



## Bryozoan fauna from the Permian (Artinskian-Kungurian) Zhongba Formation of southwestern Tibet

Andrej Ernst

### ABSTRACT

The bryozoan assemblage from the Zhongba Formation of southwestern Tibet includes 30 species of 25 genera. Seven species are new: *Fistulipora sakagamii* n. sp., *Dybowskiella hupehensiformis* n. sp., *Etherella tibetensis* n. sp., *Dyscritella lii* n. sp., *Streblotrypa (Streblotrypa) parviformis* n. sp., *Timanotrypa australis* n. sp., and *Protoretzpora irregularis* n. sp. One genus with one species is also new: *Tibetiporella ornata* n. gen. n. sp. The described fauna implies a Cisuralian (Artinskian-Kungurian) age of the Zhongba Formation and shows relationships to the Cisuralian faunas of Thailand, Western Australia, Oman, Timor, central Pamir, Iran, Urals, and other Tibetan localities. The bryozoan fauna from the Zhongba Formation shows an intermixture of both Boreal and Gondwana elements, and implies stronger faunal migrations into the tropical region from both the north and south. Palaeoecological analysis suggests that the Zhongba Formation was deposited in a middle shelf setting some distance from shoreline, probably influenced by local currents.

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Keywords: Bryozoa; taxonomy; palaeobiogeography; new genus; new species

Submission: 8 July 2015. Acceptance: 10 April 2016.

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### INTRODUCTION

The Indus-Tsangbo (Yarlung-Zangbo) Suture Zone in southern Tibet marks the collision between the Indian and Eurasian plates (Hodges, 2000). In the middle part (southwestern Tibet) of the suture, a small stratigraphical terrane called the Zhongba microterrane (Li et al., 2014a) narrowly pinches out between the two mélangé branches of the suture.

The eastern part of the Zhongba microterrane has been assigned to the middle-late Permian in

Chinese regional geological (unpublished) reports, but it was recently dated as Ordovician through Triassic and disaggregated as three lithostratigraphic units: the Ordovician–Silurian Ziqupu Group, Devonian Nadeng'er Formation and Carboniferous–Permian Quga Group (Li et al., 2014b). The Quga Group was subdivided into three parts: Carboniferous–Lower Permian Gangzhutang Formation, Lower–Middle Permian Zhongba Formation, and Middle–Upper Permian Kazhale Formation (Li et al., 2014b).

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Ernst, Andrej. 2016. Bryozoan fauna from the Permian (Artinskian-Kungurian) Zhongba Formation of southwestern Tibet. *Palaeontologia Electronica* 19.2.15A: 1-59  
[palaeo-electronica.org/content/2016/1462-bryozoan-fauna-of-tibet](http://palaeo-electronica.org/content/2016/1462-bryozoan-fauna-of-tibet)

The Zhongba Formation is composed of pinkish red dolomites and variegated dolomitic bioclastic limestones, ranging from 20–100 m thick. This formation contains abundant benthic fossils: crinoids, bryozoans, brachiopods, gastropods, and solitary corals. Fusulinds are few, whereas small agglutinating foraminifers are ubiquitous.

Bryozoa is very important animal group, which was widely distributed in marine habitats in the past. During the Palaeozoic, bryozoans played significant role in reefs and other shallow marine biotopes (Cuffey, 1977). Due to their mostly calcitic and diagenetically stable skeletons, bryozoans can be used for various purposes in palaeontology and stratigraphy (Bancroft, 1987; Taylor and Allison, 1998; Smith et al., 2006).

Permian Bryozoa display a high diversity and wide distribution worldwide. Well-studied faunas are known from North America, Eurasia, and Australia, which were successfully used for palaeobiogeographical reconstructions (Ross and Ross, 1990; Ross 1995; Gilmour and Morozova, 1999). Ross (1995) assigned Tibet to the Central Tethys province which also includes Transcaucasia, part of Afghanistan, Mongolia, and northeastern, central eastern, and southwestern China. Tibetan faunas belong to the Tethys occurring in tropical conditions.

One of the earliest publications regarding Permian bryozoans from Tibet was that of Metz (1946) who described several bryozoan species from northern Tibet. A series of more recent publications by Chinese authors describe extensive bryozoan faunas from the Permian of Tibet (e.g., Yang et al., 1981; Yang and Lu, 1983; Liu and Wang, 1987; Xia, 1991). Sakagami et al. (2006) mentioned some bryozoans from the Lower Permian (Sakmarian) of the southern Tibet.

The present paper is devoted to the taxonomic description of a bryozoan fauna from the Zhongba Formation (Lower–Middle Permian) of the Zhongba area in southwestern Tibet. This fauna includes 30 species of 25 genera. Palaeobiogeographical, stratigraphical, and ecological implications of this fauna are discussed here.

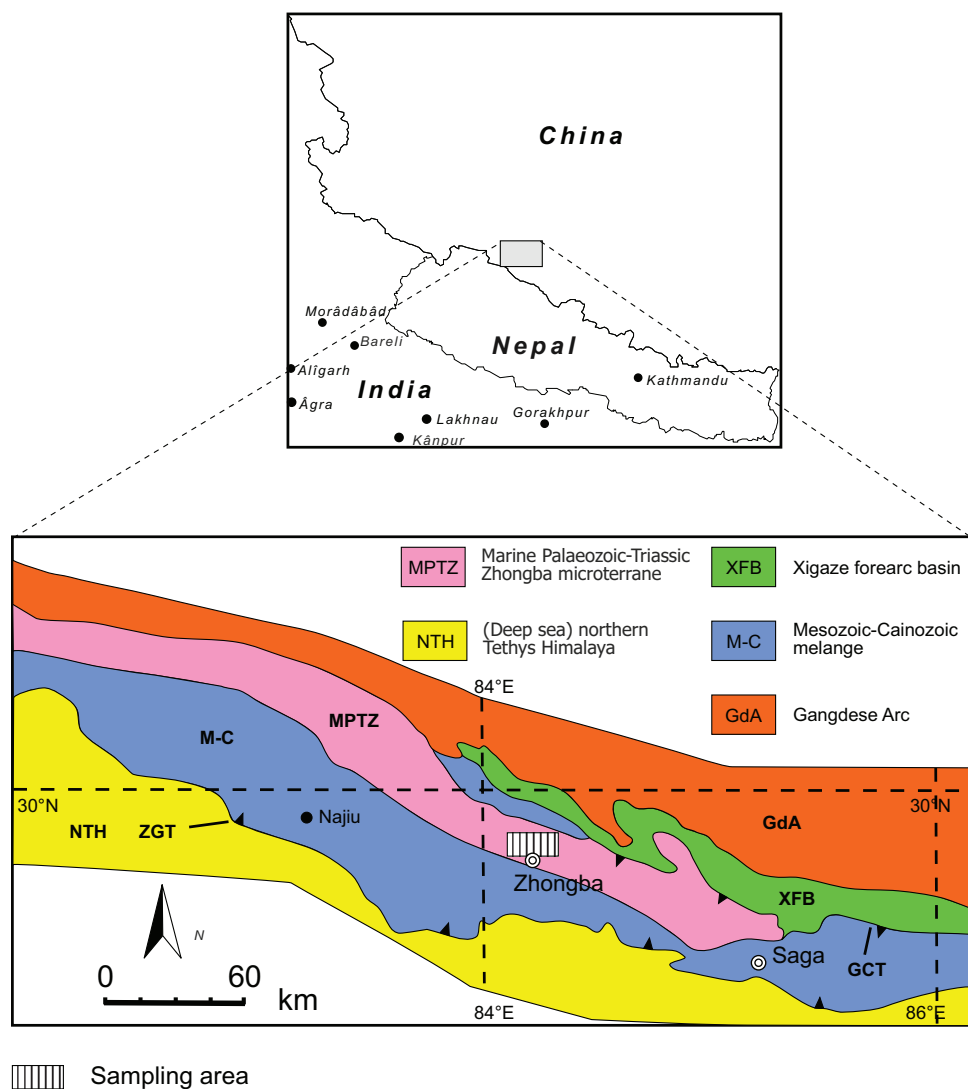
## MATERIAL AND METHODS

Material for this study was collected by Xianghui Li (Nanjing University, China) and his colleagues from the Zongba Formation in Zhongba area (Figure 1) of southwestern Tibet in the summers of 2010–2012 during 1:50,000 geological mapping and provided to the author for a taxonomic investigation on bryozoans (Li et al., 2014a,

b). The material comes from the lower part of the Zhongba Formation (Xianghui Li, personal commun., 2011) and is deposited at the Senckenberg Museum (Frankfurt am Main, Germany). The following samples are from the Zhongba Formation (GPS coordinates in brackets): D4437F8 (E 84.31536, N 29.74233), D4437F9 (E 84.31536, N 29.74233), D4437F10 (E 84.31536, N 29.74233), D4437F11 (E 84.31536, N 29.74233), D4437F12 (E 84.31536, N 29.74233), D4437F13 (E 84.31536, N 29.74233), D4437F14 (E 84.31536, N 29.74233), D4437F15 (E 84.31536, N 29.74233), D4437F17 (E 84.31536, N 29.74233), D4439F2 (E 84.31111, N 29.73889), P5170F1 (E 83.76894, N 29.93333), S09-01F4 (E 83.79028, N 29.89667), S09-01F4 (E 83.79028, N 29.89667), S09-01F6 (E 83.79028, N 29.89667).

The studied samples comprise grey to blackish, fossil-rich limestones (Figure 2.1), which are mainly represented by rudstones, grainstones, packstones, and bindstones (Figure 2.2–4). Besides bryozoans, the limestones contain crinoids, brachiopods, and gastropods. From this material, 150 randomly oriented thin sections of various sizes (28 x 48 mm [n = 92], 50 x 50 mm [n = 49], and 50 x 70 mm [n = 9]) were prepared. Thin sections are deposited at the Senckenberg Museum (Frankfurt am Main, Germany). Material included in the present publication is numbered SMF 23.007–SMF 23.098 and SMF 23.131–SMF 23.268. These numbers refer to the separate bryozoan fragments in thin sections, the system used at the Senckenberg Museum. Bryozoans were investigated in thin sections using a binocular microscope in transmitted light. The spacing of morphological structures was measured as a distance between their centres. Statistics were summarized using arithmetic mean, sample standard deviation, coefficient of variation, and minimum and maximum values.

The author does not follow the complete taxonomic procedure suggested by Snyder (1991) for fenestrates. It is often impossible to measure all the 43 morphological characters involved in this taxonomic system. The available material does not allow the preparation of ideally oriented thin sections or acetate peels, and the number of measurements per colony would not provide the necessary statistic background for such an approach. Moreover, some of the measured characters like the thickness of the reverse-wall laminated layer can vary strongly depending on the age of the colony part. The minimum chamber width varies strongly in various deep sections. Therefore, a reduced set



**FIGURE 1.** Position of the sampling area and tectonic setting of the Tibetan Plateau and Southern China (simplified after Dai et al., 2011). GCT: Great Counter thrust; ZGT: Zhongba-Gyangze thrust.

of characters suggested by Snyder (1991) has been used in this publication for the discrimination of fenestrate species.

#### SYSTEMATIC PALAEOLOGY

Phylum BRYOZOA Ehrenberg, 1831  
 Class STENOLAEMATA Borg, 1926  
 Superorder PALAEOSTOMATA Ma, Buttler, and Taylor, 2014  
 Order CYSTOPORATA Astrova, 1964  
 Suborder FISTULIPORINA Astrova, 1964  
 Family FISTULIPORIDAE Ulrich, 1882  
 Genus *FISTULIPORA* M'Coy, 1849

**Type species.** *Fistulipora minor* M'Coy, 1849. Carboniferous; England.

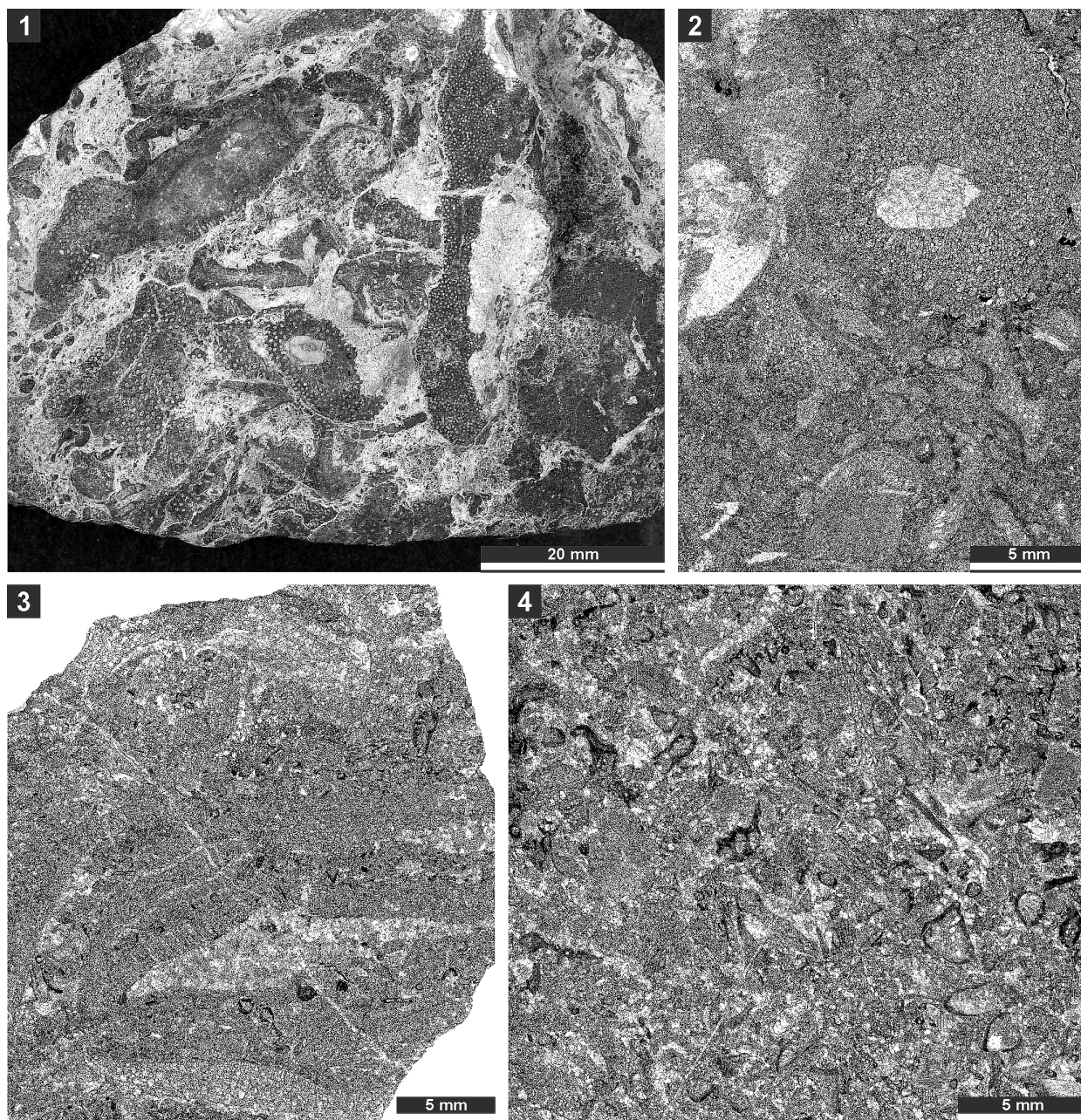
**Diagnosis.** Massive, encrusting, or ramose colonies. Cylindrical autozoecia with thin walls and complete diaphragms. Apertures rounded, possessing horseshoe-shaped lunaria. Autozoecia separated by the extrazooecial vesicular skeleton.

**Remarks.** *Fistulipora* M'Coy, 1849 differs from *Eridopora* Ulrich, 1882 in having rounded, horseshoe-shaped lunaria instead of triangular ones. Furthermore, *Eridopora* develops persistently encrusting colonies, whereas *Fistulipora* may also develop massive and branched colonies.

**Occurrence.** Ordovician to Permian; worldwide.

*Fistulipora enodata* Gorjunova, 1970  
 Figure 3.1-4; Table 1

1970 *Fistulipora enodata* Gorjunova, p. 61, pl. 21, fig. 4.

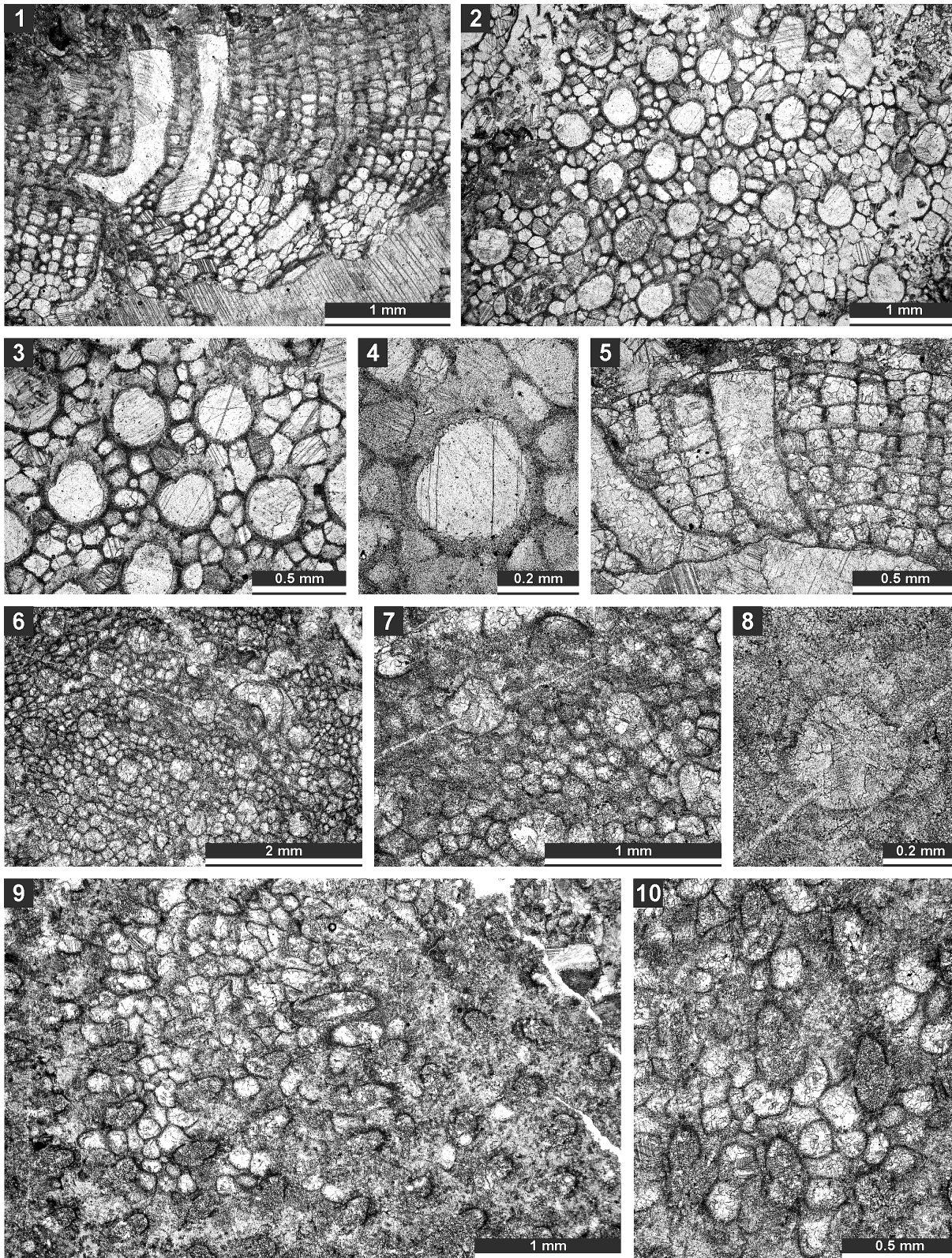


**FIGURE 2.** Lithological characteristics of the limestones from the Zhongba Formation. 1, limestone sample with abundant bryozoans (SMF 23.262); 2, rudstone containing crinoids, cystoporate (*Fistulipora enodata* Gorjunova, 1970) and fenestrate bryozoans (SMF 23.263); 3, bindstones with *Fistulipora guttata* Trizna and Klautzan, 1961 (SMF 23.264); and 4, grain- to packstones with bryozoan and crinoid fragments (SMF 23.265).

- 1975 *Fistulipora enodata* Gorjunova, 1970; Gorjunova, p. 42, pl. 1, fig. 1.
- 1987 *Fistulipora enodata* Gorjunova, 1970; Liu and Wang, p. 4, pl. 1, figs. 4a-b, pl. 2, figs. 1-a-b.
- 1991 *Fistulipora enodata* Gorjunova, 1970; Xia, p. 957, pl. 5, figs. 13-14.

**Material.** SMF 23.007–SMF 23.021.

**Description.** Encrusting, partly multilayered colony, separate sheets 1.8–2.8 mm thick. Autozoecia growing from thin epitheca, bending at their bases to the colony surface. Autozoecial diaphragms rare to absent, thin. Autozoecial apertures circular to oval. Lunaria well-developed, rounded, disappearing in deeper sections; ends of lunaria not indenting into autozoecia. Vesicles small to medium, high, separating autozoecia in



**FIGURE 3.** Thin section photographs of *Fistulipora enodata* Gorjunova, 1970, SMF 23.014 (1–4); *Fistulipora guttata* Trizna and Klautzan, 1961, SMF 23.025 (5–8); and *Fistulipora sakagamii* n. sp., holotype SMF 23.028 (9 and 10). 1 and 5, longitudinal section showing autozooeal chambers and vesicular skeleton; and 2–4, 6–8, 9, and 10, tangential sections showing autozooeal apertures and vesicles.

**TABLE 1.** Measurements of *Fistulipora enodata* Gorjunova, 1970. Abbreviations: N = number of measurements; X = mean; SD = standard deviation; CV = coefficient of variation; MIN = minimal value; MAX = maximal value.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	35	0.30	0.032	10.87	0.24	0.38
Autozooeical aperture spacing, mm	35	0.58	0.067	11.47	0.45	0.75
Vesicle diameter, mm	35	0.13	0.034	27.24	0.07	0.21
Vesicle spacing, mm	35	0.11	0.025	21.80	0.08	0.17
Vesicles per aperture	20	12.6	1.188	9.43	11.0	15.0
Lunarium length, mm	20	0.14	0.024	17.26	0.10	0.18
Lunarium width, mm	20	0.25	0.028	11.30	0.20	0.29

**TABLE 2.** Measurements of *Fistulipora guttata* Trizna and Klautzan, 1961. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	30	0.28	0.038	13.89	0.23	0.38
Autozooeical aperture spacing, mm	30	0.66	0.073	11.04	0.55	0.80
Vesicle diameter, mm	30	0.11	0.030	28.08	0.05	0.19
Vesicle spacing, mm	25	0.10	0.022	21.78	0.05	0.13
Vesicles per aperture	30	12.0	1.564	13.07	9.0	16.0
Lunarium length, mm	15	0.14	0.037	26.91	0.08	0.23
Lunarium width, mm	15	0.21	0.030	14.18	0.17	0.29
Lunarium thickness, mm	15	0.08	0.031	40.31	0.03	0.13

1–2 rows, 11–15 surrounding each autozooeical aperture, with rounded to flat roofs, polygonal in tangential section. Autozooeical walls granular prismatic, 0.005–0.015 mm thick. Maculae not observed.

**Remarks.** *Fistulipora enodata* Gorjunova, 1970 differs from *F. timorensis* Bassler, 1929 in larger autozooeical apertures (aperture width 0.24–0.38 mm vs. 0.22–0.28 mm in *F. timorensis*).

**Occurrence.** Lower Permian, Artinskian; Tajikistan (Pamir). Lower Permian; Rutog, southwestern Tibet. Xiala Formation, ?Middle Permian; Xainza, southwestern Tibet. Zhongba Formation, Permian (late Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Fistulipora guttata* Trizna and Klautzan, 1961  
Figure 3.5-8; Table 2

1961 *Fistulipora guttata* Trizna and Klautzan, p. 379-380, pl. 1, figs. 1-3.

**Material.** SMF 23.022–SMF 23.027.

**Description.** Encrusting, partly multilayered colony, separate sheets 1.0–1.5 mm thick. Autozooeical growing from thin epitheca, bending at their bases to the colony surface. Autozooeical diaphragms rare to absent, thin. Autozooeical apertures circular to oval. Lunaria well-developed, rounded, disappearing in deeper sections; ends of lunaria not indenting into autozooeical. Vesicles

small to medium, high, separating autozooeical in 2–4 rows, 9–16 surrounding each autozooeical aperture, with rounded to flat roofs, polygonal in tangential section. Autozooeical walls granular prismatic, 0.005–0.015 mm thick. Small maculae consisting of vesicular skeleton present, 1.0–1.3 mm in diameter.

**Remarks.** *Fistulipora guttata* Trizna and Klautzan, 1961 differs from *F. milleporacea* Bassler, 1929 from the Lower Permian of Timor in smaller autozooeical apertures (average aperture width 0.28 mm vs. 0.35 mm in *F. milleporacea*). *Fistulipora guttata* differs from *F. enodata* Gorjunova, 1970 in smaller apertures and larger distances between aperture centres (average aperture width 0.28 mm vs. 0.30 mm in *F. enodata*; average aperture spacing 0.66 mm vs. 0.58 mm in *F. enodata*), and in vesicles separating autozooeical.

**Occurrence.** Lower Permian (Artinskian) of Urals. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Fistulipora sakagami* n. sp.  
Figures 3.9-10, 4.1-2; Table 3

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1975 *Fistulipora* sp. indet. Sakagami, p. 35, pl. 4, figs. 5-6.

**TABLE 3.** Measurements of *Fistulipora sakagami* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	13	0.15	0.014	9.39	0.14	0.19
Autozooeical aperture spacing, mm	7	0.42	0.034	8.20	0.36	0.46
Vesicle diameter, mm	10	0.12	0.021	17.78	0.09	0.16
Vesicles per aperture	4	8.5	1.000	11.76	8.0	10.0
Lunarium length, mm	7	0.13	0.030	23.01	0.09	0.16
Lunarium width, mm	7	0.14	0.023	16.55	0.10	0.18
Lunarium thickness, mm	7	0.07	0.015	21.35	0.05	0.09

**Etymology.** The species is named in honour of Sumio Sakagami, who has contributed greatly to the research on Palaeozoic bryozoans.

**Holotype.** SMF 23.028.

**Paratype.** SMF 23.029.

**Type locality.** Zhongba area of southwestern Tibet (E 84.31536, N 29.74233).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Thin encrusting colony; lunaria well-developed, horseshoe-shaped; apertures separated by 1–3 rows of vesicles; 8–10 vesicles surrounding each aperture.

**Description.** Thin encrusting colony. Autozooeia growing from thin epitheca, bending at their bases to the colony surface. Autozooeical diaphragms rare to absent, thin. Autozooeical apertures circular to oval. Lunaria well-developed, long, horseshoe-shaped; ends of lunaria slightly indenting into autozooeia. Vesicles small to medium, high, separating autozooeia in 1–3 rows, 8–10 surrounding each autozooeia aperture, with rounded to flat roofs, polygonal in tangential section. Autozooeical walls granular prismatic, 0.005–0.015 mm thick. Maculae not observed.

**Remarks.** *Fistulipora sakagami* n. sp. differs from *F. rutogensis* Xia, 1991 from the Chainaha Formation (Middle Permian) of southwestern Tibet, in smaller autozooeical apertures (0.14–0.19 mm vs. 0.24–0.30 mm in *F. rutogensis*).

**Occurrence.** Lower Permian (Artinskian); Khao Hin Kling, Thailand. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *DYBOWSKIELLA* Waagen and Wentzel, 1886

**Type species.** *Dybowskiella grandis* Waagen and Wentzel, 1886. Permian; India.

**Diagnosis.** Ramose, hollow ramose, massive, or encrusting colonies. Autozooeia cylindrical, sub-circular in transverse section of endozone, having rounded apertures, isolated by abundant polygonal

vesicles. Basal diaphragms thin, straight or curved. Lunaria horseshoe-shaped, present in endozone and exozone; ends of lunaria inflect into autozooeical chamber. Autozooeical walls with granular boundary and light-coloured granular-prismatic cortex. Vesicular skeleton in endozone and exozone. Vesicles subrectangular with flat to slightly curved roofs. Small acanthostyles or tubuli in exterior stereom present. Monticules elevated or flash, with central cluster of vesicles surrounded by larger autozooeia in radial arrangement.

**Remarks.** *Dybowskiella* Waagen and Wentzel, 1886 differs from *Fistulipora* M'Coy, 1849 in the shape of lunaria, the ends of which inflect autozooeical chambers in *Dybowskiella*. *Dybowskiella* differs from *Eridopora* Ulrich, 1882 in having horseshoe-shaped lunaria instead of triangular ones. The shape of lunaria with inflecting ends is the only significant character for discrimination of *Dybowskiella*. However, the inflection grade of ends of lunaria varies strongly in the species of *Fistulipora*, *Dybowskiella* and *Fistuliramus*. Therefore, the discrimination of the genus *Dybowskiella* is relatively uncertain.

