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., Dybowskiiella hupehensiformis n. sp., Etherella tibetensis n. sp., Dyscritella lii n. sp., Streblotrypa (Streblotrypa) parviformis n. sp., Timanotrypa australis n. sp., and Proterotrypa 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.

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eastern part of the Zhongba microterrane has been assigned to the middle–late Permian in Chinese regional geological (unpublished) reports, but it was recently dated as Ordovician through Triassic and disaggregated as three lithostratigraphic units: the Ordovician–Silurian Ziqupu Group,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).
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
of characters suggested by Snyder (1991) has been used in this publication for the discrimination of fenestrate species.

**SYSTEMATIC PALAEONTOLOGY**

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 autozooecia with thin walls and complete diaphragms. Apertures rounded, possessing horseshoe-shaped lunaria. Autozooecia 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.
**Material.** SMF 23.007–SMF 23.021.

**Description.** Encrusting, partly multilayered colony, separate sheets 1.8–2.8 mm thick. Autozoocia growing from thin epitheca, bending at their bases to the colony surface. Autozoocial diaphragms rare to absent, thin. Autozoocial apertures circular to oval. Lunaria well-developed, rounded, disappearing in deeper sections; ends of lunaria not indenting into autozoocia. Vesicles small to medium, high, separating autozoocia 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 autozooecial chambers and vesicular skeleton; and 2–4, 6–8, 9, and 10, tangential sections showing autozooecial 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.

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

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

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

1–2 rows, 11–15 surrounding each autozooecial aperture, with rounded to flat roofs, polygonal in tangential section. Autozooecial 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 autozooecial 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* and Klautzan, 1961

**Figure 3.5-8; Table 2**


**Material.** SMF 23.022–SMF 23.027.

**Description.** Encrusting, partly multilayered colony, separate sheets 1.0–1.5 mm thick. Autozooecia growing from thin epithea, bending at their bases to the colony surface. Autozooecial diaphragms rare to absent, thin. Autozooecial apertures circular to oval. Lunaria well-developed, rounded, disappearing in deeper sections; ends of lunaria not indenting into autozooecia. Vesicles small to medium, high, separating autozooecia in 2–4 rows, 9–16 surrounding each autozooecial aperture, with rounded to flat roofs, polygonal in tangential section. Autozooecial 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 autozooecial 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 autozooecia.

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

*Fistulipora sakagamii* n. sp.

Figures 3.9-10, 4.1-2; Table 3

1975 *Fistulipora* sp. indet. Sakagami, p. 35, pl. 4, figs. 5-6.
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. Autozooecia growing from thin epitheca, bending at their bases to the colony surface. Autozooecial diaphragms rare to absent, thin. Autozooecial apertures circular to oval. Lunaria well-developed, long, horseshoe-shaped; ends of lunaria slightly indenting into autozooecia. Vesicles small to medium, high, separating autozooecia in 1–3 rows of vesicles; 8–10 vesicles surrounding each aperture.

Remarks. Fistulipora sakagamii n. sp. differs from Fistulipora rutogensis XIA, 1991 from the Chainaha Formation (Middle Permian) of southwestern Tibet, in smaller autozooecial apertures (0.14–0.19 mm vs. 0.24–0.30 mm in Fistulipora rutogensis).

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

Genus DYBOWSKIHELLA Waagen and Wentzel, 1886

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

Diagnosis. Ramose, hollow ramose, massive, or encrusting colonies. Autozooecia cylindrical, subcircular 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 autozooecial chamber. Autozooecial 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 autozooecia in radial arrangement.

Remarks. Dybowskiella Waagen and Wentzel, 1886 differs from Fistulipora MCCoy, 1849 in the shape of lunaria, the ends of which inflect autozooecial 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 hupehensiformis n. sp.

Etymology. The species is named after the species Fistulipora sakagamii 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-shaped, present in endozone and exozone; ends of lunaria inflect into autozooecial chamber. Autozooecial 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 autozooecia in radial arrangement.

Remarks. Dybowskiella Waagen and Wentzel, 1886 differs from Fistulipora MCCoy, 1849 in the shape of lunaria, the ends of which inflect autozooecial 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 hupehensiformis n. sp.

Figure 4.3-7; Table 4
FIGURE 4. Thin section photographs of Fistulipora sakagamii n. sp., holotype SMF 23.028 (1 and 2); Dybowskiella hupehensiformis 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 autozooecial apertures and vesicles; 3 and 4, longitudinal section showing autozooecial chambers and vesicular skeleton; and 8, branch transverse section.
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. Autozoecia growing from thin epitheca, bending in the early exozone to the colony surface. Autozoecial diaphragms few to absent. Autozoecial apertures circular to oval. Lunaria well-developed, horse-shoe-shaped, directed towards the next macula, disappearing in deeper sections; ends of lunaria indenting into autozoecia. Vesicles small to medium in size, high, separating autozoecia in 1–2 rows, 11–15 surrounding each autozoecia aperture, with rounded to flat roofs, polygonal in tangential section. Autozoecial walls granular prismatic, 0.005–0.015 mm thick. Maculae consisting of vesicular skeleton, 0.9–1.3 mm in diameter.

**Remarks.** *Dybowskiella hupehensiformis* n. sp. resembles the species described as *Dybowskiella hupehensis* Yang, 1956 by Yang and Lu (1983) from the Lower Permian Balaqliq 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 autozoecial apertures than the species described by Yang and Lu (1983) (aperture width 0.34–0.42 mm vs. 0.26–0.33 mm in the material of Yang and Lu). *Dybowskiella hupehensiformis* 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 hupehensiformis* n. sp. is similar to the species *Dybowskiella* sp. described by Yang and Lu (1983) from the Balaqliq 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. hupehensiformis* differs from *D. crescens* (Crockford, 1944) from the Lower Permian (Artinskian) of Western Australia in smaller autozoecial apertures (aperture width 0.26–0.33 mm vs. 0.29–0.43 mm in *D. crescens*).

