Diverse labechiid stromatoporoids from the Upper Ordovician Xiazhen Formation of South China and their paleobiogeographic implications

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Abstract.—A diverse labechiid stromatoporoid assemblage that includes 16 species in 8 genera was found in the Upper Ordovician Xiazhen Formation (mid-late Katian) at Zhuzhai, Jiangxi Province of South China. The assemblage is characterized by a combination of: a) North China provincial species succeeding from their origination in the Darriwilian, including *Pseudostylodictyon poshanense* Ozaki, 1938, *Labechia shanhsiensis* Yabe and Sugiyama, 1930, *Lb*. *variabilis* Yabe and Sugiyama, 1930 and *Labechiella regularis* (Yabe and Sugiyama, 1930), and b) South China endemic species, including three new species (*Lb. zhuzhainus* Jeon sp. nov., *Lblla*. *beluatus* Jeon sp. nov., *Sinabeatricea luteolus* Jeon gen. et sp. nov.), and four species in open nomenclature (*Rosenella* sp., *Cystostroma* sp., *Pseudostylodictyon* sp. and *Labechia* sp.). The finding of *Lblla*. *gondwanense* Jeon sp. nov., *Stylostroma bubsense* Webby, 1991, *Sty*. *ugbrookense* Webby, 1991 and *Thamnobeatricea gouldi* Webby, 1991 in the formation indicates that Tasmania was closely related to South China, and had a closer paleobiogeographical relation with peri-Gondwanan terranes than Laurentia. In addition, the occurrences of *Labechia altunensis* Dong and Wang, 1984 and *Stylostroma* species support a close biogeographic link between Tarim and South China through the Middle to Late Ordovician interval, corresponding with the results from other fossil groups such as brachiopods, conodonts and chitinozoans. The diverse labechiids from the Xiazhen Formation improve our understanding of the diversity of Ordovician stromatoporoids in peri-Gondwanan terranes and the biogeographic affinities among

Australia (especially Tasmania rather than central New South Wales), Tarim and South China.

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Introduction

The Ordovician is a crucial period for the early evolution of stromatoporoids, manifested by their first-known appearance (Li et al., 2017; Jeon et al., 2019) and early diversification (Webby, 2004). Stromatoporoids achieved one of their highest diversity and widest circum-equatorial distributions throughout the late Middle to Late Ordovician times, as many as 26 genera on a global scale (Webby, 1979c, 1980, 1994, 2004, 2015; Stock et al., 2015). Among them, labechiids, which are grouped by common internal morphological characteristics of cyst plates, denticles and pillars, were predominant stromatoporoids (Webby, 2015a).

After the appearance of the pioneering genus *Cystostroma* in the early Floian in South China (Li et al., 2017; Jeon et al., 2019), 12 labechiid genera demonstrate stromatoporoid diversification in the late Darriwilian from North China, Sibumasu, Siberia, Tasmania and Laurentia (Stock et al., 2015), in conjunction with significant global-scale development of reef-building organisms including bryozoans, sponges and corals (Carrera and Rigby, 2004; Webby, 2004, 2015a; Ernst, 2018; Servais and Harper, 2018). During this period, stromatoporoid species in different terranes show a high level of endemism (Nestor and Webby, 2013; Stock et al., 2015). Subsequently, provincial species gradually dispersed to other neighboring regions, resulting in an increased diversity level, with 19 genera recorded in the Katian (Webby, 2004; Stock et al., 2015).

Upper Ordovician carbonate successions of South China yield skeletal-dominated reefs within the Jiangshan−Changshan−Yushan (JCY) triangle area near the border between Jiangxi and Zhejiang provinces of southeastern China (Fig. 1.2; Chen et al., 1987; Webby, 2002; Zhang et al., 2007; Lee et al., 2012; Li et al., 2015). Stromatoporoids are among the most common reef components, in both volume and abundance, through the Upper Ordovician succession of South China, but these taxa have not been studied in detail. Only brief information is available in previous geological and stratigraphic studies (Bian et al., 1996; Chen et al., 1987; Chen, 1995, 1996; Lee et al., 2012; Webby, 2002; Zhang et al., 2007). As a result, South China was not considered significant in terms of the biogeographic patterns of Ordovician stromatoporoids in recent publications (e.g., Nestor and Webby, 2013; Stock et al., 2015). It has been postulated that South China and Australia (especially New South Wales) may have had a close biogeographical relationship during Late Ordovician time, judging from the occurrence of few common clathrodictyid stromatoporoids (Lin and Webby, 1988, 1989), but species-level taxa of labechiids have not been evaluated.

A recent study of Late Ordovician stromatoporoids revealed a total of eleven stromatoporoid genera from the Xiazhen Formation and indicated that South China was also one of the loci for the diversification of early stromatoporoids (Jeon et al. 2020a), in accordance with extensive reef developments during the Great Ordovician Biodiversification Event (Servais and Harper 2018). Labechiids in the formation belong to 8 genera and are much more diversified than the clathrodictyids (Jeon et al., 2020a). In this study, we carried out detailed species-level taxonomic work and report 16 labechiid species from the Xiazhen Formation. Based on the occurrences of labechiid species, we propose a paleobiogeographic relationship between peri-Gondwanan terranes and others during the Ordovician Period.

