

Bryozoans from the lower Silurian (Telychian) Hanchiatien Formation from southern Chongqing, South China

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Abstract.—Eight bryozoan species are described from the Hanchiatien Formation (lower Silurian, Telychian) of southern Chongqing, South China. Four species are new: the trepostomes *Asperopora sinensis* n. sp., *Trematopora jiebeiensis* n. sp., and *Trematopora tenuis* n. sp., and the fenestrate *Moorephylloporina parvula* n. sp. One species, the cystoporate *Hennigopora* sp. indet., is described in open nomenclature. *Moorephylloporina parvula* n. sp. is eurytopic, occurring in all types of facies within the bioherms. Erect *Moorephylloporina* Bassler, 1952, *Trematopora* Hall, 1852, and *Leioclema* Ulrich, 1882 formed pioneering communities on weakly cemented substrata, whereas encrusting *Fistulipora* M'Coy, 1849, *Hennigopora* Bassler, 1952, and *Asperopora* Owen, 1969 occurred on hardgrounds and formed densely compact framestones. Robust branched *Trematopora* and *Leioclema* tend to occur out of the reef core (framework) where they could have formed reef-flank thickets in more agitated conditions. The generic composition of the studied fauna correlates with other localities in South China, and they show general paleobiogeographic relations to Siberia and Indiana, USA.

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Introduction

Lower Silurian (Llandovery) marine sediments are distributed along a NNE-SSW trend on the South China plate, which was largely occupied by the Yangtze region in the northwestern sector. During the Llandovery, the Yangtze region has been interpreted to represent a tropical or subtropical 'epeiric platform' in western Gondwana (e.g., Rong and Cocks, 2014). In the earliest Silurian (Rhuddanian stage), black shales with flysch are dominant sediments in the Yangtze region. Due to the rapid rise of sea level, late Aeronian limestone facies became widespread in the epeiric sea of the Yangtze region, however, the early Telychian is dominated by terrigenous sediments with minor calcareous interbeds due to the expansion of the Yangtze Uplift (Rong et al., 2003, 2012; Deng et al., 2012). The early Telychian rocks are represented by the Hanchiatien (or Majiaochong) Formation, usually over a kilometer in thickness, spanning from northern Guizhou to southern Sichuan provinces and the southern Chongqing District. Li et al. (2018) provided an in-depth study of the meter-sized, bryozoan-bearing bioherms, described preliminarily earlier in Chinese by Li et al. (2012). The bryozoan fauna in those bioherms have not yet been given a systematic treatment. Previous studies of the early Telychian bryozoan fauna of the Yangtze region are scarce (Hu, 1982; Xia and Qi, 1989), thus, a detailed description of the Hanchiatien bryozoans can provide valuable insights into the faunal composition in the region.

Telychian bryozoans from South China were previously described in several papers. Hu (1982) identified six bryozoan species from the Cuijiagou Formation (lower Telychian) of Guangyuan, Sichuan: *Fistulipora guangyuanensis* Hu, 1982, *Fistuliramus eximius* Hu, 1982, *Hennigopora multilamellosa* Hu, 1982, *Hennigopora* sp. indet., *Trematopora sinensis* Hu, 1982, and *Trematopora* sp. indet. From the upper Telychian Ningqiang Formation of Ningqiang (Shanxi), he identified 14 species (Hu, 1982, 1990): *Calloporella silurica* Hu, 1982, *Cyclotrypa solidoscens* Hu, 1990, *Cyphotrypa undulata* Hu, 1990, *Fistulipora ningqiangensis* Hu, 1990, *Fistuliramus transversus* Hu, 1982, *Hennigopora petaliformis* Hu, 1982, *Hallopora aggregata* Hu, 1982, *Homotrypa ningqiangensis* Hu, 1990, *Leioclema speciosum* Hu, 1982, *Leioclema* sp. indet., *Monotrypa shaanxiensis* Hu, 1990, *Orbignyella curvata* Hu, 1982, *O. globata* Yang, 1951, and *O. mui* Yang, 1951.

Xia and Qi (1989) described four species from the lower Telychian Chenxiacun Formation of Hanshan (Anhui): *Hallopora elegantula* (Hall, 1852), *Hallopora hanshanensis* Xia and Qi, 1989, *Hallopora raritabulata* Xia and Qi, 1989, and *Trematopora reflua* Xia and Qi, 1989.

Geological settings and depositional environment

The Hanchiatien Shale was originally defined by Ting (1930) and was subsequently treated as the Hanchiatien Group (e.g.,

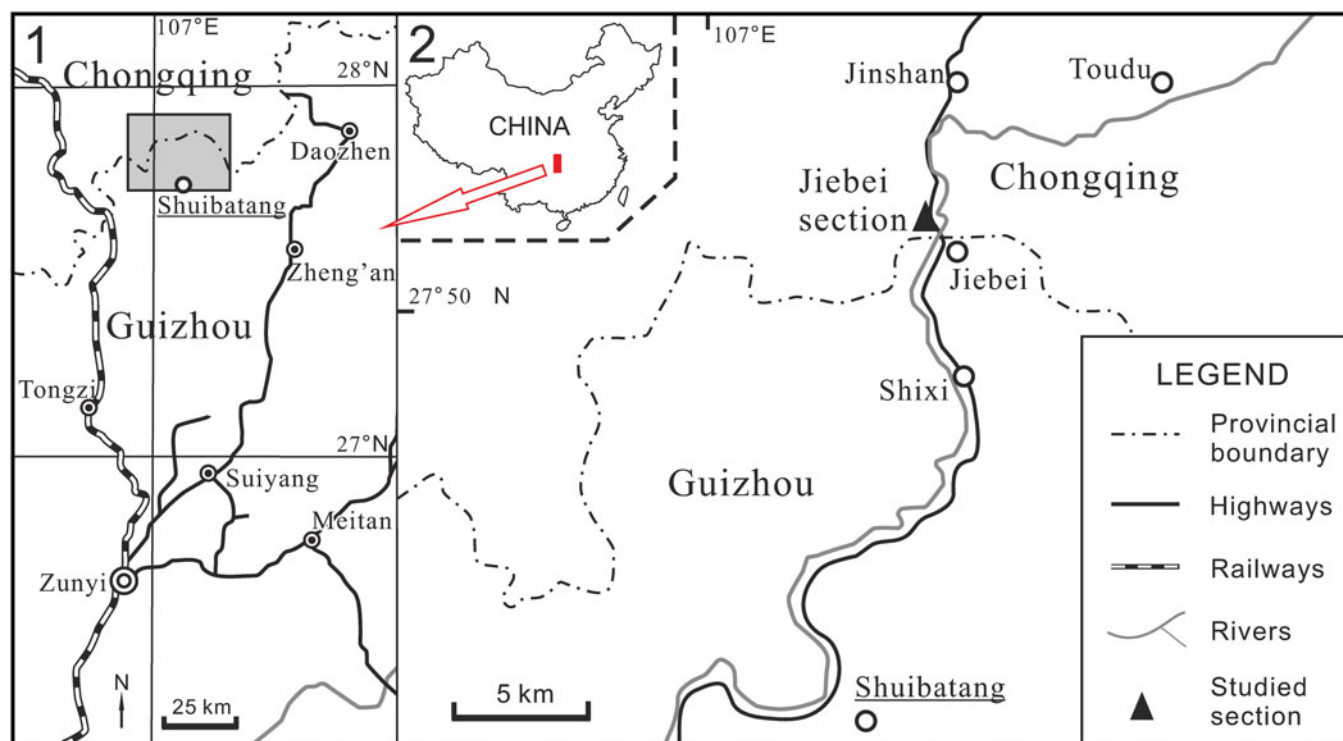


Figure 1. Location of the studied section between Chongqing and Guizhou provinces, South China: (1) region between Chongqing and Guizhou provinces; (2) detail of the shaded-box area in (1), showing the study section.

Yin, 1949; Mu, 1962). Since 1978, it has been formally named the Hanchiatien Formation (e.g., Southwest Institute of Geologic Sciences, 1978; Rong et al., 1990), characterized by brownish to greenish shales. The shales are usually disconformably underlain by the upper Aeronian Shihniulan Formation and disconformably capped by the lower Permian Liangshan or Tongkuangxi formations (Zhan and Jin, 2007). In most cases, there is a unit (normally < 10 m thick) of purplish red shales known as the Lower Red Beds at the base of the Hanchiatien Formation. Stratigraphically, the Lower Red Beds are a well-known marker unit in the Yangtze region (Rong et al., 2012).

Although the Hanchiatien Formation is poorly fossiliferous, diagnostic chitinozoans and graptolites were reported at the top of the formation in the Northeast Guizhou: *Ancyrochitina brevicollis* Geng, 1986 and *Streptograptus plumosus* Bailly, 1871 suggest the formation should be correlated to early Telychian (Chen, 1986; Geng et al., 1997). Some carbonate interbeds (or marls) occur in the Hanchiatien Formation in a few localities (e.g., Li et al., 2012). Macrofossils (e.g., brachiopods, trilobites, echinoderms, bryozoans, and corals) are abundant in some of the carbonate interbeds. To date, no systematic study has been done on the bryozoans from this formation. Here, we provide the first taxonomic description of the bryozoans from the lower Hanchiatien Formation at the border of Guizhou Province.