**Occurrence.** Balaqliq 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. Autozoecia long, subcircular in transverse section of endozone; isolated by vesicular skeleton in exozones. Autozoecial apertures rounded to oval, usually arranged in regularly alternating longitudinal rows; maculae absent or poorly developed. Autozoecial diaphragms present in both in endozone and exozone, 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. Autozoecial 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 autozoecia. *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

<table>
<thead>
<tr>
<th>TABLE 4. Measurements of <em>Dybowskiella hupehensiformis</em> n. sp. Abbreviations as for Table 1.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>N</strong></td>
</tr>
<tr>
<td>Autozoecial aperture width, mm</td>
</tr>
<tr>
<td>Autozoecial aperture spacing, mm</td>
</tr>
<tr>
<td>Vesicle diameter, mm</td>
</tr>
<tr>
<td>Vesicle spacing, mm</td>
</tr>
<tr>
<td>Vesicles per aperture</td>
</tr>
<tr>
<td>Lunarium length, mm</td>
</tr>
<tr>
<td>Lunarium width, mm</td>
</tr>
<tr>
<td>Lunarium thickness, mm</td>
</tr>
</tbody>
</table>
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 autozooecial apertures and vesicles.
1987  *Fistuliramus xianzaensis* Liu and Wang, 1987, 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. Autozooecia long in endozones, bending at low angles in exozones. Autozooecial diaphragms few, thin, planar, or concave, concentrated in the transition zone between endozone and exozone. Autozooecial 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 autozooecia in 1–3 rows and 10–13 surrounding each autozooecial aperture; in endozone usually twice as high as those in exozone. Autozooecial 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 autozooecial 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.

---

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

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

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 autozooecia 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. Autozooecia growing from thin epitheca, bending in the early exozone to the colony surface. Basal diaphragms abundant. Autozooecial apertures circular to oval. Basal diaphragms abundant. Autozooecial apertures circular to oval. Lunaria well-developed, triangular; ends of lunaria indenting into autozooecia on the opposite side of the aperture. Vesicles small to large, separating autozooecia in 1–2 rows, 11–16 surrounding each autozooecial aperture, with rounded roofs, polygonal in tangential section. Autozooecial 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 autozooecia (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 uncaeta* 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 autozooecial apertures with lunarial ends indenting into the aperture (arrow); 7, tangential section showing autozooecia and macrozooecia (arrow); 8 and 9, branch transverse section showing autozooecial chambers and vesicular skeleton; and 10 and 11, longitudinal section showing autozooecial chambers and vesicular skeleton.
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 autozooecial apertures.

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

**Genus CYCLOTRYPRA** Ulrich, 1896

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


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

**Cyclotrypa alexanderi** Sakagami, 1963

Figure 6.4-7; Table 7


**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 exozoone and 5.1–7.0 mm wide endozoones. Encrusting colonies 1.3–1.9 mm thick. In branched colonies, cylindrical autozooecia long in endozoones, bending sharply in exozoones, rounded–polygonal in transverse section. In secondary overgrowths and encrusting sheets, autozooecia growing from laminated epithea. Epitheca 0.025–0.030 mm thick. Autozooecial diaphragms few to common. Autozooecial apertures rounded to oval. Granular material well-developed at colony surface. Acanthostyles in granular material developed, 0.05–0.07 mm in diameter. Locally macrozooecia occurring. Vesicular skeleton well-developed. Vesicles small, separating autozooecia in 1–2 rows, 5–11 surrounding each autozooecial aperture, with rounded roofs, polygonal in tangential section. Autozooecial walls granular prismatic, 0.003–0.008 mm thick. Low maculae without autozooecia 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 autozooecial 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 autozooecial 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

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

<table>
<thead>
<tr>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>31</td>
<td>0.26</td>
<td>0.046</td>
<td>17.72</td>
<td>0.18</td>
</tr>
<tr>
<td>Autozooecial aperture spacing, mm</td>
<td>31</td>
<td>0.47</td>
<td>0.068</td>
<td>14.39</td>
<td>0.33</td>
</tr>
<tr>
<td>Vesicle diameter, mm</td>
<td>31</td>
<td>0.09</td>
<td>0.024</td>
<td>25.76</td>
<td>0.05</td>
</tr>
<tr>
<td>Vesicles per aperture</td>
<td>10</td>
<td>13.7</td>
<td>1.703</td>
<td>12.43</td>
<td>11.0</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>50</td>
<td>0.20</td>
<td>0.017</td>
<td>8.71</td>
<td>0.17</td>
</tr>
<tr>
<td>Autozooecial aperture spacing, mm</td>
<td>50</td>
<td>0.39</td>
<td>0.050</td>
<td>12.86</td>
<td>0.27</td>
</tr>
<tr>
<td>Vesicle diameter, mm</td>
<td>50</td>
<td>0.13</td>
<td>0.029</td>
<td>22.74</td>
<td>0.07</td>
</tr>
<tr>
<td>Vesicles per aperture</td>
<td>22</td>
<td>7.64</td>
<td>1.432</td>
<td>18.76</td>
<td>5.0</td>
</tr>
<tr>
<td>Maculae diameter, mm</td>
<td>11</td>
<td>0.6</td>
<td>0.163</td>
<td>26.67</td>
<td>0.4</td>
</tr>
<tr>
<td>Macrozooecial aperture width, mm</td>
<td>7</td>
<td>0.31</td>
<td>0.041</td>
<td>13.25</td>
<td>0.25</td>
</tr>
</tbody>
</table>
Genus *HEXAGONELLA* Waagen and Wentzel, 1886

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

**Diagnosis.** Colonies consisting of compressed to subcyllindrical 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 Pilllevuit, 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; Carluke (Scotland).

