 p.
- Ushatinskaya, G.T., 1992, [New middle Cambrian lingulates from the Batenev region (Altay-Sayan)], in Repina, L.N., and Rozanov, A.Yu., eds., *Drevneyshie brachiopody territorii severnoy Evrazii: Novosibirsk, Obiedinenniy Institut Geologii, Geofiziki i Mineralologii*, p. 80–88. [in Russian]
- Ushatinskaya, G.T., and Holmer, L.E., 2001, Brachiopoda, in Alexander, E.M., Jago, J.B., Rozanov, A.Yu., and Zhuravlev, A.Yu., eds., *The Early Cambrian Biostratigraphy of the Stansbury Basin, South Australia: Transactions of the Palaeontological Institute*, v. 282, p. 120–132.
- Ushatinskaya, G.T., and Korovnikov, I.V., 2019, Revision of the early–middle Cambrian acrotretids (Brachiopoda, Linguliformea) from the Siberian Platform: *Paleontological Journal*, v. 53, p. 689–714.

- Ushatinskaya, G.T., and Malakhovskaya, Ya.E., 2001, Origin and development of the Cambrian brachiopod bioheres: Stratigraphy and Geological Correlation, v. 9, p. 540–556.
- Voronova, L.G., Drozdova, N.A., Esakova, N.V., Zhegallo, E.A., Zhuravlev, A.Yu., Rozanov, A.Yu., Sayutina, T.A. and Ushatinskaya, G.T., 1987, Lower Cambrian fossils of the Mackenzie Mountains (Canada): Trudy, Paleontologicheskii Institut, Akademiya Nauk SSSR, v. 224, p. 1–88.
- Walcott, C.D., 1885, Paleontologic notes: American Journal of Science, v. 29, p. 114–117.
- Walcott, C.D., 1902, Cambrian Brachiopoda: *Acrotreta*; *Linnarssonella*; *Oboolus*; with descriptions of new species: Proceedings of the United States National Museum, v. 25, p. 577–612.
- Walcott, C.D., 1908, Cambrian geology and paleontology, no. 3, Cambrian Brachiopoda, descriptions of new genera and species: Smithsonian Miscellaneous Collections, v. 53, p. 53–137.
- Walcott, C.D., 1912, Cambrian Brachiopoda: U.S. Geological Survey Monographs, v. 51, 700 p.
- White, C.A., 1874, Preliminary report upon invertebrate fossils collected by the expeditions of 1871, 1872 and 1873 with descriptions from species: Geological Surveys West of the 100th Meridian, Report, Washington, D.C., Government Printing Office, p. 5–27.
- Williams, A., Carlson, S.J., Branton, C.H.C., Holmer, L.E., and Popov, L., 1996, A supra-ordinal classification of the Brachiopoda: Philosophical Transactions of the Royal Society of London, v. B351, p. 1171–1193.
- Wotte, T., and Mergl, M., 2007, Brachiopods from the lower-middle Cambrian Láncara Formation of the Cantabrian Mountains, Northwest Spain: Memoirs of the Association of Australasian Palaeontologists, v. 33, p. 101–122.
- Zhang, Z.L., Popov, L.E., Holmer, L.E., and Zhang, Z.F. 2018, Earliest ontogeny of early Cambrian acrotretoid brachiopods—first evidence for metamorphosis and its implications: BMC Evolutionary Biology, v. 18, 42. <https://doi.org/10.1186/s12862-018-1165-6>.
- Zhao, Y.L., Zhu, M.Y., Babcock, L.E., and Peng, J., 2011, The Kaili Biota: Marine Organisms from 508 Million Years Ago: Guiyang, Guizhou Publishing Group, 251 p. [in Chinese]
- A6.—Siberia, Toyon Regional Stage (Pelman, 1977; Ushatinskaya and Malakhovskaya, 2001); *Botsfordia*, *Eoobolus*, *Kyrshabaktella*, *Linnarssonella*, *Paterina*.
- A7.—Australasian segment of Gondwana; South Australia, Parara and Ramsey limestone formations (Ushatinskaya and Holmer, 2001); *Eoobolus*, *Kyrshabaktella*, *Schizopholis*, *Vandalotreta*.
- A8.—Sub-Himalaya; *Botsfordia*, *Eoobolus*, *Neobolus*, *Schizopholis*, *Wynnina*.
- A9.—Spity, Tethyan Himalaya; Parahio Formation, *Haydenaspis parvarya* Level; *Aksarinaia*, *Eohadrotreta*, *Eoobolus*, *Paterina*, *Schizopholis*.
- A10.—Australasian segment of Gondwana, central Australia, southern Georgina Basin, Thornton Limestone (Percival and Kruse, 2014), *Aksarinaia*, *Dictyonina*, *Hadrotreta*, *Kostjubella*, *Kyrshabaktella*, *Micromitra*, *Schizopholis*, *Vandalotreta*, *Westonia*, *Wynnina*?
- A11.—South China, Yunnan Province, Wulongqing Formation, Guanshan Fauna (Zhao et al., 2011); *Acanthotretella*, *Diaandongia*, *Eoobolus*, *Lingulellotreta*, *Palaeobolus*.