The Hanchiatien Formation is thought to have been deposited in a subtidal setting, mainly based on the distributional pattern of the brachiopods (Rong et al., 2003). However, different facies of the Hanchiatien Formation display a fluctuation of marine environments (Li et al., 2018). The paleogeographical setting of the Hanchiatien Formation indicates a seaward ramp

oriented northward. Depositional environments could have varied from place to place in the Yangtze epeiric sea.

The Jiebei section is located at the boundary between Chongqing and Guizhou provinces (Fig. 1). The stratigraphic details were given by Li et al. (2018) who described the lower Hanchiatien Formation as brownish to greenish shales with minor siltstones, which cap the Shihniulan Formation disconformably. In this section, there are two bioherms 85–120 m above the base of the Hanchiatien Formation. At the bottom of the second bioherm, there is a layer (~1.7 m thick) of cross-bedded, oolitic grainstone with ripples (Fig. 2). Lacking any photic-related fossils, the bryozoan bioherms demonstrate an unusual heterozoan marine community, mainly produced by internal waves (Li et al., 2018). Our interpretation is that the lower Hanchiatien Formation in Jiebei represents mid-outer ramp settings.

Material and methods

All bryozoans were collected from the bioherms (Figs. 2, 3) in June 2016 by QJL. Thin sections were made in the laboratory of the GeoZentrum Nordbayern, Friedrich-Alexander University Erlangen-Nuremberg, Germany. Bryozoans were studied in thin sections using a binocular microscope under transmitted light. In total, 42 thin sections were prepared from rock samples. The spacing of structures is measured as the distance between their centers. Statistics were summarized using arithmetic means, sample standard deviations, coefficients of variation, and minimum and maximum values.

Based on the genus-level occurrence databases of Silurian bryozoans (Hu, 1982, 1990; Xia and Qi, 1989; Anstey et al., 2003), pair-group cluster analysis (Euclidean similarity index)

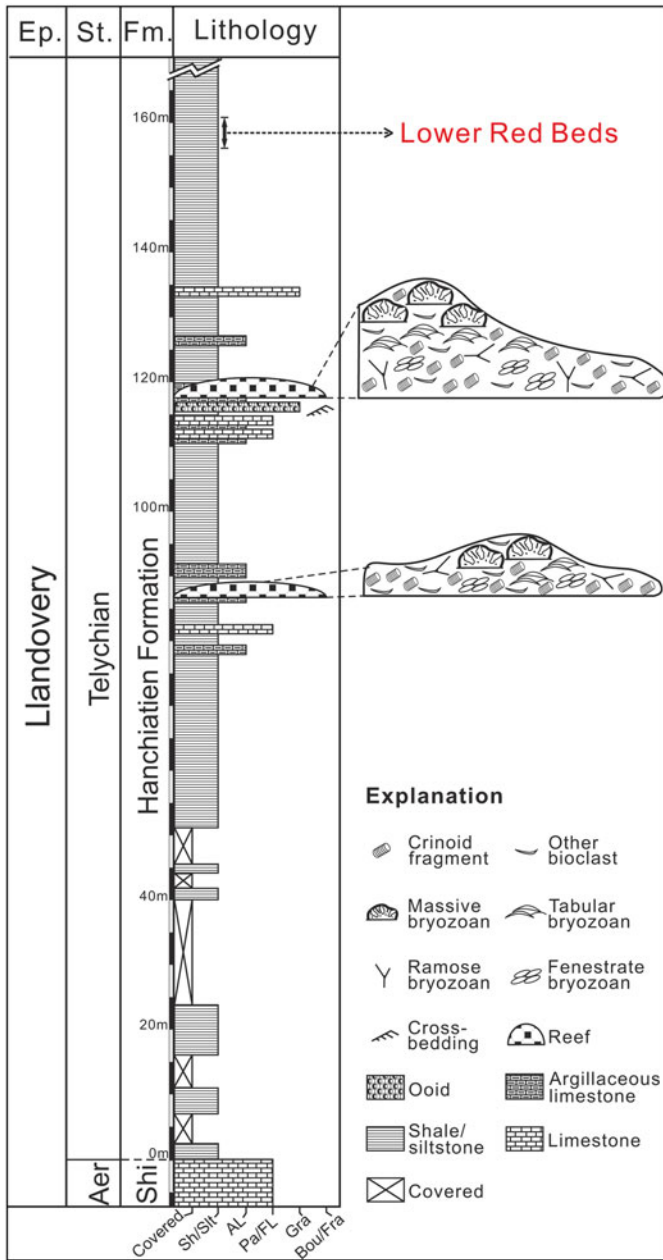


Figure 2. Lithologic column of the Jiebei section (from Li et al., 2018). Stratigraphic positions of reefs are indicated. Aer = Aeronian; AL = argillaceous limestone; Bou/Fra = boundstone/framestone; Ep. = epoch; Fm. = formation; Gra = grainstone; Pa/FL = packstone/floatstone; Sh/Silt = shale/siltstone; Shi = Shihniulan Formation; St. = stage.

and detrended correspondence analysis were implemented with the PAST statistical package (version 2.16; Hammer et al., 2001) to assess the paleobiogeographical relationship of the Telychian bryozoan fauna from the South China Block. Both cluster analysis and detrended correspondence analysis make no assumptions about the data structure, so they were suitable for our large-scale paleobiogeographical studies (Shi, 1993). To ensure the robustness of our results, taxa that were potentially poorly known were removed from the published presence-absence dataset (see Appendix).

Repositories and institutional abbreviations.—The newly studied material is deposited at the Naturmuseum Senckenberg (SMF), Frankfurt am Main, Germany. Other cited repositories are: NIGP = Nanjing Institute of Geology and Paleontology, China.

Systematic paleontology

- 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.

Fistulipora guangyuanensis Hu, 1982
Figure 4.1–4.5; Table 1

1982 *Fistulipora guangyuanensis* Hu, p. 296, pl. 3, figs. 11, 12.

Holotype.—NIGP 63771; Cuijiagou Formation, Telychian, Llandoverly, lower Silurian; Sichuan Province, China.

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandoverly, lower Silurian.

Materials.—SMF 60500–60538.

Remarks.—*Fistulipora guangyuanensis* differs from *Fistulipora ningqiangensis* from the lower Silurian of Ningqiang, China in its smaller apertures (aperture width 0.12–0.18 mm vs. 0.17–0.25 mm [Hu, 1990], respectively) and larger lunaria. *Fistulipora guangyuanensis* differs from *Fistulipora ternavensis* Astrova, 1965 from the lower–middle Silurian of Russia in its smaller autozooeical apertures (aperture width 0.12–0.18 mm vs. 0.18–0.23 mm [Astrova, 1965], respectively), larger lunaria, and less abundant vesicles (7–9 per autozooeical aperture vs. 8–10 vesicles [Astrova, 1965], respectively).

Family Xenotrypidae Utgaard, 1983
Hennigopora Bassler, 1952

Type species.—*Callopora florida* Hall, 1852; Niagaran Group, Rochester Shale, Sheinwoodian, Wenlock, Silurian; Lockport, New York, USA.

Hennigopora multilamellosa Hu, 1982
Figure 4.6–4.10; Table 2

1982 *Hennigopora multilamellosa* Hu, p. 295, pl. 2, figs. 4, 5. *Holotype.*—NIGP 63765; Cuijiagou Formation, Telychian, Llandoverly, lower Silurian; Sichuan Province, China.