**Occurrence.** Middle Devonian–Upper Permian; worldwide.

*Dybowskiella hupehensis* n. sp.

Figure 4.3-7; Table 4

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1983 *Dybowskiella hupehensis* Yang, 1956; Yang and Lu, p. 266, pl. 9, figs. 1-4.

**Etymology.** The species is named after the species *Dybowskiella hupehensis* Yang, 1956 because of its close similarity.

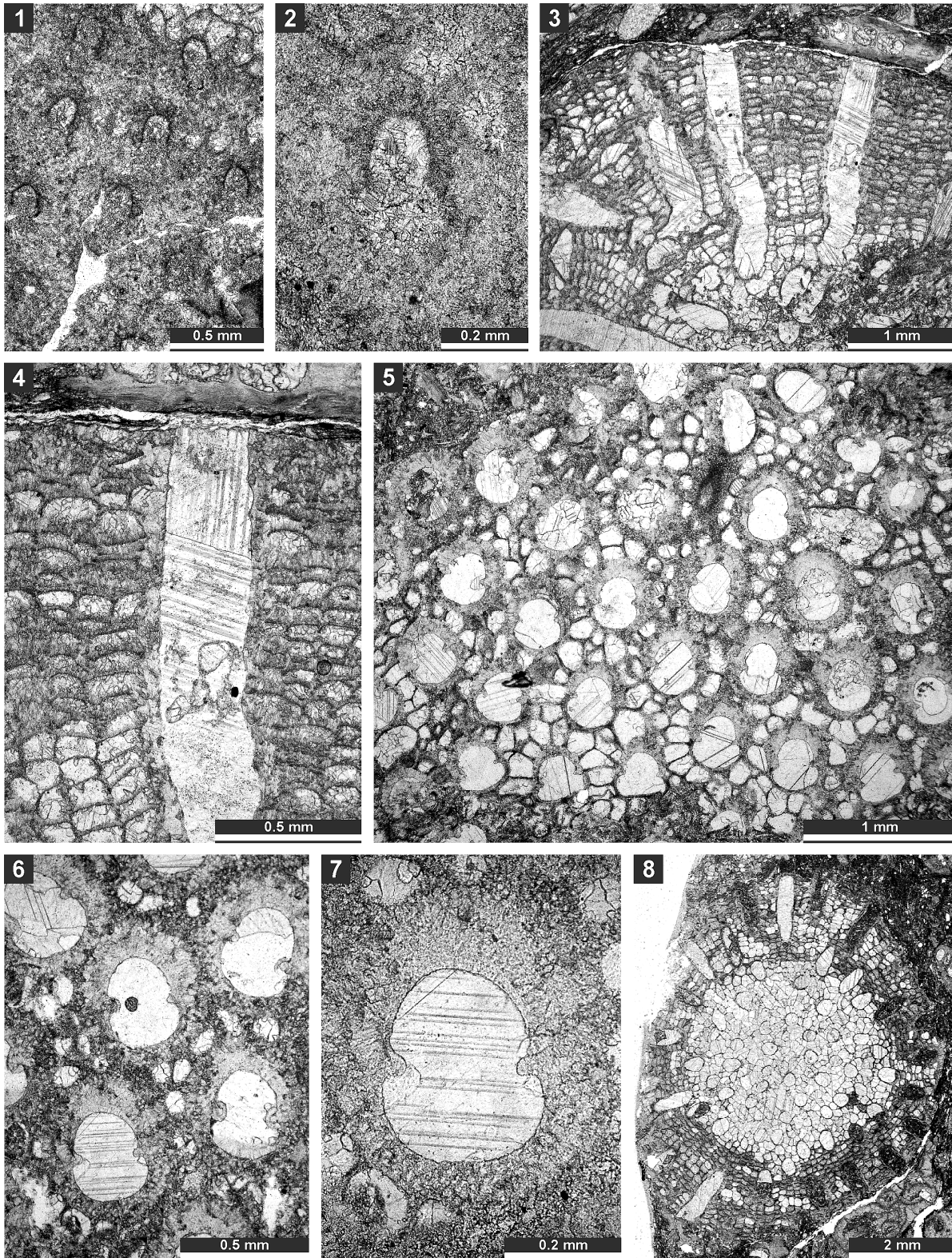
**Holotype.** SMF 23.030.

**Paratypes.** SMF 23.031–SMF 23.035.

**Type locality.** Zhongba area of southwestern Tibet (E 84.31536, N 29.74233).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Encrusting colony; diaphragms few to absent; lunaria well-developed, horseshoe-



**FIGURE 4.** Thin section photographs of *Fistulipora sakagamii* n. sp., holotype SMF 23.028 (1 and 2); *Dybowskiella hupehensisformis* n. sp., holotype SMF 23.030 and paratype SMF 23.032 (3–7); and *Fistuliramus xianzaensis* Liu and Wang, 1987, SMF 23.037 (8). 1, 2, 5–7, tangential section showing autozoecial apertures and vesicles; 3 and 4, longitudinal section showing autozoecial chambers and vesicular skeleton; and 8, branch transverse section.



**TABLE 4.** Measurements of *Dybowskiella hupehensisformis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	30	0.30	0.019	6.43	0.26	0.33
Autozooeical aperture spacing, mm	30	0.57	0.056	9.75	0.45	0.67
Vesicle diameter, mm	30	0.11	0.026	22.76	0.06	0.18
Vesicle spacing, mm	30	0.09	0.013	15.18	0.06	0.11
Vesicles per aperture	10	13	1.563	12.03	11.0	15.0
Lunarium length, mm	30	0.19	0.021	11.06	0.15	0.24
Lunarium width, mm	30	0.21	0.021	10.28	0.17	0.28
Lunarium thickness, mm	30	0.12	0.024	20.27	0.07	0.18

shaped; apertures separated by 1–2 rows of vesicles; 11–15 vesicles surrounding each aperture; maculae consisting of vesicular skeleton.

**Description.** Encrusting, partly multilayered colony, separate sheets 1.15–1.75 mm thick. Autozooeia growing from thin epitheca, bending in the early exozone to the colony surface. Autozooeical diaphragms few to absent. Autozooeical apertures circular to oval. Lunaria well-developed, horse-shoe-shaped, directed towards the next macula, disappearing in deeper sections; ends of lunaria indenting into autozooeia. Vesicles small to medium in size, high, separating autozooeia in 1–2 rows, 11–15 surrounding each autozooeia aperture, with rounded to flat roofs, polygonal in tangential section. Autozooeical walls granular prismatic, 0.005–0.015 mm thick. Maculae consisting of vesicular skeleton, 0.9–1.3 mm in diameter.

**Remarks.** *Dybowskiella hupehensisformis* n. sp. resembles the species described as *Dybowskiella hupehensis* Yang, 1956 by Yang and Lu (1983) from the Lower Permian Baliqliq Group of Kalpin in Western Xinjiang, China. However, *D. hupehensis* Yang, 1956, originally described from the Chihsia Formation (Lower Permian, Artinskian–Kungurian) of Hupei, China, has significantly larger autozooeical apertures than the species described by Yang and Lu (1983) (aperture width 0.34–0.42 mm vs. 0.26–0.36 mm in the material of Yang and Lu). *Dybowskiella hupehensisformis* differs insignificantly from the material of *D. hupehensis* Yang, 1956 described by Yang and Lu (1983): aperture width 0.26–0.33 mm vs. 0.26–0.36 mm, and aperture spacing 0.45–0.67 mm vs. 0.35–0.50 mm.

*Dybowskiella hupehensisformis* n. sp. is similar to the species *Dybowskiella* sp. described by Yang and Lu (1983) from the Baliqliq Group of Kalpin in Western Xinjiang, China (aperture width 0.26–0.33 mm vs. 0.30–0.33 mm in *Dybowskiella* sp.; aperture spacing 0.45–0.67 mm vs. 0.38–0.64 mm in

*Dybowskiella* sp.). Furthermore, *D. hupehensisformis* differs from *D. crescens* (Crockford, 1944) from the Lower Permian (Artinskian) of Western Australia in smaller autozooeical apertures (aperture width 0.26–0.33 mm vs. 0.29–0.43 mm in *D. crescens*).

**Occurrence.** Baliqliq Group, Lower Permian; Kalpin, Western Xinjiang, China. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *FISTULIRAMUS* Astrova, 1960

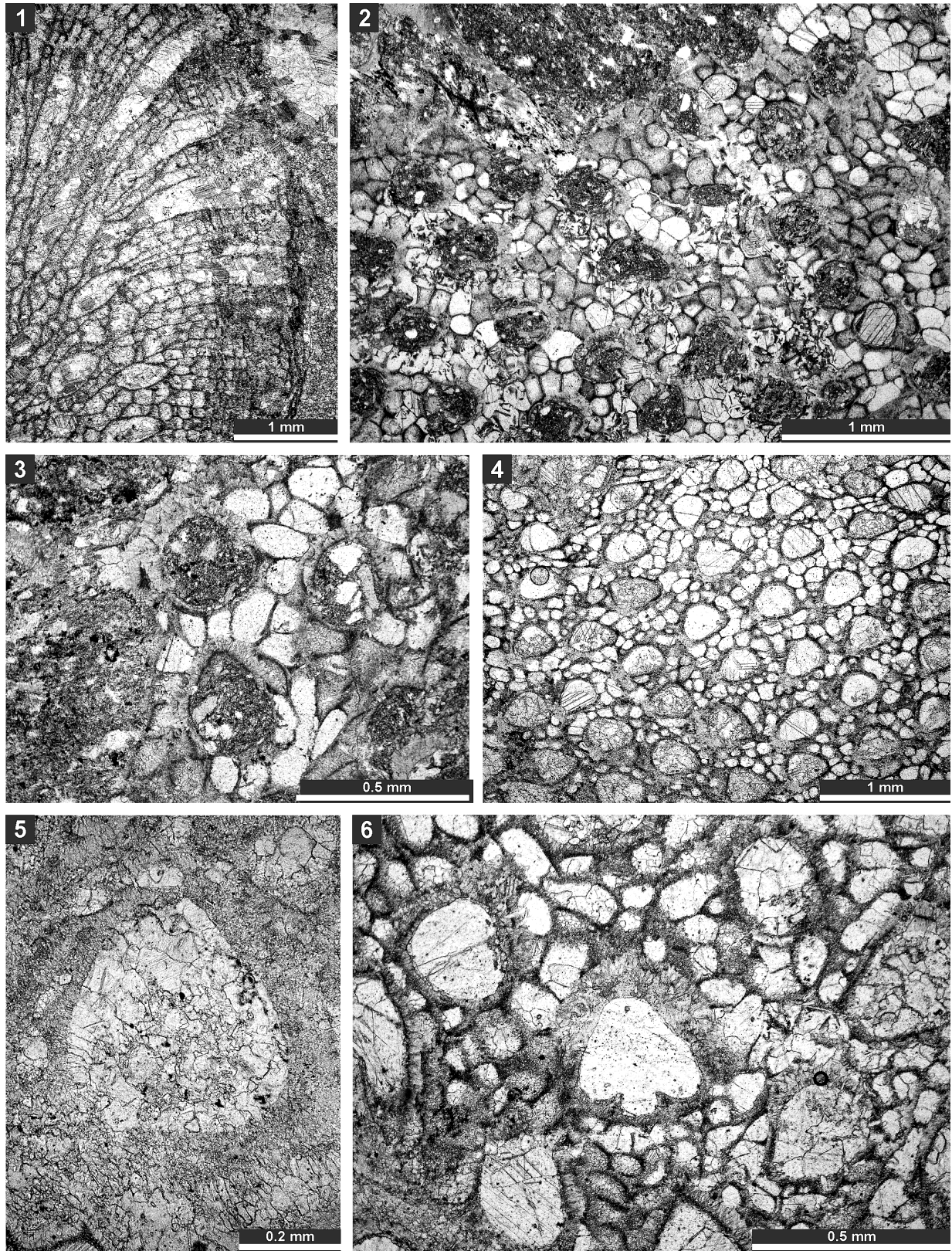
**Type species.** *Fistuliramus sinensis* Astrova, 1960. Upper Silurian (Ludlowian); Arctic Urals, Russia.

**Diagnosis.** Branched colonies; secondary overgrowths common. Autozooeia long, subcircular in transverse section of endozone; isolated by vesicular skeleton in exozones. Autozooeical apertures rounded to oval, usually arranged in regularly alternating longitudinal rows; maculae absent or poorly developed. Autozooeical diaphragms present in both in endozones and exozones, usually abundant. Lunaria in outer endozones and exozones, consisting of granular material, well-developed. Vesicles in long blisters in endozones, becoming more subquadrate in the transition region, decreasing in height in outer exozones. Autozooeical walls thin, granular in endozones; with thick laminated lining in exozones.

**Remarks.** *Fistuliramus* Astrova, 1960 differs from the similar genus *Fistulipora* M'Coy, 1849 in having constantly ramose colony form and monticules with a ring of larger autozooeia. *Eofistulipora* Morozova, 1959 differs from *Fistuliramus* in absence of vesicular skeleton in endozone and less abundant diaphragms in exozones.

**Occurrence.** Silurian–Permian; worldwide.

*Fistuliramus xianzaensis* Liu and Wang, 1987  
Figures 4.8, 5.1-3; Table 5



**FIGURE 5.** Thin section photographs of *Fistuliramus xianzaensis* Liu and Wang, 1987, SMF 23.042 (1) and SMF 23.038 (2 and 3); and *Eridopora uncata* Yang and Lu, 1983, SMF 23.052 (4 and 6) and SMF 23.051 (5). 1, longitudinal section; and 2–6, tangential section showing autozooeal apertures and vesicles.

**TABLE 5.** Measurements of *Fistuliramus xianzaensis* Liu and Wang, 1987. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch diameter, mm	6	7.4	0.928	12.49	5.9	8.3
Exozone width, mm	6	1.7	0.417	24.76	1.1	2.3
Endozone width, mm	6	4.1	0.613	15.04	3.3	5.1
Autozooeical aperture width, mm	50	0.29	0.031	10.58	0.23	0.34
Autozooeical aperture spacing, mm	50	0.51	0.072	14.13	0.35	0.65
Vesicle diameter, mm	50	0.12	0.029	24.54	0.05	0.19
Vesicles per aperture	16	11.7	0.873	7.47	10.0	13.0
Vesicle spacing, mm	50	0.12	0.033	26.52	0.07	0.24
Lunarium length, mm	29	0.16	0.042	26.36	0.08	0.24
Lunarium width, mm	29	0.24	0.036	15.28	0.16	0.31
Lunarium thickness, mm	29	0.11	0.025	23.33	0.06	0.15

1987 *Fistuliramus xianzaensis* Liu and Wang, p. 5, pl. 2, figs. 2a-c, pl. 3, fig. 1a-c.

**Material.** SMF 23.036-SMF 23.050.

**Description.** Branched colonies 5.9–8.3 mm in diameter, with 3.3–5.1 mm wide endozones and 1.1–2.3 mm wide exozones. Autozooeia long in endozones, bending at low angles in exozones. Autozooeical diaphragms few, thin, planar, or concave, concentrated in the transition zone between endozone and exozone. Autozooeical apertures rounded. Lunaria well-developed, horseshoe-shaped, originating in endozone, consisting of granular material. Vesicles abundant both in endozone and exozone, moderately large, box-like, polygonal in tangential section, having flattened roofs, separating autozooeia in 1–3 rows and 10–13 surrounding each autozooeical aperture; in endozone usually twice as high as those in exozone. Autozooeical walls granular prismatic, 0.005–0.010 mm thick. Maculae not observed. Granular skeleton on colony surface poorly developed.

**Remarks.** *Fistuliramus xianzaensis* Liu and Wang, 1987 is similar to *F. bifidus* Yang and Xia, 1975 from the Lower Permian of China, but differs by wider branches (5.9–8.3 mm vs. 3.2–5.6 mm in *F. bifidus*) and by larger and more abundant vesicles (average vesicle diameter 0.12 mm vs. 0.09 mm in *F. bifidus*). *Fistuliramus xianzaensis* differs from *F. elevatus* Liu and Wang, 1987 from the Lower Permian of China in larger autozooeical apertures (average aperture width 0.29 mm vs. 0.19 mm in *F. elevatus*).

**Occurrence.** Xiala Formation, ?Middle Permian; Xainza, southwestern Tibet. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *ERIDOPORA* Ulrich, 1882

**Type species.** *Eridopora macrostoma* Ulrich, 1882. Lower Carboniferous; North America.

**Diagnosis.** Thin encrusting colonies. Oval apertures with strongly developed lunaria of distinct triangular shape. Cylindrical autozooeia with thin walls and complete diaphragms. Vesicular skeleton consists of angular vesicles.

**Remarks.** *Eridopora* Ulrich, 1882 differs from *Fistulipora* M'Coy, 1849 and *Dybowskiella* Waagen and Wentzel, 1886 in having large triangular lunaria instead of horseshoe-shaped ones, and predominantly encrusting colonies.

**Occurrence.** Devonian to Permian; worldwide.

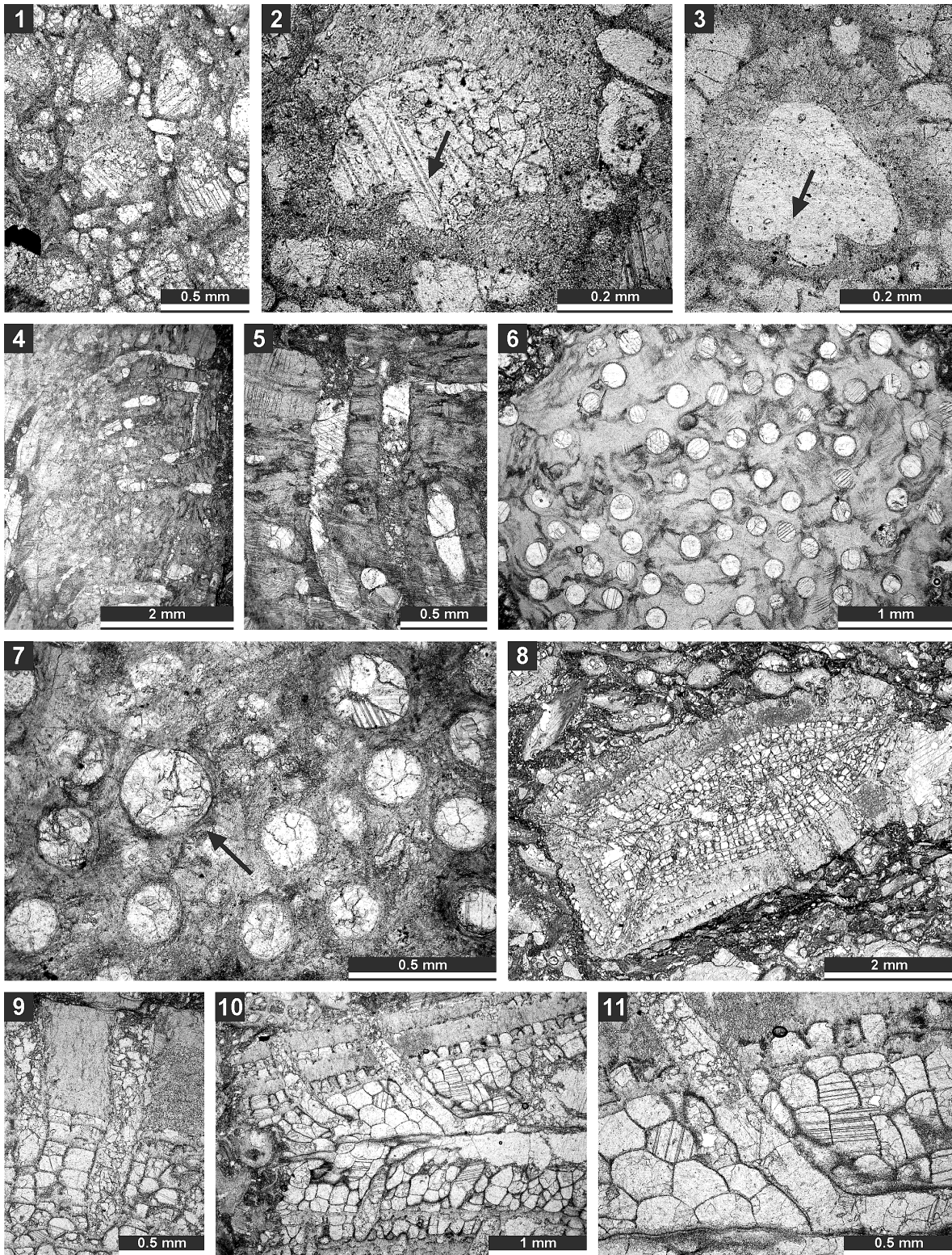
*Eridopora uncata* Yang and Lu, 1983  
Figures 5.4-6, 6.1-3; Table 6

1983 *Eridopora ? uncata* Yang and Lu, 269, pl. 5, fig. 5; pl. 6, figs. 1-4.

**Material.** SMF 23.051–SMF 23.052.

**Description.** Thin encrusting colony. Autozooeia growing from thin epitheca, bending in the early exozone to the colony surface. Basal diaphragms abundant. Autozooeical apertures circular to oval. Lunaria well-developed, triangular; ends of lunaria indenting into autozooeia on the opposite side of the aperture. Vesicles small to large, separating autozooeia in 1–2 rows, 11–16 surrounding each autozooeia aperture, with rounded roofs, polygonal in tangential section. Autozooeical walls granular prismatic, 0.005–0.010 mm thick. Maculae not observed.

**Remarks.** *Eridopora uncata* Yang and Lu, 1983 differs from *E. triangulariformis* Yang and Lu, 1983 from the Kankerin Formation (Upper Carboniferous) of Kalpin (Western Xinjiang, China) in smaller autozooeia (0.18–0.37 mm vs. 0.25–0.40 mm in *E. triangulariformis*). *Eridopora uncata* differs from



**FIGURE 6.** Thin section photographs of *Eridopora uncata* Yang and Lu, 1983, SMF 23.052 (1–3); *Cyclotrypa alexanderi* Sakagami, 1963 SMF 23.056 (4–5), SMF 23.061 (6), and SMF 23.056 (7); and *Hexagonella kobayashii* Sakagami, 1968, SMF 23.069 (8–9) and SMF 23.070 (10 and 11). 1–3, tangential section showing autozooezial apertures with lunarial ends indenting into the aperture (arrow); 7, tangential section showing autozooezia and macrozooezia (arrow); 8 and 9, branch transverse section showing autozooezial chambers and vesicular skeleton; and 10 and 11, longitudinal section showing autozooezial chambers and vesicular skeleton.

**TABLE 6.** Measurements of *Eridopora uncata* Yang and Lu, 1983. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	31	0.26	0.046	17.72	0.18	0.37
Autozooeical aperture spacing, mm	31	0.47	0.068	14.39	0.33	0.62
Vesicle diameter, mm	31	0.09	0.024	25.76	0.05	0.15
Vesicles per aperture	10	13.7	1.703	12.43	11.0	16.0

**TABLE 7.** Measurements of *Cyclotrypa alexanderi* Sakagami, 1963. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	50	0.20	0.017	8.71	0.17	0.25
Autozooeical aperture spacing, mm	50	0.39	0.050	12.86	0.27	0.50
Vesicle diameter, mm	50	0.13	0.029	22.74	0.07	0.18
Vesicles per aperture	22	7.64	1.432	18.76	5.0	11.0
Maculae diameter, mm	11	0.6	0.163	26.67	0.4	0.9
Macrozooeical aperture width, mm	7	0.31	0.041	13.25	0.25	0.36

*E. oculata* Bassler, 1929 in less closely spaced apertures (average distance between aperture centres 0.47 mm vs. 0.40 mm in *E. oculata*) and in absence of ridges between autozooeical apertures. **Occurrence.** Baliqliq Group, Lower Permian; Kalpin, Western Xinjiang, China. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *CYCLOTRYPA* Ulrich, 1896

**Type species.** *Fistulipora communis* Ulrich, 1890. Middle Devonian; Iowa, USA.

**Diagnosis.** Encrusting colonies, often with multiple overgrowths. Cylindrical autozooeia with thin walls and complete diaphragms. Autozooeical apertures rounded. Lunaria absent. Autozooeia separated by vesicular skeleton. Acanthostyles occurring in roofs of vesicles. Low maculae often developed.

**Remarks.** *Cyclotrypa* Ulrich, 1896 differs from *Fistulipora* M'Coy, 1849 and *Eridopora* Ulrich, 1882 in the absence of lunaria.

**Occurrence.** Silurian to Permian; Europe, North America, Asia.

*Cyclotrypa alexanderi* Sakagami, 1963

Figure 6.4-7; Table 7

1963 *Cyclotrypa alexanderi* Sakagami, p. 206, pl. 12, figs. 1-7.

1976 *Cyclotrypa alexanderi* Sakagami, 1963; Sakagami, pl. 25, figs. 1-2.

**Material.** SMF 23.053–SMF 23.066.

**Description.** Colonies branched ramose or encrusting. Branched colonies 7.5–9.6 mm in diameter, with 1.2–1.3 mm wide exozone and 5.1–7.0 mm wide endozones. Encrusting colonies 1.3–

1.9 mm thick. In branched colonies, cylindrical autozooeia long in endozones, bending sharply in exozones, rounded–polygonal in transverse section. In secondary overgrowths and encrusting sheets, autozooeia growing from laminated epitheca. Epitheca 0.025–0.030 mm thick. Autozooeical diaphragms few to common. Autozooeical apertures rounded to oval. Granular material well-developed at colony surface. Acanthostyles in granular material developed, 0.05–0.07 mm in diameter. Locally macrozooeia occurring. Vesicular skeleton well-developed. Vesicles small, separating autozooeia in 1–2 rows, 5–11 surrounding each autozooeical aperture, with rounded roofs, polygonal in tangential section. Autozooeical walls granular prismatic, 0.003–0.008 mm thick. Low maculae without autozooeia regularly spaced on colony surface, 0.4–0.9 mm in diameter.

**Remarks.** *Cyclotrypa alexanderi* Sakagami, 1963 differs from *C. uralica* Nikiforova, 1939 from the Lower Permian (Artinskian) of Urals in smaller autozooeical apertures (aperture width 0.17–0.25 mm vs. 0.35 mm in *C. uralica*). *Cyclotrypa alexanderi* differs from *C. exposita* Gorjunova, 1975 from the Lower Permian (Artinskian) of Pamir in smaller autozooeical apertures (aperture width 0.17–0.25 mm vs. 0.35–0.40 mm in *C. exposita*).

**Occurrence.** Noonkanbah Formation, Lower Permian (upper Artinskian–Kungurian); Western Australia (unpublished data). Lower Permian (Artinskian); Malaysia. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Suborder HEXAGONELLINA Morozova, 1970  
Family HEXAGONELLIDAE Crockford, 1947

Genus *HEXAGONELLA* Waagen and Wentzel,  
1886

**Type species.** *Hexagonella ramosa* Waagen and Wentzel, 1886. Upper Permian; Pakistan.

**Diagnosis.** Colonies consisting of compressed to subcylindrical bifoliate branches. Mesotheca straight, three-layered, with central granular and granular-prismatic outer layers. Autozoecia recumbent, widely isolated by vesicular skeleton throughout the colony. Diaphragms rare, planar. Lunaria well-developed in exozone, consisting of granular-prismatic material. Vesicles large, irregular in endozone, box-like in inner exozone, blister-like and low in outer exozone. Stereom of granular-prismatic material well-developed, containing tubules. Autozoecial walls granular-prismatic. Monticules consisting of central cluster of vesicular skeleton and radiating rows of autozoecia with lunaria directed towards the centre of the monticule. Each monticule surrounded by elevated ridges of vesicular skeleton producing hexagonal pattern.

**Remark.** *Hexagonella* Waagen and Wentzel, 1886 differs from *Coscinotrypa* Hall and Simpson, 1887 by colony form and presence of crests on the colony surface. Some species placed in *Hexagonella* do not have typical crests of the colony surface (e.g., *H. australis* {Bretnall, 1926}).

**Occurrence.** Twenty-five species have been reported from the Permian of Australia, Asia, and Northern Russia. The genus seems to be absent in North and South America.

*Hexagonella kobayashii* Sakagami, 1968

Figures 6.8-11, 7.1-4; Table 8

- 1968 *Hexagonella kobayashii* Sakagami, p. 50-51, pl. 9, figs. 3-5; 1976, pl. 25, figs. 7-9.
- 1976 *Hexagonella kobayashii* Sakagami, 1968; Sakagami, pl. 25, figs. 7-9.
- 1997 *Hexagonella kobayashii* Sakagami, 1968; Sakagami and Pillecuit, p. 206, figs. 2.4-5, 3.1-3.
- 2008 *Hexagonella kobayashii* Sakagami, 1968; Ernst, Weidlich and Schäfer, p. 680-682, figs. 3.5, 3.7, 3.8, 4.1.

**Material.** Six thin sections of single colony SMF 23.067–SMF 23.072.

**Description.** Free-branched bifoliate colony. Branches elliptical in transverse section, 6.9–8.6 mm wide and 3.0–4.5 mm thick. Mesotheca straight, three-layered, 0.05–0.10 mm thick, containing median tubules. Autozoecia long, tubular, bending gently in exozone. Apertures rounded to oval. Lunaria distinct. Diaphragms rare, 1–2 in

each autozoecium, thin, planar. Vesicles large, box-like with rounded roofs, separating autozoecia in 2–3 rows, 8–10 surrounding each autozoecia aperture. Autozoecial walls granular, 0.008–0.018 mm thick. Thick layer of granular skeleton in the outermost exozone. Crests on the colony surface building regular hexagonal patterns. Maculae not observed.