**Diagnosis.** Reticulate colonies with polygonal fenestrales. 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* Toula, 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 autozooecial chamber; 4, transverse section showing mesotheca with median tubules (arrow); and 5, external view of the colony form the reverse side.
**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; autozoecia arranged in 4–6 rows on branches; autozoecial apertures with lunaria; vesicular skeleton well-developed, consisting of small vesicles; extrazoecial 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. Autozoecia tubular, semicircular 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 autozoecial 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. Autozoecial 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. Autozoecial walls 0.02–0.04 mm thick, granular–prismatic. Extrazoecial skeleton (stereom) granular. Vesicular skeleton consisting of low small vesicles with flattened roofs, concentrated mostly in endzone.

**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 zoecial 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 hemisepa, 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 autozoecial apertures (aperture width 0.15–0.22 mm vs. 0.20–0.24 mm in *G. yongzhuensis*; aperture 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 hemisepa.

**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 autozooecial chambers, mesotheca and hemisepta (arrow); 3–5, tangential sections showing autozoocelial apertures; 7, longitudinal section showing autozooecial chamber with superior hemisepta (arrow); and 8, branch oblique section showing mesotheca, autozooecial chambers with hemisepta and vesicular skeleton.
**Ernst: Bryozoan Fauna of Tibet**

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

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

**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 autozoecial 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 autozoecia. Autozoecia 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, autozoocelial chambers with hemisepta and vesicular skeleton; 3 and 4, mid-tangential section showing autozoocelial chambers with hemisepta; 5, tangential section showing autozoocelial apertures; and 6, transverse section showing extrazoocelial skeleton and sparse vesicles.
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. Autozooecial walls granular–prismatic, 0.013–0.015 mm thick. Autozooecial 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. Extrazooecial 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. Autozooecia 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 extrazooecial 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. Autozooecial walls granular-prismatic, with dark median zone continuous into boundary zone in mesotheca. Extrazooecial skeleton well-developed, displaying cloudy structure; acanthostyles absent. Monticules absent.


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

**Etherella tibetensis** n. sp.

**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 autozooecia and wall microstructure; 5–7, oblique section showing hemisepta and mesotheca (arrows); and 8 and 9, branch transverse section showing autozooecial chambers and extrazooecial skeleton.

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; autozooecia arranged in 8–10 rows on branches; lunaria absent; vesicular skeleton scarcely developed, vesicles small; extrazooecial 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. Autozooecia 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. Autozooecial walls granular-prismatic, 0.015–0.040 mm thick. Autozooecial 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. Extrazooecial skeleton well-developed, displaying cloudy structure produced by stabb-sided 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 autozooecial apertures as well as an extremely thick extrazooecial 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 extrazooecial 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 autozooecial apertures (average autozooecial 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.

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>10</td>
<td>3.60</td>
<td>0.790</td>
<td>21.99</td>
<td>2.8</td>
<td>5.1</td>
</tr>
<tr>
<td>Fenestrule width, mm</td>
<td>20</td>
<td>2.33</td>
<td>0.477</td>
<td>20.50</td>
<td>1.6</td>
<td>3.3</td>
</tr>
<tr>
<td>Fenestrule length, mm</td>
<td>20</td>
<td>3.2</td>
<td>0.376</td>
<td>11.75</td>
<td>2.1</td>
<td>4.0</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>30</td>
<td>0.17</td>
<td>0.025</td>
<td>14.40</td>
<td>0.12</td>
<td>0.21</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>30</td>
<td>0.53</td>
<td>0.066</td>
<td>12.52</td>
<td>0.45</td>
<td>0.66</td>
</tr>
<tr>
<td>Autozooecial aperture spacing diagonally, mm</td>
<td>30</td>
<td>0.50</td>
<td>0.056</td>
<td>11.15</td>
<td>0.4</td>
<td>0.6</td>
</tr>
<tr>
<td>Vesicle diameter, mm</td>
<td>20</td>
<td>0.09</td>
<td>0.030</td>
<td>32.88</td>
<td>0.05</td>
<td>0.15</td>
</tr>
</tbody>
</table>
Diagnosis. Ramose, encrusting, cylindrical, or massive colonies. Autozoecia with basal dia-
phragms and ring septa. Autozoecial walls irregularly thickening with development of monilae. Exilazoecia rare. Acanthostyles of two sizes: small microacanthostyles and large macroacantho-
styles.

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

Occurrence. Carboniferous–Permian; worldwide.

Tabulipora xinjiangensis Yang and Lu, 1983

Figure 11.1-2; Table 12


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 autozo-
cecial 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. Endozoal walls granular, 0.015–0.020 mm thick; exozonal walls monilae-shaped thickened, laminated, serrated, with distinct autozoecial boundar-
ies, 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 Ghanahina Formation (Middle Permian) of the Rutog region of Tibet, in possessing fewer acan-
thostyles (8–14 vs. 6–9 around each aperture and more abundant acanthostyles and fewer exi-
azoecia, as well as larger autozoecia (autozo-
ecial aperture width 0.18–0.30 mm vs. 0.13–0.17 mm in D. phetchabunensis). 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 Danaeua and Morozova, 1967

Genus DYSRITELLA Girty, 1911

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

Diagnosis. Dendroid and encrusting colony with abundant acanthostyles and exilazoecia. Autozo-
ecia parallel to longitudinal direction of the colony in endozone; gradually bending outward in exo-
zone. 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. Zoo-
ceial 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 Danaeua 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, hav-
ing rounded to polygonal transverse section, restricted to the exozone, 0.04–0.11 mm in diamet-
er. Abundant acanthostyles in the walls of the exo-
zone, 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; rapidly thickening, 0.08–0.13 mm thick in exo-
zone. 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 exi-
azoecia, as well as larger autozoecia (autozo-
ceial aperture width 0.18–0.30 mm vs. 0.13–0.17 mm in D. phetchabunensis). Dyscritella lii n. sp. dif-
ers 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 autozooecial apertures and acanthostyles; and 7 and 8, oblique section.
oecial aperture width 0.18–0.30 mm vs. 0.18–0.20 mm in *D. fida*).