Geological setting

The Upper Ordovician Xiazhen Formation at Zhuzhai, Yushan County, is one of the best-exposed Ordovician carbonate successions in the Jiangshan-Changshan-Yusahn (JCY) area. It is well-known for the occurrence of diverse invertebrate marine organisms including spiculate sponges and stromatoporoids, corals, bryozoans, brachiopods, trilobites, as well as graptolites, (Chen et al., 1987; Chen, 1995, 1996; Kwon et al., 2012; Lee et al., 2012; Lee, 2013; Dai et al., 2015; Lee, et al. 2016a, 2016b, 2019; Liang et al., 2016; Sun et al., 2016; Zhang, 2016; Park et al., 2017; Zhang et al., 2018; Jeon et al., 2020a, b). The formation has been interpreted as a mixed carbonate-siliciclastic ramp-type platform (Park et al., 2021), which developed along the northern margin of the Cathaysian landmass of South China (Li et al., 2004; Zhang et al., 2007).

The measured section of the Xiazhen Formation is approximately 190 m thick, and exposed at three small hills (named as sub-sections ZU 1, ZU 2, and ZU 3; Fig. 1.3), separated by Quaternary sedimentary deposits (Lee et al., 2012). The stratigraphy of the formation at Zhuzhai has been revised according to detailed lithological and paleontological data (see Lee et al., 2012) and adopted in the present study (Fig. 2). The formation was divided into the lower limestone member, the lower shale member, the middle mixed lithology member and the upper shale member in ascending order, judging from different lithofacies (Lee et al., 2012; Fig. 2).

The Xiazhen Formation has been estimated to be the middle to late Katian, judging from corals and the rough correlation with the Sanqushan and Changwu formations (Zhang et al., 2007). A recent discovery of the graptolite *Anticostia uniformis* (Mu and Lin in Mu et al., 1993) in the upper shale member of ZU 1 (see fig. 1b of Chen et al. 2016 for detailed specimen location) indicated that the upper part of Xiazhen Formation ranges from the

Dicellograptus complanatus Biozone to the *Paraorthograptus pacificus* Biozone (*Diceratograptus mirus* Subzone) of the late Katian (Chen et al., 2016). Overall, the Xiazhen Formation is most likely to be the mid to late Katian in age.

Materials and methods

The occurrence and abundance of stromatoporoids in the Xiazhen Formation are considered to be largely governed by depositional environment (e.g., water depth, substrate adaptability, siliciclastic sediment input, depositional energy level). Stromatoporoids are not only common in patch reef environments but also present in non-reef environments. The general co-occurrence of stromatoporoids and calcareous algae in the formation indicates that stromatoporoids lived within the photic zone. Labechiid stromatoporoids exhibited shorter stratigraphic ranges compared with those of tabulate corals and clathrodictyid stromatoporoids (see Liang et al., 2016; Sun et al., 2016; Jeon et al., 2020a).

Eighteen stromatoporoid-bearing intervals are recognized from the Xiazhen Formation at Zhuzhai (Jeon et al., 2020a; labelled as S1 to S18; Fig. 2, 3). Among approximately 420 randomly collected stromatoporoid specimens, approximately 110 specimens are labechiid stromatoporoids collected from the S2 to S8 intervals in sub-section ZU 2 (more than 70 specimens), S8 to S18 in sub-section ZU 1 (40 specimens) and the upper part of sub-section ZU 3 (three fragmented specimens, indicative of transportation before burial) (Fig. 2). Transverse and longitudinal thin sections of the stromatoporoid specimens were prepared for species identification. The majority of specimens are well preserved while a few poorly-preserved specimens were studied by the “white card technique” to enhance views of stromatoporoid internal structures (e.g., Delgado, 1977; Zenger, 1979; Folk, 1987; Jeon et al., 2019; Fig. 4.2, 4.3). The suprageneric taxonomic assignments and terminology used in this study follow those of Webby (2015b, 2015c).

Network analysis, which provides a clear visible network diagram to understand paleobiogeographic links and connections with specific nodes and edges, has been applied in both modern biology and paleobiology (e.g., Sidor et al., 2013; Kiel, 2017; Rojas et al., 2017; Huang et al., 2018; Fang et al., 2019). The occurrences of Ordovician stromatoporoids are organized as a binary dataset (i.e., terranes and labechiid species) and imported into the network analysis software Gephi version 0.9.2 (Bastian et al., 2009). Lines in the diagram (called “edges” in network analysis terminology) connect a source node (terrane) to a target node (labechiid species). A target node linked to only a single source node represents an endemic labechiid. A cosmopolitan species is represented by a multi-connected node. The size of a target node reflects the degree of cosmopolitanism, and larger node size indicates higher degree of cosmopolitanism. There are several options within Gephi for displaying the data, and the layout option called Force Atlas 2 was applied here for the diagram layout. The following parameters within Gephi were used in this study: scaling 2.0, gravity 1.0, edge weight influence 1.0, number of threads 7, tolerance 1.0 and approximation 1.2