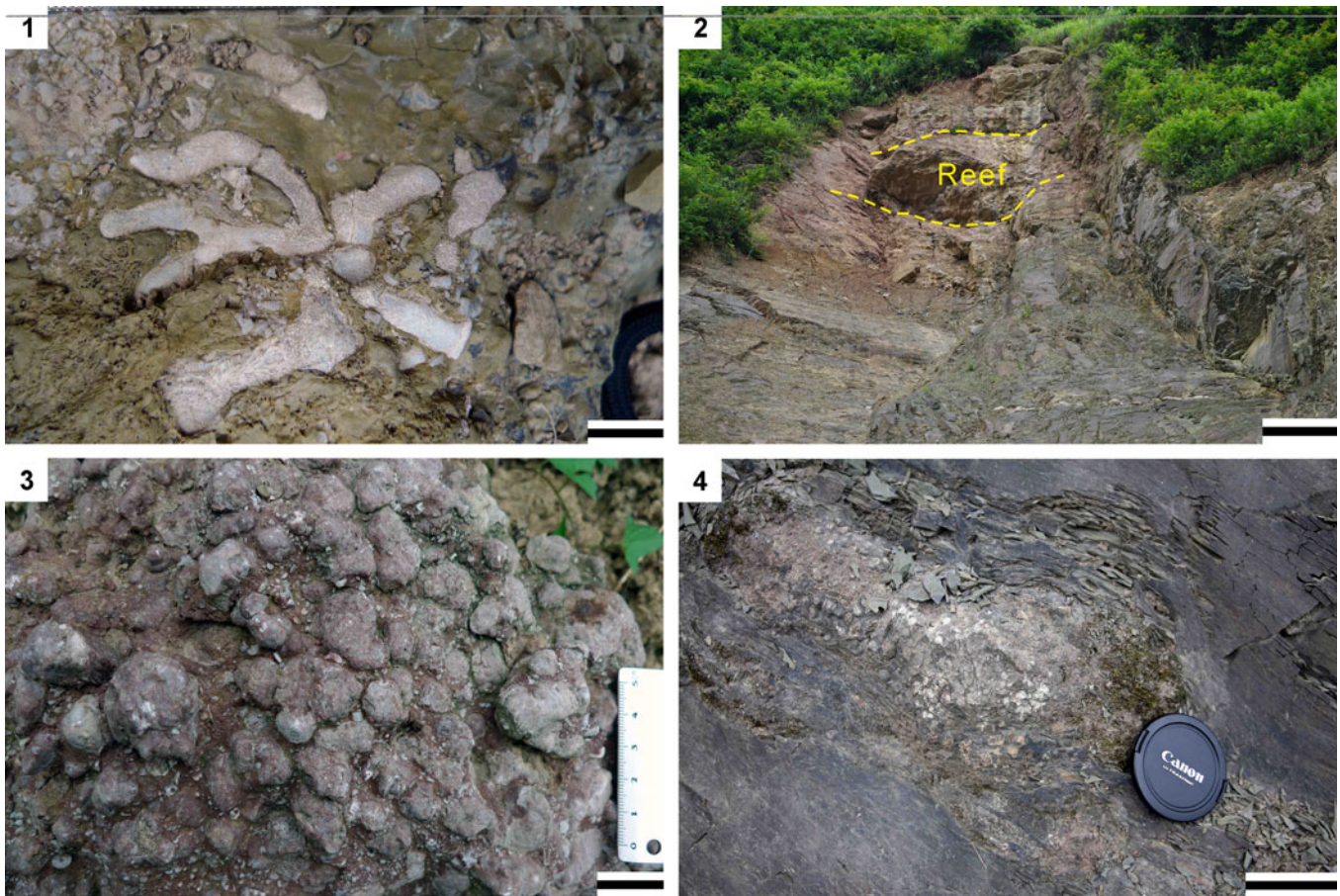


Figure 3. Field aspects of the studied section: (1) the flank facies of the second reef horizon, showing the branched bryozoan *Trematopora*; (2) the core facies of the second reef horizon; (3) plan view of the framestone, showing bulbous and knobby colonies of the first reef horizon; (4) the flank facies of the first reef horizon. Scale bars = 2 m (2); 8 cm (4); 2 cm (3); 1 cm (1).

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Materials.—SMF 60539–60576.

Remarks.—*Hennigopora multilamellosa* differs from *Hennigopora florida* (Hall, 1852) from the middle Silurian of New York, USA in its smaller autozooeical apertures (aperture width 0.17–0.28 mm vs. 0.28–0.35 mm [Bassler, 1906], respectively). *Hennigopora multilamellosa* differs from *Hennigopora hunanensis* Yang and Xia, 1974 from the lower Silurian of China in having smaller autozooeical apertures (aperture width 0.17–0.28 mm vs. 0.20–0.30 mm [Yang and Xia, 1974], respectively) and in its less abundant vesicles (6–11 per aperture vs. 8–13, respectively). *Hennigopora multilamellosa* differs from *Hennigopora apta* Perry and Hattin, 1960 from the lower Silurian of Indiana, USA in the presence of 4–7 acanthostyles per autozooeical aperture instead of 3–5 (Ernst et al., 2019) in the latter species. *Hennigopora multilamellosa* differs from *Hennigopora petaliformis* from the Ningqiang Formation (upper Telychian) of Shanxi in its encrusting instead of branched erect colony and in the presence of 4–7 acanthostyles per autozooeical aperture instead of 2–4 (Hu, 1982) in the latter species.

Hennigopora sp. indet.

Figure 4.11–4.15; Table 3

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Description.—Encrusting colony, 0.40–1.25 mm thick. Autozooeia originating from thin epitheca, bending in the early exozone to the colony surface, with rounded-polygonal, often petaloid, apertures due to indenting acanthostyles. Basal diaphragms rare, straight, thin. Vesicles generally large, separating autozooeia in one or two rows, 8–10 surrounding each autozooeical aperture, with rounded roofs, polygonal in tangential section. Acanthostyles abundant, relatively large, often deeply indenting autozooeical chambers, six or seven surrounding each autozooeical aperture. Autozooeical walls displaying obscure granular microstructure, 0.005–0.010 mm thick. Maculae not observed.

Materials.—Single specimen, SMF 60577.

Remarks.—*Hennigopora* sp. indet. differs from *Hennigopora multilamellosa* in its smaller autozooeical apertures (mean aperture width 0.15 mm vs. 0.22 mm [Table 2], respectively)

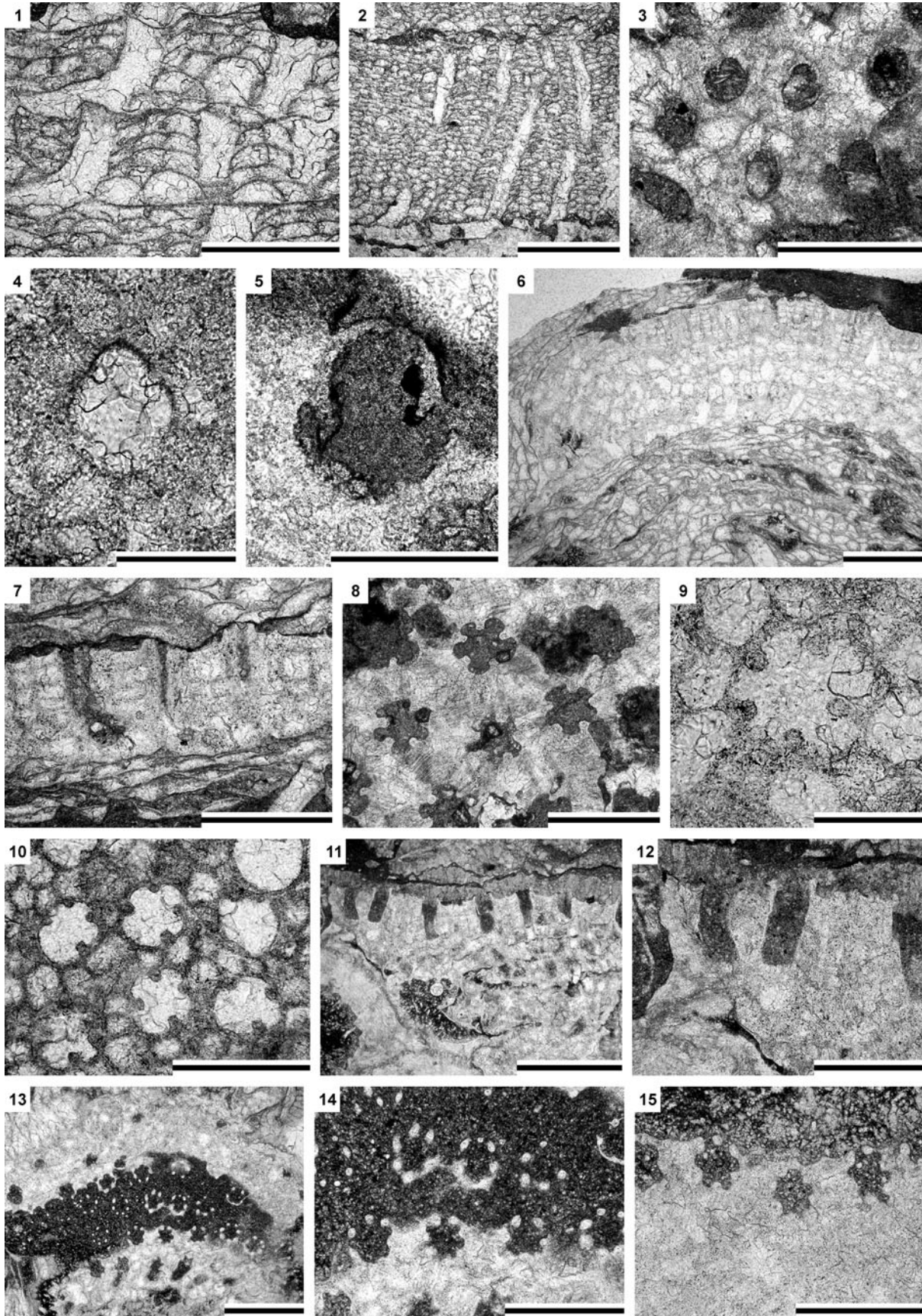


Figure 4. (1–5) *Fistulipora guangyuanensis* Hu, 1982: (1) longitudinal section of a multilayered encrusting colony, SMF 60526; (2) longitudinal section of an encrusting colony, SMF 60526; (3, 4) tangential section showing autozoecial apertures and vesicles, SMF 60525; (5) tangential section showing autozoecial aperture with lunarium, SMF 60524; (6–10) *Hennigopora multilamellosa* Hu, 1982: (6) longitudinal section, SMF 60570; (7) longitudinal section showing autozoecia and vesicles, SMF 60552; (8–10) tangential sections showing autozoecial apertures, acanthostyles, and vesicles: (8) SMF 60544; (9) SMF 60542; (10) SMF 60554; (11–15) *Hennigopora* sp. indet., SMF 60577: (11, 12) longitudinal section of an encrusting colony; (13–15) tangential sections showing autozoecial apertures, acanthostyles, and vesicles. Scale bars = 1 mm (2, 6, 11, 13); 0.5 mm (1, 3, 7, 8, 10, 12, 14, 15); 0.2 mm (4, 5, 9).