**Remarks.** *Hexagonella kobayashii* Sakagami, 1968 is similar to *H. turgida* Bassler, 1929 from Permian of Timor. The latter species differs in having smaller autozoecial apertures (ca. 0.20 mm vs. 0.19–0.25 mm in *H. kobayashii*).

**Occurrence.** Rat Buri Limestone (Khao Phrick), Lower Permian (Artinskian); Thailand. Aseelah Unit, Saal Formation, Lower–?Middle Permian; Batain Coast (eastern Oman). Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Family GONIOCLADIIDAE Waagen and Pichl,  
1885

Genus *GONIOCLADIA* Etheridge, 1876

**Type species.** *Carinella cellulifera* Etheridge, 1873. Lower Carboniferous; Carlisle (Scotland).

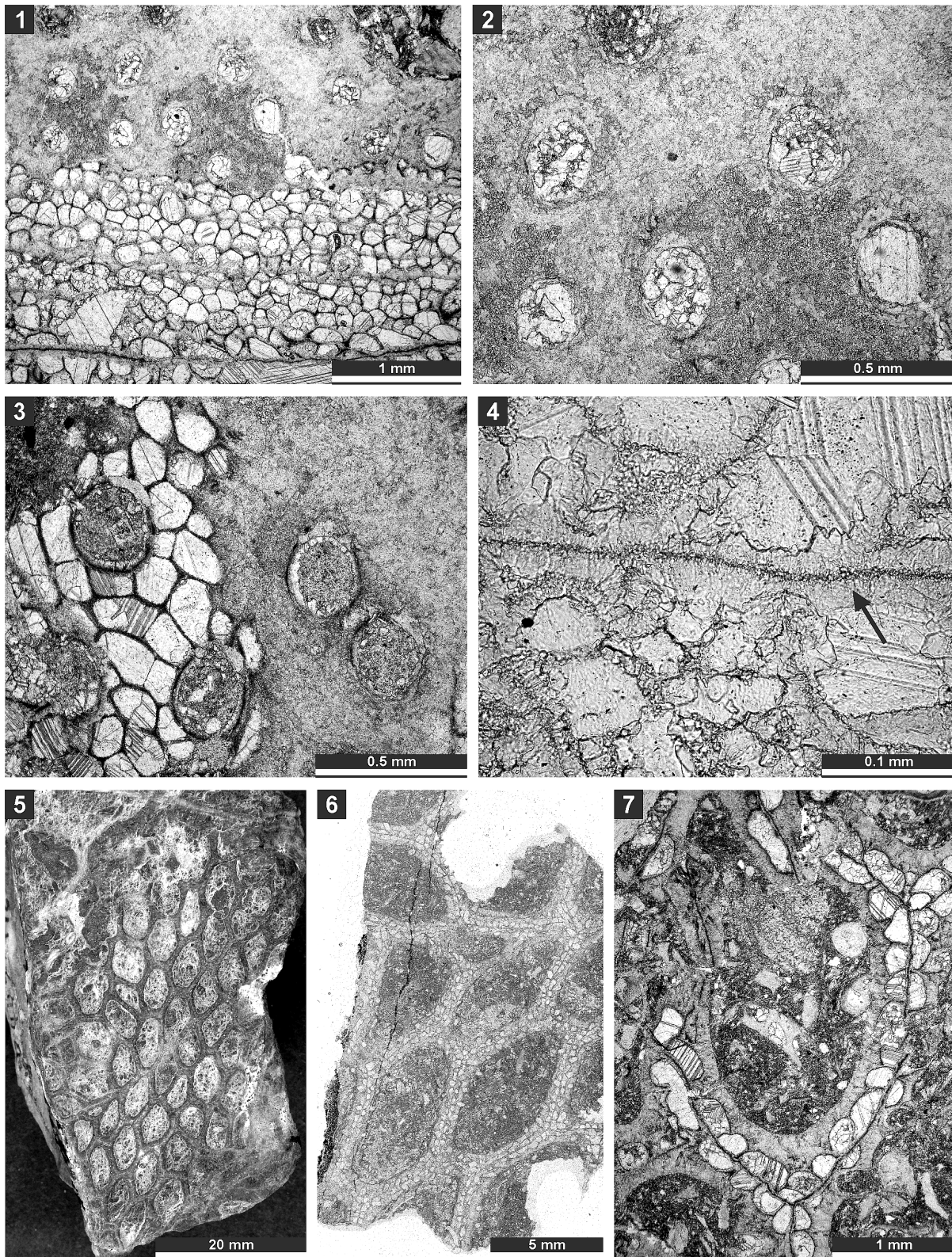
**Diagnosis.** Reticulate colonies with polygonal fenestrules. Branches bifoliate, joined by anastomoses or rarely by dissepiments. Autozoecia in two or more rows on each side of the mesotheca. Apertures with more or less developed lunaria and apertural styles. Thin mesotheca protruding as ridge on the circular reverse side and as sharp keel on peaked obverse side. Median rods in mesotheca usually lacking, in few species present. Thin walled autozoecia usually separated by vesicular skeleton.

**Remarks.** *Goniocladia* Etheridge, 1876 differs from *Ramipora* Toulou, 1875 in having reticulate colony shape instead of pinnate one (consisting of main branch with diverging lateral branches).

**Occurrence.** Carboniferous–Permian; worldwide.

*Goniocladia* aff. *indica* Waagen and Pichl, 1885  
Figures 7.5-7, 8.1-7; Table 9

- aff. 1885 *Goniocladia indica* Waagen and Pichl, p. 805, pl. 93, fig. 3.
- aff.? 1929 *Goniocladia indica* Waagen and Pichl, 1885; Bassler, p. 88.
- aff.? 1957 *Goniocladia indica* Waagen and Pichl, 1885; Crockford, p. 38.
- aff. 1981 *Goniocladia indica* Waagen and Pichl, 1885; Yang, Lu and Xia, p. 92-93, pl. 1, fig. 5, pl. 3, fig. 4.
- aff. 1986 *Goniocladia* cf. *indica* Waagen and Pichl, 1885; Xia, pl. 11, figs. 1-2.



**FIGURE 7.** Thin section photographs of *Hexagonella kobayashii* Sakagami, 1968, SMF 23.067 (1–3) and SMF 23.072 (4); and *Goniocladia* aff. *indica* Waagen and Pichl, 1885, SMF 23.266 (5), SMF 23.077 (6), and SMF 23.073 (7). 1–3 and 6, tangential section; 7, mid-tangential section showing autozooeical chamber; 4, transverse section showing mesotheca with median tubules (arrow); and 5, external view of the colony form the reverse side.

**TABLE 8.** Measurements of *Hexagonella kobayashii* Sakagami, 1968. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	22	0.22	0.016	7.15	0.19	0.25
Autozooeical aperture spacing, mm	22	0.53	0.047	8.81	0.42	0.60
Vesicle diameter, mm	30	0.12	0.031	25.96	0.04	0.19
Vesicles per aperture	10	9.0	0.667	7.41	8.0	10.0
Vesicle spacing, mm	13	0.10	0.023	23.09	0.07	0.14

aff. 1991 *Goniocladia indica* Waagen and Pichl, 1885; Xia, p. 191, pl. 7, fig. 10.

**Material.** SMF 23.073–SMF 23.080, SMF 23.266.

**Diagnosis.** Reticulate colony consisting of anastomosing bifoliate branches of intermediate width and thickness; fenestrules oval to circular, intermediate in size; autozooeicia arranged in 4–6 rows on branches; autozooeical apertures with lunaria; vesicular skeleton well-developed, consisting of small vesicles; extrazoeical skeleton well-developed.

**Description.** Reticulate colony consisting of anastomosing bifoliate branches. Branches 0.88–2.00 mm wide and 0.63–1.26 mm thick. Fenestrules oval to polygonal (pentagonal to hexagonal), occasionally nearly circular. Autozooeicia tubular, semi-circular in transverse section at their bases, relatively short, budding in 4–6 rows from each side of thin mesotheca, opening on both sides of the median carina. Superior hemisepta positioned on the distal side of the autozooeical chamber near its bend; inferior hemisepta positioned on the proximal side (at mesotheca). Basal diaphragms rare. Mesotheca straight or slightly undulating, consisting of granular–prismatic material, with dark median layer, 0.02–0.04 mm thick, protruding on the obverse side as a median carina and as a sharp keel on the reverse side. Autozooeical apertures arranged regularly in 2–6 diagonal rows on both sides of the median carina, rounded to oval. Outermost parts of median lamina containing median rods, 0.010–0.015 mm in diameter. Lunaria moderately developed, directed towards median carina. Autozooeical walls 0.02–0.04 mm thick, granular–prismatic. Extrazoeical skeleton (steriom) granular. Vesicular skeleton consisting of low small vesicles with flattened roofs, concentrated mostly in endozoe.

**Remarks.** The present material superficially resembles the species *Goniocladia indica* Waagen and Pichl, 1885, originally described from the *Productus* Limestone (?Kungurian–Wordian) of Salt Range, Pakistan. The original description of this species is based on external characters without

use of thin sections. Only figure 3e from plate 93 (Waagen and Pichl, 1885) shows a broken piece of branch, which reveals zooeical shape and vesicular skeleton typical for *Goniocladia*. Some important measurements such as aperture size and spacing of the original material are also unknown. Therefore, the assignment to this species by later authors was justified according to external parameters. Waagen and Pichl (1885, p. 805–806) provided the following measurements: branch width ca 1.5 mm, fenestrule length 3–7 mm, and fenestrule width 1–4 mm. They correspond in general with those of the present material. However, the present material possesses superior and inferior hemisepta, which were neither mentioned nor depicted in the original material.

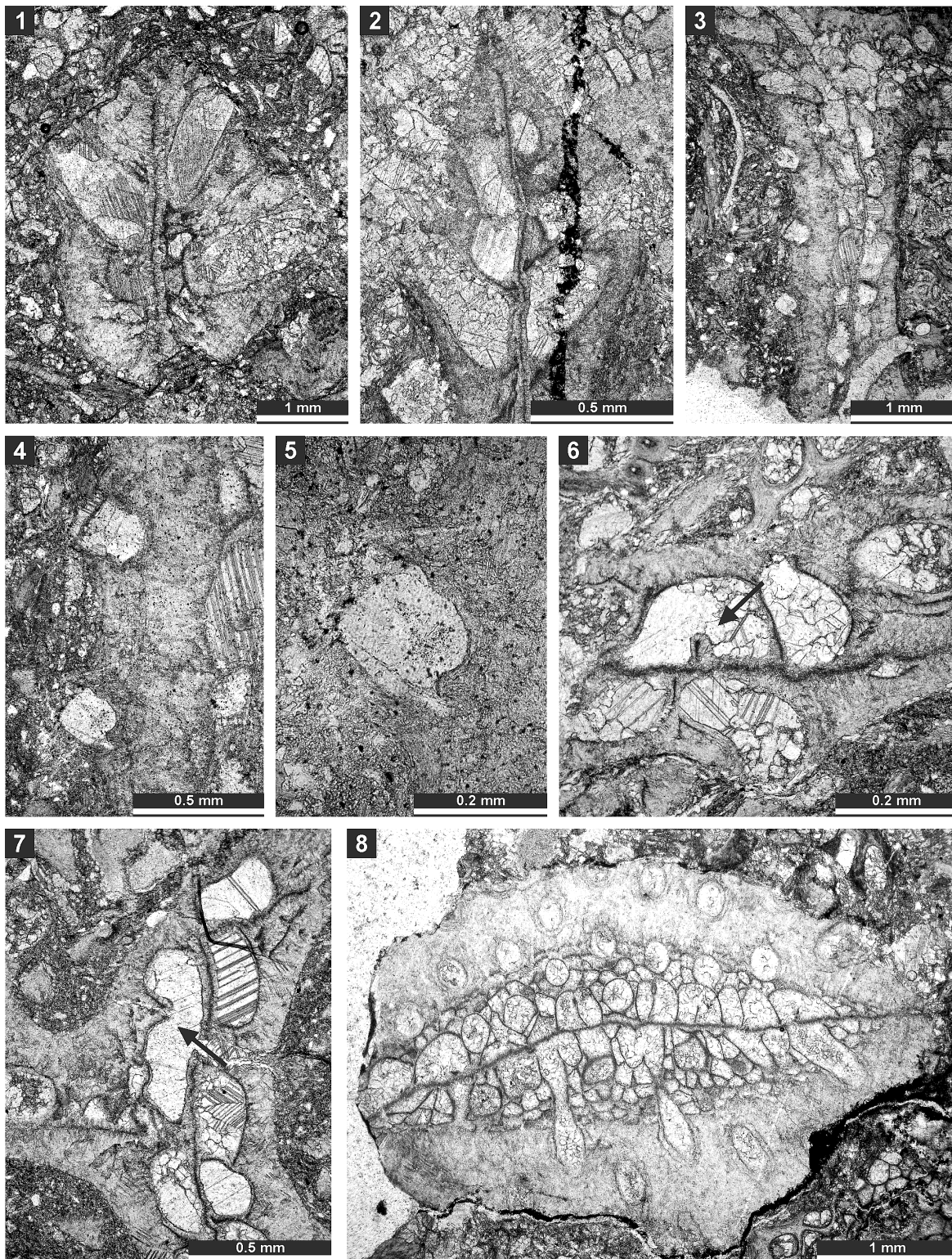
The present species is, therefore, only tentatively assigned with *Goniocladia indica* Waagen and Pichl, 1885. It differs from *G. afghana* (Termier and Termier, 1971) from the Lower Permian of Afghanistan and Iran (Ernst and Gorgij, 2013) by larger fenestrules (fenestrule length 4.3–6.9 mm vs. 1.26–2.73 mm in *G. afghana*; fenestrule width 2.4–3.7 mm vs. 0.75–1.56 mm in *G. afghana*). Moreover, the present species has wider spaced apertures (average aperture spacing 0.60 mm vs. 0.45 mm in *G. afghana*).

The present species differs from *Goniocladia yongzhuensis* Liu and Wang, 1987 from the Lower Permian (Artinskian) of Tibet in possessing smaller autozooeical apertures (aperture width 0.15–0.22 mm vs. 0.20–0.24 mm in *G. yongzhuensis*) and larger fenestrules (fenestrule length 4.3–6.9 mm vs. 0.64–5.6 mm in *G. yongzhuensis*).

Bassler (1929) and Crockford (1957) mentioned *Goniocladia indica*, but they did not provide either descriptions or illustrations of their material. Chinese citations of *Goniocladia indica* Waagen and Pichl, 1885 (Yang et al., 1981; Xia 1986, 1991) seem to correspond to the species described here. However, no description mentioned hemisepta.

**Occurrence.** ?Lower Permian; Tibet. ?*Productus* Limestone (?Kungurian–Wordian) of Salt-range, Pakistan. ?Lower Permian; Western Australia.





**FIGURE 8.** Thin section photographs of *Goniocladia* aff. *indica* Waagen and Pichl, 1885, SMF 23.076 (1 and 2), SMF 23.077 (3–5), and SMF 23.073 (6 and 7); and *Liguloclema meridianus* (Etheridge, 1926), SMF 23.093 (8). 1–2, and 6, branch transverse sections showing autozooeceia chambers, mesotheca and hemisepta (arrow); 3–5, tangential sections showing autozooeceial apertures; 7, longitudinal section showing autozooeceial chamber with superior hemisepta (arrow); and 8, branch oblique section showing mesotheca, autozooeceial chambers with hemisepta and vesicular skeleton.

**TABLE 9.** Measurements of *Goniocladia* aff. *indica* Waagen and Pichl, 1885. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	6	1.22	0.405	33.36	0.88	2.00
Branch thickness, mm	10	0.99	0.220	22.34	0.63	1.26
Fenestrule width, mm	8	3.2	0.412	13.04	2.4	3.7
Fenestrule length, mm	8	5.8	0.989	17.03	4.3	6.9
Distance between branch centres, mm	8	6.5	0.316	4.82	6.0	7.0
Distance between dissepiment centres, mm	6	7.7	0.359	4.67	7.2	8.1
Autozooeical aperture width, mm	20	0.19	0.022	11.29	0.15	0.22
Autozooeical aperture spacing, mm	20	0.60	0.097	16.37	0.42	0.70
Lunarium length, mm	6	0.08	0.018	21.29	0.06	0.10
Lunarium width, mm	6	0.14	0.019	14.03	0.10	0.15
Lunarium thickness, mm	5	0.03	0.009	36.19	0.02	0.04

?Lower Permian; Timor. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Family ETHERELLIDAE Crockford, 1957  
Genus *LIGULOCLEMA* Crockford, 1957

**Type species.** *Liguloclema typicalis* Crockford, 1957. Noonkanbah Formation, Lower Permian (Artinskian–Kungurian); Western Australia.

**Diagnosis.** Colony narrow bifoliate branches, branching dichotomously in plane of mesotheca. Mesotheca consisting of granular-prismatic material, straight; median tubules present. Autozooeical tubular, with rounded to elongate apertures, rhombically arranged on branches, lacking on lateral sides of branches; subquadrate, trapezoid to sub-hemispherical in transverse section at mesotheca; angular shaped in deep tangential section in mid exozone and partially isolated by vesicles. Long and thin hook-shaped superior hemisepta present, curved proximally, club-shaped. Lunaria absent. Vesicular skeleton well-developed, restricted to exozone; vesicles blister-like, low to moderately high with flat to rounded roofs, polygonal in tangential section. Autozooeical walls granular-prismatic, with dark median zone continuous into boundary zone in mesotheca. Extrazoeical skeleton well-developed, displaying cloudy structure; acanthostyles present. Monticules absent.

**Remarks.** *Liguloclema* Crockford, 1957 differs from *Etherella* Crockford, 1957 in having narrow belt-shaped colonies instead of reticulate one in *Etherella*. *Liguloclema* differs from *Wysejacksonella* Ernst and Gorgij, 2013 by the club-shaped hemisepta vs. blunt hemisepta representing buckling of the autozooeical wall at the transition between endo- and exozone in *Wysejacksonella*.

Furthermore, *Liguloclema* possesses median tubules in mesotheca.

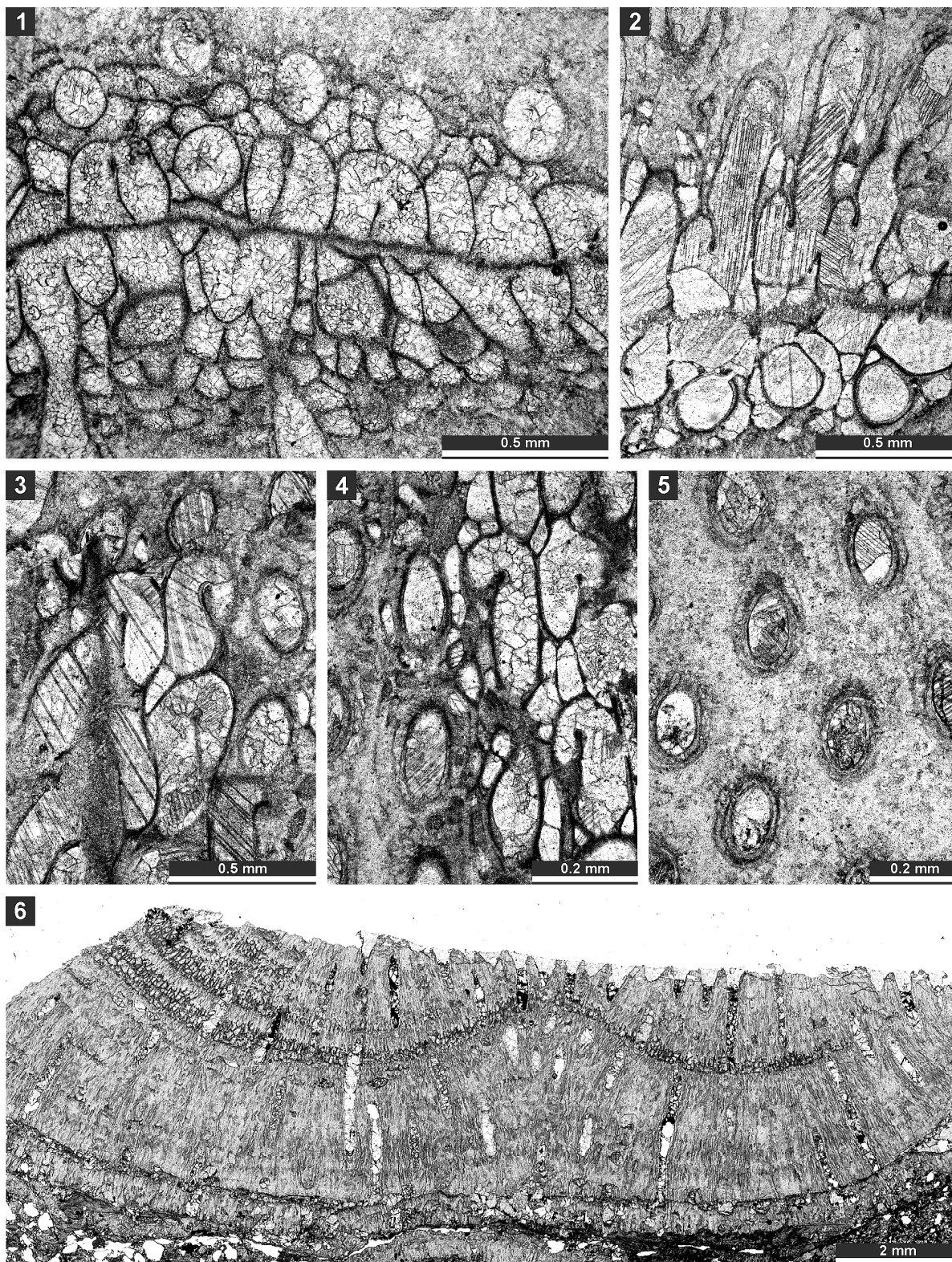
**Occurrence.** Lower Permian (Artinskian); Western Australia. Xiala Formation (?Middle Permian); Xainza, southwestern Tibet. ?Lower Permian (Artinskian); Thailand. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Liguloclema meridianus* (Etheridge, 1926)  
Figures 8.8, 9.1-5; Table 10

- 1926 *Sulcoretepora* (?) *meridianus* Etheridge, in Bretnall, p. 19, pl. 1, fig. 9.
- 1931 *Sulcoretepora* (?) *meridianus* Etheridge, 1926; Hosking, p. 15.
- 1944 "*Sulcoretepora*" *meridianus* Etheridge, 1926; Crockford, p. 156, pl. 4, fig. 6, text-figs. 29-30.
- 1957 *Liguloclema meridianus* (Etheridge, 1926); Crockford, p. 37.
- 1988 *Liguloclema meridianus* (Etheridge, 1926); Yanagida, J. a Research Group, p. 17, figs. 2-3.
- 1987 *Liguloclema* cf. *meridianus* (Etheridge, 1926); Liu and Wang, p. 7, figs. 7-8.
- 1993 *Liguloclema meridianus* (Etheridge, 1926); Engel and Ross, p. 17, pl. 13, figs. 1-3.
- 1973 *Liguloclema* cf. *meridianus* (Etheridge, 1926); Sakagami, p. 77-78, pl. 11, figs. 1-4.
- 1999 *Liguloclema meridianus* (Etheridge, 1926); Sakagami, p. 86-87, pl. 21, figs. 1-3.

**Material.** SMF 23.081–SMF 23.098.

**Description.** Colony narrow bifoliate branches, dichotoming in plane of mesotheca. Branches 1.4–3.4 mm wide and 1.1–1.9 mm thick, lens-shaped in transverse section. Branch edges rounded, lacking autozooeical. Autozooeical tubular, rhombically arranged in 8–13 longitudinal rows on branches,



**FIGURE 9.** Thin section photographs of *Liguloclema meridianus* (Etheridge, 1926), SMF 23.093 (1), SMF 23.085 (2), and SMF 23.083 (3–5); and *Etherella tibetensis* n. sp., paratype SMF 23.217 (6). 1 and 2, branch oblique section showing mesotheca, autozooeical chambers with hemisepta and vesicular skeleton; 3 and 4, mid-tangential section showing autozooeical chambers with hemisepta; 5, tangential section showing autozooeical apertures; and 6, transverse section showing extrazooeical skeleton and sparse vesicles.

**TABLE 10.** Measurements of *Liguloclema meridianus* (Etheridge, 1926). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	30	0.14	0.012	8.54	0.12	0.16
Autozooeical aperture spacing, mm	30	0.65	0.105	16.17	0.52	0.95
Aperture spacing diagonally, mm	30	0.47	0.045	9.59	0.37	0.55
Vesicle diameter, mm	30	0.08	0.018	22.51	0.05	0.12

lacking on lateral sides of branches; subquadrate, trapezoid to subhemispherical in transverse section at mesotheca; angular shaped in deep tangential section in mid exozone and partially isolated by vesicles. Long and thin hook-shaped superior hemisepta present at the transition between endo- and exozone, curved proximally, club-shaped. Basal diaphragms rare. Mesotheca consisting of granular-prismatic material, straight, 0.03–0.04 mm thick; median tubules present, 0.010–0.015 mm in diameter; longitudinal ridges absent. Autozooeical walls granular-prismatic, 0.013–0.015 mm thick. Autozooeical apertures arranged regularly in 9–13 diagonal rows on branches, rounded to oval. Lunaria absent. Vesicular skeleton well-developed, restricted to exozone; vesicles blister-like, low to moderately high with flat to rounded roofs, polygonal (mainly rectangular) in tangential section. Extrazooeical skeleton well-developed, displaying cloudy structure. Acanthostyles absent. Monticules absent.

**Remarks.** Two species are placed in the genus *Liguloclema*, *L. typicalis* Crockford, 1957 and *L. meridianus* (Etheridge, 1926), both originally known from the Noonkanbah Formation, Lower Permian (Artinskian–Kungurian) of Western Australia. Crockford (1957, p. 37) provided neither detailed description of *L. meridianus* nor made a comprehensive comparison between *L. typicalis* and *L. meridianus*. The only difference she mentioned was the smaller branch width of *L. meridianus* against *L. typicalis* (less than 1.8 mm vs. 3.3–5.0 mm in *L. typicalis*). The present material of *Liguloclema meridianus* differs from *L. typicalis* in larger distances between aperture centres (0.52–0.95 mm vs. 0.43–0.55 mm in *L. typicalis*).

**Occurrence.** Noonkanbah Formation, Lower Permian (upper Artinskian–Kungurian); Western Australia. Rat Buri Limestone, Lower Permian (?Artinskian–Kungurian); Khao Raen, Thailand. Permian, ?Wordian; Khao Hin Kling area, north-central Thailand. Xiala Formation, ?Middle Permian; Xainza, southwestern Tibet. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *ETHERELLA* Crockford, 1957

**Type species.** *Etherella porosa* Crockford, 1957. Lower Permian, Noonkanbah Formation (Artinskian–Kungurian); Western Australia.

**Diagnosis.** Reticulate colonies formed by fused branches; branches bifoliate, lenticular, rounded, or oval in transverse section; fenestrules circular to oval. Mesotheca consisting of granular-prismatic material, straight; median tubules present. Autozooeical tubular, with rounded to elongate apertures, rhombically arranged on branches, lacking on lateral sides of branches; subquadrate, trapezoid to subhemispherical in transverse section at mesotheca; angular shaped in deep tangential section in mid exozone and isolated by vesicles and extrazooeical skeleton. Long and thin hook-shaped superior hemisepta present, curved proximally, club-shaped. Lunaria absent. Vesicular skeleton scarcely developed; vesicles small, blister-like, low to moderately high with flat to rounded roofs, polygonal in tangential section. Autozooeical walls granular-prismatic, with dark median zone continuous into boundary zone in mesotheca. Extrazooeical skeleton well-developed, displaying cloudy structure; acanthostyles absent. Monticules absent.

**Remarks.** *Etherella* Crockford, 1957 differs from *Liguloclema* Crockford, 1957 in having reticulate colonies instead of narrow belt-shaped type in *Liguloclema*. *Etherella* differs from *Wysejacksonella* Ernst and Gorgij, 2013 by the club-shaped hemisepta vs. blunt hemisepta representing buckling of the autozooeical wall at the transition between endo- and exozone in *Wysejacksonella*. Furthermore, *Etherella* possesses median tubules in mesotheca.