The dataset of the Ordovician labechiid stromatoporoids for the network analysis was compiled from previous publications as well as this study, including 181 labechiid species from peri-Gondwanan regions, including South China, North China (Yabe and Sugiyama, 1930a, b; Endo, 1932; Ozaki, 1938; Sugiyama, 1941; Dong, 1982; Kano et al., 1994; Jeon et al., 2017, 2019), Sibumasu (Webby et al., 1985), Australian terranes (Webby, 1969, 1971, 1979b, 1991; Pickett and Percival, 2001; Percival et al., 2001), and Tarim (Dong and Wang, 1984), Laurentia (Galloway, 1957; Galloway and St. Jean, 1961; Kapp and Stearn, 1975; Webby, 1977; Bolton, 1988; Nestor et al., 2010; Copper et al., 2013), Baltica (Nestor, 1960, 1964; Bogoyavlenskaya, 1973; Webby, 1979a), Siberia (Yavorsky, 1955, 1961; Nestor, 1976; Khromykh, 2001), Altai-Sayan Fold Belt (Khalifina, 1960), Tuva (Bogoyavlenskaya, 1971), and Kazakh terranes (Yavorsky, 1961; Karimova and Lessovaya, 2007). A few Ordovician labechiid species are not added in this study due to problematic taxonomic assignment (e.g., Bol'shakova and Ulitina, 1985; Jiang et al., 2011), inaccessibility of original publications, or impoverished occurrence of data. Due to insufficient biostratigraphic precision (i.e., conodonts, graptolites) from carbonate successions, stromatoporoid study relies on relatively coarse temporal resolution. Thus, in this study, we compiled all the data within the Ordovician, using the updated genera-level taxonomic revision of Webby (2015c).

Repository and institutional abbreviation. — All labechiid stromatoporoid specimens and thin sections in this study are housed in Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

Systematic paleontology

Phylum Porifera Grant, 1836

Class Stromatoporoidea Nicholson and Murie, 1878

Order Labechiida Kühn, 1927

Family Rosenellidae Yavorsky in Khalfina and Yavorsky, 1973

Cystostroma Galloway and St. Jean in Galloway, 1957

Type species.—*Cystostroma vermontense* Galloway and St. Jean in Galloway, 1957.

Cystostroma sp. indet.

Figure 4.1, 4.2, 4.3

2020 *Cystostroma* Jeon, Liang, Park, Choh and Lee: p. 200, fig. 5a.

Occurrence — The S2 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeletons are thin laminar, less than 3 mm in height (0.8 mm in average), exclusively encrusting on fragmented shells.

The majority of the skeletons are poorly preserved and fragmented. In longitudinal section, cyst plates are moderately convex, of variable cyst sizes, ranging from 0.13–0.35 mm in height (n=13, species average 0.19 mm) and 0.31–0.71 mm in width (n=13, species average 0.44 mm). Cyst width/height ratio ranges from 1.42 to 3.80, and average 2.38 (n=13). Denticles, latilaminae and mamelons are not observed.

Material.— Two specimens, including NIGP 168771 and 175160 from the S2 interval.

Remarks.— The distinguishable characteristic of the present specimen of this taxon is that its cyst size is more variable than in other species from peri-Gondwanan regions (*Cystostroma* sp. in Webby et al., 1985 and *Cystostroma primordia* Jeon et al., 2019). *C. primordia*, which is the earliest known species of *Cystostroma*, possessed the smallest cysts, ranging from 0.04–0.20 mm in height and 0.09–0.39 mm in length (Jeon et al., 2019). Cysts in *Cystostroma* sp. from Sibumasu range from 0.2–0.6 mm high and 0.7–1.0 mm wide (Webby et al., 1985), bigger than both *C. primordia* and the Xiazhen species. Denticles were not found in all peri-Gondwanan species.

Genus *Rosenella* Nicholson, 1886a

Type species.—*Rosenella macrosystis* Nicholson, 1886a

Rosenella sp. indet.

Figure 4.4, 4.5, 4.6

2020 *Rosenella* Jeon, Liang, Park, Choh and Lee: p. 200, fig. 5b, c.

Occurrence.— The S11 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.— The skeleton is thin laminar, 31 mm in width and 9 mm in height. It was preserved in upside-down position, encrusted by another stromatoporoid (*Ecclimadictyon*). In longitudinal section, cysts are small, low-profile and long, ranging from 0.17–0.53 mm high (n=12, species average 0.31 mm) and 0.99–2.91 mm width (n=12, species average 1.89 mm). Cyst width/height ratio ranges from 3.60 to 13.13, with an average of 6.6 (n=12). Denticles are sporadically developed, appearing as small dots in transverse sections. Latilaminae are not observed. Mamelon-like up-growths are found, approximately 2 mm in height.

Material.— One specimen of NIGP 168772 from the S11 interval.

Remarks.—*Rosenella. woyuensis* Ozaki, 1938 and *R. amzassensis* Khalfina, 1960 differ in having much larger cysts. The cysts of *R. amzassensis* commonly range from 1–3 mm in height and 1–9 mm in width, but in rare cases up to 5 mm in height (Khalfina, 1960), while the cysts of *R. woyuensis* range from 0.3–0.5 mm in height and 0.4–12 mm in width (Ozaki, 1938; Webby, 1969, 1991; Webby et al., 1985).

Genus *Pseudostylodictyon* Ozaki, 1938

Type species.—*Pseudostylodictyon poshanense* Ozaki, 1938.