Family **ULRICHOTRYPLELLIDAE** Romantchuk in Romantchuk and Kiseleva, 1968

Genus **ULRICHOTRYPSELLA** Romantchuk, 1967

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


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

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

*Ulrichotrypella omanica* Ernst, Weidlich and Schäfer, 2008

**Figures 11.7-8, 12.1; Table 14**

**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 autozooecia constricted to exozone. Autozooecial apertures rounded to angular. Exilazooecia few, having a rounded to polygonal transverse section, restricted to the exozone, 0.09–0.12 mm in diameter. Abundant aktinotyles 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 exilazooecia.

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

Family **ERIDOTRYPSELLIDAE** Morozova, 1960

Genus **NEOERIDOTRYPSELLA** Morozova, 1970

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


**Remarks.** *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. Autozooecial diaphragms absent. Autozooecial apertures rounded to slightly angular. Exilazooecia few, having rounded to polygonal transverse section shape, restricted to the exozone, 0.04–0.11 mm in diameter.
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.
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 autozooecial 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 autozooecial 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 autozooecial 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
**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. Autozooecia 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. Autozooecial apertures rounded to oval. Diaphragms rare.

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

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

*Streblotrypa* (*Streblotrypa*) *parviformis* n. sp.

Figures 12.8-10, 13.1-3; Table 16

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

---

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>17</td>
<td>0.28</td>
<td>0.048</td>
<td>17.11</td>
<td>0.21</td>
<td>0.38</td>
</tr>
<tr>
<td>Autozooecial aperture spacing, mm</td>
<td>13</td>
<td>0.47</td>
<td>0.076</td>
<td>16.33</td>
<td>0.38</td>
<td>0.67</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>6</td>
<td>0.10</td>
<td>0.023</td>
<td>23.29</td>
<td>0.06</td>
<td>0.12</td>
</tr>
<tr>
<td>Aktinotostyle diameter, mm</td>
<td>10</td>
<td>0.06</td>
<td>0.012</td>
<td>21.43</td>
<td>0.04</td>
<td>0.07</td>
</tr>
<tr>
<td>Exozonal wall thickness, mm</td>
<td>8</td>
<td>0.11</td>
<td>0.031</td>
<td>28.22</td>
<td>0.07</td>
<td>0.15</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>4</td>
<td>4.66</td>
<td>0.550</td>
<td>11.79</td>
<td>4.10</td>
<td>5.40</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>4</td>
<td>0.65</td>
<td>0.136</td>
<td>20.94</td>
<td>0.54</td>
<td>0.82</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>4</td>
<td>3.36</td>
<td>0.305</td>
<td>9.07</td>
<td>3.02</td>
<td>3.76</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>30</td>
<td>0.22</td>
<td>0.024</td>
<td>11.00</td>
<td>0.17</td>
<td>0.26</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>30</td>
<td>0.47</td>
<td>0.051</td>
<td>10.85</td>
<td>0.40</td>
<td>0.57</td>
</tr>
<tr>
<td>Macroacanthostyle diameter, mm</td>
<td>21</td>
<td>0.16</td>
<td>0.028</td>
<td>17.42</td>
<td>0.10</td>
<td>0.22</td>
</tr>
<tr>
<td>Microacanthostyle diameter, mm</td>
<td>30</td>
<td>0.07</td>
<td>0.013</td>
<td>17.64</td>
<td>0.04</td>
<td>0.10</td>
</tr>
</tbody>
</table>
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.
Etymology. The species is named after its similarity with *Streblotrypa* (*Streblotrypa*) *parva* Morozova, 1965.

**Holotype.** SMF 23.251.


**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. Autozooecia 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. Autozooecial apertures oval, arranged in regular diagonal rows. Autozooecial diaphragms locally present. Hemisepta absent. Metazooecia small, 12–20 of them arranged in three rows between apertures. Acanthostyles present, irregularly distributed between autozooecial apertures. Autozooecial 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 (STREBLASCOPORA) Bassler, 1929

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

**Diagnosis.** Branched colonies. Clearly defined bundle of the axial zooecia in the endozone. Autozooecia 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. Autozooecial apertures rounded to oval. Diaphragms rare. Inferior hemisepta commonly present, sometimes accompanied by superior hemisepta; in some species hemisepta absent. Metazooecia between the autozooecial apertures and beyond the distolateral margins of autozooecial apertures. Autozooecial walls laminated, without distinct autozooecial boundaries.