Table 1. Descriptive statistics of *Fistulipora guangyuanensis* Hu, 1982.

CV = coefficient of variation; Max = maximum value; Min = minimum value; N = number of measurements; SD = sample standard deviation; X = mean.

	N	X	SD	CV	MIN	MAX
Aperture width (mm)	30	0.15	0.014	9.65	0.12	0.18
Aperture spacing (mm)	30	0.34	0.039	11.62	0.23	0.40
Vesicle diameter (mm)	30	0.08	0.020	25.63	0.04	0.12
Vesicles per aperture	20	8.25	0.639	7.74	7.0	9.0
Lunaria width (mm)	30	0.10	0.013	13.62	0.07	0.12
Lunaria length (mm)	30	0.07	0.014	20.20	0.05	0.10
Vesicle spacing (mm)	30	0.07	0.014	20.20	0.05	0.10

and more abundant acanthostyles (mean 6.6 acanthostyles per autozoecial aperture vs. 5 [Table 2], respectively). *Hennigopora* sp. indet. differs from *Hennigopora apta* from the lower Silurian of Indiana, USA in the presence of six or seven acanthostyles per autozoecial aperture instead of 3–5 (Ernst et al., 2019) in the latter species.

Order Trepodomata Ulrich, 1882
 Suborder Halloporina Astrova, 1965
 Family Heterotrypidae Ulrich, 1890
 Genus *Leioclema* Ulrich, 1882
 [= *Lioclema* Ulrich, 1882]

Type species.—*Callopora punctata* Hall, 1858; lower Carboniferous, Iowa, USA.

Leioclema speciosum Hu, 1982
 Figure 5.1–5.6; Table 4

1982 *Leioclema speciosum* Hu, p. 295, pl. 2, figs. 9–13.

1990 *Leioclema speciosum*; Hu, p. 29, pl. 2, figs. 4–6.

Holotype.—NIGP 63767; Cuijiagou Formation, Telychian, Llandovery, lower Silurian; Sichuan Province, China.

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Materials.—SMF 60578–60598.

Table 2. Descriptive statistics of *Hennigopora multilamellosa* Hu, 1982.

Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width (mm)	55	0.22	0.029	13.19	0.17	0.28
Aperture spacing (mm)	55	0.39	0.046	11.85	0.28	0.50
Vesicle diameter (mm)	55	0.10	0.024	23.05	0.06	0.16
Acanthostyle diameter (mm)	55	0.05	0.010	19.88	0.03	0.08
Acanthostyles per aperture	55	5.0	0.680	13.65	4.0	7.0
Vesicles per aperture	55	9.3	1.171	12.56	6.0	11.0
Vesicle spacing (mm)	45	0.08	0.028	35.35	0.04	0.15

Table 3. Descriptive statistics of *Hennigopora* sp. indet. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width (mm)	20	0.15	0.010	6.79	0.14	0.17
Aperture spacing (mm)	20	0.32	0.039	12.20	0.25	0.37
Vesicle diameter (mm)	20	0.08	0.017	19.76	0.06	0.12
Acanthostyle diameter (mm)	20	0.031	0.004	14.04	0.025	0.038
Acanthostyles per aperture	17	6.6	0.507	7.70	6.0	7.0
Vesicle spacing (mm)	10	0.08	0.023	27.61	0.05	0.11

Remarks.—*Leioclema speciosum* is similar to *Leioclema tuvaensis* Astrova, 1959 from the Wenlock of Tuva (Russia), but differs in having smaller colonies and less abundant and smaller acanthostyles (acanthostyle diameter 0.030–0.045 mm vs. 0.01–0.03 mm [Astrova, 1959], respectively). *Leioclema speciosum* differs from *Leioclema densiporum* Owen, 1965 from the Llandovery of England in having larger autozoecial apertures (aperture width 0.10–0.20 mm vs. 0.10–0.12 mm [Owen, 1965], respectively).

Genus *Asperopora* Owen, 1969

Type species.—*Callopora aspera* Hall, 1852; Silurian (Wenlock), New York, USA.

Asperopora sinensis new species
 Figure 5.7–5.11; Table 5

Type specimens.—Holotype, SMF 60599; paratypes, SMF 60600–60635.

Diagnosis.—Thin encrusting colonies; endozones short; autozoecial apertures rounded-polygonal; basal diaphragms few to common in exozone; one or two acanthostyles surrounding each autozoecial aperture; 6–10 mesozoecia surrounding each autozoecial aperture; maculae absent.

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Description.—Encrusting colonies, 0.4–1.0 mm thick. Autozoecia budding from a thin epitheca, growing a short distance parallel to the substratum, then bending sharply to the colony surface. Epitheca 0.003–0.005 mm thick. Autozoecial apertures rounded-polygonal. Basal diaphragms common in exozone, thin, slightly deflected orally. Acanthostyles common, one or two surrounding each autozoecial aperture, small, originating in the outer exozone, having distinct calcite cores and dark, laminated sheaths, indenting into autozoecial space. Mesozoecia abundant,