Remarks.—The original description of genus *Pseudostylodictyon* mentioned the existence of vertical elements, which penetrate through two or even more thinner and low cyst plates (p. 209 in Ozaki, 1938). Vertical elements are best described as pillars, but not well-matched with the rosenellid family group, which mainly comprises cyst plates and accessory denticles. However, subsequent descriptions of stromatoporoid genus previously attributed to *Pseudostylodictyon* and its species did not mention the existence of pillars (e.g., Galloway, 1957; Galloway and St. Jean, 1961; Webby, 1969; Kapp and Stearn, 1975). The most specific characters of long and low cyst plates and mamelon columns have been considered as the most important distinguishable features of this genus (e.g., Galloway, 1957; Galloway and St. Jean, 1961). The most recent description of the type specimens (NIGP 121556a, b; *Ps. poshanense* Ozaki, 1938) described this penetrating vertical structure as 'a vague impression of one or two, more continuous, upwardly and outwardly radiating, pillar-like structures' and 'weakly developed pattern of concentrically arranged cyst plates, outwardly radiating structures, mainly denticles and a few incomplete pillars' in p. 719 of Webby (2015a). Our materials from the Xiazhen Formation, which are identified as *P. poshanense* Ozaki, 1938 and *Pseudostylodictyon* sp., have well-developed pillar-like structures (see Fig. 4.8, 4.9), restricted to mamelon columns. Such features in *P. poshanense* imply that the genus *Pseudostylodictyon* may not be included in the family Rosenellidae and therefore raises the question as to defining the difference between genera *Stylostroma* and *Pseudostylodictyon*. Thus, a follow-up study is required to investigate the presence of pillars in other *Pseudostylodictyon* species.

Pseudostylodictyon poshanensis Ozaki, 1938

Figure 4.7, 4.8

1938 *Pseudostylodictyon poshanensis* Ozaki: p. 208, pl. 24, fig. 2, pl. 25, fig. 1a–e.

Type specimen.—Syntype, longitudinal section of the *Pseudostylodictyon poshanense* Ozaki, 1938 skeleton (NIGP 121556) from the Machiakou Formation (Middle Ordovician, Darriwilian), north of Woyu, Boshan County, Shandong Province, China (Ozaki, 1938, pl. 24, fig. 2; pl. 25, 1a−e).

Occurrence.— The upper part (rudstone interval) of sub-section ZU 3 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Description.—The specimens are transported fragments (thus difficult to determine growth form), up to 30 mm in width and 45 mm in height. Mamelon columns are regularly spaced, 5.52–9.75 mm apart and 4.51–6.72 mm in diameter. Latilaminae are not found.

Cysts are commonly long and low, and range 0.19–1.67 mm in height (n=64, species average 0.57 mm), and 0.59–4.32 mm in width (n=64, species average 1.80 mm). Cyst width/height ratio ranges from 0.38 to 8.53 (n=64, species average 3.65). Cysts, composed of mamelon columns, closely spaced and range 0.19–1.60 mm in height (n=44, species average 0.45 mm) and 0.60–3.57 mm in width (n= 44, species average 1.49 mm). Cyst width/height ratios are from 1.30 to 6.38 (n=44, species average 3.70). Sediment-filled cysts are common, particularly placed between mamelon columns. Vertical elements commonly penetrate through two to three cysts, thus corresponding to the concept of 'pillar' in labechiids. These pillar-like structures are slender and only restricted in mamelon columns (Fig. 4.8), and range 0.46–2.11 mm (n=11, species average 0.99) in height and 0.10–0.21 mm in diameter (n=11, species average 0.16), with flanged and hollow preservation. Denticles are well-developed (Fig. 4.7, 4.8).

Materials.—Two specimens, including NIGP 175161 and 175162 from the upper rudstone interval of sub-section ZU 3 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Remarks.—The most recent description of the type specimens of *Pseudostylodictyon poshanense* Ozaki, 1938 skeleton (NIGP 121556) includes vertical elements, which are presented as 'vague pillar-like structures' (see p. 719 of Webby, 2015a). These vague structures seem to be due to the oblique section of mamelon columns in the limited material available and caused the incomplete morphological shape of pillars. However, subsequent study of *Pseudostylodictyon* species did not describe pillar-like structures (e.g., Galloway, 1957; Galloway and St. Jean, 1961; Webby, 1969; Kapp and Stearn, 1975). Further interspecific comparison of internal morphological features of each *Pseudostylodictyon* species is required.

Pseudostylodictyon sp. indet.

Figure 4.9

2020a *Pseudostylodictyon* Jeon, Liang, Park, Choh and Lee: p. 200, fig. 5d.

Occurrence.—The S15 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Description.—The specimens are fragmentary, with evidence of small domical growth forms, encrusted by other stromatoporoid (*Clathrodictyon*) and spiculate sponges. Fragmentary specimens are up to 20 mm wide and 30 mm high. Mamelon columns are regularly spaced, 5.52–5.74 mm apart and 3.47–4.86 mm in diameter.

The majority of the cyst plates are silicified and poorly preserved. Cysts are long, low and variable, ranging from 0.11–0.48 mm (n=29, species average 0.19 mm) in height and 0.44–1.55 mm in width (n=29, species average 0.85 mm). Cyst width/height ratio ranges from 0.38–8.53 (n=29, species average 4.65). Sediment-filled cysts commonly occur between mamelon columns. Stout pillar-like vertical structures pass through two or more cyst plates. These structures are restricted to mamelon columns, ranging from 0.52–2.70 mm in height (n=14, species average 1.21 mm) and 0.13–0.23 mm in diameter (n=14, species average 0.17 mm).