**Occurrence.** Lower Permian of Australia and Tibet, Upper Permian of the Russian Far East.

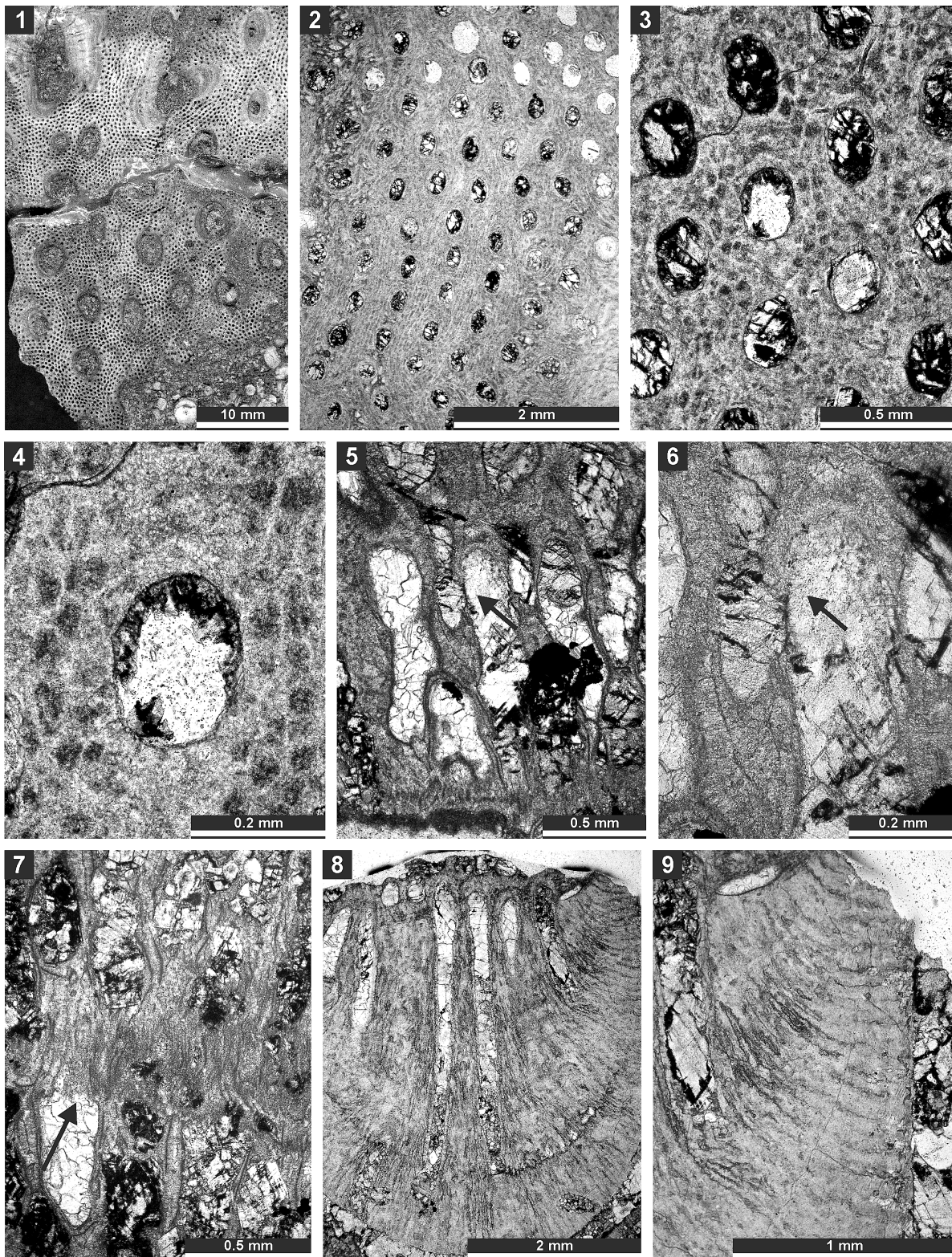
*Etherella tibetensis* n. sp.

Figures 9.6, 10; Table 11

zoobank.org/1610F4FA-934D-4255-ADF6-1DFF0931FBA1

**Etymology.** The species is named after its occurrence in Tibet.

**Holotype.** SMF 23.214.



**FIGURE 10.** Thin section photographs of *Etherella tibetensis* n. sp., paratype SMF 23.267 (1), paratype SMF 23.216 (2), paratype SMF 23.219 (3 and 4), holotype SMF 23.214 (5–7), and paratype SMF 23.230 (8 and 9). 1, external view of the colony (split along mesotheca); 2–4, tangential section showing arrangement of autozoocidia and wall microstructure; 5–7, oblique section showing hemisepta and mesotheca (arrows); and 8 and 9, branch transverse section showing autozoocelial chambers and extrazoocelial skeleton.

**TABLE 11.** Measurements of *Etherella tibetensis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	10	3.60	0.790	21.99	2.8	5.1
Fenestrule width, mm	20	2.33	0.477	20.50	1.6	3.3
Fenestrule length, mm	20	3.2	0.376	11.75	2.1	4.0
Autozooeical aperture width, mm	30	0.17	0.025	14.40	0.12	0.21
Autozooeical aperture spacing along branch, mm	30	0.53	0.066	12.52	0.45	0.66
Autozooeical aperture spacing diagonally, mm	30	0.50	0.056	11.15	0.4	0.6
Vesicle diameter, mm	20	0.09	0.030	32.88	0.05	0.15

**Paratypes.** SMF 23.215–SMF 23.223, SMF 23.230, SMF 23.231, SMF 23.267.

**Type locality.** Zhongba area of southwestern Tibet (E 83.76894, N 29.93333).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Reticulate colonies formed by fused branches; branches bifoliate, lenticular, rounded to oval in transverse section; fenestrules circular to oval; autozooeia arranged in 8–10 rows on branches; lunaria absent; vesicular skeleton scarcely developed, vesicles small; extrazooeical skeleton well-developed; monticules absent.

**Description.** Studied material represent a bifoliate reticulate colon split in the plane of mesotheca (Figures 9.6, 10.8). Branches 2.8–5.1 mm wide and 8.0–10.3 mm thick, rounded to oval in transverse section. Fenestrules circular to oval, 1.6–3.3 mm wide and 2.1–4.0 mm long. Autozooeia tubular, long, rhombically arranged in 8–10 longitudinal rows on branches, lacking on lateral sides of branches; subquadrate, trapezoid to subhemispherical in transverse section at mesotheca; angular shaped in deep tangential section in mid exozone and partially isolated by vesicles. Long and thin hook-shaped superior hemisepta present at the transition between endo- and exozone, curved proximally, club-shaped. Basal diaphragms rare. Mesotheca consisting of granular-prismatic material, straight, 0.02–0.03 mm thick; median tubules present, 0.015–0.030 mm in diameter; longitudinal ridges absent. Autozooeical walls granular-prismatic, 0.015–0.040 mm thick. Autozooeical apertures arranged regularly in 9–13 diagonal rows on branches, rounded to oval. Lunaria absent. Vesicular skeleton well-developed, restricted to exozone; vesicles blister-like, low to moderately high with flat to rounded roofs, polygonal in tangential section. Extrazooeical skeleton well-developed, displaying cloudy structure produced by stab-shaped elements. Acanthostyles absent. Monticules absent.

**Remarks.** *Etherella tibetensis* n. sp. differs from *Etherella porosa* Crockford, 1957 and *E. porosa minor* Crockford, 1957 from the Lower Permian (Artinskian–Kungurian) of Western Australia, in having larger and more closely spaced autozooeical apertures as well as an extremely thick extrazooeical skeleton. *Etherella tibetensis* n. sp. shows intermediate dimensions of colony elements comparable to both Australian species:

*Etherella porosa*—branch width: 4.0–5.5 mm; fenestrule width: 3.0–5.0 mm; fenestrule length: 5.0–7.0 mm; aperture width: 0.13–0.16 mm; aperture spacing: 0.5–0.7 mm.

*Etherella porosa minor*—branch width: 2.0–3.3 mm; fenestrule width: 2.0–2.5 mm; fenestrule length: 2.0–3.5 mm; aperture width: 0.14 mm; aperture spacing: 0.50–0.83 mm.

*Etherella tibetensis*—branch width: 2.8–5.1 mm; fenestrule width: 1.6–3.3 mm; fenestrule length: 2.1–4.0 mm; aperture width: 0.12–0.21 mm (0.17 mm at average); aperture spacing: 0.45–0.66 mm (0.53 mm at average).

The species *Coscinotrypa orientalis* Sakagami, 1968 from the Permian of Khao Ta Mong Rai, Thailand, may belong to *Etherella*. It shows oval apertures without lunaria, scarce vesicular skeleton and extensive extrazooeical skeleton. However, the presence of the hook-shaped hemisepta cannot be confirmed on that material because the part of the colony at mesotheca is strongly affected by diagenesis. This species also possesses larger autozooeical apertures (average autozooeical width 0.24 mm vs. 0.17 mm in *E. tibetensis*).

Order TREPOSTOMATA Ulrich, 1882

Suborder AMPLEXOPORINA Astrova, 1965

Family STENOPORIDAE Waagen and Wentzel, 1886

Genus *TABULIPORA* Young, 1883

**Type species.** *Cellepora urii* Fleming, 1828. Carboniferous; Scotland.

**Diagnosis.** Ramose, encrusting, cylindrical, or massive colonies. Autozoecia with basal diaphragms and ring septa. Autozoecial walls irregularly thickening with development of monilae. Exilazoecia rare. Acanthostyles of two sizes: small microacanthostyles and large macroacanthostyles.

**Remarks.** The genus *Tabulipora* Young, 1883 differs from the genera *Stenopora* Lonsdale, 1844 and *Stenodiscus* Crockford, 1945 by the development of ring septa.

**Occurrence.** Carboniferous–Permian; worldwide.

*Tabulipora xinjiangensis* Yang and Lu, 1983  
Figure 11.1-2; Table 12

1983 *Tabulipora xinjiangensis* Yang and Lu, p. 271, pl. 2, figs. 1-2.

**Material.** SMF 23.232–SMF 23.234.

**Material.** Encrusting colony, 0.75–1.26 mm thick. Autozoecia prismatic, having polygonal shape in transverse section, containing rare diaphragms and abundant ring septa. Ring septa concentrated in exozones, occupying about a half of the autozoecial chamber space. Acanthostyles 0.05–0.11 mm in diameter, having narrow hyaline cores and wide laminated sheaths, 1–3 surrounding each autozoecial aperture. Exilazoecia not observed. Endozonal walls granular, 0.015–0.020 mm thick; exozonal walls monilae-shaped thickened, laminated, serrated, with distinct autozoecial boundaries, 0.075–0.120 mm thick. Tubules abundant in exozonal walls, 0.010–0.015 mm in diameter.

**Remarks.** *Tabulipora xinjiangensis* Yang and Lu, 1983 differs from *T. angjiensis* Xia, 1986 from the Ghainaha Formation (Middle Permian) of the Rutog region of Tibet, in possessing fewer acanthostyles and having larger autozoecial apertures (0.25–0.35 mm vs. 0.15–0.25 mm in *T. angjiensis*). *Tabulipora xinjiangensis* differs from *T. sinensis* Yang and Lu, 1984 and *T. wangcangensis* Yang and Lu, 1984 from the Lower Permian of southwest China in having an encrusting colony instead of a branched colony.

**Occurrence.** Baliqliq Group, Lower Permian; Kalpin, Western Xinjiang, China. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Family DYSTRITELLIDAE Dunaeva and Morozova, 1967

Genus DYSCRITELLA Girty, 1911

**Type species.** *Dyscritella robusta* Girty, 1911. Lower Carboniferous; Arkansas, USA.

**Diagnosis.** Dendroid and encrusting colony with abundant acanthostyles and exilazoecia. Autozo-

oecia parallel to longitudinal direction of the colony in endozone; gradually bending outward in exozone. Diaphragms in autozoecia lacking or very rare; lacking in exilazoecia. Exilazoecia circular to angular in cross section and separated from the autozoecia and from each other by thick walls. Two sizes of acanthostyles may be present. Zoecial walls thin in endozone, rapidly thickening in the exozone (modified after Ernst and Gorgij, 2013).

**Remarks.** *Dyscritella* Girty, 1911 generally lacks diaphragms which are commonly developed in the similar genus *Dyscritellina* Morozova in Dunaeva and Morozova, 1967.

**Occurrence.** Devonian to Triassic; worldwide.

*Dyscritella lii* n. sp.  
Figure 11.3-6; Table 13

zoobank.org/C2A7C366-334C-46E5-BB66-375EBFE2FC98

**Etymology.** The species is named in honour of Dr. Xianghui Li, who provided material for this study and helped during the manuscript preparation.

**Holotype.** SMF 23.235.

**Paratypes.** SMF 23.236 and SMF 23.237.

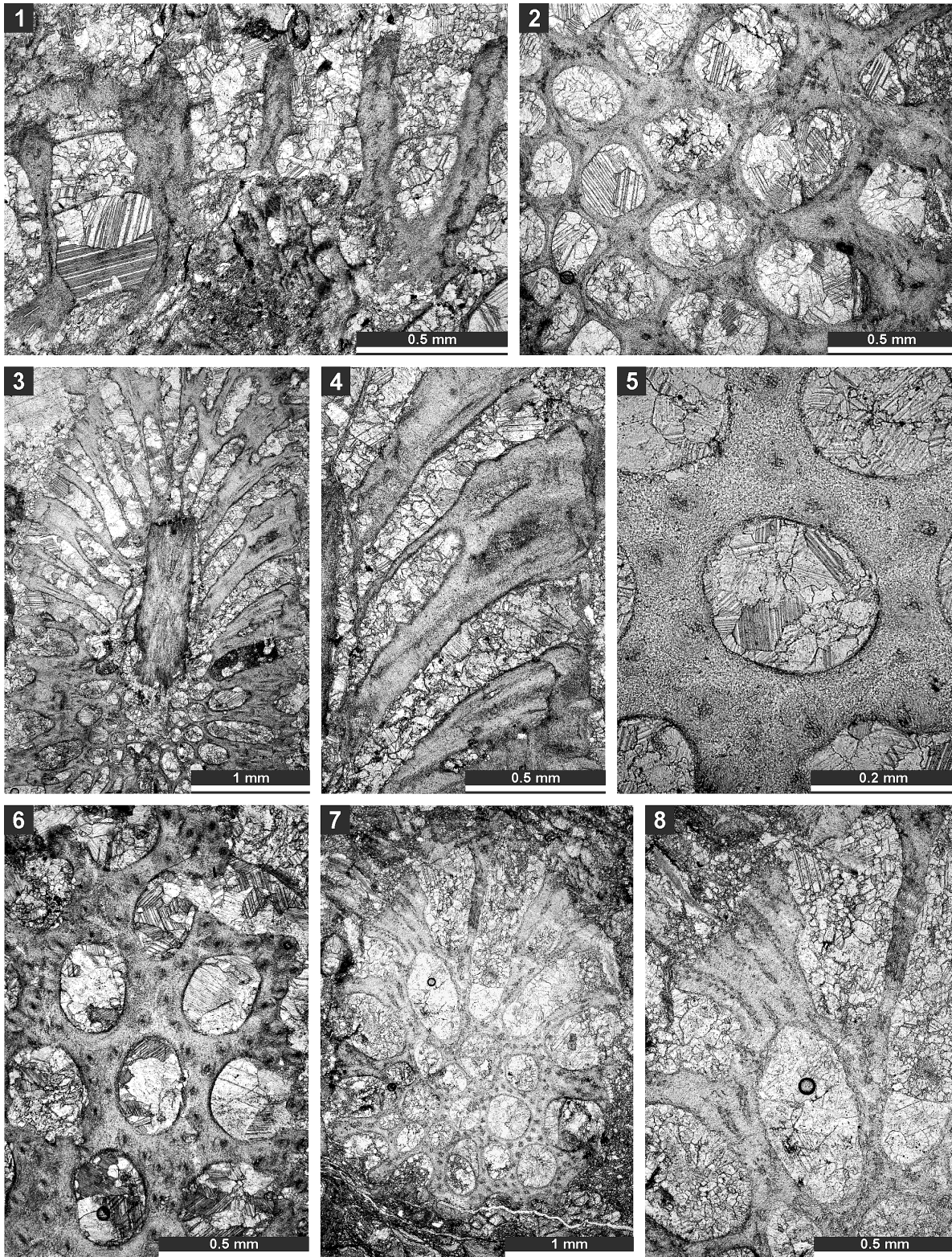
**Type locality.** Zhongba area of southwestern Tibet (E 84.31536, N 29.74233).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Encrusting colony; exilazoecia few; acanthostyles large, abundant, 8–14 surrounding each autozoecial aperture; exozonal walls thick.

**Description.** Encrusting colony, 0.99–1.05 mm thick, with 0.54–0.64 mm wide exozone. Autozoecial diaphragms absent. Autozoecial apertures rounded to slightly angular. Exilazoecia few, having rounded to polygonal transverse section, restricted to the exozone, 0.04–0.11 mm in diameter. Abundant acanthostyles in the walls of the exozone, originating from transitional zone between endozone and exozone, 8–14 surrounding each autozoecial aperture. Walls granular-prismatic, 0.02–0.03 mm thick in the endozone; laminated, regularly thickened, 0.08–0.13 mm thick in exozone. Maculae not observed.

**Remarks.** *Dyscritella lii* n. sp. differs from *Dyscritella phetchabunensis* Sakagami, 1975 from the Lower Permian of Thailand, by having larger and more abundant acanthostyles and fewer exilazoecia, as well as larger autozoecia (autozoecial aperture width 0.18–0.30 mm vs. 0.13–0.17 mm in *D. phetchabunensis*). *Dyscritella lii* n. sp. differs from *D. fida* Morozova, 1991 from the Lower Permian of Mongolia in possessing more abundant acanthostyles (8–14 vs. 6–9 around each aperture in *D. fida*), as well as larger autozoecia (autozo-



**FIGURE 11.** Thin section photographs of *Tabulipora xinjiangensis* Yang and Lu, 1983, SMF 23.233 (1 and 2); *Dyscritella lii* n. sp., holotype SMF 23.235 (3, 4, and 6) and paratype SMF 23.236 (5); and *Ulrichotrypella omanica* Ernst et al., 2008, SMF 23.242 (7 and 8). 1, longitudinal section showing ring septa; 2, oblique section showing macroacanthostyles and tubules; 3 and 4, oblique section through the colony; 5 and 6, tangential section showing autozoecial apertures and acanthostyles; and 7 and 8, oblique section.



**TABLE 12.** Measurements of *Tabulipora xinjiangensis* Yang and Lu, 1983. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	12	0.30	0.027	9.19	0.25	0.35
Autozooeical aperture spacing, mm	7	0.40	0.060	15.08	0.32	0.50
Exozonal wall thickness, mm	7	0.094	0.014	14.50	0.075	0.120

**TABLE 13.** Measurements of *Dyscritella lii* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	29	0.24	0.030	12.28	0.18	0.30
Autozooeical aperture spacing, mm	22	0.38	0.057	15.06	0.26	0.48
Acanthostyle diameter, mm	20	0.08	0.022	28.54	0.04	0.12
Acanthostyles per aperture	14	10.1	1.657	16.34	8.0	14.0

oeical aperture width 0.18–0.30 mm vs. 0.18–0.20 mm in *D. fida*).

Family ULRICHOTRYPELLIDAE Romantchuk in Romantchuk and Kiseleva, 1968  
Genus ULRICHOTRYPELLA Romantchuk, 1967

**Type species.** *Ulrichotrypella prima* Romantchuk, 1967. Upper Permian; Khabarovsk region, Russia.

**Diagnosis.** Ramose and rarely encrusting colonies. Autozooeia with circular to polygonal apertures. Diaphragms rare, thin, planar. Autozooeical walls in the exozone irregularly thickened. Exilazooeia rare to common. Abundant aktinostyles present (modified after Astrova, 1978).

**Remarks.** *Ulrichotrypella* Romantchuk, 1967 differs from *Ulrichotrypa* Bassler, 1929 by the presence of diaphragms in autozooeia and aktinostyles in the walls of the autozooeia.

**Occurrence.** Lower Permian–Upper Permian; Indonesia, Iran, Russia, Canada.

*Ulrichotrypella omanica* Ernst, Weidlich and Schäfer, 2008

Figures 11.7-8, 12.1; Table 14

2008 *Ulrichotrypella omanica* Ernst, Weidlich and Schäfer, p. 686, figs. 5.12-17.

**Material.** SMF 23.238–SMF 23.242.

**Description.** Ramose colony, 2.2 mm in diameter, with 0.65 mm wide exozone and 0.9 mm wide endozone. Thin complete diaphragms in autozooeia constricted to exozone. Autozooeical apertures rounded to angular. Exilazooeia few, having a rounded to polygonal transverse section, restricted to the exozone, 0.09–0.12 mm in diameter. Abundant aktinostyles in the walls of the exozone, originating from transitional zone between endozone and exozone. Acanthostyles absent. Walls granular-prismatic, 0.03–0.04 mm thick in the endozone; laminated, regularly thickened, 0.07–0.15 mm thick in exozone.

**Remarks.** *Ulrichotrypella omanica* Ernst et al., 2008 differs from *U. prima* Romantchuk, 1967 in having larger apertures (0.21–0.38 mm vs. 0.20–0.29 mm in *U. prima*) and less abundant exilazooeia.

**Occurrence.** Aseelah Unit, Saal Formation, Lower–?Middle Permian; Batain Coast (eastern Oman). Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Family ERIDOTRYPELLIDAE Morozova, 1960  
Genus NEOERIDOTRYPELLA Morozova, 1970

**Type species.** *Neoeridotrypella pulchra* Morozova, 1970. Permian, Guadalupian (Kazanian); Russia.

**Diagnosis.** Branched colonies with wide exozones. Autozooeia polygonal in transverse section of endozone, bending at low angles in exozone. Autozooeical apertures oval to polygonal. Diaphragms rare. Exilazooeia rare. Autozooeical walls in the exozone irregularly thickened, traversed by tubules. Acanthostyles stellate, variable in size.

**Remarks.** *Neoeridotrypella* Morozova, 1970 differs from *Permopora* Romantchuk, 1967 in being a branched colony rather than an encrusting one.

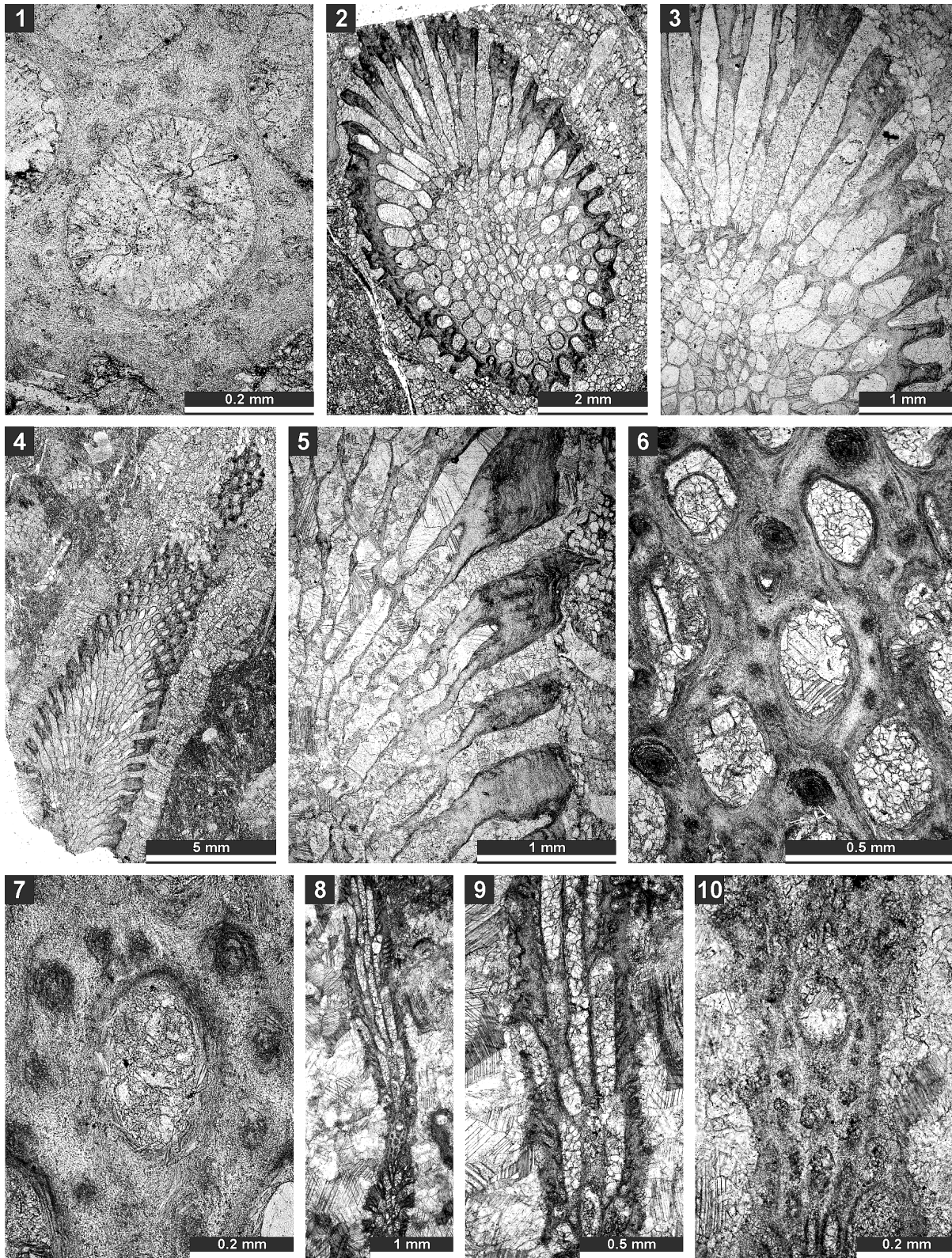
**Occurrence.** Permian; Russia, USA, Tibet.

*Neoeridotrypella astrica* (Linskaya, 1951)  
Figure 12.2-7; Table 15

1951 *Rhombotrypella astrica* Linskaya, p. 150, pl. 3, figs. 3-4.

**Material.** SMF 23.243–SMF 23.250.

**Description.** Ramose colonies, 4.10–5.40 mm in diameter, with 0.54–0.82 mm wide exozone and 3.02–3.76 mm wide endozone. Autozooeical diaphragms absent. Autozooeical apertures rounded to slightly angular. Exilazooeia few, having rounded to polygonal transverse section shape, restricted to the exozone, 0.04–0.11 mm in diame-



**FIGURE 12.** Thin section photographs of *Ulrichotrypella omanica* Ernst et al., 2008, SMF 23.242 (1); *Neoeridotrypella astrica* (Linskaya, 1951), SMF 23.245 (2 and 3), SMF 23.246 (4–6), and SMF 23.249 (7); and *Streblotrypa (Streblotrypa) parviformis* n. sp., holotype SMF 23.251 (8–10). 1, 6, 7, and 10, tangential section; 2–5, oblique branch section; and 8 and 9, longitudinal section.

**TABLE 14.** Measurements of *Ulrichotrypa omanica* Ernst et al., 2008. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	17	0.28	0.048	17.11	0.21	0.38
Autozooeical aperture spacing, mm	13	0.47	0.076	16.33	0.38	0.67
Exozone width, mm	6	0.10	0.023	23.29	0.06	0.12
Aktinostyle diameter, mm	10	0.06	0.012	21.43	0.04	0.07
Exozonal wall thickness, mm	8	0.11	0.031	28.22	0.07	0.15

**TABLE 15.** Measurements of *Neoeridotrypella astrica* (Linskaya, 1951). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	4	4.66	0.550	11.79	4.10	5.40
Exozone width, mm	4	0.65	0.136	20.94	0.54	0.82
Endozone width, mm	4	3.36	0.305	9.07	3.02	3.76
Autozooeical aperture width, mm	30	0.22	0.024	11.00	0.17	0.26
Autozooeical aperture spacing along branch, mm	30	0.47	0.051	10.85	0.40	0.57
Macroacanthostyle diameter, mm	21	0.16	0.028	17.42	0.10	0.22
Microacanthostyle diameter, mm	30	0.07	0.013	17.64	0.04	0.10

ter. Abundant stellate acanthostyles in the walls of the exozone, originating from transitional zone between endozone and exozone, strongly varying in size. Usually 1–4 macroacanthostyles and 5–10 microacanthostyles surrounding each autozooeical aperture. Walls granular-prismatic, 0.018–0.025 mm thick in the endozone; laminated, regularly thickened, 0.15–0.26 mm thick in exozone. Tubules and spherules abundant in exozonal walls.

**Remarks.** *Neoeridotrypella astrica* (Linskaya, 1951) differs from *N. pulchra* Morozova, 1970 from the Upper Permian (Kazanian) of Russia, in having slightly larger autozooeical apertures (aperture width 0.17–0.26 mm vs. 0.16–0.20 mm in *N. pulchra*). *Neoeridotrypella astrica* differs from *N. schilti* Gilmour et al., 1997 from the Upper Permian (Wordian) of Nevada, USA, in having smaller autozooeical apertures (average aperture width 0.22 mm vs. 0.25 mm in *N. schilti*). Furthermore, *Neoeridotrypella astrica* has no diaphragms instead of the few present in *N. schilti*, and stellate acanthostyles instead of normal ones.

**Occurrence.** Cisuralian (Artinskian–Kungurian); Northern Urals, Russia. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Order CRYPTOSTOMATA Vine, 1884  
Suborder RHABDOMESINA Astrova and Morozova, 1956  
Suborder RHABDOMESINA Astrova and Morozova, 1956  
Family HYPHASMOPORIDAE Vine, 1885

Genus *STREBLOTRYPA* Vine, 1885  
Sub-genus *STREBLOTRYPA* (*STREBLOTRYPA*)  
Vine, 1885

**Type species.** *Streblotrypa nicklesi* Vine, 1885. Middle Carboniferous; England.

**Diagnosis.** Branched colonies. Indistinct bundle of about 10 or fewer axial zooecia in the endozone. Autozooeia budding from axial bundle, having long inflated proximal parts, rounded-polygonal in transverse section in the endozone, bending abruptly at the transition between endo- and exozone. Autozooeical apertures rounded to oval. Diaphragms rare.