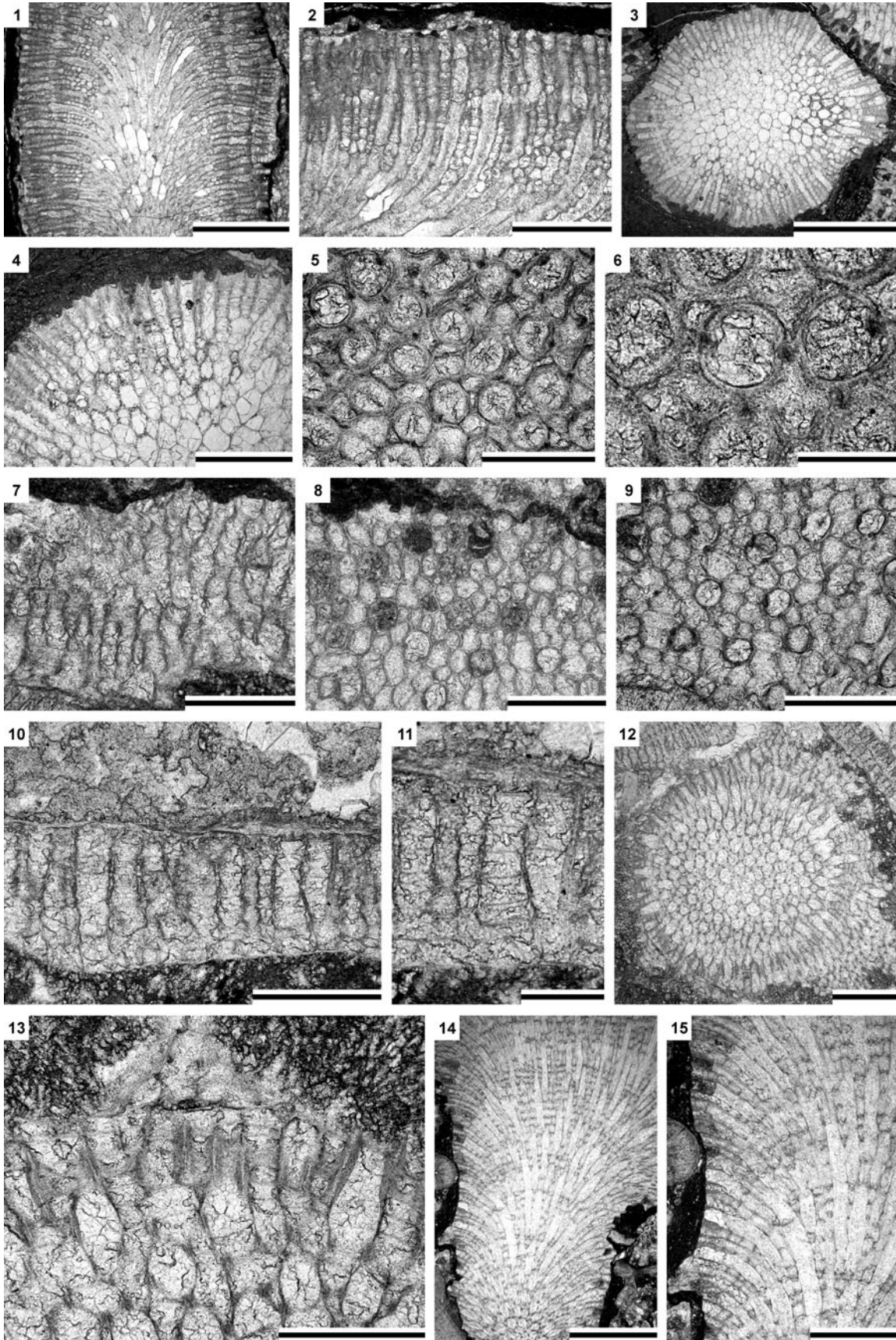


Figure 5. (1–6) *Leioclema speciosum* Hu, 1982: (1) longitudinal section of branched colony, SMF 60587; (2) longitudinal section of exozonal part of branched colony, SMF 60587; (3, 4) transverse section of branched colony, SMF 60586; (5, 6) tangential sections showing autozooeical apertures, acanthostyles, and mesozooecia, SMF 60587; (7–11) *Asperopora sinensis* n. sp.: (7) longitudinal section, holotype, SMF 60599; (8, 9) tangential sections showing autozooeical apertures, acanthostyles, and mesozooecia, holotype, SMF 60599; (10, 11) longitudinal section showing autozooeical and mesozooecia, paratype, SMF 60606; (12–15) *Trematopora jiebeiensis* n. sp.: (12, 13) branch transverse section, paratype, SMF 60644; (14, 15) branch longitudinal section, paratype, SMF 60643. Scale bars = 2 mm (1, 3, 14); 1 mm (2, 4, 12, 15), 0.5 mm (5, 7–10, 13); 0.2 mm (6, 11).

6–10 surrounding each autozooeical aperture, rounded-polygonal in transverse section, originating at the base of exozone, slightly beaded. Autozooeical walls granular, 0.003–0.005 mm thick in endozone, laminated, merged, 0.02–0.03 mm thick in exozone. Maculae not observed.

Etymology.—The species is named after its occurrence in China.

Remarks.—*Asperopora sinensis* n. sp. differs from *Asperopora bellum* (Pushkin, 1976) from the middle Silurian of Belarus and Norway in its slightly smaller autozooeical apertures (mean aperture width 0.11 mm vs. 0.14 mm [Pushkin, 1976], respectively) and in its more abundant mesozooecia (mean 8.12 per aperture vs. 7.4 [Pushkin, 1976], respectively). *Asperopora sinensis* n. sp. differs from *Asperopora aspera* (Hall, 1852) from the middle Silurian of North America and Europe in its less abundant and larger mesozooecia (mean 8.12 per aperture vs. 10.5 [Ernst et al., 2015], respectively), and in having one or two acanthostyles around each autozooeical aperture instead of 1–5 (Ernst et al., 2015) in the latter species.

Family Trematoporidae Miller, 1889
Genus *Trematopora* Hall, 1852

Type species.—*Trematopora tuberculosa* Hall, 1852; lower Silurian (Niagaran), North America.

Trematopora jiebeiensis new species
Figures 5.12–5.15, 6.1–6.3; Table 6

Type specimens.—Holotype, SMF 60636; paratypes, SMF 60637–60660.

Diagnosis.—Branched colonies with distinct exozones; autozooeical apertures rounded to slightly angular; basal diaphragms rare; mesozooecia beaded, 5–8 surrounding each autozooeical aperture; acanthostyles moderately large,

2–6 surrounding each autozooeical aperture, originating in endozone; maculae absent.

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Description.—Ramosely branched colonies; branch width 2.25–5.20 mm. Exozone distinct, 0.45–1.13 mm wide; endozone 1.35–3.26 mm wide. Secondary overgrowths common. Autozooeical apertures long, polygonal in cross section in endozone, bending sharply in exozone, with rounded to slightly angular apertures. Basal diaphragms rare, thin, concentrated mainly in the transition between exo- and endozones. Mesozooecia abundant, originating at base of exozone, beaded in places of development of diaphragms, 5–8 surrounding each autozooeical aperture. Diaphragms in mesozooecia straight, abundant. Acanthostyles moderately large, prominent, having distinct hyaline cores, 2–6 surrounding each autozooeical aperture, originating in endozone. Autozooeical walls 0.003–0.005 mm thick, granular-prismatic in endozone, showing reversed V-shaped lamination, integrated with locally visible dark border between zooecia, 0.02–0.06 mm thick in exozone. Maculae absent.

Etymology.—The species is named after the type locality, the village of Jiebei in China.

Remarks.—*Trematopora jiebeiensis* n. sp. differs from *Trematopora sinensis* from the lower Silurian (Llandovery) of China in having smaller autozooeical apertures (aperture width 0.07–0.14 mm vs. 0.30–0.36 mm [Hu, 1982], respectively). *Trematopora jiebeiensis* n. sp. differs from *Trematopora whitfieldi* Ulrich, 1883 from the Silurian (Wenlock) of North America in its smaller autozooeical apertures (mean aperture width 0.11 mm vs. 0.14 mm [Ulrich, 1883], respectively).

Trematopora tenuis new species
Figure 6.4–6.9; Table 7

Type specimens.—Holotype, SMF 60661; SMF 60662–60667.

Diagnosis.—Thin, branched colonies with distinct exozones; autozooeical apertures rounded to slightly angular; basal

Table 4. Descriptive statistics of *Leioclema speciosum* Hu, 1982. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width (mm)	10	3.16	0.743	23.56	2.40	4.50
Exozone width (mm)	10	0.75	0.154	20.56	0.45	0.90
Endozone width (mm)	10	1.66	0.647	38.98	0.78	2.78
Aperture width (mm)	70	0.13	0.022	16.80	0.10	0.20
Aperture spacing (mm)	70	0.22	0.033	15.26	0.16	0.30
Mesozooecia width (mm)	70	0.08	0.020	25.57	0.03	0.13
Mesozooecia per aperture	40	7.5	1.339	17.80	6.0	11.0
Acanthostyle diameter (mm)	20	0.036	0.005	14.54	0.030	0.045
Acanthostyles per aperture	20	3.0	0.918	30.59	2.0	5.0
Mesozooecial diaphragm spacing (mm)	70	0.09	0.020	21.73	0.05	0.15
Exozone wall thickness (mm)	20	0.038	0.009	22.57	0.025	0.055

Table 5. Descriptive statistics of *Asperopora sinensis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width (mm)	50	0.11	0.015	13.28	0.09	0.15
Aperture spacing (mm)	50	0.25	0.037	14.84	0.17	0.34
Mesozooecia width (mm)	50	0.07	0.017	22.37	0.03	0.11
Acanthostyle diameter (mm)	43	0.03	0.007	21.37	0.02	0.045
Mesozooecia per aperture	50	8.12	1.003	12.35	6.0	10.0
Mesozooecial diaphragm spacing (mm)	50	0.06	0.021	34.35	0.02	0.10