Materials.—Two specimens, including NIGP 168773 and 175163 from the S15 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Remarks.—The present specimen has cysts of various sizes, but it possesses smaller cysts and stouter pillars than those of *Pseudostylodictyon poshanense* Ozaki, 1938.

Family Labechiidae Nicholson, 1879

Genus *Labechia* Edwards and Haime, 1951

Type species. *Monticularia conferta* Lonsdale, 1839

Labechia altunensis Dong and Wang, 1984

Figure 5.1, 5.2

1984 *Labechia altunensis* Dong and Wang: p. 248, pl. 1, fig 3a, b.

1984 *Labechia sibirica* Yavorsky; Dong and Wang: p. 247, pl. 1, fig 1a, b.

Type specimen.—Syntype, one thin section of *Labechia altunensis* Yang and Dong 1984 (NIGP 70384) from the Malieziken Group (probably upper Darriwilian to lower Sandbian), eastern Ruoqiang County, Xinjiang Province, China (Dong and Wang, 1984, pl. 1, fig 3a, b).

Occurrence.— The S15 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Description.— The specimens are fragmented, thus the original growth form is unknown. Latilaminae, mamelon columns and astrorhizae are not found.

Cysts are relatively small, round and regular in shape, and range from 0.19–0.47 mm high (n=67, species average 0.30 mm) and 0.29–1.86 mm wide (n=67, species average 1.86 mm). Cyst plates have low to moderate convexity and cyst width/height ratio ranges from 1.55–6.43 (n=67, species average 3.17). Pillars are vertically and continuously well-developed with downward-opening growth lines (also often referred to as 'cone-in-cone structure'), and range 1.17–5.44 mm in height (n=14, species average 2.58 mm) and 0.10–0.37 mm in diameter (n=155, species average 0.18 mm). Tops of the pillars are moderately round, but slightly sharp shapes are also seen.

Materials.— One specimen of NIGP 175164 from the S15 interval.

Remarks.—Two *Labechia* species (i.e., *Lb. altunensis* Dong and Wang, 1984 and *Labechia sibirica* Yavorsky, 1955 in Dong and Wang, 1984) from the Middle Ordovician of Tarim Basin, are closely similar to the present species. *Labechia sibirica* Yavorsky 1955 is first reported from the uppermost Silurian of the Stony Tunguska River, Siberian Platform (Yavosky, 1955). Although this Silurian species has similar thicknesses of pillars (about 2 mm; Yavorsky, 1995) with the former two species, it is distinguishable with bigger cysts, ranging from 0.40–1.0 mm high (Yavorsky, 1955) than those earlier species. The specimen of *Lb. sibirica* (NIGP 70382), described by Dong and Wang (1984) possesses very similar morphological measurements of both cysts (cysts ranging from 0.2–0.5 mm high and 0.3–1.4 mm wide) and pillars (0.1–0.2 mm in diameter) with *Lb. altunensis* in Dong and Wang 1984 and present study. Judging from the possession of key morphological characteristics and numeric features of *Lb. altunensis* in the specimens of *Lb. sibirica* (NIGP 70382), i.e., small, round and regular shaped cysts, continuously developed solid pillars and the identical dimension of measurements, thus herein it is regarded as being conspecific with *Lb. altunensis* Dong and Wang, 1984.

Labechia variabilis Yabe and Sugiyama 1930

Figure 5.3, 5.4, 5.5

1930a *Labechia variabilis* Yabe and Sugiyama: p. 54, pl. 17, figs. 1−9.

1938 *Labechia variabilis* Yabe and Sugiyama; Ozaki: p. 211, pl. 28, fig. 1a−d.

1982 *Cystistroma donnellii* Etheridge; Dong: p. 578, pl.1, figs. 1, 2.

1982 *Cystistroma canadense* Nicholson and Murie; Dong: p. 578, pl. 1, figs. 3, 4

1982 *Rosenella cf. woyuensis* Ozaki; Dong: p. 579, pl.1, figs. 5, 6

1982 *Labechia changchiuensis* Ozaki; Dong: p. 579, pl. 2, figs. 1, 2

1985 *Labechia variabilis* Yabe and Sugiyama; Webby et al.: p. 161, fig. 3a−e.

2017 *Labechia yeongwolense* Jeon, Park, Choh and Lee: p. 336, fig. 4f–h.

2020 *Labechiella* Jeon, Liang, Park, Choh and Lee: p. 201, fig. 6b.

Type specimen.—Syntype 37679a, b, 37680a, b, 37682a, b, c in Tohoku University, Japan (Yabe and Sugiyama, 1930a, p. 54, pl. 17, figs. 1−9).

Occurrence.—The S17 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—The skeletons are laminar, up to 50 mm in height and 180 mm in width. Latilaminae, mamelon columns and astrorhizae are not found.

Cysts range from 0.40–1.72 mm high (n=69, species average 0.81 mm) and 1.33–6.02 mm wide (n=69, species average 2.71 mm). Cyst plates have low to moderate convexity, and their cyst width/ height ratios range from 1.76 to 6.21 (n=69, species average 3.42). The preservation of cysts is variable from normal cement-filled, dissolved spar-filled and sediment-filled spaces.