**Remarks.** *Streblotrypa* (*Strebascopora*) 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* (*Strebascopora*) *delicatula* Sakagami, 1961

- Figure 13.4-8; Table 17

<table>
<thead>
<tr>
<th>Sub-genus STREBLOTRYPA (STREBLASCOPORA) Bassler, 1929</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Type species.</strong> <em>Streblotrypa fasciculata</em> Bassler, 1929. Upper Permian, Indonesia.</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Mean</th>
<th>Standard Deviation</th>
<th>Coefficient of Variation</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>0.68</td>
<td>0.091</td>
<td>13.45</td>
<td>0.51</td>
<td>0.92</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>0.13</td>
<td>0.027</td>
<td>20.66</td>
<td>0.09</td>
<td>0.17</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>0.42</td>
<td>0.066</td>
<td>15.84</td>
<td>0.31</td>
<td>0.58</td>
</tr>
<tr>
<td>Axial bundle width, mm</td>
<td>0.15</td>
<td>0.039</td>
<td>25.61</td>
<td>0.10</td>
<td>0.26</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>0.10</td>
<td>0.011</td>
<td>11.15</td>
<td>0.08</td>
<td>0.12</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>0.53</td>
<td>0.059</td>
<td>11.20</td>
<td>0.48</td>
<td>0.61</td>
</tr>
<tr>
<td>Autozooecial aperture spacing diagonally, mm</td>
<td>0.25</td>
<td>0.026</td>
<td>10.58</td>
<td>0.22</td>
<td>0.27</td>
</tr>
<tr>
<td>Metazooecia width, mm</td>
<td>0.02</td>
<td>0.006</td>
<td>28.30</td>
<td>0.01</td>
<td>0.03</td>
</tr>
</tbody>
</table>

**1961**

*Streblotrypa* (*Strebascopora*) *delicatula* Sakagami, p. 52, pl. 25, figs. 7-10, pl. 26, fig. 2-18, pl. 27, figs. 1-5.

**1973**

*Streblotrypa* (*Strebascopora*) *delicatula* Sakagami, 1961; Sakagami, p. 84-85, pl. 8, figs. 1-4.

**1984**

*Streblotrypa* (*Strebascopora*) *delicatula* Sakagami, 1961; Yang and Lu, p. 53-54, pl. 1, fig. 5b, pl. 2, 3a, b.

**1997**

*Streblotrypa* (*Strebascopora*) *delicatula* Sakagami, 1961; Sakagami and Pillevuit, p. 212, figs. 4-(9-11), 5-1.
TABLE 17. Measurements of Streblotrepa (Streblascopora) delicatula Sakagami, 1961. Abbreviations as for Table 1.

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


**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. Autozoecia budding from the axial bundle, having long inflated proximal parts, rounded to polygonal in transverse section in the endozeone. Autozoecial 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. Autozoecial walls laminated, 0.005–0.010 mm thick in endozone.

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

Streblotrepa (Streblascopora) marmionensis (Etheridge, 1926)

Figures 13.9, 14.1-3; Table 18

1926 Streblotrepa marmionensis Etheridge in Bretnall, p. 22, pl. 1, fig. 1, pl. 2, fig. 3.

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

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

1957 Streblotrepa marmionensis Etheridge, 1926; Crockford, p. 80.

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

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

1970 Streblascopora marmionensis (Etheridge, 1926); Gorjunova, p. 151-152, pl. 28, fig. 1.

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

1975 Streblascopora marmionensis (Etheridge, 1926); Gornjovina, p. 65, pl. 9, fig. 1.

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

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

2013 Streblascopora 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. Autozoecia budding from the axial bundle, having long inflated proximal parts, rounded to polygonal in transverse section in the endozone. Autozoecial 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. Autozoecial walls laminated, 0.005–0.010 mm thick in endozone.

**Remarks.** Streblotrepa (Streblascopora) marmionensis (Etheridge, 1926) differs from S. (S.) germana (Bassler, 1929) in possessing hemisepta, thicker branches and a larger diameter of the axial bundle. Streblotrepa (Streblascopora) 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.
family RHABDOMESIDAE Vine, 1884
Genus RHABDOMESON Young and Young, 1874 [= Coeloconus Ulrich, 1889]


Diagnosis. Rhabdomesid with delicate dendroid colony with irregularly dichotomizing branches. Autozoecia regularly budding around central axial cylinder in an annual or spiral manner. Hemisepta common. Autozoecial apertures elliptical, pyriform or rhombic, closely spaced, arranged in quincunx on colony surface; of constant or variable dimensions around branch. Stylets abundant and structurally diverse (modified after Wyse Jackson and Bancroft, 1995).

Remarks. Rhabdomeson differs from other rhadomesines in the presence of a central axial cylinder. Rhabdomeson differs from Silenella Gorjunova, 1992 in the absence of aktinotostyles 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 aktinotostyles.

Occurrence. Middle Devonian to Upper Permian; worldwide.

Rhabdomeson bretnalli Crockford, 1957
Figure 14.4-9; Table 19


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. Autozoecia budding in a spiral pattern from the axial cylinder, rhomboid in transverse section. Autozoecial 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. Autozoecial 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 *Primorea 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.
Lu, 1983 from the Baliqliq Group of western Xinjiang, China, but differs from it by the regular presence of four macroacanthostyles surrounding autozooecial 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 autozooecial 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. Autozooecia budding in a spiral pattern from the axial cylinder, rhomboid in transverse section. Autozooecial 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. Autozooecial 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. 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 tubelike autozooecia budding in spiral pattern. Oval apertures arranged in regular diagonal rows. Abundant aktinotostyles in walls of the exozone (modified after Gorjunova, 1985).

**Remarks.** *Primorella* differs from other genera of the family Rhomboporidae by the presence of aktinotostyles. *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*

**Material.** SMF 23.161–SMF 23.164.

**Description.** Branched colonies, 1.4–1.6 mm in diameter. Autozooecia growing from median axis. Apertures oval. Aktinotostyles abundant, arranged in a single row around apertures. Autozooecial 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*). *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.