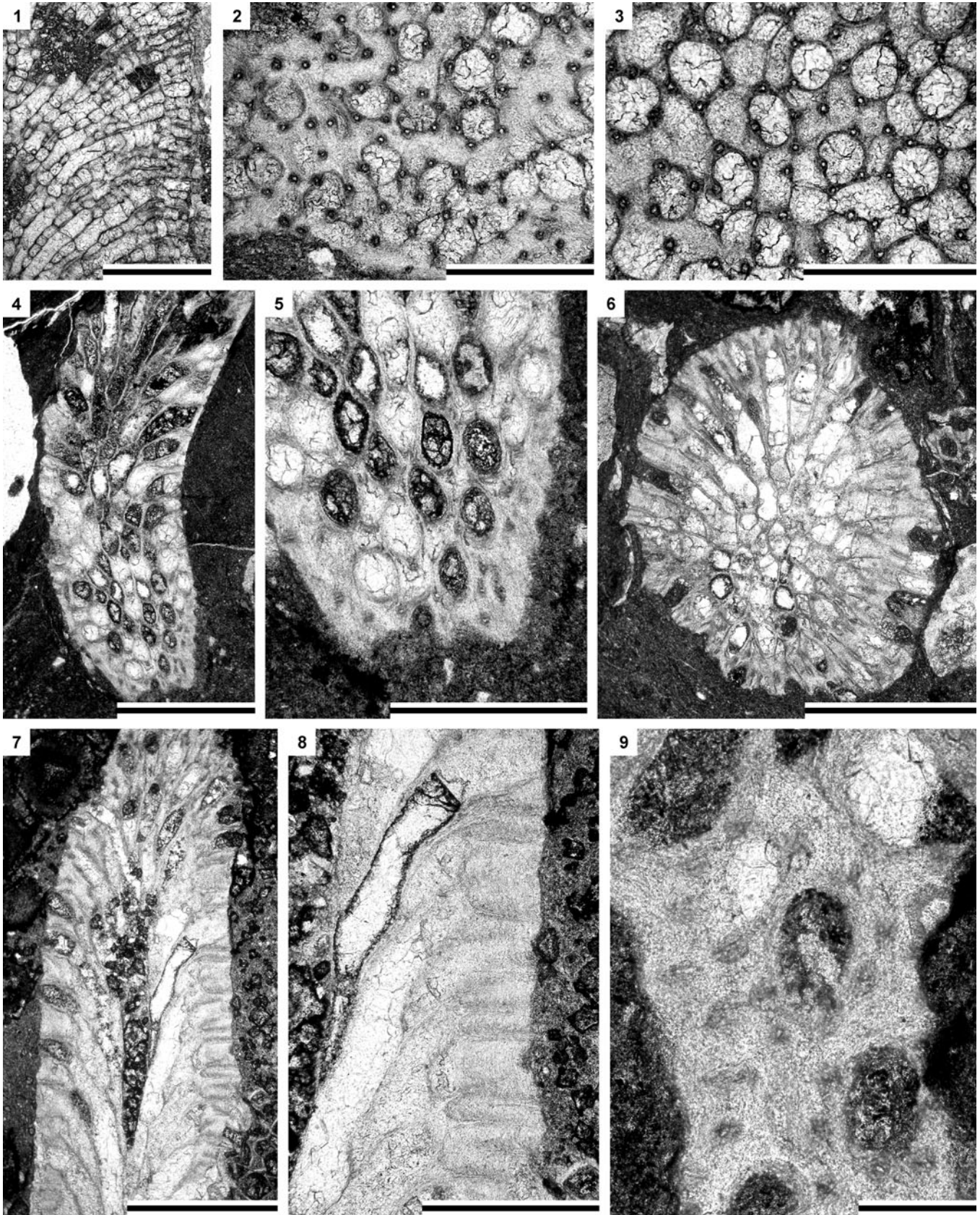


Figure 6. (1–3) *Trematopora jiebeiensis* n. sp.: (1) branch longitudinal section showing secondary overgrowth, autozoecia, mesozoecia, and acanthostyles, holotype, SMF 60636; (2, 3) tangential sections showing autozoecial apertures, acanthostyles, and mesozoecia, holotype, SMF 60636; (4–9) *Trematopora tenuis* n. sp., holotype, SMF 60661: (4, 5) oblique section of a branch; (6) branch transverse section; (7, 8) longitudinal section of a branch showing autozoecia and acanthostyles; (9) tangential sections showing autozoecial apertures, acanthostyles, and mesozoecia. Scale bars = 1 mm (1, 4, 6–8); 0.5 mm (2, 3, 5); 0.2 mm (9).

Table 6. Descriptive statistics of *Trematopora jiebeiensis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width (mm)	10	3.63	1.043	28.77	2.25	5.20
Exozone width (mm)	10	0.64	0.211	33.15	0.45	1.13
Endozone width (mm)	10	2.35	0.705	30.00	1.35	3.26
Aperture width (mm)	40	0.11	0.017	15.24	0.07	0.14
Aperture spacing (mm)	40	0.19	0.023	11.76	0.15	0.25
Acanthostyle diameter (mm)	40	0.04	0.008	20.29	0.03	0.06
Mesozoocia width (mm)	40	0.08	0.020	24.91	0.04	0.13
Acanthostyles per aperture	40	4.1	0.859	21.08	2.0	6.0
Mesozoocia per aperture	30	6.4	0.809	12.70	5.0	8.0
Mesozoocial diaphragm spacing (mm)	40	0.08	0.027	32.27	0.04	0.16

diaphragms rare; mesozoocia common, slightly beaded; acanthostyles moderately large, 6–8 surrounding each autozoocial aperture, originating in endozone; maculae absent.

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Description.—Ramosely branched colonies; branch width 0.72–1.88 mm. Exozone distinct, 0.20–0.38 mm wide; endozone 0.32–1.12 mm wide. Secondary overgrowths not observed. Autozoocia long, polygonal in cross section in endozone, bending sharply in exozone, with rounded to slightly angular apertures. Basal diaphragms rare, thin, concentrated mainly in the transition between exo- and endozones. Mesozoocia common, originating at base of exozone, slightly beaded in places of development of diaphragms. Diaphragms in mesozoocia straight, abundant. Acanthostyles moderately large, prominent, having distinct hyaline cores, 6–8 surrounding each autozoocial aperture, originating at the base of exozone. Autozoocial walls 0.003–0.005 mm thick, granular-prismatic in endozone, showing reversed V-shaped lamination, integrated with locally visible, dark border between zooecia, 0.003–0.005 mm thick in exozone. Maculae absent.

Etymology.—The species is named because of its thin branches (Latin *tenuis* = thin, narrow).

Remarks.—*Trematopora tenuis* n. sp. is similar to *Trematopora cristata* Kopajevitch, 1984 from the Wenlock of Mongolia, but differs from the latter in having more abundant acanthostyles (6–8 per autozoocial aperture vs. 1–4 [Kopajevitch, 1984], respectively). *Trematopora tenuis* n. sp. differs from *Trematopora minima* Ernst in Suttner and Ernst, 2007 from the Upper Ordovician of India in its less abundant mesozoocia and more abundant acanthostyles (6–8 per autozoocial aperture vs. four or five [Suttner and Ernst, 2007], respectively).

Order Fenestrata Elias and Condra, 1957

Suborder Fenestellina Astrova and Morozova, 1956

Family Fenestellidae King, 1849

Genus *Moorephylloporina* Bassler, 1952

Type species.—*Moorephylloporina typica* Bassler, 1952; Middle Ordovician, Black Riverian, Virginia, USA.

Table 7. Descriptive statistics of *Trematopora tenuis* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width (mm)	4	1.28	0.479	37.56	0.72	1.88
Exozone width (mm)	4	0.29	0.084	29.57	0.20	0.38
Endozone width (mm)	4	0.71	0.327	46.45	0.32	1.12
Aperture width (mm)	15	0.08	0.008	9.45	0.07	0.09
Aperture spacing (mm)	15	0.21	0.021	10.23	0.17	0.24
Acanthostyle diameter (mm)	15	0.04	0.006	16.83	0.03	0.05
Mesozoocia width (mm)	15	0.06	0.009	16.54	0.04	0.07

Moorephylloporina parvula new species

Figure 7.1–7.8; Table 8

Type specimens.—Holotype, SMF 60668; paratypes SMF 60669–60710.

Diagnosis.—Reticulate colonies with straight branches; dissepiments short, wide; fenestrules small, oval; autozoocial apertures rounded, two or three spaced per fenestrule length; keel wide, low, with high and moderately large nodes; hemisepta lacking; diaphragms present; vesicular skeleton present.

Occurrence.—Jiebei village, Chongqing, China; lower part of the Hanchiatien Formation, lower Telychian, Llandovery, lower Silurian.

Description.—Reticulate colonies with straight, frequently bifurcating branches, joined by short, wide dissepiments. Autozoocia arranged in two alternating rows on branches, having circular apertures with moderately high peristomes, two or three spaced per length of a fenestrule. Peristomes containing 10–12 nodes. Peristomal nodes 0.015–0.020 mm in diameter. Fenestrules oval. Keels wide, low. Keel nodes high, with moderate diameter and spacing, rounded to oval in their cross sections. Microacanthostyles on the reverse colony surface abundant, regularly spaced in longitudinal rows, 0.010–0.015 mm in diameter.

Interior description.—Autozoocia long, rectangular in the mid-tangential section, with well developed vestibule; axial wall straight; aperture positioned at distal end of chamber. Hemisepta absent. Diaphragms present. Internal granular skeleton thin,

Table 8. Descriptive statistics of *Moorephylloporina parvula* n. sp. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width (mm)	20	0.24	0.028	11.73	0.19	0.29
Branch thickness (mm)	10	0.25	0.022	9.03	0.22	0.29
Dissepiment width (mm)	10	0.17	0.026	15.64	0.13	0.21
Fenestrule width (mm)	10	0.21	0.037	17.96	0.16	0.26
Fenestrule length (mm)	10	0.39	0.042	10.80	0.34	0.46
Distance between branch centers (mm)	10	0.44	0.057	13.11	0.34	0.56
Distance between dissepiment centers (mm)	10	0.58	0.051	8.90	0.52	0.65
Aperture width (mm)	20	0.08	0.006	7.68	0.07	0.09
Aperture spacing along branch (mm)	20	0.24	0.022	9.13	0.20	0.28
Apertures per fenestrule	10	2.5	0.527	21.08	2.0	3.0
Maximal chamber width (mm)	10	0.07	0.008	11.40	0.06	0.09
Node width (mm)	10	0.06	0.011	19.20	0.04	0.07
Distance between node centers (mm)	10	0.24	0.040	16.35	0.19	0.30