Pillars are sporadically developed, and short, ranging from 1.33–4.77 mm in height (n=25, species average 2.56 mm) and 0.21–0.80 mm in diameter (n=84, species average 0.41 mm). In tangential sections, pillars appear as ellipsoidal to circular shapes. Preservation is variable and selective as solid, hollow and flanged, and dissolved unflanged pillars.

Materials.— Four specimens, including NIGP 168778, 175166–175168 from the S17 interval.

Remarks.— *Labechia variabilis* Yabe and Sugiyama 1930 was first known from the Middle Ordovician Toufangkou and Shanpingchou formations (upper Darriwilian) of northeastern China and Sangsori 'Series' (Sandbian to Katian; see p. 217 in Lee et al., 2017 for the problem of stratigraphic nomenclature in North Korea) of northeastern Korean Peninsula (Yabe and Sugiyama, 1930). One of the key characteristic features of this species is round, stout and small pillars, which are not persistently developed. Its wide range of skeletal variation caused taxonomic confusion, particularly between *Labechia* and *Labechiella*, together with the poor quality of old illustrations in Yabe and Sugiyama, 1930. Recent confirmation of the syntypes deposited in Tohoku University and detailed comparisons with subsequently reported *Labechia* species through China (deposited in NIGPAS, Nanjing; Dong et al., 1982) and Korea (deposited in National Heritage Center of the Cultural Heritage Administration in Korea, Daejeon; Jeon et al., 2017) prove that they are conspecific with *Cystistroma donnellii* Etheridge 1895 in Dong (1982), *Cystistroma canadense* Nicholson and Murie, 1878 in Dong (1982), *Rosenella cf. woyuensis* Ozaki, 1938 in Dong (1982), *Labechia changchiuensis* Ozaki, 1938 in Dong (1982), *Labechia yeongwolense* Jeon, Park, Choh and

Lee, 2017 and *Labechiella* sp. in Jeon et al. (2020), judging from the morphological characteristics and numerical measurements.

Labechia shanhsiensis Yabe and Sugiyama, 1930

Figure 5.6, 5.7

1930a *Labechia shanhsiensis* Yabe and Sugiyama: p. 56, pl. 18, figs. 2−4.

Type specimen.—Syntype IGPS 37685a, b, c, d in Tohoku University, Japan (Yabe and Sugiyama, 1930a, p. 56, pl. 18, figs. 2−4).

Occurrence.—The S18 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeleton is thin laminar, up to 18 mm high and 115 mm wide. Latilaminae, mamelon columns and astrorhizae are not found.

Cysts range 0.33–1.25 mm high (n=96, species average 0.57 mm) and 0.18–3.89 mm wide (n=96, species average 1.29 mm). Cyst plates have moderately to highly convexity, and cyst width/height ratio ranges 0.31–6.98 (n=96, species average 2.29). Pillars are consistently well-developed with long and slender shapes, ranging from 1.62–7.84 mm in height (n=32, species average 3.32 mm) and 0.17–0.52 mm (n=45, species average 0.36 mm) in diameter, and exclusively preserved as flanged and hollow with downward-opening growth lines. In some cases, pillars are curved, perhaps indicating geotrophic growth (white arrow in Fig. 5.6). In the tangential section, pillars are well rounded circular shape.

Materials.—One specimen of NIGP 175165 from the S18 interval.

Remarks.—*Labechia shanhsiensis* Yabe and Sugiyama, 1930, described in Yabe and Sugiyama (1930), has slightly thinner pillars (0.10–0.21 mm in diameter) than the present specimens, and this is considered as the intraspecific variation.

Labechia zhuzhainus Jeon new species

Figure 6.1, 6.2, 6.3, 6.4, 6.5

Type specimen.—Holotype NIGP 175169, paratype NIGP 168777 and 175170

Diagnosis.—A species of *Labechia* with low to moderately convex cyst plates and well-developed continuous stout pillar; cysts, ranging from 0.09–0.99 mm (species average 0.52 mm) high and 0.46–3.99 mm (species average 1.62 mm) wide, with cyst width/height ratio from 1.00 to 22.04, in general, 3.31; pillars ranging from 1.03–5.18 mm (species average 2.44 mm) high and 0.08–0.80 mm (species average 0.35 mm) in thickness.

Occurrence.—The S10 and S16−S18 intervals of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeletons are laminar, up to 40 mm high and 130 mm wide, as having either smooth or ragged skeletal margins. The internal structures are commonly silicified. Latilaminae, rhythmic changes, mamelon columns, and astrorhizae are not found. It commonly encrusted on tabulate coral *Catenipora*, perhaps caused its growth termination (Fig. 6.5), but no evidence of intergrowth association is seen.

Cysts range 0.09–0.99 mm high (n=132, species average 0.52 mm) and 0.46–3.99 mm wide (n=132, species average 1.62 mm). Cyst plates have low to moderate convexity, and cyst width/height ratio ranges from 1.00 to 22.04 (n=132, species average 3.31). Pillars are persistent, stout and short, ranging from 1.03–5.18 mm in height (n=82, species average 2.44

mm) and 0.08–0.80 mm (n=314, species average 0.35 mm) in diameter and dominantly preserved as solid form. Branching pillars are not found.

