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 Mooreophyllum parvula n. sp. One species, the cystoporate Hennigopora n. sp. indet., is described in open nomenclature. Mooreophyllum parvula n. sp. is eurytopic, occurring in all types of facies within the bioherms. Erect Mooreophyllum parvula 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 ‘eperic platform’ in western Gondwana (e.g., Rong and Cocks, 2014). In the earliest Silurian (Rhuddanian stage), black shales with 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.

Telychian bryozoans from South China were previously described in several papers. Hu (1982) identified six bryozoan species from the Cuijiagou Formation (lower Telychian) of Guanyuan, Sichuan: Fistulipora guangyuanensis Hu, 1982, Fistuliramus eximus Hu, 1982, Hennigopora multilamelllosa 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): Callopora silicara Hu, 1982, Cyclotrypa solidiscens Hu, 1990, Cyphotrypa undulata Hu, 1990, Fistulipora ningqiensis Hu, 1990, Fistuliramus transversus Hu, 1982, Hennigopora petaliformis Hu, 1982, Hallopora aggregata Hu, 1982, Homotrypa ningqiensis Hu, 1990, Leioclema speciosum Hu, 1990, Leioclema sp. indet., Monotrypa shaanxiensis Hu, 1990, Orbignyella curvata Hu, 1982, O. globata Yang, 1951, and O. mai Yang, 1951.

Xia and Qi (1989) described four species from the lower Telychian Chenxiancun Formation of Hanshan (Anhui): Hallopora eleganesta (Hall, 1852), Hallopora hanshanensis Xia and Qi, 1989, Hallopora raritabulata Xia and Qi, 1989, and Trematopora refiu 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.,
Yin, 1949; Mu, 1962). Since 1978, it has been formally named the Hanchiatien Formation (e.g., Southwest Institute of Geo-
logic Sciences, 1978; Rong et al., 1990), characterized by brownish to greenish shales. The shales are usually disconform-
ably 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 fossilifer-
ous, diagnostic chitinozoans and graptolites were reported at the top of the formation in the Northeast Guizhou: Ancyrochitina brevicollis Geng, 1986 and Streptograptus plumosus Baily, 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)
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, Buttlar, and Taylor, 2014  
Order Cystoporata Astrov, 1964  
Suborder Fistuliporina Astrov, 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, Llandovery, lower Silurian; Sichuan Province, China.

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

Materials.—SMF 60500–60538.

Remarks.—*Fistulipora guangyuanensis* differs from *Fistulipora ninggiangensis* 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* Astrov, 1965 from the lower–middle Silurian of Russia in its smaller autozooecial apertures (aperture width 0.12–0.18 mm vs. 0.18–0.23 mm [Astrov, 1965], respectively), larger lunaria, and less abundant vesicles (7–9 per autozooecial aperture vs. 8–10 vesicles [Astrov, 1965], respectively).

Family Xenotrypidae Utgaard, 1983  
*Hennigopora* Bassler, 1952

*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, Llandovery, lower Silurian; Sichuan Province, China.
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 autozoecal 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 autozoecal 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 autozoecal 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 autozoecal aperture instead of 2–4 (Hu, 1982) in the latter species.

*Hennigopora* sp. indet.

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. Autozoecia 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 autozoecia in one or two rows, 8–10 surrounding each autozoecal aperture, with rounded roofs, polygonal in tangential section. Acanthostyles abundant, relatively large, often deeply indenting autozoecial chambers, six or seven surrounding each autozoecal aperture. Autozoecial 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 autozoecal apertures (mean aperture width 0.15 mm vs. 0.22 mm [Table 2], respectively).
Vesicle spacing (mm) 30 0.07 0.014 20.20 0.05 0.10
Lunaria length (mm) 30 0.07 0.014 20.20 0.05 0.10
Lunaria width (mm) 30 0.10 0.013 13.62 0.07 0.12
Aperture spacing (mm) 30 0.34 0.039 11.62 0.23 0.40

N = number of measurements; SD = sample standard deviation; X = mean.

CV = coefficient of variation; Max = maximum value; Min = minimum value;

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

|                      | 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 autozooecial 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 autozooecial aperture instead of 3–5 (Ernst et al., 2019) in the latter species.

Order Trepostomata 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; Cuijiangou 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 | 7.9 |
| 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 autozooecial 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; autozooecial apertures rounded-polygonal; basal diaphragms few to common in exozones; one or two acanthostyles surrounding each autozooecial aperture; 6–10 mesozooecia surrounding each autozooecial aperture; maculae absent.

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

Materials.—SMF 60578–60598.

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 exozones, thin, slightly deflected orally. Acanthostyles common, one or two surrounding each autozooecial aperture, small, originating in the outer exozones, having distinct calcite cores and dark, laminated sheaths, indenting into autozoecial space. Mesozooecia abundant,
6–10 surrounding each autozooecial aperture, rounded-polygonal in transverse section, originating at the base of exozone, slightly beaded. Autozooecial walls granular, 0.003–0.005 mm thick in exozone, laminated, merged, 0.02–0.03 mm thick in exozone. Maculae not observed.

**Etyymology.**—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 autozooecial 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 autozooecial 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; autozooecial apertures rounded to slightly angular; basal diaphragms rare; mesozooecia beaded, 5–8 surrounding each autozooecial aperture; acanthostyles moderately large, 2–6 surrounding each autozooecial aperture, originating in endozone; maculae absent.