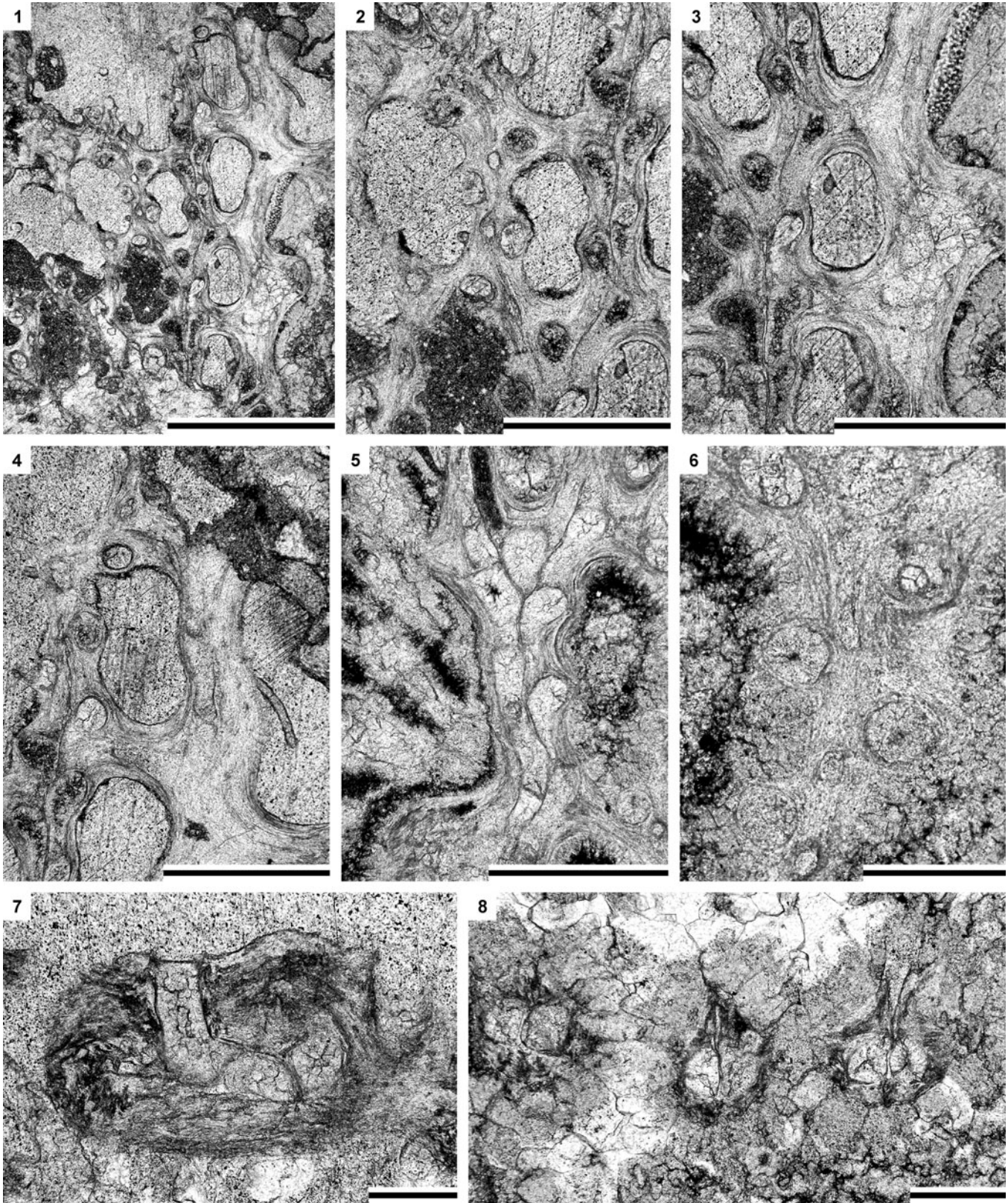


Figure 7. *Moorephylloporina parvula* n. sp.: (1–4) tangential section showing autozooeal apertures and keel nodes, holotype, SMF 60668; (5) midtangential section showing autozooeal chambers, paratype, SMF 60708; (6) tangential section showing autozooeal apertures and nodes, paratype, SMF 60708; (7) transverse section showing autozooeal chamber, paratype, SMF 60682; (8) transverse section showing autozooeal chambers, paratype, SMF 60702. Scale bars = 1 mm (1); 0.5 mm (2–5); 0.2 mm (6–8).

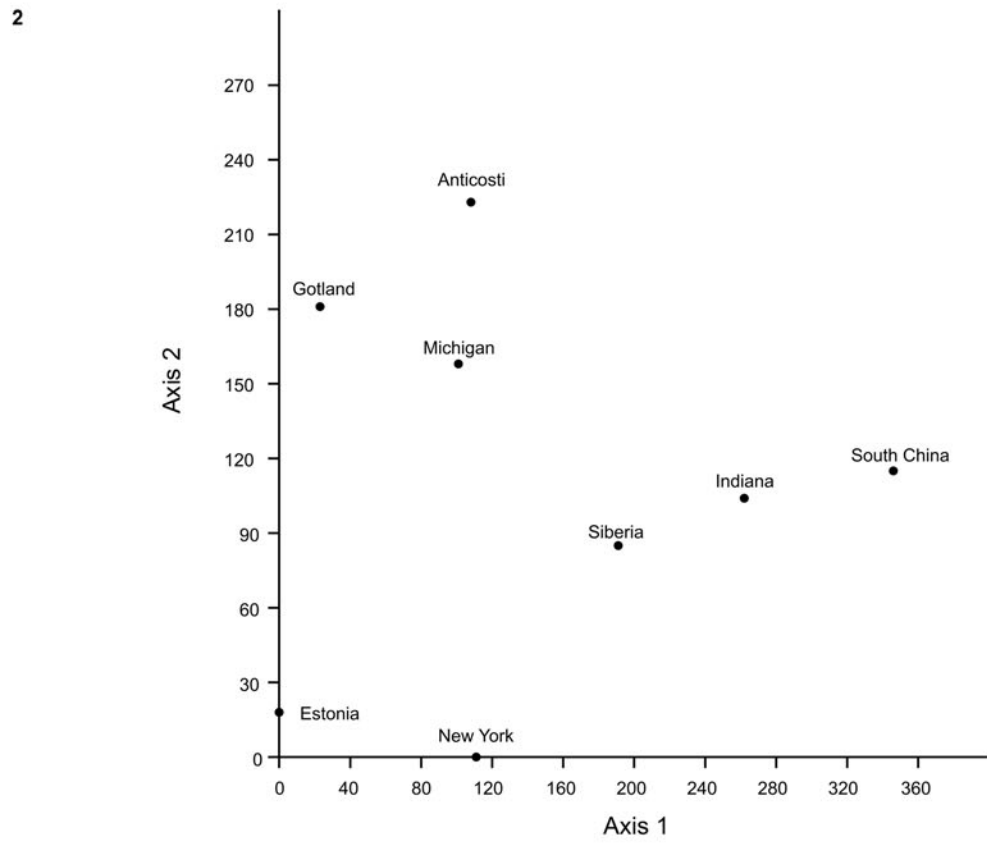
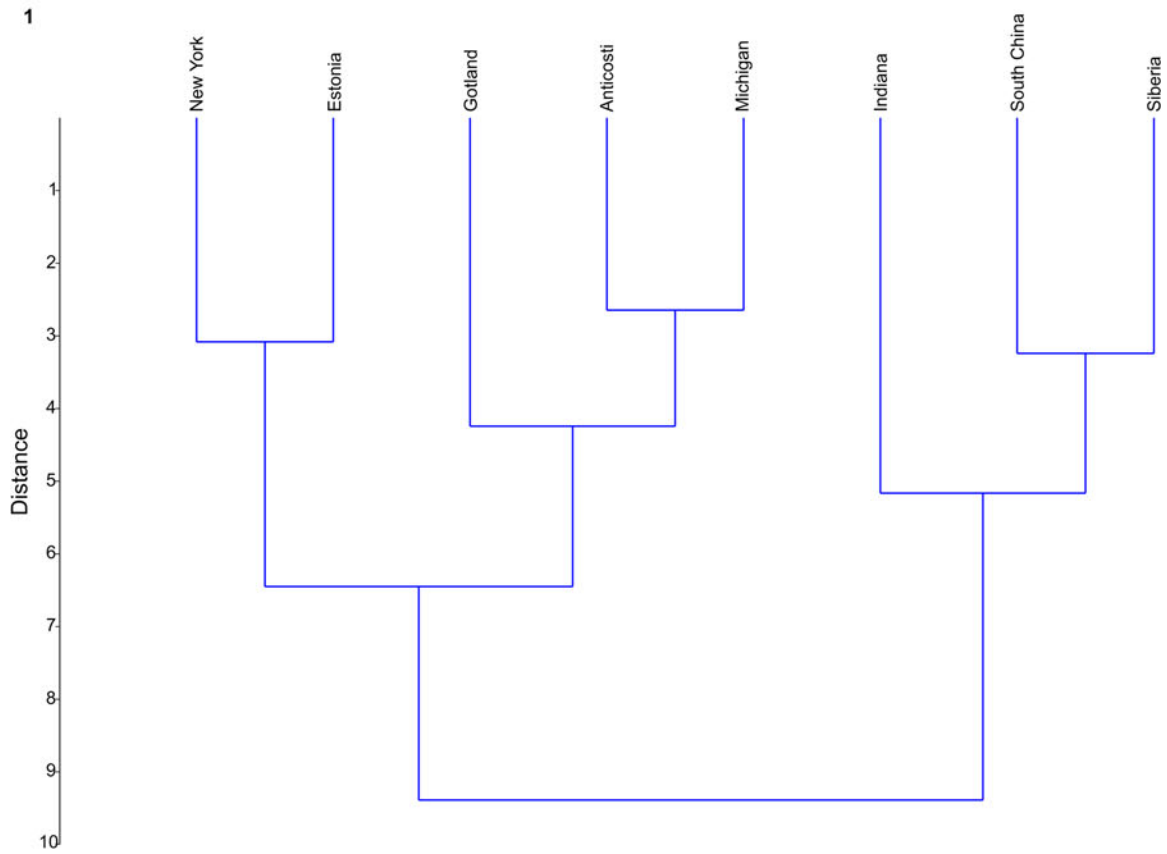