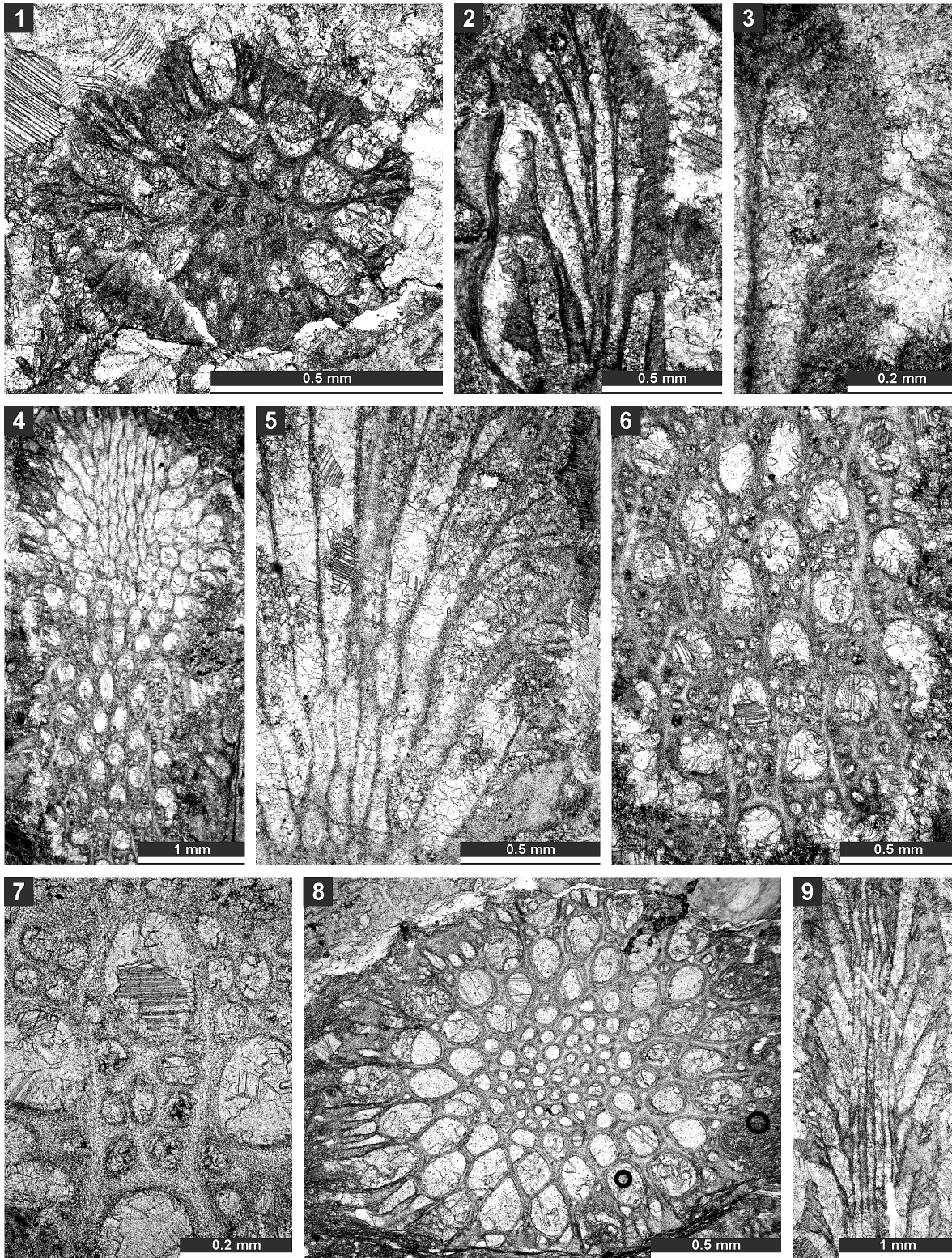
Hemisepta usually present. Metazooeia usually restricted to rows between the autozooeical apertures; styles usually lacking but poorly developed acanthostyles sometimes occurring. Autozooeical walls laminated, without distinct autozooeical boundaries.

**Remarks.** *Streblotrypa* (*Streblotrypa*) Vine, 1885 differs from *S. (Streblascopora)* Bassler, 1929 by possessing an indistinctly defined axial bundle of 10 or less axial zooecia. *Streblotrypa* (*Streblotrypa*) differs from *Hyphasmopora* Etheridge, 1875 by the presence of an axial bundle and having a wall structure without distinct autozooeical boundaries.

**Occurrence.** Carboniferous to Permian; world-wide.

*Streblotrypa* (*Streblotrypa*) *parviformis* n. sp.  
Figures 12.8-10, 13.1-3; Table 16

zoobank.org/5E091691-0A97-45F9-8BD6-091335B75870



**FIGURE 13.** Thin section photographs of *Streblotrypa* (*Streblotrypa*) *parviformis* n. sp., paratype SMF 23.260 (1) and paratype SMF 23.256 (2 and 3); *Streblotrypa* (*Streblascopora*) *delicatula* Sakagami, 1961, SMF 23.205 (4, 6, and 7), SMF 23.206 (5), and SMF 23.143 (8); and *Streblotrypa* (*Streblascopora*) *marmionensis* (Etheridge, 1926), SMF 23.145 (9). 1 and 8, branch transverse section; 2, 3, 5, and 9, longitudinal section; 4, branch oblique section; and 6 and 7, tangential section.

**TABLE 16.** Measurements of *Streblotrypa (Streblotrypa) parviformis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	20	0.68	0.091	13.45	0.51	0.92
Exozone width, mm	19	0.13	0.027	20.66	0.09	0.17
Endozone width, mm	19	0.42	0.066	15.84	0.31	0.58
Axial bundle width, mm	17	0.15	0.039	25.61	0.10	0.26
Autozooeical aperture width, mm	25	0.10	0.011	11.15	0.08	0.12
Autozooeical aperture spacing along branch, mm	4	0.53	0.059	11.20	0.48	0.61
Autozooeical aperture spacing diagonally, mm	3	0.25	0.026	10.58	0.22	0.27
Metazooecia width, mm	15	0.02	0.006	28.30	0.01	0.03

**Etymology.** The species is named after its similarity with *Streblotrypa (Streblotrypa) parva* Morozova, 1965.

**Holotype.** SMF 23.251.

**Paratypes.** SMF 23.131–SMF 23.142, SMF 23.252–SMF 23.261.

**Type locality.** Zhongba area of southwestern Tibet (E 84.31536, N 29.74233).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Thin branched colonies; axial bundle consisting of 3–7 axial zooecia; hemisepta absent; 12–20 metazooecia arranged between apertures; acanthostyles present.

**Description.** Branched colonies, 0.51–0.92 mm in diameter, with 0.09–0.17 mm wide exozones and 0.31–0.58 mm wide endozones. Autozoecia long, tubular, growing from a distinct axial bundle, rounded to slightly polygonal in transverse section. Axial bundle small, formed by 3–7 axial zooecia, 0.10–0.26 mm in diameter. Autozooeical apertures oval, arranged in regular diagonal rows. Autozooeical diaphragms locally present. Hemisepta absent. Metazooecia small, 12–20 of them arranged in three rows between apertures. Acanthostyles present, irregularly distributed between autozooeical apertures. Autozooeical walls laminated, 0.010–0.015 mm thick in endozone.

**Remarks.** *Streblotrypa (Streblotrypa) parviformis* n. sp. is similar to *Streblotrypa (Streblotrypa) parva* Morozova, 1965 from the Upper Permian of Caucasus, but differs from it by the presence of acanthostyles. *Streblotrypa (Streblotrypa) parviformis* differs from *S. (S.) quadrata* Liu, 1976 from the Lower Permian of China by the presence of acanthostyles and thinner branches (branch diameter 0.51–0.92 mm vs. 0.60–1.40 mm in *S. (S.) quadrata*). *Streblotrypa (Streblotrypa) parviformis* differs from *S. (S.) elegans* Sakagami, 1970 from the Lower Permian of Thailand by possessing acanthostyles and lacking hemisepta.

Sub-genus STREBLOTRYPA  
(STREBLASCOPIORA) Bassler, 1929

**Type species.** *Streblotrypa fasciculata* Bassler, 1929. Upper Permian, Indonesia.

**Diagnosis.** Branched colonies. Clearly defined bundle of the axial zooecia in the endozone. Autozoecia budding from axial bundle, having long inflated proximal parts, rounded-polygonal in transverse section in the endozone, bending abruptly at the transition between endo- and exozone. Autozooeical apertures rounded to oval. Diaphragms rare. Inferior hemisepta commonly present, sometimes accompanied by superior hemisepta; in some species hemisepta absent. Metazooecia between the autozooeical apertures and beyond the distolateral margins of autozooeical apertures. Autozooeical walls laminated, without distinct autozooeical boundaries.

**Remarks.** *Streblotrypa (Streblotrypa) parviformis* Bassler, 1929 differs from *S. (Streblotrypa) Vine*, 1885 by having a distinct axial bundle with more than 10 axial zooids.

**Occurrence.** Carboniferous to Permian; worldwide.

*Streblotrypa (Streblotrypa) delicatula* Sakagami, 1961

Figure 13.4-8; Table 17

- 1961 *Streblotrypa delicatula* Sakagami, p. 52, pl. 25, figs. 7-10, pl. 26, fig. 2-18, pl. 27, figs. 1-5.
- 1973 *Streblotrypa delicatula* Sakagami, 1961; Sakagami, p. 84-85, pl. 8, figs. 1-4.
- 1984 *Streblotrypa delicatula* Sakagami, 1961; Yang and Lu, p. 53-54, pl. 1, fig. 5b, pl. 2, 3a, b.
- 1997 *Streblotrypa delicatula* Sakagami, 1961; Sakagami and Pillecuit, p. 212, figs. 4-(9-11), 5-1.

**TABLE 17.** Measurements of *Streblotrypa (Streblascopea) delicatula* Sakagami, 1961. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	4	1.68	0.288	17.14	1.30	2.00
Axial bundle width, mm	4	0.58	0.092	15.97	0.45	0.67
Autozooeical aperture width, mm	19	0.16	0.010	6.53	0.13	0.17
Autozooeical aperture spacing along branch, mm	15	0.45	0.055	12.15	0.37	0.55
Autozooeical aperture spacing diagonally, mm	15	0.29	0.034	11.50	0.24	0.35
Metazooecia width, mm	15	0.03	0.009	27.91	0.02	0.05
Metazooecia per aperture	7	7.4	0.976	13.14	6.0	9.0

2008 *Streblascopea delicatula* Sakagami, 1961; Ernst, Weidlich and Schäfer, p. 692, figs. 9.1-9.2.

**Material.** SMF 23.143, SMF 23.205–SMF 23.208.

**Description.** Branched colonies, 1.3–2.0 mm in diameter. Axial bundle 0.45–0.67 mm in diameter. Axial zooecia arranged in 6–8 rows. Autozooeica budding from the axial bundle, having long inflated proximal parts, rounded to polygonal in transverse section in the endozone. Autozooeical apertures oval, arranged in regular diagonal rows. Superior hemisepta weakly developed; inferior hemisepta long. Terminal diaphragms common. Metazooecia small, oval to rounded, 6–9 of them arranged in 2–3 rows between apertures. Autozooeical walls laminated, 0.005–0.010 mm thick in endozone.

**Remarks.** *Streblotrypa (Streblascopea) delicatula* Sakagami, 1961 differs from *S. (S.) marmionensis* (Etheridge, 1926) in having wider and less closely spaced autozooeical apertures (average aperture width 0.16 mm vs. 0.10 mm in *S. [S.] marmionensis*). *Streblotrypa (Streblascopea) delicatula* differs from *S. (S.) germana* Bassler, 1929 by the presence of hemisepta and wider autozooeical apertures (average aperture width 0.16 mm vs. 0.10 mm in *S. [S.] germana*).

**Occurrence.** Lower Permian; Japan, Thailand. Aseelah Unit, Saal Formation (Lower–?Middle Permian); Batain Coast (eastern Oman). Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Streblotrypa (Streblascopea) marmionensis*  
(Etheridge, 1926)

Figures 13.9, 14.1-3; Table 18

1926 *Streblotrypa marmionensis* Etheridge in Brethall, p. 22, pl. 1, fig. 1, pl. 2, fig. 3.

1931 *Streblotrypa marmionensis* Etheridge, 1926; Hosking, p. 14, pl. 6, fig. 1, text-fig. 1.

1944 *Streblotrypa marmionensis* Etheridge, 1926; Crockford, p. 168-169, pl. 5, figs. 10-11, text-figs. 34-37.

1957 *Streblotrypa marmionensis* Etheridge, 1926; Crockford, p. 80.

1966 ? *Streblascopea cf. marmionensis* (Etheridge, 1926); Sakagami, p. 166-167, pl. 6, fig. 11.

1983 *Streblascopea cf. marmionensis* (Etheridge, 1926); Yang and Lu, p. 291, pl. 2, fig. 6, pl. 4, figs. 8-9.

?1970 *Streblascopea marmionensis* (Etheridge, 1926); Morozova, p. 151-152, pl. 28, fig. 1.

1971 *Streblascopea marmionensis* (Etheridge, 1926); Termier and Termier, p. 24 (pars.), pl. 9, figs. 1-3, non 4-5.

1975 *Streblascopea marmionensis* (Etheridge, 1926); Gorjunova, p. 65, pl. 9, fig. 1.

1991 *Streblascopea marmionensis* (Etheridge, 1926); Xia, p. 184-185, pl. 5, figs. 7-10.

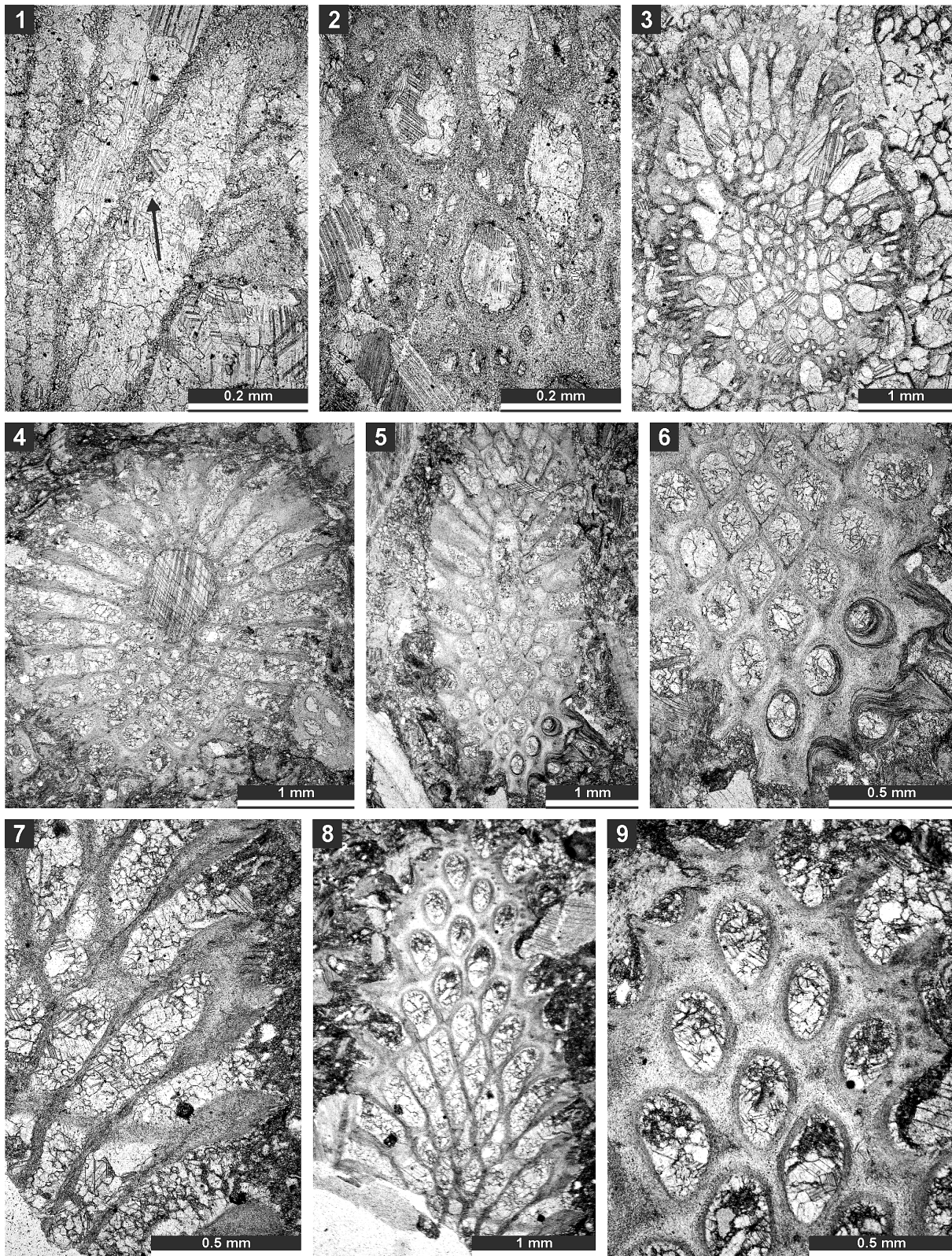
2008 *Streblascopea marmionensis* (Etheridge, 1926); Ernst, Weidlich and Schäfer, p. 694, figs. 8.10-8.11, 8.13.

2013 *Streblascopea marmionensis* (Etheridge, 1926); Ernst and Gorgij, p. 298, figs. 13d-h.

**Material.** SMF 23.144–SMF 23.151.

**Description.** Branched colonies, 1.00–1.55 mm in diameter, with 0.14–0.26 mm wide exozones and 0.65–1.15 mm wide endozones. Axial bundle 0.26–0.54 mm in diameter. Axial zooecia arranged in 5–6 rows, 0.05–0.08 mm in diameter. Autozooeica budding from the axial bundle, having long inflated proximal parts, rounded to polygonal in transverse section in the endozone. Autozooeical apertures oval, arranged in regular diagonal rows. Inferior hemisepta present. Terminal diaphragms common. Metazooecia small, oval to rounded, 8–10 of them arranged in 2–3 rows between apertures. Autozooeical walls laminated, 0.005–0.010 mm thick in endozone.

**Remarks.** *Streblotrypa (Streblascopea) marmionensis* (Etheridge, 1926) differs from *S. (S.) germana* (Bassler, 1929) in possessing hemisepta, thicker branches and a larger diameter of the axial bundle. *Streblotrypa (Streblascopea) marmionensis* is similar to *S. (S.) erecta* Baranova, 1960a



**FIGURE 14.** Thin section photographs of *Streblotrypa (Streblascopora) marmionensis* (Etheridge, 1926), SMF 23.145 (1 and 2), and SMF 23.148 (3); and *Rhabdomeson bretnalli* Crockford, 1957, SMF 23.155 (4–6) and SMF 23.157 (7–9). 1, longitudinal section; 2 and 7, tangential section; 3 and 4, branch transverse section; and 5, 6, 8 and 9; branch oblique section.

**TABLE 18.** Measurements of *Streblotrypa (Streblascopora) marmionensis* (Etheridge, 1926). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	12	1.25	0.198	15.88	1.00	1.55
Axial bundle width, mm	12	0.38	0.077	20.26	0.26	0.54
Exozone width, mm	12	0.19	0.034	17.95	0.14	0.26
Endozone width, mm	12	0.87	0.165	18.88	0.65	1.15
Autozooeical aperture width, mm	12	0.11	0.010	9.22	0.10	0.13
Metazooecia width, mm	11	0.02	0.006	30.05	0.01	0.03

**TABLE 19.** Measurements of *Rhabdomeson bretnalli* Crockford, 1957. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	7	2.45	0.610	24.91	1.60	3.30
Axial tube diameter, mm	7	0.53	0.158	29.76	0.27	0.80
Autozooeical aperture width, mm	18	0.17	0.021	12.58	0.12	0.20
Autozooeical aperture spacing along branch, mm	10	0.41	0.068	16.60	0.36	0.56
Autozooeical aperture spacing diagonally, mm	12	0.27	0.028	10.44	0.22	0.31

from the Lower Permian of northeastern Russia, but differs from it by more metazooecia between autozooeical apertures (8–10 vs. 6–9). *Streblotrypa (Streblascopora) marmionensis* differs from *S. (S.) tscharlakensis* Trizna, 1950 from the Lower Permian (Sakmarian–Artinskian) of Urals in having a larger number of axial zooecia in the axial bundle and a larger number of metazooecia between autozooeical apertures (8–10 vs. 6–8).

**Occurrence.** Lower Permian (Noonkanbah Series and Liveringa Formation); Western Australia. Lower Permian; Pamir, Tajikistan. Aseelah Unit, Saal Formation (Lower–?Middle Permian); Batain Coast (eastern Oman). Chili Formation, Lower Permian (Sakmarian–Artinskian); Kalmard area, central Iran. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of south-western Tibet.

Family RHABDOMESIDAE Vine, 1884

Genus *RHABDOMESON* Young and Young, 1874  
[= *Coeloconus* Ulrich, 1889]

**Type species.** *Rhabdomeson progradile* Wyse Jackson and Bancroft, 1995 (ICZN Opinion 1874). Lower Carboniferous; Ireland.

**Diagnosis.** Rhabdomesid with delicate dendroid colony with irregularly dichotomizing branches. Autozooeical apertures regularly budding around central axial cylinder in an annual or spiral manner. Hemisepta common. Autozooeical apertures elliptical, pyriform or rhombic, closely spaced, arranged in quincunx on colony surface; of constant or variable dimensions around branch. Stylets abundant and struc-

turally diverse (modified after Wyse Jackson and Bancroft, 1995).

**Remarks.** *Rhabdomeson* differs from other rhabdomesines in the presence of a central axial cylinder. *Rhabdomeson* differs from *Silenella* Gorjunova, 1992 in the absence of aktinostyles and from *Pseudorhabdomeson* Gorjunova, 2002 in having a rounded axial tube instead of a polygonal one as well as the presence of differentiated styles instead of aktinostyles.

**Occurrence.** Middle Devonian to Upper Permian; worldwide.

*Rhabdomeson bretnalli* Crockford, 1957

Figure 14.4-9; Table 19

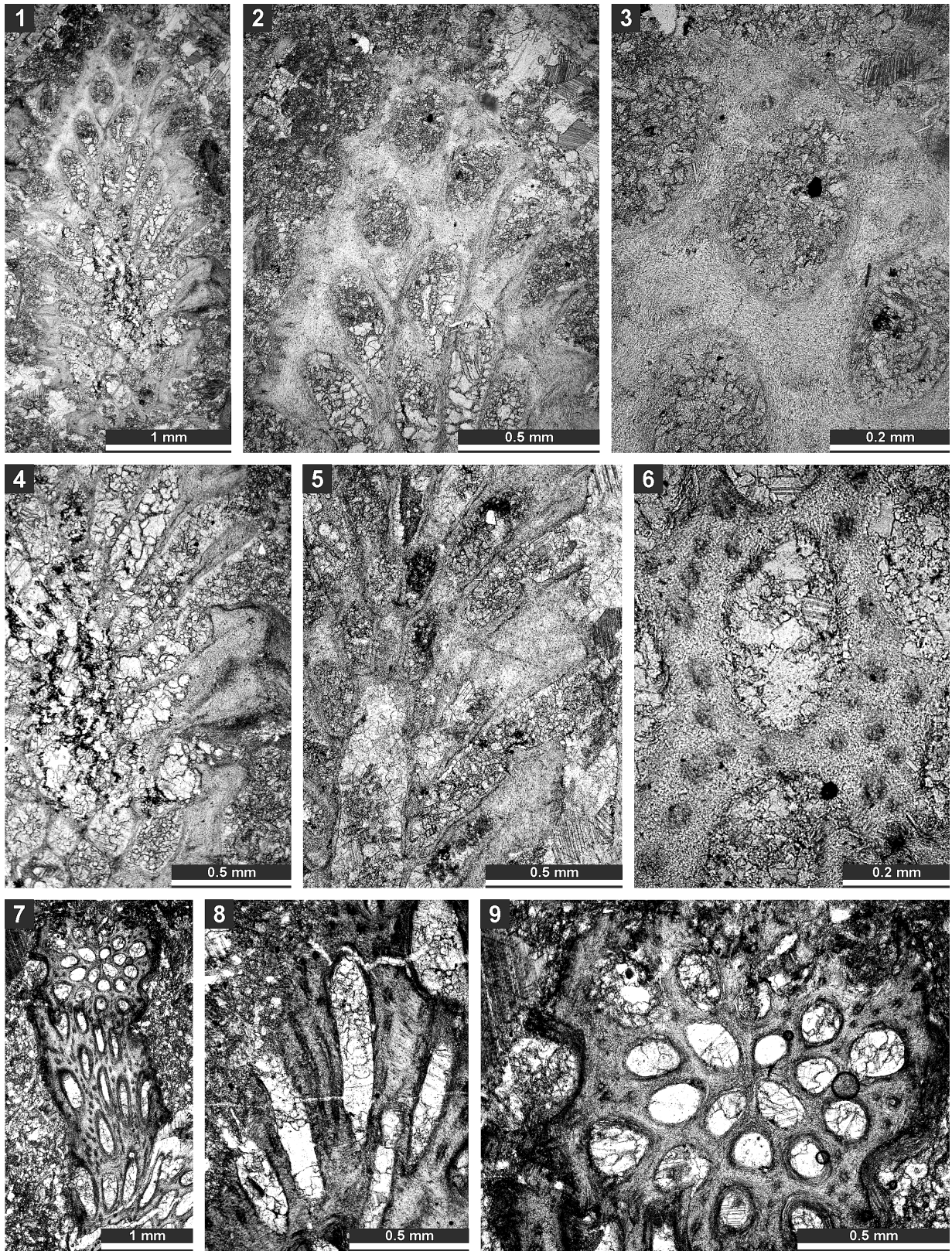
1957 *Rhabdomeson bretnalli* Crockford, p. 75, pl. 20, figs. 4-7.

**Material.** SMF 23.152–SMF 23.157.

**Description.** Branched colonies with small axial cylinder. Branches 1.6–3.3 mm in diameter. Axial cylinder circular, 0.27–0.80 mm in diameter. Autozooeical budding in a spiral pattern from the axial cylinder, rhomboid in transverse section. Autozooeical apertures oval, arranged in regular diagonal rows. Single macroacanthostyle between each aperture present building a regular rhombic pattern, 0.03–0.07 mm in diameter. Microacanthostyles abundant, arranged in 1–2 rows between macroacanthostyles, 0.02–0.03 mm in diameter. Hemisepta absent. Diaphragms rare. Autozooeical walls laminated, 0.010–0.015 mm thick in endozone.

**Remarks.** *Rhabdomeson bretnalli* Crockford, 1957 is similar to *Rhabdomeson xinjiangense* Yang and





**FIGURE 15.** Thin section photographs of *Rhabdomeson* sp. SMF 23.160 (1–4) and SMF 23.158 (5); and *Primorella rotunda* Gorjunova, 1985, SMF 23.163 (6) and SMF 23.162 (7–9). 1–3, branch oblique section; 4 and 5, longitudinal section; 6, tangential section; and 7–9, oblique section.

**TABLE 20.** Measurements of *Primorella rotunda* Gorjunova, 1975. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooeical aperture width, mm	30	0.17	0.026	15.98	0.12	0.22
Autozooeical aperture spacing along branch, mm	5	0.53	0.050	9.33	0.48	0.61
Autozooeical aperture spacing diagonally, mm	5	0.36	0.050	14.02	0.32	0.44
Aktinostyle diameter, mm	20	0.027	0.007	25.38	0.010	0.038

Lu, 1983 from the Baliqliq Group of western Xinjiang, China, but differs from it by the regular presence of four macroacanthostyles surrounding autozooeical apertures instead of 7–10 acanthostyles in the latter species. *Rhabdomeson bretnalli* differs from *R. ofukuensis* Sakagami, 1964 from the Permian of Japan in having larger autozooeical apertures (average aperture width 0.17 mm vs. 0.13 mm in *R. ofukuensis*).

**Occurrence.** Lower Permian (Noonkanbah Series and Liveringa Formation); Western Australia. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Rhabdomeson* sp.  
Figure 15.1-5

**Material.** SMF 23.158–SMF 23.160.

**Description.** Branched colonies with small axial cylinder. Branches 1.48–1.53 mm in diameter. Axial cylinder circular, 0.26–0.34 mm in diameter. Autozooeia budding in a spiral pattern from the axial cylinder, rhomboid in transverse section. Autozooeical apertures oval, arranged in regular diagonal rows, 0.15–0.19 mm wide. Two macroacanthostyles between each aperture present, 0.05–0.08 mm in diameter. Microacanthostyles abundant, arranged in one row between macroacanthostyles, 0.015–0.020 mm in diameter. Superior hemisepta present, curved proximally. Diaphragms absent. Autozooeical walls laminated, 0.010–0.015 mm thick in endozone.