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

**Description.**—Ramose 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. Autozooecia 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 endozoecae. Meso-zooecia abundant, originating at base of exozone, beaded in places of development of diaphragms, 5–8 surrounding each autozooecial aperture. Diaphragms in mesozooecia straight, abundant. Acanthostyles moderately large, prominent, having distinct hyaline cores, 2–6 surrounding each autozooecial aperture, originating in endozone. Autozooecia 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.

**Etyymology.**—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 autozooecial apertures (aperture width 0.07–0.14 mm vs. 0.30–0.36 mm [Hu, 1982], respectively). *Trematopora jiebeiensis* n. sp. differs from *Trematopora whitfieldii* Ulrich, 1883 from the Silurian (Wenlock) of North America in its smaller autozooecial 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; autozooecial apertures rounded to slightly angular; basal diaphragms rare; mesozooecia beaded, 5–8 surrounding each autozooecial aperture; acanthostyles moderately large, 2–6 surrounding each autozooecial aperture, originating in endozone; maculae absent.

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

**Description.**—Branched colonies; branch width 2.10–5.20 mm. Exozone distinct, 0.35–1.13 mm wide; endozone 1.35–3.26 mm wide. Secondary overgrowths common. Autozooecia 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 endozoecae. Meso-zooecia abundant, originating at base of exozone, beaded in places of development of diaphragms, 5–8 surrounding each autozooecial aperture. Diaphragms in mesozooecia straight, abundant. Acanthostyles moderately large, prominent, having distinct hyaline cores, 2–6 surrounding each autozooecial aperture, originating in endozone. Autozooecia 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.

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

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

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**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 |
| Meso-zooecia width (mm)| 70 | 0.08 | 0.020 | 25.57 | 0.03 | 0.13 |
| Meso-zooecia 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 |
| Meso-zooecial 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 |

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

|                      | N  | X  | SD | CV | MIN | MAX |
|----------------------|----|----|----|----|-----|-----|
| Aperture width (mm)  | 50 | 0.25 | 0.037 | 14.84 | 0.17 | 0.34 |
| Aperture spacing (mm)| 50 | 0.25 | 0.037 | 14.84 | 0.17 | 0.34 |
| Meso-zooecia width (mm) | 50 | 0.07 | 0.017 | 22.37 | 0.02 | 0.045 |
| Acanthostyle diameter (mm) | 43 | 0.03 | 0.007 | 21.37 | 0.02 | 0.045 |
| Meso-zooecia per aperture | 50 | 8.12 | 1.003 | 12.35 | 6.0 | 10.0 |
| Meso-zooecial 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, autozooecia, mesozooecia, and acanthostyles, holotype, SMF 60636; (2, 3) tangential sections showing autozoocelial apertures, acanthostyles, and mesozooecia, 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 autozoecelial apertures, acanthostyles, and mesozooecia. Scale bars = 1 mm (1, 4, 6–8); 0.5 mm (2, 3, 5); 0.2 mm (9).
diaphragms rare; mesozoecia common, slightly beaded; acanthostyles moderately large, 6–8 surrounding each autozoecial aperture, originating in endozone; maculae absent.

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

**Description.**—Ramose 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. Autozoecia 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 endozone. Mesozoecia common, originating at base of exozone, slightly beaded in places of development of diaphragms. Diaphragms in mesozoecia straight, abundant. Acanthostyles moderately large, prominent, having distinct hyaline cores, 6–8 surrounding each autozoecial aperture, originating at the base of exozone. Mesozoecial walls 0.003–0.005 mm thick, granular-prismatic in endozone, showing reversed V-shaped lamination, integrated with locally visible, dark border between zoecia, 0.003–0.005 mm thick in exozone. Maculae absent.

**Etymology.**—The species is named because of its thin branches (Latin *tenus* = 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 autozoecial 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 mesozoecia and more abundant acanthostyles (6–8 per autozoecial aperture vs. four or five [Suttner and Ernst, 2007], respectively).

**Order Fenestrate 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 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 |
| Mesozoecia width (mm)| 40 | 0.08| 0.020| 24.91| 0.04 | 0.13 |
| Acanthostyles per aperture | 40 | 0.41| 0.859| 21.08| 2.0  | 6.0  |
| Mesozoecia per aperture | 30 | 6.4 | 0.809| 12.70| 5.0  | 8.0  |
| Mesozoecial diaphragm spacing (mm) | 40 | 0.08| 0.027| 32.27| 0.04 | 0.16 |

**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 |
| Mesozoecia width (mm)| 15 | 0.06| 0.009| 16.54| 0.04 | 0.07 |

**Moorephylloporina parvula** new species

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

**Diagnosis.**—Reticulate colonies with straight branches; disseipments short, wide; fenestrules small, oval; autozoecial 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 disseipments. Autozoecia 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.—Autozoecia 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 |
| Disseipment 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 disseipment 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 |
| Distance between node centers (mm) | 10 | 0.24| 0.040| 16.35| 0.19 | 0.30 |
Moorephyllopora parvula n. sp.: (1–4) tangential section showing autozooecial apertures and keel nodes, holotype, SMF 60668; (5) midtangential section showing autozooecial chambers, paratype, SMF 60708; (6) tangential section showing autozooecial apertures and nodes, paratype, SMF 60708; (7) transverse section showing autozooecial chamber, paratype, SMF 60682; (8) transverse section showing autozooecial chambers, paratype, SMF 60702. Scale bars = 1 mm (1); 0.5 mm (2–5); 0.2 mm (6–8).
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 hardgrounds and occupied a large proportion in the reefs, layered on top of one another and so forming densely compact framesones (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 *Leiotolaena* 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 *Leiotolaena* 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 (Llandovery) 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 Torvik, 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**

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