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>30</td>
<td>0.17</td>
<td>0.026</td>
<td>15.98</td>
<td>0.12</td>
<td>0.22</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>5</td>
<td>0.53</td>
<td>0.050</td>
<td>9.33</td>
<td>0.48</td>
<td>0.61</td>
</tr>
<tr>
<td>Autozooecial aperture spacing diagonally, mm</td>
<td>5</td>
<td>0.36</td>
<td>0.050</td>
<td>14.02</td>
<td>0.32</td>
<td>0.44</td>
</tr>
<tr>
<td>Aktinotostyle diameter, mm</td>
<td>20</td>
<td>0.027</td>
<td>0.007</td>
<td>25.38</td>
<td>0.010</td>
<td>0.038</td>
</tr>
</tbody>
</table>

Family RHOMBOPORIDAE Simpson, 1895

Genus PRIMORELLA Romantchuk and Kiseleva, 1968

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


**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. von 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; autozooecia 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 autozooecia 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. Autozooecia tubular, semicircular in endozone, recumbent at mesotheca, bending sharply in exozone. Autozooecial apertures rounded to oval, arranged in 8–15 alternating rows. Autozooecial 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 autozooecia, positioned between pinnae across branch axis. Elliptical nodes regularly spaced between autozooecial 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 Girtyporiidae, 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 Gorunova (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 autozooecial 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 autozooecial apertures, nodes (arrows) and microstyles; and 4 and 5, branch transverse section.
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 southwestern 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. Autozooecia arranged in two rows on the branches. Autozooecia 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 autozooecia 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.


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. Autozooecia arranged in two rows on branches. Autozooecial 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. Autozooecia short, triangular to trapezoidal in mid-tangential section; with short to moderately long vestibule in longitudinal section. Axial wall between autozooecial 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 southwestern Tibet.

Spinofenestella subquadratopora (Schulga-Nesterenko, 1952)

Figure 17.6-8; Table 23

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

---

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>4</td>
<td>4.9</td>
<td>1.458</td>
<td>29.76</td>
<td>3.2</td>
<td>6.7</td>
</tr>
<tr>
<td>Branch thickness, mm</td>
<td>5</td>
<td>1.7</td>
<td>0.415</td>
<td>24.69</td>
<td>1.1</td>
<td>2.2</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>35</td>
<td>0.16</td>
<td>0.012</td>
<td>7.60</td>
<td>0.13</td>
<td>0.19</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>8</td>
<td>0.79</td>
<td>0.044</td>
<td>5.55</td>
<td>0.72</td>
<td>0.85</td>
</tr>
<tr>
<td>Autozooecial aperture spacing diagonally, mm</td>
<td>30</td>
<td>0.44</td>
<td>0.051</td>
<td>11.57</td>
<td>0.37</td>
<td>0.55</td>
</tr>
<tr>
<td>Node diameter, mm</td>
<td>5</td>
<td>0.08</td>
<td>0.015</td>
<td>18.05</td>
<td>0.06</td>
<td>0.10</td>
</tr>
</tbody>
</table>
FIGURE 17. Thin section photographs of Spinofenestella sp., SMF 23.178 (1–5); and Spinofenestella subquadratopora (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.
Fenestella subquadratopora Schulga-Nesterenko, 1952; Gorjunova, p. 84, pl. 19, fig. 3, pl. 20, fig. 1.

Alternifenestella subquadratopora Schulga-Nesterenko, 1952; Nakrem, p. 94, fig. 17A-B.

Alternifenestella subquadratopora Schulga-Nesterenko, 1952; Ernst, p. 97, pl. 21, figs. 3-5.


Exterior description. Reticulate colony formed by straight branches joined by wide dissepiments. Fenestrules oval to rectangular, long, narrow. Autozooecia arranged in two rows on branches. Autozooecial 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. Autozooecia short, triangular in mid-tangential section; with short to moderately long vestibule in longitudinal section. Axial wall between autozooecial 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

| 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|
| Autozooecial aperture width, mm  | 20  | 0.07| 0.007| 9.13| 0.06| 0.09|
| Autozooecial aperture spacing along branch, mm| 20  | 0.26| 0.015| 5.72| 0.24| 0.29|
| Autozooecial 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|
| Autozooecial aperture width, mm  | 10  | 0.10| 0.007| 7.45| 0.09| 0.11|
| Autozooecial aperture spacing along branch, mm| 10  | 0.29| 0.018| 6.03| 0.27| 0.32|
| Autozooecial 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.

larger fenestrules (average fenestrule width 0.33 mm vs. 0.28 mm in \textit{S. macronodata}; average fenestrule length 0.46 mm vs. 0.40 mm in \textit{S. macronodata}). \textit{Spinofenestella subquadratopora} differs from \textit{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 \textit{S. pulcherrima}) and an irregular distribution of nodes on the reverse side of the colony; the nodes in \textit{S. pulcherrima} are arranged in regular rows.

**Occurrence.** Upper Carboniferous, late Gzhelian, lowermost part of the Tyrrlefjellet 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.** \textit{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.** \textit{Polypora} M’Coy, 1844 is similar to \textit{Paucipora} Termier and Termier, 1971. The latter has well-developed hemisepta and shorter autozoecia. \textit{Polypora} differs from \textit{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.

\textit{Polypora consanguinea} Bassler, 1929  
**Figure 18.1-4; Table 24**

1929 \textit{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. Autozoocelial apertures rounded to oval, 4–10 spaced per length of fenestrule. Fenestrules long, oval, narrow. Node regularly spaced between subsequent autozoocelial apertures, 0.03–0.04 mm in diameter. Reverse colony surface smooth.