Etymology.—*Labechia zhuzhainus*: from Zhuzhai, a regional name of the place where this species commonly occurs.

Materials.—Eleven specimens, including NIGP 168777 and 175169–175178 from the S18 interval, four specimens, including NIGP 168779–168782 from the S16 interval, one specimen NIGP 175183 from the S10 interval.

Remarks.—This species is distinguishable with its persistently developed pillars, comparable with *Labechia altunensis* Dong and Wang, 1984 and *Lb. shanhsiensis* Yabe and Sugiyama, 1930 from this formation. However, the internal structure of the present species has larger sizes of cyst than *Lb. altunensis* (Cysts ranging from 0.19–0.47 mm high and 0.29–1.86 mm wide; pillar ranging from 0.10–0.37 mm in diameter). *Lb. shanhsiensis* possesses a similar cyst size to the present species, but it is differentiated by shapes of pillars; *Labechia zhuzhainus* has rounder and stouter pillars than *Lb. shanhsiensis*.

Labechia sp.

Figure 6.6, 6.7

Occurrence.—The S18 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeletons are thin laminar, up to 4 mm high and 72 mm wide. One specimen (NIGP 169634) encrusts the growth surface of *Clathrodictyon* and shows irregularly developed physical contacts between those two species with deformed internal structures.

Cysts range 0.35–1.93 mm high (n=15, species average 0.72 mm) and 0.60–3.52 mm wide (n=15, species average 1.43 mm). Cyst plates have moderate to high convexity, having cyst width/height ratio from 1.00 to 3.85 (n=15, species average 2.04). Pillars are generally preserved as flanged and hollow, with blade-like sharp top margin, ranging from 1.03–5.18 mm in height (n=82, species average 2.44 mm) and 0.15–0.66 mm in diameter (n=65, species average 0.29 mm).

One specimen (NIGP 169634), interpreted spatial competition with a species of *Clathrodictyon* (Jeon et al., 2020b), shows a variety of internal skeletal morphology and variation of cysts and pillars in both structure and size. Deformed cysts up to 2.08 mm high and 5.76 mm wide with irregular thickness. The shape of pillars is also variable, ranging from sharply triangular to stoutly round. The majority of pillars are preserved as hollow and flanged, but solid pillars are also present.

Material.—Three specimens including NIGP 169634, 175184, 175185 from the S18 interval.

Remarks. — The present species is distinguishable with its blade-like sharp and short pillars. However, owing to the thin shape and small size of the entire skeleton, with a wide range of internal skeletal morphological features, it is currently required that the species remains in open nomenclature.

This is the only *Labechia* species showing paleoecological interaction (in this case competition) with *Clathrodictyon*, with *Labechia* probably a paleoecological subordinate to *Clathrodictyon* (Jeon et al., 2020b).

Genus *Labechiella* Yabe and Sugiyama, 1930

Type species. —*Labechia serotina* Nicholson, 1886b

Labechiella beluatus Jeon new species

Figure 7.1, 7.2, 7.3, 7.4

Type specimen. —Holotype NIGP 175187, paratype NIGP 175188

Diagnosis. —A species of *Labechiella* with moderately convex cyst plates and very large persistent pillars; cysts, ranging from 0.25–0.84 mm (species average 0.84 mm) high and 0.30–11.08 mm, (species average 2.56 mm) wide; cyst width/height ratio ranging from 0.58–7.48, (species average 3.02); pillars ranging from 0.26–0.93 mm (species average 5.37 mm) high and 0.15–0.54 mm (species average 0.32 mm) in diameter.

Occurrence. —The S15 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description. — Skeletons are fragmented, perhaps pieces of large laminar in growth forms, up to 50 mm high 110 mm wide. Latilaminae, rhythmic changes, mamelon columns, and astrorhizae are not found.

Cysts range 0.25–0.84 mm (n=186, species average 0.84 mm) high and 0.30–11.08 mm (n=186, species average 2.56 mm) wide. Cyst plates have moderate convexity, and cyst width/height ratio ranges 0.58–7.48 (n=186, species average 3.02). Pillars are very large and persistently distributed, ranging from 0.25–0.84 mm in height (n=186, species average 0.84 mm) and 0.30–11.08 mm (n=186, species average 2.56 mm) in diameter. Branching pillars are commonly seen.

Etymology. —*Labechiella beluatus*: from Latin *béluae*, the meaning of beast, wild animal, monster, in referring to persistently well-developed large pillars.

Materials. —Three specimens, including NIGP 175187–175189.

Remarks. —This new species is distinguishable from previously known Ordovician *Labechiella* species in that the former has very large and multi-branching pillars.

Labechiella gondwanense Jeon new species

Figure 7.5, 7.6, 7.7

1969 *Labechia variabilis* Yabe and Sugiyama; Webby: p. 650, pl. 121, figs. 1, 2.

1991 *Labechiella variabilis* (Yabe and Sugiyama); Webby: p. 198, figs. 3a−d, 4e−f.

2011 *Cystistroma donnellii* (Etheridge 1895) Jiang et al. p. 302 pl. 1 figs 1,2

Type specimen.— Holotype NIGP 175186

Diagnosis.— A species of *Labechiella* with low to moderately convex cyst plates, and persistently well-developed slender pillar with slightly-developed downward-opening growth lines; cysts ranging from 0.45–1.07 mm (species average 0.78 mm) high and 1.47–10.01 mm (species average 3.27 mm) wide; cyst width/height ratio ranging from 1.71–11.08 (species average 4.16); pillars ranging from 0.44–9.53 mm in height (species average 4.58 mm) and 0.16–3.81 mm (species average 0.45 mm) in diameter.