**Remarks.** *Rhabdomeson* sp. is similar to *R. bispinosum* Crockford, 1944 from the Lower Permian (Artinskian) of Western Australia, but differs in the presence of hemisepta and by having wider autozooeical apertures (aperture width 0.15–0.19 mm vs. 0.08–0.10 mm in *R. bispinosum*). *Rhabdomeson* sp. differs from *R. consimile* Bassler, 1929 from the Upper Permian of Timor, by having wider apertures (aperture width 0.15–0.19 mm vs. ca 0.12 mm in *R. consimile*).

**Occurrence.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Family RHOMBOPORIDAE Simpson, 1895  
Genus *PRIMORELLA* Romantchuk and Kiseleva, 1968

**Type species.** *Primorella polita* Romantchuk and Kiseleva, 1968. Upper Permian, Primorje, East Russia.

**Diagnosis.** Branched colonies with long and tube-like autozooeia budding in spiral pattern. Oval apertures arranged in regular diagonal rows. Abundant aktinostyles in walls of the exozone (modified after Gorjunova, 1985).

**Remarks.** *Primorella* differs from other genera of the family Rhomboporidae by the presence of aktinostyles. *Primorella* differs from *Pamirella* Gorjunova, 1975 by the absence of acanthostyles.

**Occurrence.** Carboniferous and Permian of the Russian Plate, Mongolia, Iran, and Arctic.

*Primorella rotunda* Gorjunova, 1985  
Figure 15.6-9; Table 20

- 1985 *Primorella rotunda* Gorjunova, p. 92, pl. 11, figs. 2-3.
- 2008 *Primorella* cf. *rotunda* Gorjunova, 1985; Ernst, Weidlich and Schäfer, p. 704, figs. 11.10-11.14.
- 2013 *Primorella rotunda* Gorjunova, 1985; Ernst and Gorgij, p. 298, figs. 14A-E.

**Material.** SMF 23.161–SMF 23.164.

**Description.** Branched colonies, 1.4–1.6 mm in diameter. Autozooeia growing from median axis. Apertures oval. Aktinostyles abundant, arranged in a single row around apertures. Autozooeical diaphragms and heteromorphs not observed. Walls laminated, 0.010–0.015 mm thick in endozone, 0.07–0.09 mm thick in exozone.

**Remarks.** *Primorella rotunda* Gorjunova, 1985 differs from *P. opulenta* Gorjunova, 1985 from the Lower Permian (Sakmarian) of Russia, in having thicker branches (branch diameter 1.4–1.6 mm vs. 0.7–0.8 mm in *P. opulenta*) and wider autozooeical apertures (aperture width 0.12–0.22 mm vs. 0.11–0.13 mm in *P. opulenta*). *Primorella rotunda* differs from *P. serena* Gorjunova, 1975 from the Lower Permian (Sakmarian) of Tajikistan in having thinner colonies (branch diameter 1.4–1.6 mm vs. 2.15–2.30 mm in *P. serena*) and wider autozooeical

apertures (aperture width 0.12–0.22 mm vs. 0.12–0.14 mm in *P. serena*).

**Occurrence.** Lower Permian (Artinskian); Pamir (Tajikistan). Chili Formation, Lower Permian (Sakmarian–Artinskian); Kalmard area, central Iran. Aseelah Unit, Saal Formation (?Lower Permian); Batain Coast (eastern Oman). Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Suborder TIMANODICTYINA Morozova, 1966  
Family TIMANODICTYIDAE Morozova, 1966  
Genus *TIMANOTRYPA* Nikiforova, 1938

**Type species.** *Timanotrypa foliata* Nikiforova, 1938. Lower Permian, Sakmarian; Russia.

**Diagnosis.** Bifoliate, frondose, leaf-shaped colonies. Branched colonies; branches bifoliate, lenticular, rounded or oval in transverse section. Autozooezia tubular, widened proximally and bending at low angles in exozone. Mesotheca straight or zigzag folded. Median tubules absent. Autozooezial diaphragms rare. Exozonal walls laminated, traversed by abundant microstyles. Maculae lacking autozooezia present. Heterozooezia absent.

**Remarks.** *Timanotrypa* Nikiforova, 1938 differs from *Timanodictya* Nikiforova, 1938 in having frondose or leaf-shaped colonies instead of branched ones.

**Occurrence.** Lower Permian of Arctic, Tibet and Australia, Upper Permian (Kazanian) of the Russian Plate.

*Timanotrypa australis* n. sp.  
Figure 16; Table 21

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1973 *Timanodictya?* sp. Sakagami, p. 85, pl. 14, fig. 3.

**Etymology.** The species is named after its occurrence in southern hemisphere (from Latin "*australis*" southern).

**Holotype.** SMF 23.165.

**Paratypes.** SMF 23.166–SMF 23.177.

**Type locality.** Zhongba area of southwestern Tibet (E 84.31536, N 29.74233).

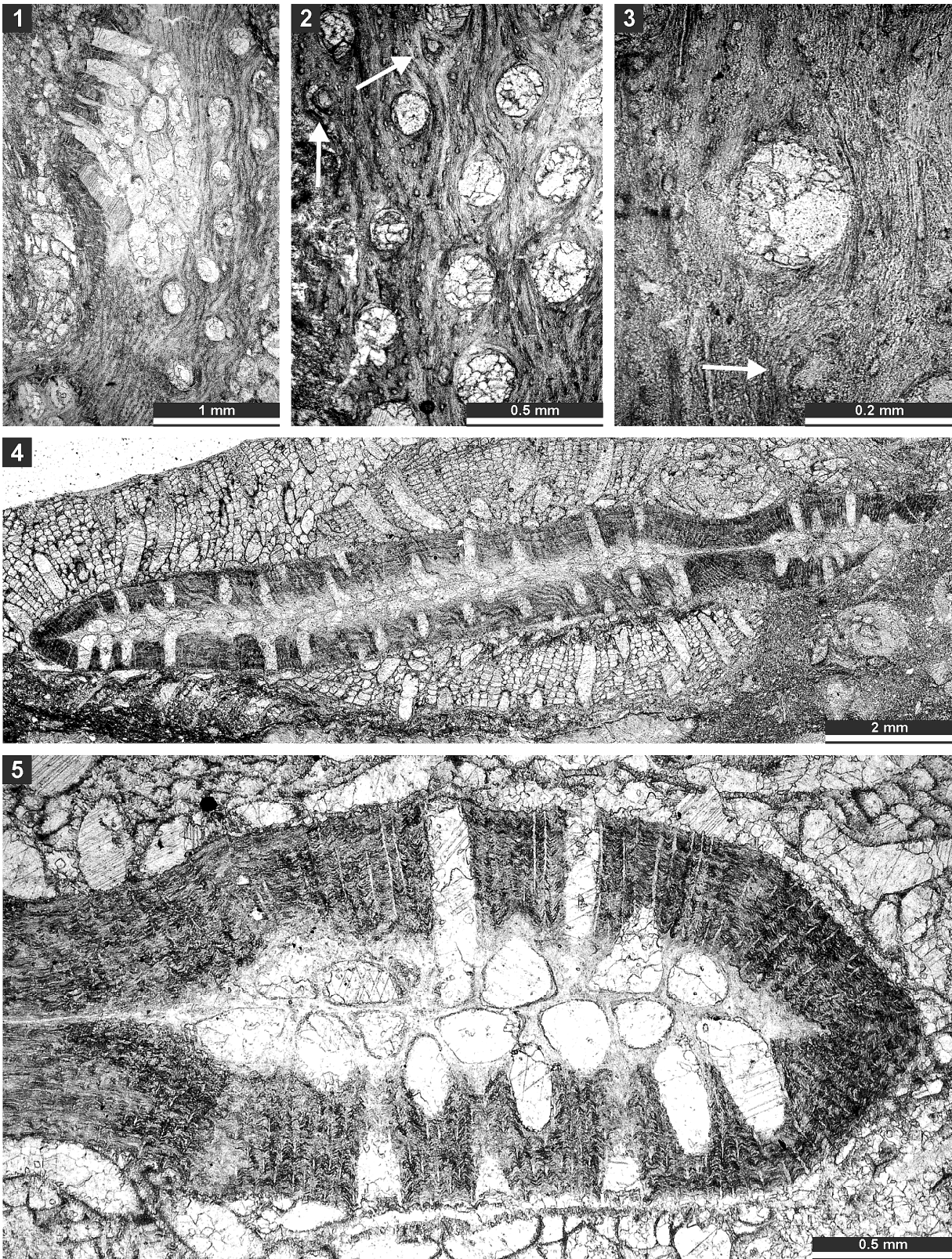
**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Colonies consisting of narrow bifoliate ribbons growing in the same plane, apparently pinnate; mesotheca straight to slightly zigzag folded; autozooezia tubular, semicircular in endozone, recumbent at mesotheca, bending sharply in exozone; diaphragms and hemisepta absent; exozonal walls laminated, traversed by abundant microstyles; depressed maculae without autozooezia occurring between pinnae.

**Description.** Colonies consisting of narrow bifoliate ribbons growing in the same plane, apparently pinnate (complete colony shape unknown). Separate ribbons 3.2–6.7 mm wide and 1.1–2.2 mm thick, with 0.26–0.65 mm wide exozone and 0.58–0.90 mm wide endozones. Mesotheca straight to slightly zigzag folded, 0.025–0.038 mm thick. Autozooezia tubular, semicircular in endozone, recumbent at mesotheca, bending sharply in exozone. Autozooezial apertures rounded to oval, arranged in 8–15 alternating rows. Autozooezial diaphragms not observed. Hemisepta absent. Endozonal walls hyaline, 0.015–0.020 mm thick. Exozonal walls laminated, traversed by abundant microstyles. Microstyles 0.015–0.025 mm in diameter. Maculae depressed, narrow, lacking autozooezia, positioned between pinnae across branch axis. Elliptical nodes regularly spaced between autozooezial apertures, 0.06–0.10 mm in diameter.

**Remarks.** *Timanodictya?* sp. Sakagami, 1973 (p. 85, plate 14, figure 3) fits with the new species (average aperture width 0.16 (range 0.14–0.18 mm) vs. 0.16 (range 0.13–0.19 mm) in the present species). *Timanotrypa australis* n. sp. differs from *T. borealis* Morozova, 1970 from the Upper Permian (Kazanian) of the Russian Platform, by possessing smaller fronds (frond width 3.2–6.7 mm vs. 6–9 mm in *T. borealis*; frond thickness 1.1–2.2 mm vs. 2.0–3.0 mm in *T. borealis*).

The wall structure in timanodictyid bryozoans is quite variable and includes such structures as microstyles and stenostyles. The term "stenostyle" has been suggested by Gilmour and Snyder (1986) instead of "cappilares" used by the Russian authors (cf. Morozova, 1970; Gorjunova, 1994). However, these structures are not uniform in their morphology among timanodictyines. Gilmour (personal commun., 2015) understands rods of stellate appearance in transverse section as stenostyles, whereas others are of circular shape in their transverse sections (as known in the Family Girtyporidae, for example). The original diagnosis of the genus *Timanotrypa* Nikiforova (1938) includes "stellate acanthostyles". However, her figures 5-6 of plate 50 and figures 1-4 of plate 52 do not reveal any of such styles. Instead, they show small styles of circular shape in their transverse section. Neither the sample of *Timanotrypa* depicted by Gorjunova (1994, plate 3, figure 1) shows any kind of stellate styles. The assignment of the present material to *Timanotrypa* followed largely on the base of the autozooezial shape, which is a very important character in the bryozoan morphology.



**FIGURE 16.** Thin section photographs of *Timanotrypa australis* n. sp., holotype SMF 23.165 (1), paratype SMF 23.166 (2 and 3), paratype SMF 23.169 (4), and paratype SMF 23.171 (5). 1, oblique section of the pinnate branch; 2 and 3, tangential section showing autozooeal apertures, nodes (arrows) and microstyles; and 4 and 5, branch transverse section.

**TABLE 21.** Measurements of *Timanotrypa australis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	4	4.9	1.458	29.76	3.2	6.7
Branch thickness, mm	5	1.7	0.415	24.69	1.1	2.2
Autozooeal aperture width, mm	35	0.16	0.012	7.60	0.13	0.19
Autozooeal aperture spacing along branch, mm	8	0.79	0.044	5.55	0.72	0.85
Autozooeal aperture spacing diagonally, mm	30	0.44	0.051	11.57	0.37	0.55
Node diameter, mm	5	0.08	0.015	18.05	0.06	0.10

**Occurrence.** Rat Buri Limestone, Lower Permian (?Artinskian–Kungurian); Khao Raen, Thailand. Noonkanbah Formation, Lower Permian (upper Artinskian–Kungurian); Western Australia (unpublished data). Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of south-western Tibet.

Order FENESTRATA Elias and Condra, 1957  
Suborder FENESTELLINA Astrova and Morozova, 1956

Family FENESTELLIDAE King, 1849  
Genus *SPINOFENESTELLA* Termier and Termier, 1971

[= *Alternifenestella* Termier and Termier, 1971]

**Type species.** *Fenestella spinosa* Condra, 1902. Lower Permian (Wolfcampian); North America.

**Diagnosis.** Reticulate colonies with relatively wide and thick branches and relatively thin dissepiments. Autozooea arranged in two rows on the branches. Autozooea triangular in mid-tangential section, triangular to pentagonal proximal to bifurcations. Narrow keel with single row of nodes developed.

**Remarks.** *Spinofenestella* Termier and Termier, 1971 differs from the genus *Rectifenestella* Morozova, 1974 by the triangular shape of the autozooea in mid-tangential section.

*Alternifenestella* Termier and Termier, 1971 is a synonym of *Spinofenestella* due to the close morphological similarities of their type species, according to Hageman and McKinney (2010), though Gorjunova and Weis (2012) retained *Alternifenestella* as a valid genus.

**Occurrence.** Lower Devonian–Upper Permian.

*Spinofenestella* sp.  
Figure 17.1-5; Table 22

**Material.** SMF 23.178.

**Exterior description.** Reticulate colony formed by straight branches joined by wide dissepiments. Fenestrules oval to rectangular, short, narrow. Autozooea arranged in two rows on branches.

Autozooeal apertures circular, with stellate structure; two apertures spaced per fenestrule length. Median keel low, narrow, containing small closely spaced rounded nodes. Large nodes on the reverse side of branches.

**Interior description.** Autozooea short, triangular to trapezoid in mid-tangential section; with short to moderately long vestibule in longitudinal section. Axial wall between autozooeal rows strongly zig-zag; aperture positioned at distal end of chamber. Superior hemisepta weakly developed; inferior hemisepta absent. External laminated skeleton well-developed on both obverse and reverse sides, traversed by small microstyles. Heteromorphs not observed.

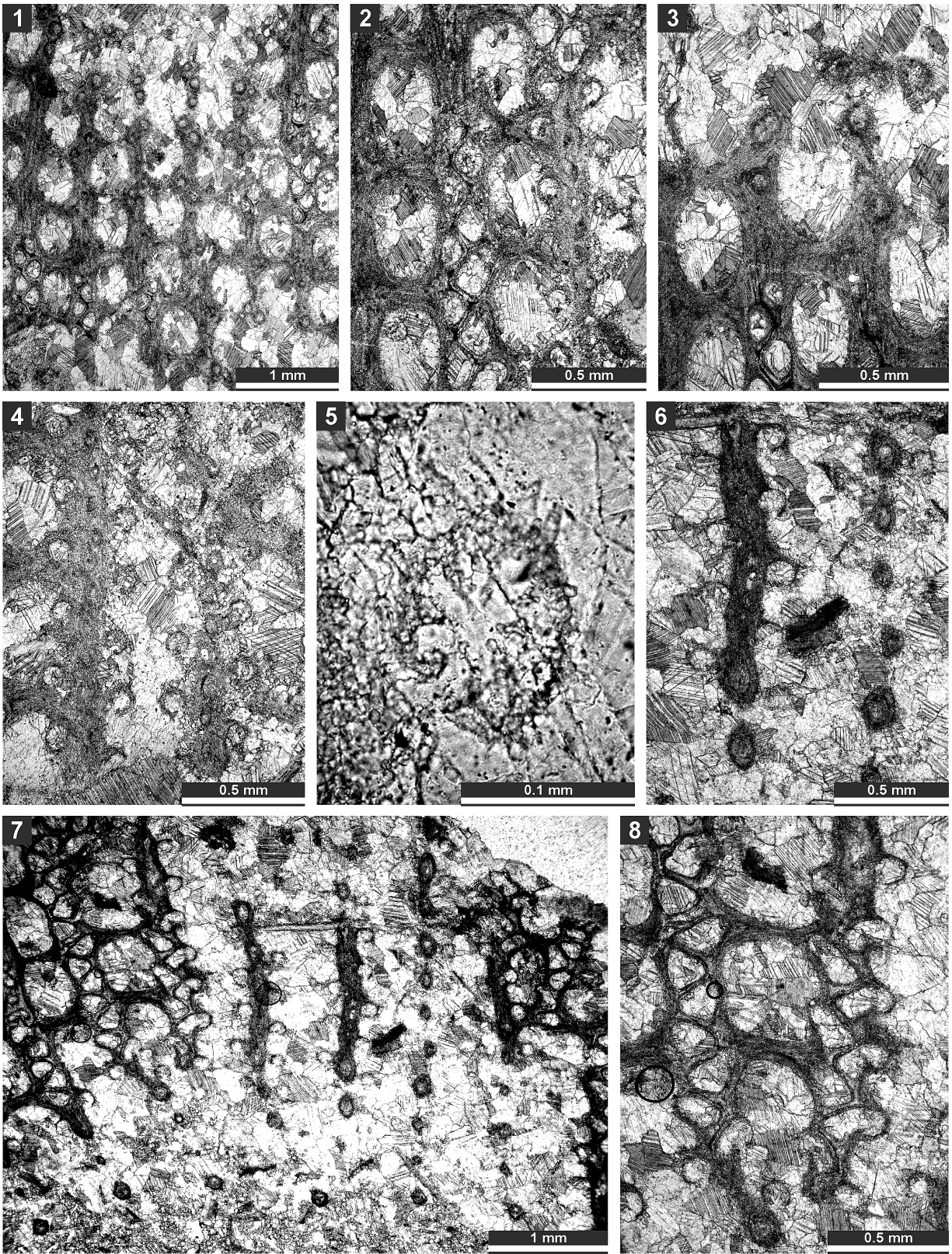
**Remarks.** *Spinofenestella* sp. is similar to *S. cibaria* (Trizna, 1950) from the Lower Permian of Russia, but differs from it in presence of nodes on the reverse colony side and wider branches (0.28–0.34 mm vs. 0.20–0.30 mm in *S. cibaria*). *Spinofenestella* sp. differs from *S. microaperturata* (Schulga-Nesterenko, 1941) from the Lower Permian of Russia in the presence of nodes on the reverse colony side and wider branches (0.38–0.34 mm vs. 0.20–0.30 mm in *S. microaperturata*).

*Minilya magnispinata* (Schulga-Nesterenko, 1952), from the Lower Permian of Urals, has similar colony dimensions and similar kinds of nodes on the reverse colony side. However, the latter species has alternating nodes on the keel (characteristic of the genus *Minilya*) and narrower branches (branch width 0.22–0.25 mm vs. 0.28–0.34 mm in the present species).

**Occurrence.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of south-western Tibet.

*Spinofenestella subquadratopora* (Schulga-Nesterenko, 1952)  
Figure 17.6-8; Table 23

1952 *Fenestella subquadratopora* Schulga-Nesterenko, 1952, p. 47, pl. 9, fig. 5.



**FIGURE 17.** Thin section photographs of *Spinofenestella* sp., SMF 23.178 (1–5); and *Spinofenestella subquadratorpora* (Schulga-Nesterenko, 1952), SMF 23. 179 (6–8). 1–3, tangential section of the reverse side; 4–7, tangential section of the obverse side; and 8, mid-tangential section.

**TABLE 22.** Measurements of *Spinofenestella* sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	15	0.30	0.020	6.67	0.28	0.34
Dissepiment width, mm	15	0.15	0.009	6.05	0.14	0.17
Fenestrule width, mm	15	0.23	0.019	8.01	0.20	0.27
Fenestrule length, mm	15	0.41	0.018	4.26	0.38	0.45
Distance between branch centres, mm	15	0.51	0.032	6.27	0.45	0.56
Distance between dissepiment centres, mm	15	0.56	0.025	4.38	0.52	0.61
Autozooeal aperture width, mm	20	0.07	0.007	9.13	0.06	0.09
Autozooeal aperture spacing along branch, mm	20	0.26	0.015	5.72	0.24	0.29
Autozooeal aperture spacing diagonally, mm	20	0.30	0.014	4.51	0.27	0.33
Maximum chamber width, mm	20	0.12	0.008	6.62	0.11	0.14
Keel node diameter, mm	15	0.06	0.008	12.94	0.05	0.08
Node spacing, mm	15	0.13	0.011	8.35	0.10	0.14
Node diameter, reverse side, mm	20	0.11	0.020	18.01	0.08	0.15

**TABLE 23.** Measurements of *Spinofenestella subquadratopora* (Schulga-Nesterenko, 1952). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	10	0.32	0.023	7.16	0.29	0.36
Dissepiment width, mm	10	0.12	0.022	18.00	0.10	0.17
Fenestrule width, mm	10	0.33	0.047	14.42	0.25	0.39
Fenestrule length, mm	10	0.46	0.036	7.82	0.40	0.50
Distance between branch centres, mm	10	0.62	0.094	15.21	0.48	0.80
Distance between dissepiment centres, mm	10	0.59	0.041	7.03	0.53	0.68
Autozooeal aperture width, mm	10	0.10	0.007	7.45	0.09	0.11
Autozooeal aperture spacing along branch, mm	10	0.29	0.018	6.03	0.27	0.32
Autozooeal aperture spacing diagonally, mm	10	0.31	0.023	7.50	0.28	0.35
Maximum chamber width, mm	10	0.17	0.018	10.70	0.14	0.19
Keel node diameter, mm	20	0.11	0.017	15.88	0.08	0.14
Node spacing, mm	20	0.30	0.021	7.03	0.25	0.34

- 1975 *Fenestella subquadratopora* Schulga-Nesterenko, 1952; Gorjunova, p. 84, pl. 19, fig. 3, pl. 20, fig. 1.
- 1994 *Alternifenestella subquadratopora* Schulga-Nesterenko, 1952; Nakrem, p. 94, fig. 17A-B.
- 2000 *Alternifenestella subquadratopora* Schulga-Nesterenko, 1952; Ernst, p. 97, pl. 21, figs. 3-5.

**Material.** SMF 23.179–SMF 23.181.

**Exterior description.** Reticulate colony formed by straight branches joined by wide dissepiments. Fenestrules oval to rectangular, long, narrow. Autozooea arranged in two rows on branches. Autozooeal apertures circular, with low smooth peristome; two apertures spaced per fenestrule length. Median keel low, relatively wide, containing large widely spaced elliptical nodes.

**Interior description.** Autozooea short, triangular in mid-tangential section; with short to moderately long vestibule in longitudinal section. Axial wall between autozooeal rows strongly zigzag; aperture positioned at distal end of chamber. Superior hemisepta long; inferior hemisepta absent. External laminated skeleton well-developed on both obverse and reverse sides, traversed by small microstyles. Microstyles 0.010–0.015 mm in diameter. Heteromorphs not observed. Nodes on the reverse side irregularly distributed, 0.035–0.051 mm in diameter.

**Remarks.** *Spinofenestella subquadratopora* (Schulga-Nesterenko, 1952) is similar to *Spinofenestella macronodata* (Sakagami, 1964) from the Lower Permian of Japan, but differs from it in having wider branches (branch width 0.29–0.36 mm vs. 0.21–0.24 mm in *S. macronodata*) and

larger fenestrules (average fenestrule width 0.33 mm vs. 0.28 mm in *S. macronodata*; average fenestrule length 0.46 mm vs. 0.40 mm in *S. macronodata*). *Spinofenestella subquadratopora* differs from *S. pulcherrima* (Schulga-Nesterenko, 1941) from the Lower Permian of Russia by having larger nodes on the keel (node diameter 0.08–0.14 mm vs. 0.03–0.06 in *S. pulcherrima*) and an irregular distribution of nodes on the reverse side of the colony; the nodes in *S. pulcherrima* are arranged in regular rows.

**Occurrence.** Upper Carboniferous, late Gzhelian, lowermost part of the Tyrrelfjellet Member; Spitsbergen. Lower Permian (Sakmarian); Urals, Russia. Trogkofel Formation, Lower Permian (late Sakmarian–late Artinskian); Carnic Alps, Austria. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Family POLYPORIDAE Vine, 1884

Genus *POLYPORA* M'Coy, 1844

**Type species.** *Polypora dendroides* M'Coy, 1844. Lower Carboniferous; Ireland.

**Diagnosis.** Reticulate colonies of different shape built by straight or slightly undulating, bifurcating branches, joined at regular intervals by straight dissepiments without autozoecia. Autozoecia arranged in four alternating rows on branches, 5–6 rows before and 2–3 after bifurcation. Autozoecial chambers tubular, short, having weakly developed inferior hemisepta and short vestibule, regularly hexagonal in mid tangential section. Autozoecial apertures rounded. Keels between longitudinal rows of autozoecia weakly developed or absent. Microacanthostyles and nodes usually present on obverse surface (after Morozova, 2001).

**Remarks.** *Polypora* M'Coy, 1844 is similar to *Paucipora* Termier and Termier, 1971. The latter has well-developed hemisepta and shorter autozoecia. *Polypora* differs from *Polyporella* Simpson, 1895 in the presence of four rows of autozoecia on branches instead of three in the latter genus.

**Occurrence.** Lower Devonian to Upper Permian; worldwide.

*Polypora consanguinea* Bassler, 1929

Figure 18.1-4; Table 24

1929 *Polypora consanguinea* Bassler, p. 79, pl. 19, figs. 5-9.

**Material.** SMF 23.182.

**Exterior description.** Reticulate colonies composed of moderately wide branches jointed by moderately wide dissepiments. Autozoecia arranged in 4–5 alternating rows on branches.

Autozoecial apertures rounded to oval, 4–10 spaced per length of fenestrule. Fenestrules long, oval, narrow. Node regularly spaced between subsequent autozoecial apertures, 0.03–0.04 mm in diameter. Reverse colony surface smooth.

**Interior description.** Autozoecial chambers moderately long, generally rhombic to roughly hexagonal in the mid tangential section. Hemisepta absent. External laminated skeleton well-developed, traversed by abundant small microacanthostyles. Heteromorphs not observed.

**Remarks.** *Polypora consanguinea* Bassler, 1929 is similar to *P. russiensis* Schulga-Nesterenko 1941 from the Lower Permian of Russia, but differs from it in having wider branches (branch width 1.08–1.45 mm vs. 0.52–0.88 mm in *P. russiensis*) and wider fenestrules (fenestrule width 1.08–1.40 mm vs. 0.45–0.70 mm in *P. russiensis*). *Polypora consanguinea* differs from *P. multiporifera* Crockford, 1944 from the Lower Permian of Western Australia in having wider branches (branch width 1.08–1.45 mm vs. 0.70–1.10 in *P. multiporifera*) as well as wider and shorter fenestrules (fenestrule width 1.08–1.40 mm vs. 0.65–1.10 mm in *P. multiporifera*; fenestrule length 2.00–2.10 mm vs. 2.1–2.45 mm in *P. multiporifera*). *Polypora consanguinea* Bassler, 1929 has been reported from the Lower Permian (Kungurian) of northern Russia (Morozova, 1981, p. 85), however, this species possesses hemisepta.

**Occurrence.** Permian (Sakmarian–Artinskian); Indonesia, Timor. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Polypora brouweri* Bassler, 1929

Figure 18.5-9; Table 25

1929 *Polypora brouweri* Bassler, p. 77, pl. 18, figs. 7-10.