**Interior description.** Autozoocelial 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.** \textit{Polypora consanguinea} Bassler, 1929 is similar to \textit{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 \textit{P. russiensis}) and wider fenestrules (fenestrule width 1.08–1.40 mm vs. 0.45–0.70 mm in \textit{P. russiensis}). \textit{Polypora consanguinea} differs from \textit{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 \textit{P. multiporifera}) as well as wider and shorter fenestrules (fenestrule width 1.08–1.40 mm vs. 0.65–1.10 mm in \textit{P. multiporifera}; fenestrule length 2.00–2.10 mm vs. 2.1–2.45 mm in \textit{P. multiporifera}). \textit{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.

\textit{Polypora brouweri} Bassler, 1929  
**Figure 18.5-9; Table 25**

1929 \textit{Polypora brouweri} Bassler, p. 77, pl. 18, figs. 7-10.

1946 \textit{Polypora goldfussi} Eichwald, 1860; Metz, p. 181, pl. 19, fig. 9.

**Material.** SMF 23.183.


**Interior description.** Autozoocelial 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 autozoocelial apertures, nodes and autozoocelial chambers; 6, reverse side of the colony; and 7–9, tangential section showing autozoocelial apertures and chambers.
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 (Sakmarian-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


Exterior description. Reticulate colonies composed of moderately wide branches jointed by moderately wide dissepiments. Autozoecia arranged in 3–4 alternating rows on branches. Autozoecial apertures rounded to oval, 4–5 mm wide, 4–5 mm long. Large nodes regularly spaced on the colony surface.

Interior description. Autozoecial 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 Perm-

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

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

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>6</td>
<td>0.91</td>
<td>0.151</td>
<td>16.55</td>
<td>0.72</td>
<td>1.13</td>
</tr>
<tr>
<td>Dissepiment width, mm</td>
<td>3</td>
<td>0.48</td>
<td>0.035</td>
<td>7.27</td>
<td>0.45</td>
<td>0.52</td>
</tr>
<tr>
<td>Fenestrule width, mm</td>
<td>4</td>
<td>1.1</td>
<td>0.200</td>
<td>18.18</td>
<td>1.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Fenestrule length, mm</td>
<td>3</td>
<td>3.1</td>
<td>0.814</td>
<td>26.56</td>
<td>2.5</td>
<td>4.0</td>
</tr>
<tr>
<td>Distance between branch centres, mm</td>
<td>6</td>
<td>1.94</td>
<td>0.191</td>
<td>9.83</td>
<td>1.80</td>
<td>2.25</td>
</tr>
<tr>
<td>Autozoecial aperture width, mm</td>
<td>20</td>
<td>0.14</td>
<td>0.009</td>
<td>6.91</td>
<td>0.12</td>
<td>0.16</td>
</tr>
<tr>
<td>Autozoecial aperture spacing along branch, mm</td>
<td>20</td>
<td>0.51</td>
<td>0.065</td>
<td>12.68</td>
<td>0.40</td>
<td>0.60</td>
</tr>
<tr>
<td>Autozoecial aperture spacing diagonally, mm</td>
<td>20</td>
<td>0.32</td>
<td>0.035</td>
<td>11.02</td>
<td>0.25</td>
<td>0.38</td>
</tr>
<tr>
<td>Maximum chamber width, mm</td>
<td>20</td>
<td>0.21</td>
<td>0.009</td>
<td>4.14</td>
<td>0.20</td>
<td>0.23</td>
</tr>
</tbody>
</table>
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 autozoocial apertures and chambers with hemisepta (arrow); 5, tangential section showing autozoocial apertures, chambers and heteromorph (arrow); 6, tangential section showing autozoocial apertures and nodes; and 7 and 8, tangential section showing autozoocial apertures and chambers.
ian of Arctic, but differs from the latter in having wider branches and larger fenestrales (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 autozooecial chamber in mid-tangential section. Typical Polypora species have regularly hexagonal autozooecia 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 Schulganesterenko, 1941. Lower Permian, southern Urals (Russia).

**Diagnosis.** Reticulated colonies of various shapes consisting of broad linear, essentially parallel branches joined by dissepsiments; dissepsiments narrow, perpendicular or at oblique angle to branches, regularly spaced at large distance; fenestrales elongate oval, sub-rectangular, or irregular in shape; keels and superstructure absent; autozooecia 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 autozooecial walls; extrazooecial skeleton laminated, traversed by abundant, moderate-size microstyles.

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

**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 dissepsiments. 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. Autozooecia arranged in 5–9 alternating rows on branches. Apertures circular, arranged in regular alternating rows, 6–8 spaced per fenestrule length. Fenestrales medium in size, elongate, sub-rectangular. Keels absent; nodes on the obverse side present, arranged irregularly between autozooecial 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.** Autozooecia rhombic in mid-tangential section; with well-developed vestibule

<table>
<thead>
<tr>
<th>TABLE 26. Measurements of Polypora aff. voluminosa Trizna and Klautzan, 1961. Abbreviations as for Table 1.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Measurements</strong></td>
</tr>
<tr>
<td>Branch width, mm</td>
</tr>
<tr>
<td>Dissepiment width, mm</td>
</tr>
<tr>
<td>Fenestrule width, mm</td>
</tr>
<tr>
<td>Fenestrule length, mm</td>
</tr>
<tr>
<td>Distance between branch centres, mm</td>
</tr>
<tr>
<td>Distance between dissepsiment centres, mm</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
</tr>
<tr>
<td>Autozooecial aperture spacing diagonally, mm</td>
</tr>
<tr>
<td>Maximum chamber width, mm</td>
</tr>
<tr>
<td>Node diameter, obverse side, mm</td>
</tr>
<tr>
<td>Node diameter, reverse side, mm</td>
</tr>
</tbody>
</table>
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 autozooeial chambers; 4, branch transverse section; 5, branch longitudinal section; and 6, external view of the reverse side of the colony.
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