Figure 8. Paleobiogeographical affinities of Jiebei bryozoan association and selected Telychian bryozoan faunas (data from Anstey et al., 2003, updated 2020): (1) the hierarchical relationship based on pair-group cluster analysis (Euclidean similarity index); (2) detrended correspondence analysis. All analyses performed using PAST (Hammer et al., 2001).

Table 9. Distribution of bryozoan species in the Telychian localities of South China.

Age Locality Formation Reference	lower Telychian			upper Telychian Ningqiang, Shanxi Ningqiang Hu, 1982, 1990
	Hanshan, Anhui Chenxiacun Xia and Qi, 1989	Guangyuan, Sichuan Cuijiagou Hu, 1982	Jiebei, Chongqing Hanchiatien This paper	
<i>Asperopora sinensis</i> n. sp.			x	
<i>Calloporella silurica</i> Hu, 1982				x
<i>Cyclotrypa solidoscens</i> Hu, 1990				x
<i>Cyphotrypa undulata</i> Hu, 1990				x
<i>Fistulipora ningqiangensis</i> Hu, 1990				x
<i>Fistulipora guangyuanensis</i> Hu, 1982		x	x	
<i>Fistuliramus transversus</i> Hu, 1982				x
<i>Fistuliramus eximius</i> Hu, 1982		x		
<i>Hallopora elegantula</i> (Hall, 1852)	x			
<i>Hallopora raritabulata</i> Xia and Qi, 1989	x			
<i>Hallopora hanshanensis</i> Xia and Qi, 1989	x			
<i>Hallopora aggregata</i> Hu, 1982				x
<i>Hennigopora petaliformis</i> Hu, 1982				x
<i>Hennigopora multilamellosa</i> Hu, 1982		x	x	
<i>Hennigopora</i> sp. indet.		x		
<i>Hennigopora</i> sp. indet.			x	
<i>Homotrypa ningqiangensis</i> Hu, 1990				x
<i>Leioclema speciosa</i> Hu, 1982			x	x
<i>Leioclema</i> sp. indet.				x
<i>Monotrypa shaanxiensis</i> Hu, 1990				x
<i>Orbignyella mui</i> Yang, 1951				x
<i>Orbignyella curvata</i> Hu, 1982				x
<i>Orbignyella globata</i> Yang, 1951				x
<i>Trematopora reflua</i> Xia and Qi, 1989	x			
<i>Trematopora sinensis</i> Hu, 1982		x		
<i>Trematopora</i> sp. indet.		x		
<i>Trematopora jiebeiensis</i> n. sp.			x	
<i>Trematopora tenuis</i> n. sp.			x	
<i>Moorephylloporina parvula</i> n. sp.			x	

continuous, with obverse keel, nodes, peristome, and across dissepiments. Outer lamellar skeleton thin to moderately thick. Vesicular skeleton present.

Etymology.—The species name refers to the small size of this species (Latin *parvulus* = very small).

Remarks.—*Moorephylloporina parvula* n. sp. is similar to *Moorephylloporina delicata* (Nekhoroshev, 1961) from the Llandovery of Siberia. The new species differs in its wider branches (branch width 0.19–0.29 mm vs. 0.16–0.19 mm [Nekhoroshev, 1961], respectively) and smaller fenestrules (fenestrule width 0.16–0.26 mm vs. 0.30–0.40 mm [Nekhoroshev, 1961], respectively; fenestrule length 0.34–0.46 mm vs. 0.58–0.60 mm [Nekhoroshev, 1961], respectively).

Discussion

In the Jiebei section, bryozoans occur exclusively in the carbonate interbeds in the lower part of the Hanchiatien Formation (Figs. 2, 3). Characterized by reticular colonies, *Moorephylloporina* can be found in all types of facies in these meter-scale reefs, indicating its eurytopic nature. However, such distribution could be also explained by taphonomic processes and

postmortem transportation of *Moorephylloporina* fragments from reef areas inhabited by this species within the whole reef. Although the abundance of *Moorephylloporina* is relatively low in the framestone (Fig. 3.3) of the reefs, these fenestellid bryozoans provide hard substrata for *Fistulipora* and *Asperopora*. In contrast, branched *Trematopora* and *Leioclema* tend to occur out of the reef core (framework) (Fig. 3.1). Like *Champlainopora* (*Atactotoechus*) *chazyensis* Ross, 1963 in some Ordovician reefs (e.g., Cuffey et al., 2002), *Trematopora* and *Leioclema* might have formed reef-flank thickets developed under more agitated conditions. *Moorephylloporina*, *Trematopora*, and *Leioclema* represent pioneering bryozoans that were able to grow on weakly lithified substrata. In contrast, encrusting *Fistulipora*, *Hennigopora*, and *Asperopora* relied more on hard-grounds and occupied a large proportion in the reefs, layered on top of one another and so forming densely compact framestones (Li et al., 2018) that represent a typical crust-mound stage from an evolutionary ecological perspective (Cuffey, 2006).

The Telychian of the Upper Yangtze Platform is characterized by terrigenous sediments (e.g., Rong et al., 2012), and bryozoans are mostly reported from interbedded argillaceous limestones (or marls) (Hu, 1982, 1990; Xia and Qi, 1989), probably related to internal-wave deposits (Li et al., 2018) in some cases. Systematic studies of Telychian bryozoans are limited

compared to other macrofossil groups, e.g., brachiopods, trilobites, and corals. Here, we provide the first detailed comparison of the composition of the bryozoan fauna (Table 9). In the South China block, *Asperopora* and *Moorephylloporina* are only reported from the Hanchiatien Formation, whereas *Fistulipora* and *Trematopora* are widely distributed across the platform during the early Telychian, recorded in all three studied sections in the literature. Apart from the Jiebei section, *Hennigopora* and *Leioclema* have been documented from one other Telychian section, indicating a moderately wide paleogeographic distribution. It is worth noting that bryozoans in some sections are not diverse, or else have been inadequately sampled. Further studies should be carried out to confirm their distributional patterns on the platform.

Bryozoans from the Jiebei section belong to genera with predominantly cosmopolitan distributions during the Telychian. Outside of South China, representatives of the genus *Fistulipora* are known from North America and Siberia. Species of *Hennigopora* are known from the USA (New York, Indiana) and Siberia. The genus *Leioclema* is known from North America, Europe (England, Ukraine), and Tuva (Russia). Records of *Asperopora* are known from North America (New York, Canada), Sweden (Gotland), and Siberia, whereas *Trematopora* is known from North America and China. The fenestrate genus *Moorephylloporina* is largely restricted to the Ordovician, except for two species from the lower Silurian (Llandoverey) of Siberia, and the new species described here. It disappeared during the lower Silurian.

The early Silurian was a period of exceptional cosmopolitanism for benthic species with dispersive larvae (e.g., Cocks, 2001). Bryozoans, as in other groups of benthic organisms, showed low provinciality (e.g., Tuckey, 1990; Anstey et al., 2003; McCoy and Anstey, 2010; Buttler et al., 2013). The cluster analysis and detrended correspondence analysis (Fig. 8) reveal distinct clustering of South China with Siberia and Indiana (USA). Bryozoan faunas of Estonia seem to be close to those of New York (USA), whereas Gotland (Sweden) clusters with Anticosti (Canada) and Michigan (USA). These results agree with existing paleogeographical reconstructions for the early Silurian (e.g., Cocks and Torsvik, 2002). However, most existing references for bryozoans in the lower Silurian need critical reassessment, because the descriptions are often far from present-day standards.

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Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/jpa.2020.86>

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