Transitional 'Eothele faunas'.—

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 gimmeljarbi* Biozone (Holmer et al., 2001); *Botsfordia*, *Lingulellotreta*, *Linnarssonella*, *Palaeobolus*.
- A3.—Australasian segment of Gondwana; Northern Territories, composite list (Wiso, Georgina and Daly Basin) (Kruse, 1990, 1991, 1998); *Westonia*, *Schizopholis*, *Kyrshabaktella*, *Vandalotreta*, *Micromitra*?
- A4.—Laurentia, North-East Greenland, Bastion and Ella Island formations (Skovsted and Holmer, 2005); *Botsfordia*, *Eoobolus*, *Micromitra*, *Vandalotreta*.
- A5.—South China, Shaanxi Province, Guojiaba and Xiannüdong formations (Li and Holmer, 2004); *Eohadrotreta*, *Eoobolus*, *Kyrshabaktella*, *Palaeobolus*, *Lingulellotreta*.
- 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. Dyeran Mackenzie Mountain (*Bonnina-Olenellus* zone) Laurentia (Voronova et al., 1987); *Palaeoschmidites*, *Linnarssonella*, *Eothele*, *Micromitra*, *Paterina*.
- B2.—Peri-Siberia, Altai-Sayany Region, 'Toyon Stage', composite list (Ushatinskaya and Malakhovskaya, 2001; *Botsfordia*, *Chakassilingula*, *Eothele*, *Kyrshabaktella*, *Linnarssonella*, *Oepikites*.
- B3.—Australasian segment of Gondwana; western New South Wales, Coonigan Formation (Roberts and Jell, 1990), *Eothele*, *Hadrotreta*, *Kleithriatreta*, *Dictyonina*, *Micromitra*, *Eoobolus* (= *Palaeoschmidites*), *Oepikites* (?) (= *Lingulella*), *Westonia*.
- B4.—Australasian segment of Gondwana; north-western New South Wales, Wydjah Formation (Pimpira Member) (Brock and Percival, 2006); *Dictyonina*, *Eothele*, *Eoobolus*, *Micromitra*, *Prototreta*.
- B5.—North African Sector of Gondwana; Morocco, composite list (Mergl, 1988; Streng, 1999; Alvaro et al., 2008), *Acanthotreta*, *Almohadella*, *Botsfordia*, *Eothele*, *Monophtalma*, *Vandalotreta*.
- B6.—Laurentia, late Dyeran – early Delamaran, Nevada, Pioche Shale (Rowell, 1980), and Harkless Formation (Skovsted and Holmer, 2006); *Dictyonina*, *Eothele*, *Hadrotreta*.
- B7.—Laurentia, Nevada, Harkless Formation (Skovsted and Holmer, 2006); *Eothele*, *Kyrshabaktella*, *Hadrotreta*.
- B8.—Caborca Terrane, Sonora, Cerro Prieto Formation; *Dictyonina*, *Eothele*, *Hadrotreta*, *Linnarssonella*, *Paterina*.

Cambrian Stage 5, *Acrothele* Fauna

- C1.—Karatau-Naryn microplate; Malyi Karatau Range, *Peronopsis? ultimus* and *Ptychagnostus intermedius* biozones (Holmer et al., 2001); *Aksarinaia*, *Akmolina?*, *Canalilatus*,

- Kotylotreta*, *Kyrshabaktella*, *Linnarssonia*, *Prototreta*, *Schizopholis*, *Stilpnotreta*.
- C2.—North Tien-Shan microplate, Kargajly Formation (Holmer et al., 2001); *Anabolotreta*?, *Canalilathus*, *Conthylotreta*, *Kleithriatreta*, *Kotylotreta*, *Kyrshabaktella*, *Neotreta*, *Paterina*.
- C3.—Chingiz-Tarbagatai island arcs; Tarbagatai Range, ‘Amga’ 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*, *Aphelotreta*, *Dictyonina*, *Micromitra*.
- C6.—Avalonia; New Brunswick (Walcott, 1912); *Acrothele*, *Acrothyra*, *Botsfordia*, *Eoobolus*, *Palaeoobolus*.
- 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, Forsemölla 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*, *Erbotreta*, *Kostjubella*, *Kyrshabaktella*, *Linnarssonia*, *Paterina*, *Prototreta*.
- C11.—Spity, Tethyan Himalaya; Parahio Formation, Cambrian Stage 5; *Acrothele*, *Amictocracens*, *Aphelotreta*, *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*.
- C14.—Australasian segment of Gondwana, central Australia, southern Georgina Basin, Arthur Creek Formation, lower part (Percival and Kruse, 2014), *Acrothele* (= *Orbithiele*), *Amictocracens*, *Anabolotreta*, *Chakassilingula*, *Kyrshabaktella*, *Linnarssonia*, *Micromitra*, *Picnotreta*, *Treptotreta*, *Stilpnotreta*.
- 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*.

Accepted: 30 March 2022