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 extrazooecial skeleton may be present between autozooecial apertures at fusion points; lateral expansions depressed relative to main branch obverse and reverse surface; typically 5–6 rows of autozooecia per branch with fewer on lateral branch expansions; zooecial apertures circular, lacking peristomes, aligned longitudinally and diagonally in alternating rows; keels and large obverse styles absent, small styles common in interapertural skeleton; autozooecial 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; zooecial 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; extrazooecial 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 autozooecia. 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 Protoretepora 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 autozoocelial apertures and chambers; 2, mid-tangential section showing autozoocelial chambers; 3, 4, 7, and 8, tangential section showing autozoocelial apertures, microstyles and nodes; 5, tangential section of obverse colony side with nodes; and 6, tangential section of the reverse side of the colony.
**Ernst: Bryozoan Fauna of Tibet**

**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; autozooecia in 6–7 rows on branches; autozooecia 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. Autozooecial apertures circular, lacking peristomes. Keels absent. Nodes spaced irregularly on the reverse colony surface.

**Interior description.** Autozooecia 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. Extrazooecial 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.** *Protoretepora irregularis* n. sp. is distinct by its broad branches, irregular meshwork and presence of large nodes on the reverse colony surface. *Protoretepora 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. *Protoretepora irregularis* differs from *P. flexuosa* Crockford, 1957 from the Lower Permian of Western Australia by the presence of 6–7 rows of autozooecia on branches instead of 4–5 rows in *P. flexuosa*. Furthermore, the new species has larger autozooecial apertures (average aperture width 0.18 mm vs. 0.13 mm in *P. flexuosa*).

**Genus *TIBETIPORELLA* n. gen.**

**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; autozooecia arranged in 3–7 rows on branches; autozooecial apertures circular; autozooecial chambers long, narrow, tubular, with long vesti- bules, 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 autozooecial walls; extrazooecial skeleton thick, laminated, traversed by abundant, moderate-size microstyles; apparent reproductive hetero- morphs in form of isolated zooecia 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 autozooecia with long vesti- bules and heteromorphs in the form of enlarged chambers in the proximal part of vestibule.

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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>20</td>
<td>1.8</td>
<td>0.332</td>
<td>18.21</td>
<td>1.2</td>
<td>2.5</td>
</tr>
<tr>
<td>Fenestrule width, mm</td>
<td>12</td>
<td>1.4</td>
<td>0.310</td>
<td>21.88</td>
<td>0.9</td>
<td>2.0</td>
</tr>
<tr>
<td>Fenestrule length, mm</td>
<td>7</td>
<td>3.9</td>
<td>1.212</td>
<td>31.19</td>
<td>2.0</td>
<td>5.5</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>40</td>
<td>0.18</td>
<td>0.017</td>
<td>9.94</td>
<td>0.14</td>
<td>0.20</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>40</td>
<td>0.33</td>
<td>0.037</td>
<td>11.18</td>
<td>0.26</td>
<td>0.40</td>
</tr>
<tr>
<td>Maximum chamber width, mm</td>
<td>40</td>
<td>0.26</td>
<td>0.018</td>
<td>6.85</td>
<td>0.23</td>
<td>0.30</td>
</tr>
<tr>
<td>Node diameter, reverse side, mm</td>
<td>20</td>
<td>0.18</td>
<td>0.036</td>
<td>20.10</td>
<td>0.14</td>
<td>0.25</td>
</tr>
</tbody>
</table>
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 autozooecial apertures, nodes and heteromorphs; 3 and 4, mid-tangential section showing autozooecial chambers; 5 and 6, tangential section showing autozooecial apertures, nodes and heteromorphs; 7 and 8, longitudinal section showing autozooecial chambers and heteromorphs; and 9, transverse section showing autozooecial chambers.
**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.


**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. Autozoecia arranged in 3–7 rows on branches. Autozoecial 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.** Autozoecial 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. Extrazoecial skeleton thick, laminated, traversed by abundant, moderate-size microstyles 0.003–0.006 mm in diameter. Apparent reproductive heteromorphs in the form of isolated zooecia 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.


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

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

---

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


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.

**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.

<table>
<thead>
<tr>
<th>Zhongba Fm.</th>
<th>Xainza</th>
<th>Pamir</th>
<th>Thailand</th>
<th>W-Australia</th>
<th>Timor</th>
<th>Urals</th>
<th>Oman</th>
<th>Xinjiang</th>
<th>Iran</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fistulipora enodata</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fistulipora guttata</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fistulipora sakagamii</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dybowskiella hupehensiformis</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Fisturiamus xianzaensis</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Eridopora uncata</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cyclotrypa alexandri</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hexagonella kobayashii</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Liguloclema meridianus</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tabulipora xinjiangensis</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Ulrichotrypella omanica</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Neoeriotrypella astrica</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>S. (S.) delicatula</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>S. (S.) marmionensis</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Rhabdomeson bretnalli</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Primorella rotunda</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Timanotrypa australis</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Spinofenestella subquadratopora</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Polypora consanguinea</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Polypora brouweri</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mackinneyella obesa</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
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 the north and south.

Brachiopods found in the Zhongba Formation along with bryozoans include the following species (Li et al., 2014b): *Stenoscisma gigantea* (Diener, 1897), *Spiriferella sinica* Zhang, 1976, *S. rajah* (Salter, 1865), *Costiferina alata* Waterhouse, 1966.
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) (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 2-3); 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, Olso 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.

REFERENCES


Yang, J., Lu, L., and Xia, F. 1981. Late Paleozoic bryozoans from Xizang, p. 81-100. In (editor unknown), *The Series of the Scientific Expedition to the Plateau of Xizang. Palaeontology Book*. Publisher and publication locality unknown. (In Chinese with English abstract)