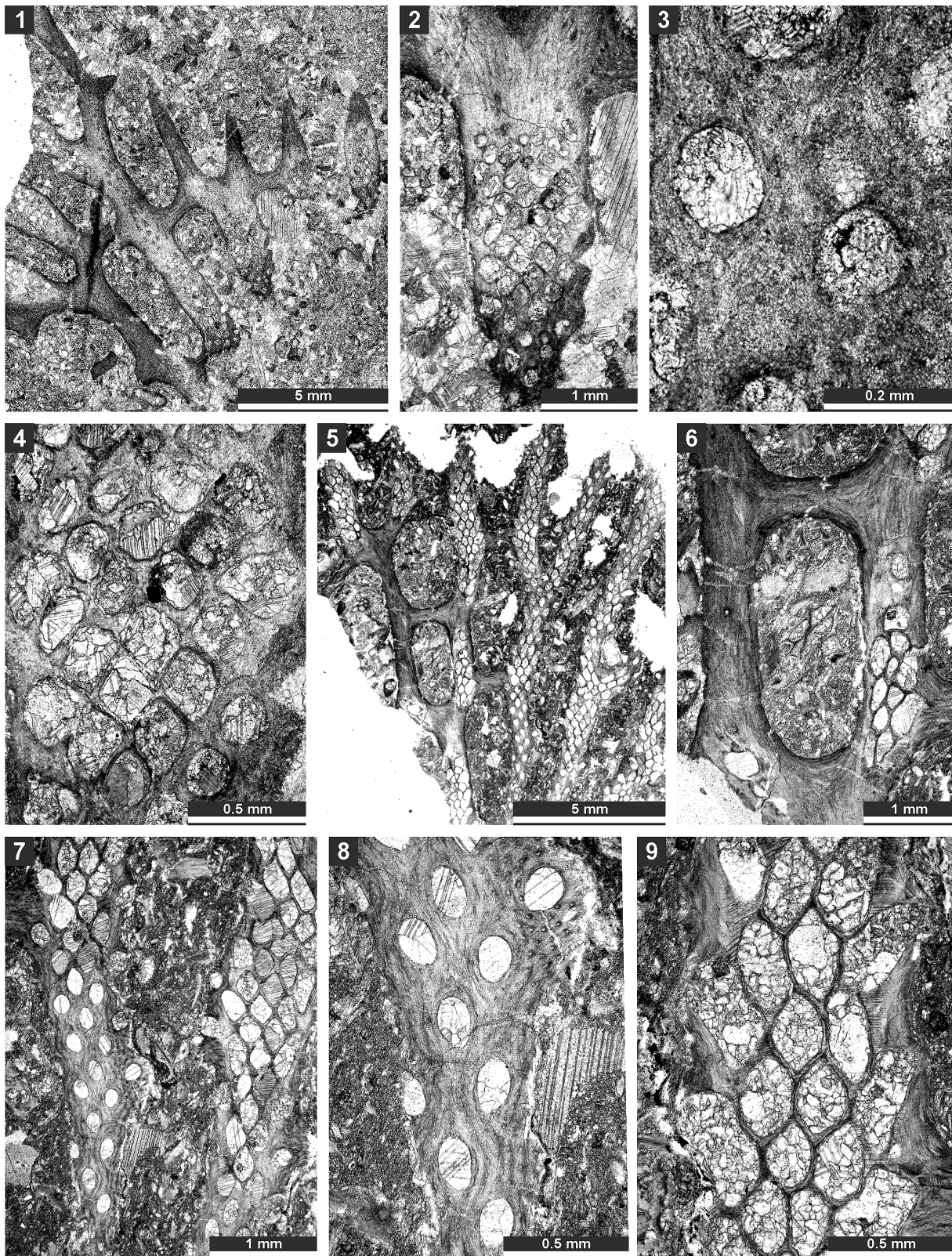
1946 *Polypora goldfussi* Eichwald, 1860; Metz, p. 181, pl. 19, fig. 9.

**Material.** SMF 23.183.

**Exterior description.** Reticulate colonies composed of moderately wide branches jointed by moderately wide dissepiments. Autozoecia arranged in 4–5 alternating rows on branches. Autozoecial apertures rounded to oval, 4–10 spaced per length of fenestrule. Fenestrules long, oval to rectangular. Keels and nodes absent. Reverse colony surface smooth.

**Interior description.** Autozoecial chambers moderately long, generally rhombic to roughly hexagonal, irregularly polygonal at places of bifurcation in the mid-tangential section. Hemisepta absent. External laminated skeleton well-developed, tra-





**FIGURE 18.** Thin section photographs of *Polypora consanguinea* Bassler, 1929, SMF 23.182 (1–4); and *Polypora brouweri* Bassler, 1929, SMF 23.183 (5–9). 1, oblique section; 2–5, tangential section showing autozoecial apertures, nodes and autozoecial chambers; 6, reverse side of the colony; and 7–9, tangential section showing autozoecial apertures and chambers.

**TABLE 24.** Measurements of *Polypora consanguinea* Bassler, 1929. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	5	1.27	0.180	14.21	1.08	1.45
Dissepiment width, mm	2	0.54	0.014	2.62	0.53	0.55
Fenestrule width, mm	4	1.24	0.159	12.79	1.08	1.40
Fenestrule length, mm	2	2.05	0.071	3.45	2.00	2.10
Autozooeical aperture width, mm	9	0.13	0.005	4.20	0.12	0.13
Autozooeical aperture spacing along branch, mm	7	0.41	0.059	14.50	0.36	0.53
Autozooeical aperture spacing diagonally, mm	7	0.28	0.025	8.99	0.25	0.32
Maximum chamber width, mm	9	0.21	0.011	4.99	0.20	0.23

**TABLE 25.** Measurements of *Polypora brouweri* Bassler, 1929. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	6	0.91	0.151	16.55	0.72	1.13
Dissepiment width, mm	3	0.48	0.035	7.27	0.45	0.52
Fenestrule width, mm	4	1.1	0.200	18.18	1.0	1.4
Fenestrule length, mm	3	3.1	0.814	26.56	2.5	4.0
Distance between branch centres, mm	6	1.94	0.191	9.83	1.80	2.25
Autozooeical aperture width, mm	20	0.14	0.009	6.91	0.12	0.16
Autozooeical aperture spacing along branch, mm	20	0.51	0.065	12.68	0.40	0.60
Autozooeical aperture spacing diagonally, mm	20	0.32	0.035	11.02	0.25	0.38
Maximum chamber width, mm	20	0.21	0.009	4.14	0.20	0.23

versed by abundant small microacanthostyles. Heteromorphs not observed.

**Remarks.** *Polypora brouweri* Bassler, 1929 differs from *P. principalis* Gorjunova, 1975 from the Lower Permian of Pamir in having wider branches as well as larger fenestrules. *Polypora brouweri* differs from *P. remota grandis* Trizna, 1939 from the Lower Permian of Urals in having narrower branches (branch width 0.72–1.13 mm vs. 1.11–1.39 mm in *P. remota grandis*) and wider apertures (aperture width 0.12–0.16 mm vs. 0.11–0.13 mm in *P. remota grandis*). *Polypora goldfussi* Eichwald, 1860, as described by Metz (1946) from the Permian of northern Tibet, corresponds to *Polypora brouweri* Bassler, 1929. The original species of Eichwald (1860), however, possesses cyclozoecia (Nikiforova, 1938).

**Occurrence.** Permian; northern Tibet. Lower Permian (Sakmariian-Artinskian); Timor. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Polypora* aff. *voluminosa* Trizna and Klautzan, 1961

Figure 19.1-6; Table 26

aff. 1961 *Polypora voluminosa* Trizna and Klautzan, p. 433, pl. 12, fig. 5, pl. 13, fig. 1, text-figs. 26a-b.

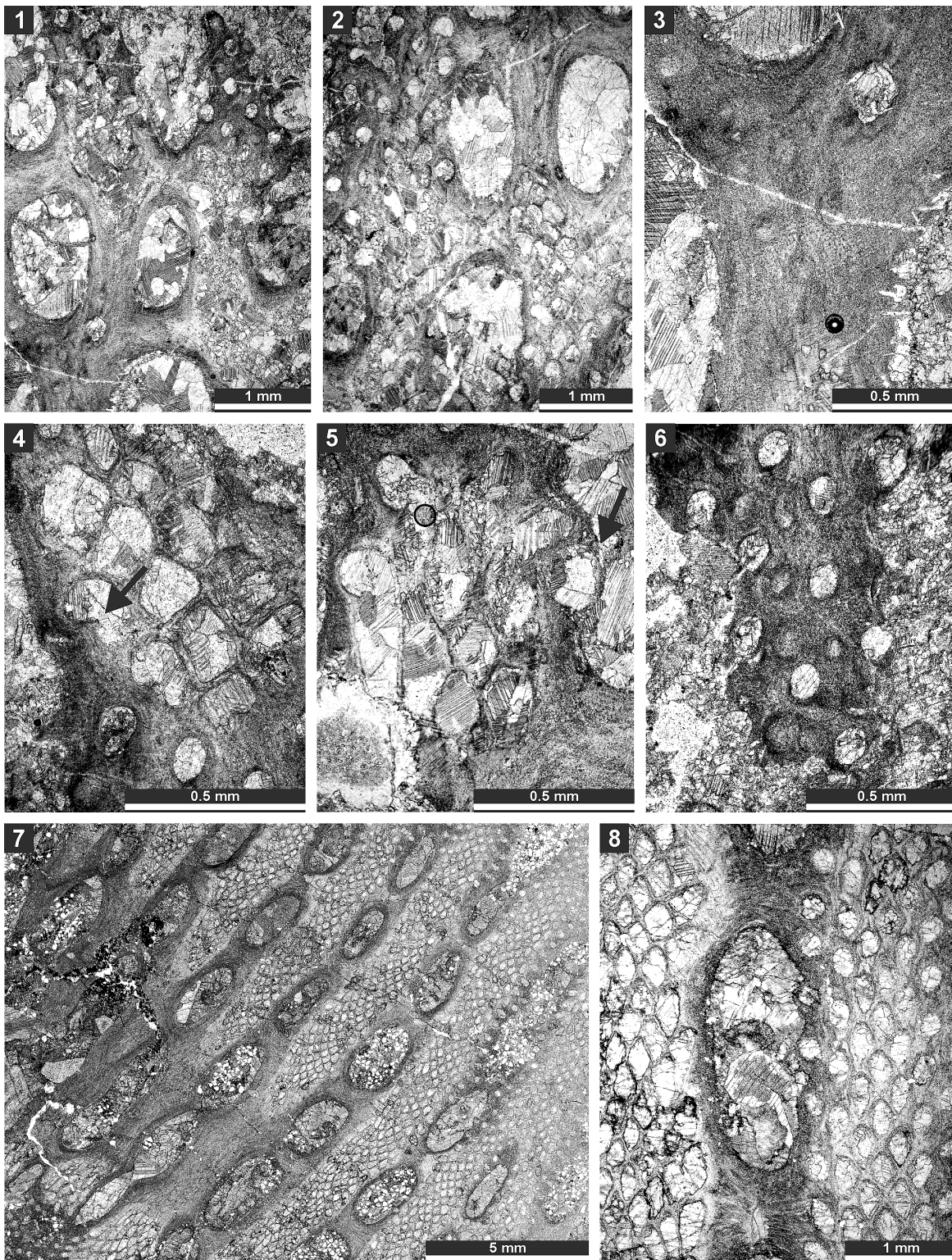
aff. 1986 *Polypora voluminosa* Trizna and Klautzan, 1961; Morozova and Krutchinina, p. 106, pl. 40, fig. 2.

**Material.** SMF 23.184–SMF 23.187.

**Exterior description.** Reticulate colonies composed of moderately wide branches jointed by moderately wide dissepiments. Autozoecia arranged in 3–4 alternating rows on branches. Autozooeical apertures rounded to oval, 4–5 spaced per length of fenestrule. Fenestrules short, oval. Large nodes regularly spaced on the colony surface.

**Interior description.** Autozooeical chambers relatively short, generally rhombic to roughly hexagonal in the mid-tangential section. Superior hemisepta well-developed, slightly curved proximally. External laminated skeleton well-developed, traversed by abundant small microacanthostyles. Apparent reproductive heteromorphs in form of isolated zoecia with enlarged distal roofed chambers, occurring on obverse colony surface, 0.19–0.21 mm in diameter.

**Remarks.** The present species is similar to *Polypora voluminosa* Trizna and Klautzan, 1961 from the Lower Permian of Urals. However, that species lacks nodes on the reverse side of the colony. It is similar to *P. subvoluminosa* Krutchinina in Morozova and Krutchinina, 1986 from the Lower Permian.



**FIGURE 19.** Thin section photographs of *Polypora* aff. *voluminosa* Trizna and Klautzan, 1961, SMF 23.187 (1–3, and 5) and SMF 23.185 (4 and 6); and *Mackinneyella obesa* (Crockford, 1957), SMF 23.191 (7) and SMF 23.192 (8). 1 and 2, tangential section branches and fenestrules; 3, tangential section of the reverse side showing nodes; 4, tangential section showing autozooeical apertures and chambers with hemisepta (arrow); 5, tangential section showing autozooeical apertures, chambers and heteromorph (arrow); 6, tangential section showing autozooeical apertures and nodes; and 7 and 8, tangential section showing autozooeical apertures and chambers.

**TABLE 26.** Measurements of *Polypora* aff. *voluminosa* Trizna and Klautzan, 1961. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	8	0.85	0.153	17.92	0.67	1.02
Dissepiment width, mm	7	0.56	0.052	9.25	0.50	0.65
Fenestrule width, mm	6	0.62	0.066	10.77	0.53	0.70
Fenestrule length, mm	3	1.25	0.218	17.44	1.10	1.50
Distance between branch centres, mm	6	1.26	0.143	11.36	1.10	1.50
Distance between dissepiment centres, mm	7	1.90	0.312	16.44	1.63	2.38
Autozooeal aperture width, mm	30	0.11	0.006	5.57	0.10	0.12
Autozooeal aperture spacing along branch, mm	30	0.42	0.038	8.98	0.36	0.56
Autozooeal aperture spacing diagonally, mm	30	0.33	0.032	9.80	0.27	0.40
Maximum chamber width, mm	15	0.22	0.015	6.65	0.20	0.25
Node diameter, obverse side, mm	29	0.10	0.022	23.60	0.06	0.15
Node diameter, reverse side, mm	10	0.10	0.015	15.89	0.07	0.12

ian of Arctic, but differs from the latter in having wider branches and larger fenestrules (branch width 0.67–1.02 mm vs. 0.45–0.60 mm in *P. subvoluminosa*; fenestrule width 0.53–0.70 mm vs. 0.50–0.60 mm in *P. subvoluminosa*; fenestrule length 1.10–1.50 mm vs. 0.90–1.15 mm in *P. subvoluminosa*). Both of these species have well-developed superior hemisepta and a rhombic autozooeal chamber in mid-tangential section. Typical *Polypora* species have regularly hexagonal autozooea and usually no distinct hemisepta. Representatives of *Paucipora* Termier and Termier, 1971 have distinct superior and inferior hemisepta dividing the hexagonal chambers in three parts.

**Occurrence.** ?Lower Permian (Artinskian); Russia (Urals). Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *MACKINNEYELLA* Morozova and Lisitsyn, 1996

**Type species.** *Polypora ornamentata* Schulga-Nesterenko, 1941. Lower Permian, southern Urals (Russia).

**Diagnosis.** Reticulated colonies of various shapes consisting of broad linear, essentially parallel branches joined by dissepiments; dissepiments narrow, perpendicular or at oblique angle to branches, regularly spaced at large distance; fenestrules elongate oval, sub-rectangular, or irregular in shape; keels and superstructure absent; autozooea arranged in 5–6 rows on branches; chambers slightly elongate, proximally recumbent on budding plate, rhomboidal or rounded hexagonal in mid tangential section, long axis parallel with branch axis; hemisepta and diaphragms absent; granular skeleton present in basal plate and axial

wall but locally absent in transverse and lateral autozooeal walls; extrazooeal skeleton laminated, traversed by abundant, moderate-size microstyles.

**Remarks.** *Mackinneyella* Morozova and Lisitsyn, 1996 differs from *Polypora* M'Coy, 1844 in having 5–6 autozooeal rows on branches instead of 3–4 and a rhombic vs. hexagonal autozooea in mid-tangential section. *Mackinneyella* differs from *Parapolypora* Morozova and Lisitsyn, 1996 in having rhombic instead of hexagonal autozooea.

**Occurrence.** Upper Devonian–Upper Permian; worldwide.

*Mackinneyella obesa* (Crockford, 1957)

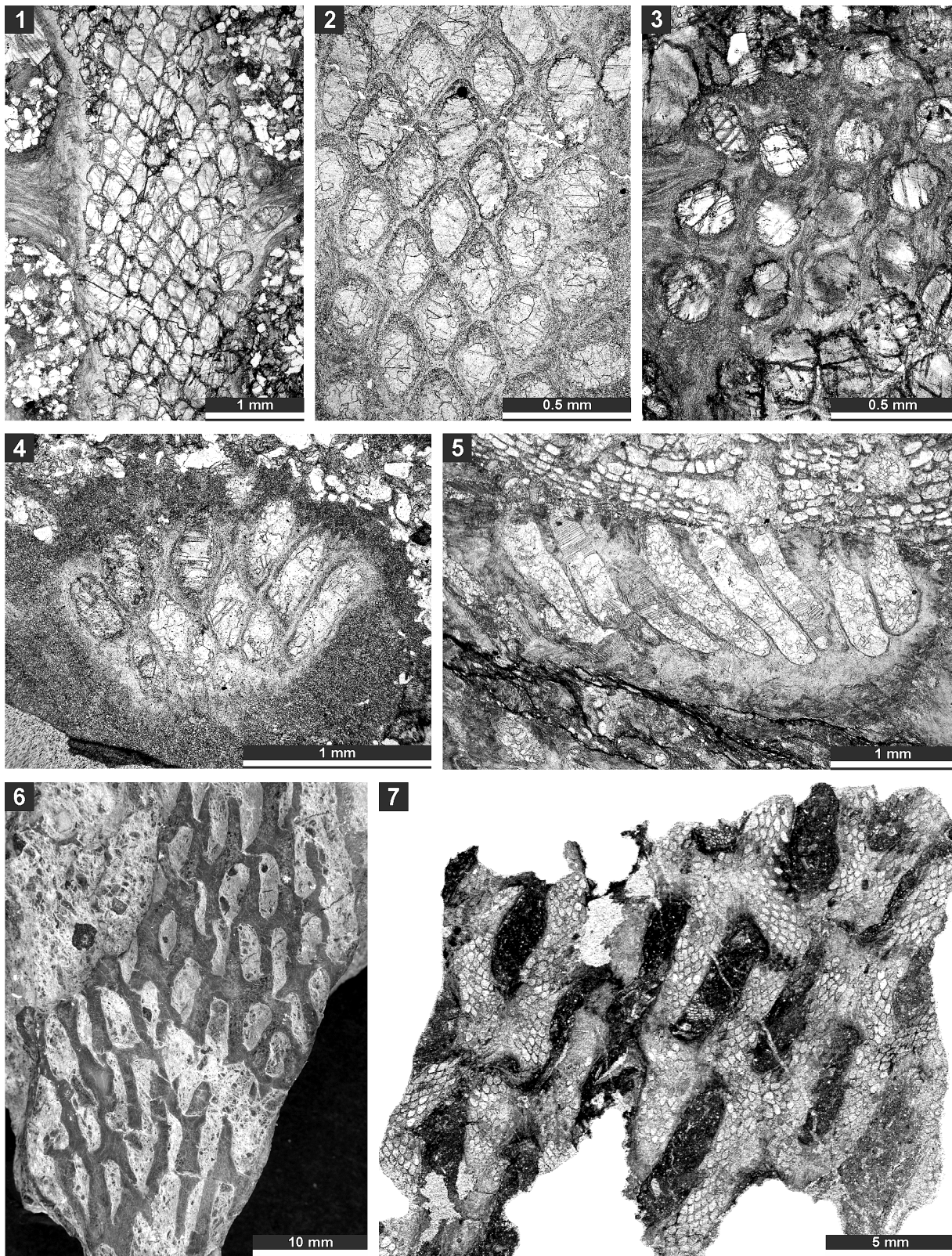
Figures 19.7–8, 20.1–4; Table 27

1957 *Polypora obesa* Crockford, p. 67, pl. 19, fig. 4.

**Material.** SMF 23.188–SMF 23.194.

**Exterior description.** Robust reticulate colony with straight branches joined by wide dissepiments. Bifurcation common. Regular branches 1.7–2.1 mm wide, widening before bifurcation to 2.4–2.6 and narrowing after the bifurcation to 1.2–1.5 mm. Autozooea arranged in 5–9 alternating rows on branches. Apertures circular, arranged in regular alternating rows, 6–8 spaced per fenestrule length. Fenestrules medium in size, elongate, sub-rectangular. Keels absent; nodes on the obverse side present, arranged irregularly between autozooeal apertures; large nodes on the reverse side present. Internal granular skeleton thick, well-developed, continuous in microstyles. Outer lamellar skeleton moderately thick. Large nodes on the reverse colony surface present.

**Interior description.** Autozooea rhombic in mid-tangential section; with well-developed vestibule



**FIGURE 20.** Thin section photographs of *Mackinneyella obesa* (Crockford, 1957), SMF 23.194 (1, 3), SMF 23.191 (2), and SMF 23.189 (4); and *Protoretepora irregularis* n. sp., paratype SMF 23.198 (5), SMF 23.268 (6), and SMF 23.195 (7). 1–3, and 7, tangential section showing autozooeal chambers; 4, branch transverse section; 5, branch longitudinal section; and 6, external view of the reverse side of the colony.

**TABLE 27.** Measurements of *Mackinneyella obesa* (Crockford, 1957). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	18	1.83	0.121	6.58	1.70	2.10
Dissepiment width, mm	23	0.86	0.112	13.00	0.67	1.08
Fenestrule width, mm	21	0.88	0.200	22.84	0.55	1.20
Fenestrule length, mm	25	1.96	0.219	11.20	1.50	2.30
Distance between branch centres, mm	16	2.55	0.297	11.63	1.75	3.00
Distance between dissepiment centres, mm	20	2.97	0.294	9.93	2.30	3.45
Autozooeal aperture width, mm	40	0.17	0.021	11.89	0.14	0.23
Autozooeal aperture spacing along branch, mm	40	0.45	0.041	9.00	0.36	0.51
Autozooeal aperture spacing diagonally, mm	40	0.30	0.034	11.53	0.24	0.38
Maximum chamber width, mm	40	0.23	0.017	7.25	0.20	0.27
Node diameter, reverse side, mm	20	0.16	0.028	17.32	0.12	0.20
Node diameter, obverse side, mm	10	0.08	0.018	22.05	0.05	0.10

protruding highly above the colony surface; elongate to branch length; aperture positioned at distal end of chamber. Hemisepta absent. Heteromorphs absent.

**Remarks.** *Mackinneyella obesa* (Crockford, 1957) differs from *M. ovalifenestrata* Sakagami, 1964 from the Lower Permian of Japan by having wider branches (1.7–2.1 mm vs. 1.2–1.4 mm in *M. ovalifenestrata*). *Mackinneyella obesa* differs from *M. granulosa* Reid, 2003 by also having wider branches (average branch width 1.84 mm vs. 1.46 mm in *M. granulosa*). *Mackinneyella obesa* differs from *M. brevicellata* Baranova, 1960b from the Lower Permian of Russia by having wider branches (1.7–2.1 mm vs. 0.52–0.95 mm in *M. brevicellata*) and larger fenestrules (fenestrule width 0.55–1.20 mm vs. 0.47–0.72 mm in *M. brevicellata*; fenestrule length 1.50–2.30 mm vs. 1.66–2.10 mm in *M. brevicellata*).

**Occurrence.** Noonkanbah Formation, Lower Permian (upper Artinskian–Kungurian); Western Australia. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

Genus *PROTORETEPORA* de Koninck, 1878

**Type species.** *Protoretepora crockfordae* Wyse Jackson, Reid and McKinney, 2011 (revised by Wyse Jackson, Reid and McKinney, 2012). Cascades Group, Lower Permian (late Artinskian–early Kungurian); Tasmania.

**Diagnosis.** Colony fan-shaped to conical, longitudinally pleated; branches broad, linear, essentially parallel, closely spaced, dichotomously dividing; regularly placed lateral expansions of branches fuse with those developed from adjacent branches to form circular to oval-shaped intermediate-sized

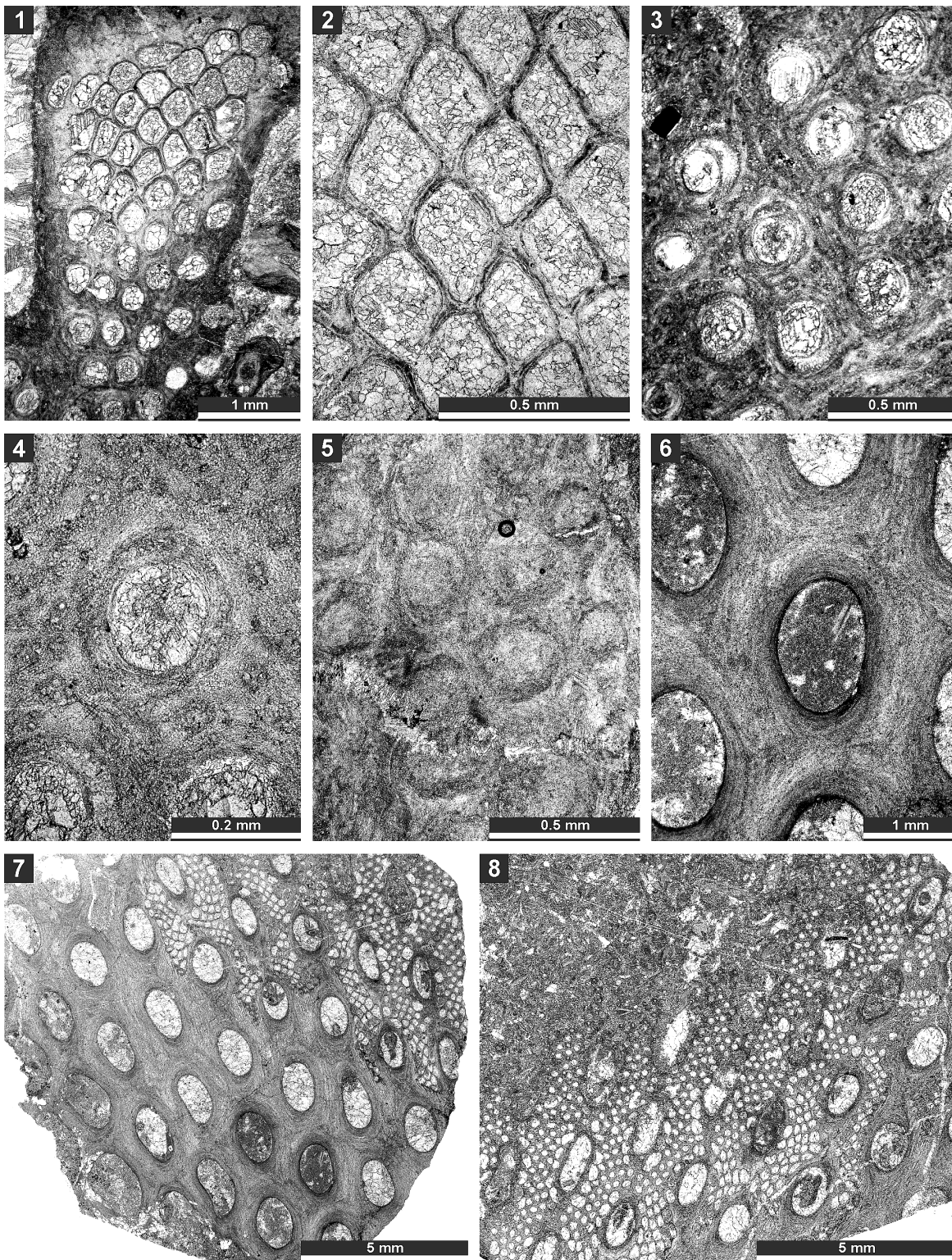
fenestrules; additional extrazooeal skeleton may be present between autozooeal apertures at fusion points; lateral expansions depressed relative to main branch obverse and reverse surface; typically 5–6 rows of autozooea per branch with fewer on lateral branch expansions; zooeal apertures circular, lacking peristomes, aligned longitudinally and diagonally in alternating rows; keels and large obverse styles absent, small styles common in interapertural skeleton; autozooeal chambers tubular, diverging from budding plate at an angle of 50–60°, with long axis directed toward obverse surface, laterally placed chambers inclined disto-laterally at acute or obtuse angle; zooeal chamber cross-sections polygonal or hexagonal in deep section parallel to base; rounded-polygonal in shallow section; hemisepta and diaphragms absent; large diameter distal tube short; reverse axial wall of varying thickness, granular skeleton present in basal plate and axial wall, basal plate with closely spaced fine ridges on reverse side; extrazooeal skeleton laminated, traversed by abundant, typically small styles closely spaced; heteromorphs not known (modified after Wyse Jackson et al., 2011).

**Remarks.** *Protoretepora* de Koninck, 1878 differs from *Anastomopora* Simpson, 1897 in the absence of exozonal tubes in autozooea. Furthermore, *Anastomopora* shows a skeletal microstructure which implies an original aragonitic skeleton, whereas *Protoretepora* has a typical low-Mg calcite laminated skeleton.

**Occurrence.** Permian (Artinskian–Ufimian); Australia, Tasmania, Indonesia, Mongolia, Thailand.

*Protoretepora irregularis* n. sp.  
Figures 20.5-7, 21.1-5; Table 28

zoobank.org/C6FD3035-7186-41C0-991C-0425C7478744



**FIGURE 21.** Thin section photographs of *Protorettepora irregularis* n. sp., paratype SMF 23.201 (1, 3, and 4), paratype SMF 23.202 (2), and holotype SMF 23.195 (5); and *Tibetiporella ornata* n. gen. n. sp., paratype SMF 23.224 (6 and 7) and holotype SMF 23.227 (8). 1, tangential section showing autozooeclial apertures and chambers; 2, mid-tangential section showing autozooeclial chambers; 3, 4, 7, and 8, tangential section showing autozooeclial apertures, microstyles and nodes; 5, tangential section of obverse colony side with nodes; and 6, tangential section of the reverse side of the colony.

**TABLE 28.** Measurements of *Protoretetpora irregularis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	20	1.8	0.332	18.21	1.2	2.5
Fenestrule width, mm	12	1.4	0.310	21.88	0.9	2.0
Fenestrule length, mm	7	3.9	1.212	31.19	2.0	5.5
Autozooeical aperture width, mm	40	0.18	0.017	9.94	0.14	0.20
Autozooeical aperture spacing along branch, mm	40	0.33	0.037	11.18	0.26	0.40
Maximum chamber width, mm	40	0.26	0.018	6.85	0.23	0.30
Node diameter, reverse side, mm	20	0.18	0.036	20.10	0.14	0.25

**Etymology.** The species is named after its irregular colony shape

**Holotype.** SMF 23.195.

**Paratypes.** SMF 23.196–SMF 23.204, SMF 23.268.

**Type locality.** Zhongba area of southwestern Tibet (E 84.31536, N 29.74233).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** Irregular meshwork formed by broad branches; fenestrules large, irregularly oval to rectangular; autozooeicia in 6–7 rows on branches; autozooeicia rhombic in mid-tangential section; hemisepta absent; abundant microstyles arranged in rosette-like pattern; nodes spaced irregularly on the reverse colony surface; heteromorphs absent.

**Exterior description.** Reticulate colony formed by broad branches irregularly fused together; colony shape unknown. Fenestrules large, having irregularly oval to rectangular shape. Autozooeicia arranged in 6–7 rows on branches. Autozooeical apertures circular, lacking peristomes. Keels absent. Nodes spaced irregularly on the reverse colony surface.

**Interior description.** Autozooeicia rhombic in mid-tangential section, irregularly shaped at branch bifurcations; with well-developed vestibule protruding highly above the colony surface; elongate to branch length; aperture positioned at distal end of chamber. Hemisepta absent. Extrazoeical skeleton laminated, traversed by abundant microstyles. Microstyles 0.005–0.015 mm in diameter, generally arranged in a rosette-like pattern. Heteromorphs not observed.

**Remarks.** *Protoretetpora irregularis* n. sp. is distinct by its broad branches, irregular meshwork and presence of large nodes on the reverse colony surface. *Protoretetpora irregularis* differs from *P. robusta* Bassler, 1929 from the Permian of Timor by having large and irregularly shaped fenestrules as well as large nodes on the reverse surface. *Protoretetpora irregularis* differs from *P. flexuosa* Crockford, 1957 from the Lower Permian of West-

ern Australia by the presence of 6–7 rows of autozooeicia on branches instead of 4–5 rows in *P. flexuosa*. Furthermore, the new species has larger autozooeical apertures (average aperture width 0.18 mm vs. 0.13 mm in *P. flexuosa*).

Genus *TIBETIPORELLA* n. gen.

zoobank.org/F1631541-0817-4F68-A475-1CA0028A0AB3

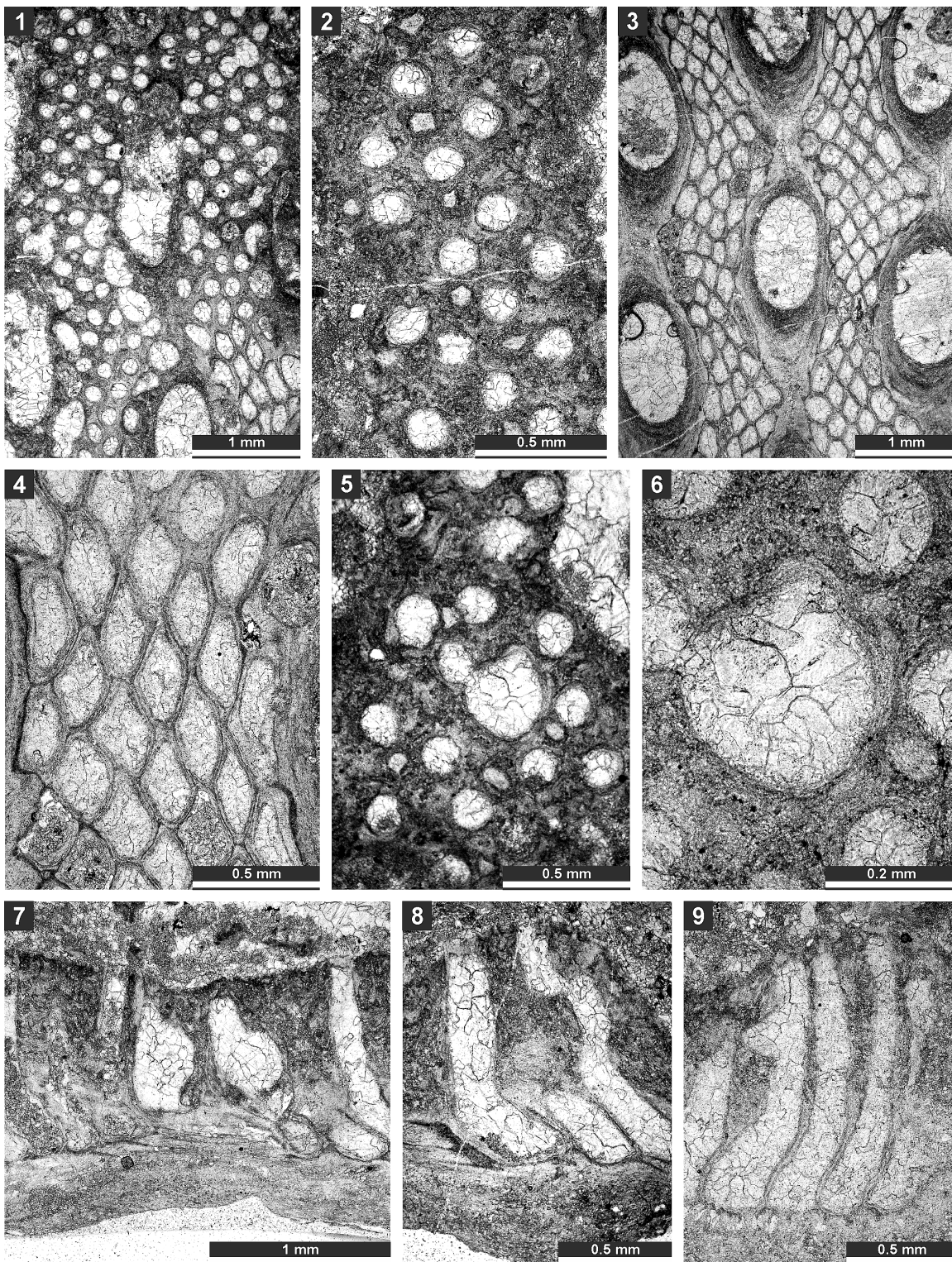
**Type species.** *Tibetiporella ornata* n. gen. n. sp. Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

**Etymology.** The genus is named after its occurrence in Tibet plus suffix *-porella* (feminine), meaning pored organism.

**Diagnosis.** Reticulate colonies consisting of broad linear branches joined by short and wide dissepiments; dissepiments narrow, perpendicular to branches, regularly spaced at large distance; fenestrules elongate oval, sub-rectangular, or irregular in shape; keels and superstructure absent; autozooeicia arranged in 3–7 rows on branches; autozooeical apertures circular; autozooeical chambers long, narrow, tubular, with long vestibules, proximally recumbent on budding plate, rhomboidal in mid tangential section, long axis parallel with branch axis; hemisepta and diaphragms absent; granular skeleton present in basal plate and axial wall but locally absent in transverse and lateral autozooeical walls; extrazoeical skeleton thick, laminated, traversed by abundant, moderate-size microstyles; apparent reproductive heteromorphs in form of isolated zooeicia with enlarged chambers in the proximal part of the vestibule, occurring on obverse colony surface; chambers rounded, oval to semicircular in tangential section; nodes and styles on the obverse colony surface present; reverse side smooth.

**Remarks.** *Tibetiporella* n. gen. differs from *Mackinneyella* Morozova and Lisitsyn, 1996 by having long autozooeicia with long vestibules and heteromorphs in the form of enlarged chambers in the proximal part of vestibule.





**FIGURE 22.** Thin section photographs of *Tibetiporella ornata* n. gen. n. sp., holotype SMF 23.227 (1 and 2), paratype SMF 23.211 (3 and 4), paratype SMF 23.210 (5 and 6), paratype SMF 23.213 (7 and 8), and paratype SMF 23.225 (9). 1 and 2, tangential section showing autozooeceal apertures, nodes and heteromorphs; 3 and 4, mid-tangential section showing autozooeceal chambers; 5 and 6, tangential section showing autozooeceal apertures, nodes and heteromorphs; 7 and 8, longitudinal section showing autozooeceal chambers and heteromorphs; and 9, transverse section showing autozooeceal chambers.

**TABLE 29.** Measurements of *Tibetiporella ornata* n. gen. n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	30	1.06	0.157	14.73	0.78	1.38
Branch thickness	10	1.87	0.308	16.42	1.40	2.25
Dissepiment width, mm	30	1.29	0.165	12.78	1.00	1.60
Fenestrule width, mm	30	0.60	0.090	15.01	0.45	0.79
Fenestrule length, mm	30	1.20	0.151	12.64	0.77	1.63
Distance between branch centres, mm	30	1.68	0.195	11.60	1.25	2.13
Distance between dissepiment centres, mm	30	2.54	0.123	4.84	2.40	2.85
Autozooeical aperture width, mm	30	0.14	0.011	7.70	0.12	0.16
Autozooeical aperture spacing along branch, mm	30	0.36	0.046	12.79	0.26	0.43
Autozooeical aperture spacing diagonally, mm	30	0.22	0.025	11.31	0.17	0.26
Apertures per fenestrule length	10	5.8	0.789	13.60	5.0	7.0
Maximum chamber width, mm	30	0.21	0.017	8.12	0.18	0.25
Node diameter, mm	30	0.09	0.018	20.85	0.05	0.12
Heteromorph width, mm	30	0.30	0.045	15.07	0.24	0.41

**Occurrence.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian); Zhongba area of southwestern Tibet.

*Tibetiporella ornata* n. gen. n. sp.  
 Figures 21.6-8, 22.1-9; Table 29

zoobank.org/D85111C2-1B35-45F2-8278-80137807B6C5

**Etymology.** The species is named after rich ornamentation due to various styles on the obverse colony surface (after Latin "*ornata*" = adorned, decorated).

**Holotype.** SMF 23.227.

**Paratypes.** SMF 23.209–SMF 23.213, SMF 23.224–SMF 23.226, SMF 23.228, SMF 23.229.

**Type locality.** Zhongba area of southwestern Tibet (E 84.31111, N 29.73889).

**Type stratum.** Zhongba Formation, Permian (upper Cisuralian–Guadalupian).

**Diagnosis.** See genus diagnosis.

**Exterior description.** Reticulate colony formed by broad branches fused together; colony shape unknown. Autozooeia arranged in 3–7 rows on branches. Autozooeical apertures circular, 6–7 apertures spaced per fenestrule length. Large nodes on the obverse colony surface, 0.05–0.12 mm in diameter. Smaller styles irregularly arranged, 0.025–0.030 mm in diameter. Reverse colony side smooth.

**Interior description.** Autozooeical chambers long, narrow, tubular, with long vestibules, proximally recumbent on budding plate, rhomboidal in mid-tangential section, long axis parallel with branch axis. Hemisepta and diaphragms absent. Extra-zooeical skeleton thick, laminated, traversed by

abundant, moderate-size microstyles 0.003–0.006 mm in diameter. Apparent reproductive heteromorphs in the form of isolated zoecia with enlarged chambers in the proximal part of the vestibule, occurring on obverse colony surface. Chambers rounded, oval to semicircular in tangential section, 0.24–0.41 mm wide.

**Remarks.** See genus diagnosis and remarks.

## DISCUSSION

### Palaeobiogeography and Stratigraphy

The bryozoan fauna of the Zhongba Formation shows high diversity and abundance. Taxa comprising this fauna belong to orders Cystoporata, Trepostomata, Cryptostomata, and Fenestrata. In total, 30 species of 25 genera were identified.

Cystoporate bryozoans (11 species of nine genera): *Fistulipora enodata* Gorjunova, 1970, *F. guttata* Trizna and Klautzan, 1961, *F. sakagami* n. sp., *Dybowskiella hupehensisiformis* n. sp., *Fistuliramus xianzaensis* Liu and Wang, 1987, *Eridopora uncata* Yang and Lu, 1983, *Cyclotrypa alexanderi* Sakagami, 1963, *Hexagonella kobayashii* Sakagami, 1968, *Goniocladia* aff. *indica* Waagen and Pichl, 1885, *Liguloclema meridianus* (Etheridge, 1926), and *Etherella tibetensis* n. sp.

Trepostome bryozoans (four species of four genera): *Tabulipora xinjiangensis* Yang and Lu, 1983, *Dyscritella lii* n. sp., *Ulrichotrypella omanica* Ernst et al., 2008, and *Neoeridotrypella astrica* (Linskaya, 1951).

**TABLE 30.** Matrix of occurrences of bryozoan species from the Zhongba Formation used for the numerical plots in the Figure 23 (1 - present, 0 - absent). Thailand and Western Australia share the highest number of species with the Zhongba area (five and four species, respectively), whereas other regions share three or fewer species with the studied area.

	Zhongba Fm.	Xainza	Pamir	Thailand	W-Australia	Timor	Urals	Oman	Xinjiang	Iran
<i>Fistulipora enodata</i>	1	1	1	0	0	0	0	0	0	0
<i>Fistulipora guttata</i>	1	0	0	0	0	0	1	0	0	0
<i>Fistulipora sakagami</i>	1	0	0	1	0	0	0	0	0	0
<i>Dybowskiella hupehensisiformis</i>	1	0	0	0	0	0	0	0	1	0
<i>Fistuliramus xianzaensis</i>	1	1	0	0	0	0	0	0	0	0
<i>Eridopora uncata</i>	1	0	0	0	0	0	0	0	1	0
<i>Cyclotrypa alexanderi</i>	1	0	0	0	1	0	0	0	0	0
<i>Hexagonella kobayashii</i>	1	0	0	1	0	0	0	1	0	0
<i>Liguloclema meridianus</i>	1	1	0	1	1	0	0	0	0	0
<i>Tabulipora xinjiangensis</i>	1	0	0	0	0	0	0	0	1	0
<i>Ulrichotrypella omanica</i>	1	0	0	0	0	0	0	1	0	0
<i>Neoeridotrypella astrica</i>	1	0	0	0	0	0	1	0	0	0
<i>S.(S.) delicatula</i>	1	0	0	1	0	0	0	1	0	0
<i>S. (S.) marmionensis</i>	1	0	1	0	1	0	0	1	0	1
<i>Rhabdomeson bretnalli</i>	1	0	0	0	1	0	0	0	0	0
<i>Primorella rotunda</i>	1	0	1	0	0	0	0	1	0	1
<i>Timanotrypa australis</i>	1	0	0	1	0	0	0	0	0	0
<i>Spinofenestella subquadratopora</i>	1	0	0	0	0	0	1	0	0	0
<i>Polypora consanguinea</i>	1	0	0	0	0	1	0	0	0	0
<i>Polypora brouweri</i>	1	0	0	0	0	1	0	0	0	0
<i>Mackinneyella obesa</i>	1	0	0	0	0	1	0	0	0	0

Cryptostome bryozoans (seven species of five genera): *Streblotrypa* (*Streblotrypa*) *parviformis* n. sp., *Streblotrypa* (*Streblascopepora*) *delicatula* Sakagami, 1961, *Streblotrypa* (*Streblascopepora*) *marmionensis* (Etheridge, 1926), *Rhabdomeson bretnalli* Crockford, 1957, *Rhabdomeson* sp., *Primorella rotunda* Gorjunova, 1985, and *Timanotrypa australis* n. sp.

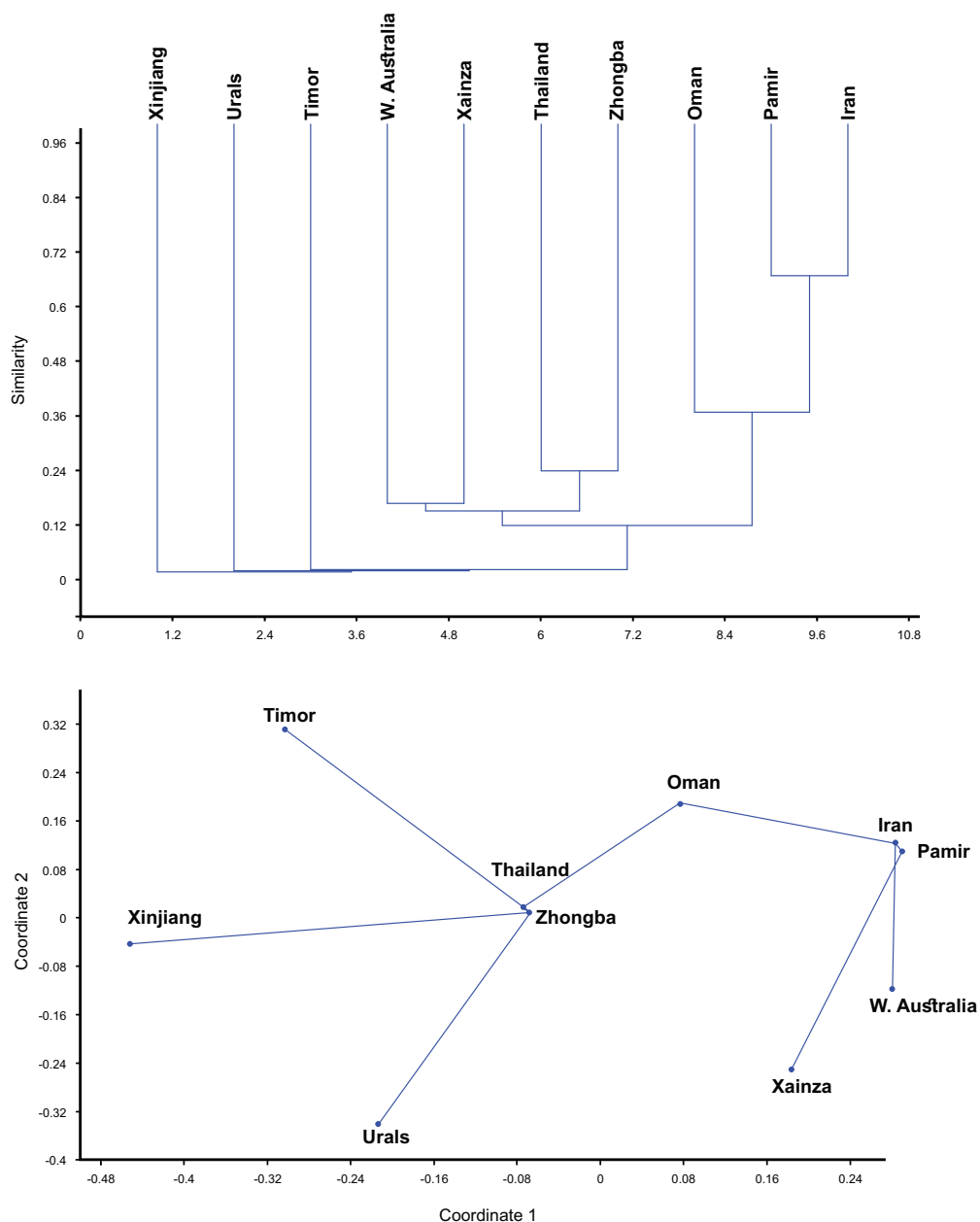
Fenestrate bryozoans (eight species of five genera): *Spinofenestella* sp., *Spinofenestella subquadratopora* (Schulga-Nesterenko, 1952), *Polypora consanguinea* Bassler, 1929, *Polypora brouweri* Bassler, 1929, *Polypora* aff. *voluminosa* Trizna and Klautzan, 1961, *Mackinneyella obesa* (Crockford, 1957), *Protorettepora irregularis* n. sp., and *Tibetiporella ornata* n. gen. n. sp.

The majority of bryozoans from the Zhongba Formation of southwestern Tibet have a Lower Permian (Artinskian–Kungurian) distribution in

such regions as Thailand, Oman, Western Australia, Timor, the Urals, Pamir, Iran, and two localities in southwestern China (Table 30).

The distribution matrix from the Table 30 was used for the cluster analysis (Jacquard's similarity index, unweighted pair-group average algorithm). The computed dendrogram suggests the closest relation of the Zhongba fauna is that of Thailand (Figure 23). These two faunas show similarity to the cluster formed by Western Australia and Xainza, and together they build a cluster that shows similarity to the cluster Oman plus Pamir and Iran. All these regions show decreasing similarity to Timor, Urals and Xinjiang.

Reid and James (2008, 2010) compared the Permian bryozoan diversity of Gondwana and northern Eurasia and concluded that Permian bryozoan faunas from higher latitudes (antitropical) showed lower diversity than those from the tropics.



**Figure 23.** Palaeobiogeographical affinities of the bryozoan assemblage from the Zhongba Formation (Zhongba). Top: dendrogram of the cluster analysis using Jacquard's similarity index (unweighted pair-group average algorithm), and bottom: plot of non-metric MDS analysis made with Jacquard's similarity index. Areas: Pamir (Tajikistan), Oman (Batain Coast), Iran (central Iran, Chili Formation), Xainza (southwestern Tibet, Xiala Fm.), Thailand, Urals, Western Xinjiang (Baliqliq Group), and W. Australia (Noonkanbah Fm.). Japan, Malaysia, and Rutog (southwestern Tibet) were omitted as sharing only one species with Zhongba assemblage.

The Zhongba area of southwestern Tibet belongs to the central Tethys (Ross, 1995) and is clearly a tropical region. The taxonomic composition of the bryozoan fauna from the Zhongba Formation shows an intermixture of both Boreal and Gondwana elements. This fact indicates that there might

be faunal migrations into the tropical region from both from the north and south.

Brachiopods found in the Zhongba Formation along with bryozoans include the following species (Li et al., 2014b): *Stenosisma gigantea* (Diener, 1897), *Spiriferella sinica* Zhang, 1976, *S. rajah* (Salter, 1865), *Costiferina alata* Waterhouse, 1966,

**TABLE 31.** Distribution of bryozoan growth forms in the Zhongba Formation.

Species	Growth form
<i>Fistulipora enodata</i>	encrusting
<i>Fistulipora guttata</i>	encrusting
<i>Fistulipora sakagamii</i>	encrusting
<i>Dybowskiella hupehensisformis</i>	encrusting
<i>Eridopora uncata</i>	encrusting
<i>Tabulipora xinjiangensis</i>	encrusting
<i>Dyscritella lii</i>	encrusting
<i>Cyclotrypa alexanderi</i>	encrusting/branched
<i>Hexagonella kobayashii</i>	branched/bifoliate/lenticular
<i>Liguloclema meridianus</i>	branched/bifoliate/lenticular
<i>Timanotrypa australis</i>	branched/bifoliate/lenticular
<i>Fistuliramus xianzaensis</i>	branched/cylindrical
<i>Ulrichotrypella omanica</i>	branched/cylindrical
<i>Neoeridotrypella astrica</i>	branched/cylindrical
<i>Streblotrypa (Streblotrypa) parviformis</i>	branched/cylindrical
<i>Streblotrypa (Streblascopora) delicatula</i>	branched/cylindrical
<i>Streblotrypa (Streblascopora) marmionensis</i>	branched/cylindrical
<i>Rhabdomeson bretnalli</i>	branched/cylindrical
<i>Rhabdomeson sp.</i>	branched/cylindrical
<i>Primorella rotunda</i>	branched/cylindrical
<i>Spinofenestella sp.</i>	reticulate/connected/biserial
<i>Spinofenestella subquadratopora</i>	reticulate/connected/biserial
<i>Polypora consanguinea</i>	reticulate/connected/ multiserial
<i>Polypora brouweri</i>	reticulate/connected/ multiserial
<i>Polypora aff. voluminosa</i>	reticulate/connected/ multiserial
<i>Mackinneyella obesa</i>	reticulate/connected/ multiserial
<i>Goniocladia aff. indica</i>	reticulate/fused/bifoliate/ multiserial
<i>Etherella tibetensis</i>	reticulate/fused/bifoliate/ lenticular
<i>Protoretetepora irregularis</i>	reticulate/fused/multiserial
<i>Tibetiporella ornata</i>	reticulate/fused/multiserial

and *Enteletes waageni* Gemmellaro, 1892. These species indicate a rather younger age (Guadalupian–Lopingian) than the bryozoan fauna (Artinskian–Kungurian). Accordingly, biostratigraphical interpretation does not correspond to the data on bryozoans. *Enteletes waageni* Gemmellaro, 1892

was originally described from the Permian on Sicily, and later recorded from the Chitichun Limestone (southern Tibet), Middle and Upper *Productus* Limestone (Pakistan), and Guadalupian (Djebel Tebaga, Tunisia) (Verna et al., 2010). Other species are known mainly from the Upper Permian of Nepal and Northern Himalaya (Waterhouse, 1966; Shen and Yugan, 1999). The age contradiction between bryozoans and brachiopods could be explained by the fact that the bryozoan samples were sampled from the lower part of the Zhongba Formation, whereas brachiopods were collected from the upper part of the formation (Xianghui Li, personal commun., 2015).

### Palaeoecology

The studied bryozoan fauna shows a great variety of growth forms, which correspond to certain functionalities. Distribution of bryozoan growth forms is controlled by extrinsic factors (e.g., Stach, 1936; McKinney and Jackson, 1989; Smith, 1995; Hageman et al., 1997, 1998; Amini et al., 2004). Therefore, an analysis of bryozoan growth forms in a palaeocommunity may reveal import insights in the palaeoenvironment. However, a taphonomic impact must be considered because bryozoan skeletons react selectively to various sea-floor processes such as abrasion or dissolution (Smith and Nelson, 1994).

The bryozoan association of the Zhongba Formation contains three main groups of growth forms (Table 31): encrusting (8), erect branched (13) and erect reticulate (10). One species, *Cyclotrypa alexanderi*, can develop both encrusting and branched ramose colonies. Erect branches can be divided in branched/cylindrical (10) and branched/lenticular (3). Reticulate bryozoans show greater diversity in their construction modes: reticulate/connected/(biserial-multiserial) (6), reticulate/fused/multiserial (3), and reticulate/fused/bifoliate/lenticular (1). The mode of the connection of branches in reticulate colonies may occur in two ways: by connection with dissepiments consisting of extrazooecial skeleton (connected) and by fusing (anastomosing) of undulating branches (fused). Furthermore, the branches may be unifoliate (apertures open on one side of branches, opposite side sterile) or bifoliate (apertures open both on obverse and reverse side of branches). The branches may bear two rows of zooecia (biserial) or three and more (multiserial).

From these growth forms, the encrusting colonies are the most universal, being adapted to various substrates and surviving also in moderate to high energy conditions (e.g., Nelson et al., 1988;

McKinney and Jackson, 1989; Amini et al., 2004). Reticulate colonies may occur in a variety of hydrodynamic conditions (e.g., Stach, 1936; Pedley, 1976, Cuffey and McKinney, 1982), whereas erect branched colonies (especially the robust ones) are considered vulnerable to damage in high energy conditions (Cheetham and Thomsen, 1981). The lithological characteristics of embedding rocks (Figure 2) indicate a moderate to high energy environment. Absence of terrigenous material indicates a large distance from the shoreline. At least the encrusting bryozoans seem to be autochthonous in this association (Figure 2.2-3); other groups show a rather low to moderate fragmentation level indicating a relatively short transport distance of the debris. The lithology, bryozoan growth form distribution and composition of the accompanying fauna (brachiopods, crinoids, gastropods) suggest a middle shelf setting, an environment quite remote from the shoreline and influenced by local currents.

### CONCLUSIONS

The described bryozoan fauna from the Zhongba Formation of the Zhongba area (south-western Tibet) supports the early Permian (Cisuralian, Artinskian–Kungurian) age of this formation. Bryozoan fauna from the Zhongba Formation shows rather close relationships to Thailand and Western Australia, and some distant relations to Oman, Timor, central Pamir, Iran, Urals, and other Tibetan localities displaying an intermixture of both Boreal and Gondwana elements. These results contradict the interpretation of brachiopod species found in the Zhongba Formation, which indicate Guadalupian to Lopingian age and suggest connections to northern Himalaya and Nepal. This discrepancy may be explained by different levels of sampling within the Zhongba Formation. The distribution of bryozoan growth forms as well as the lithological characteristics and accompanying fauna suggests a middle shelf setting some distance from shoreline likely influenced by local currents.

### ACKNOWLEDGEMENTS

Dr. X. Li, Department of Earth Sciences of Nanjing University, China, is thanked greatly for providing the bryozoan collection for study and helpful comments during the manuscript writing. This work is thanks to projects (12112011086037 and 1212011121229) aiming the 1:50,000 geological mapping of Zhongba area fund by the Chinese Bureau of Geological Survey. E. Gilmour, Washington, and P. Wyse Jackson, Dublin, are

thanked for helpful comments to the bryozoan taxonomy. C. Reid, Christchurch and H. Arne Nakrem, Oslo provided helpful comments to the manuscript. Three anonymous referees are thanked for their constructive and helpful reviews of the manuscript. The study of Permian bryozoans is supported by the Deutsche Forschungsgemeinschaft (DFG), project ER 278/7.1 and 2.

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