Occurrence.—The S17 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.— Skeleton is laminar, up to 19 mm high and 90 mm wide. Latilaminae and astrorhizae are not found. Mamelon-like upward growth is seen.

Cysts range 0.45–1.07 mm (n=52, species average 0.78 mm) high and 1.47–10.01 mm (n=52, species average 3.27 mm) wide. Cyst plates have low to moderate convexity, and cyst width/height ratio ranges from 1.71–11.08 (n=52, species average 4.16). Pillars are continuously well-developed with slightly-developed downward-opening growth, ranging from 0.44–9.53 mm in height (n=26, species average 4.58 mm) and 1.47–10.01 mm in diameter (n=52, species average 3.27 mm). Branching forms are intensely developed with particular mamelon-like upward growth. Pillars are commonly preserved as solid, but hollow and flanged pillars are also found.

Etymology.—Named after its wide distribution throughout the peri-Gondwanan regions including North China, South China and Australia during the Middle to Late Ordovician interval.

Materials.—One specimen of NIGP 178186 from the S17 interval.

Remarks.—Previously known *Labechiella variabilis* (Yabe and Sugiyama, 1930) in Webby (1969, 1991) is fairly different from the original description of type specimens of *Labechia variabilis* Yabe and Sugiyama, 1930. The former species is characterized by its flat and gently convex cyst plates and vertically persistent long pillars (Webby, 1969, 1991), which is consistent with the concept of genus *Labechiella*, rather than *Labechia* (Webby, 2015a). Both species from New South Wales and Tasmania has branching pillars (Webby, 1969, 1991), which is similar to the present specimens from the Xiazhen Formation. However, *Lb. variabilis* is characterized by variable cyst size with low to moderate convexity and sporadically developed stout, short pillars, but branching pillars have not been confirmed (Yabe and Sugiyama, 1930; Ozaki, 1938; Dong, 1982; Jeon et al., 2017; present study). Therefore, this formerly known species from New South Wales and Tasmania is considered to be an independent species of *Labechiella* from *Lb. variabilis* Yabe and Sugiyama 1930, and we named as *Lblla. gondwanense* Jeon sp. nov., judging from its morphological characteristics of *Labechiella* and numerical similarity of internal structures.

Cystistroma donnellii (Etheridge, 1895) in Jiang et al. (2011) is far from the concept of genus *Cystistroma* (see Webby, 1969, p. 652, pl. 122, figs. 3–8, pl. 123, figs. 1–5 for *Cystistroma donnellii* and Webby, 2015c, p. 785 for genus *Cystistroma*), judging from its plain and parallel cyst plates (see Jiang et al., 2011, p. 302, pl.1, fig. 1). This species has rather thick and straight pillars, punctuating up to two parallel cyst plates. The morphological features are close to the concept of genus *Labechiella*, and share morphological and numerical similarity with current Xiazhen material. Thus, herein this *Cystistroma* species from North China is regarded as being conspecific with *Lblla. gondwanense*.

Labechiella regularis (Yabe and Sugiyama, 1930)

Figure 7.8

1930a *Labechia regularis* Yabe and Sugiyama: p. 56, pl. 18, figs. 5, 6, pl. 21, fig. 8.

1930a *Labechia regularis* var. *tenuis* Yabe and Sugiyama: p. 57, pl. 21, figs. 9−10.

1930b *Labechia regularis* var. *tenuis* Yabe and Sugiyama: p. 9, pl. 3, fig. 1, pl. 4, figs. 1−2.

1938 *Labechia regularis* Yabe and Sugiyama; Ozaki: p. 210, pl. 26, fig. 2a−d.

1955 *Labechia regularis* Yabe and Sugiyama; Yavorsky: p. 59, pl. 24, figs. 4, 5.

1969 *Labechia regularis* Yabe and Sugiyama; Webby: p. 649, pl. 120, fig. 1, pl. 121, figs 3−6, pl. 124, figs 1, 2.

1971 *Tuvaechia regularis* (Yabe and Sugiyama); Bogoyavlenskaya: p. 35, pl. 2, fig. 1a, b

1991 *Labechiella regularis* (Yabe and Sugiyama); Webby: p. 200, fig. 3g.

1994 *Labechiella regularis* (Yabe and Sugiyama); Kano et al.: p. 453, figs 3, 4a−e.

2017 *Labechiella regularis* (Yabe and Sugiyama); Jeon et al.: p. 335, fig. 4a−c.

Type specimen.—Syntype 37684 in Tohoku University of Japan; others are probably missing (Yabe and Sugiyama, 1930a, pl. 18, figs. 5, 6, pl. 21, fig. 8).

Occurrence.—The S15 interval of sub-section ZU2 and the upper part (rudstone interval) of sub-section ZU 3 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeletons are low domical, up to 55 mm high and 220 mm wide. Latilaminae, mamelons and astrorhizae are not found.

Cyst plates are regularly spaced, gently parallel to slightly concave to other cyst plates, which shares morphological similarity with laminae. The height of cysts ranges from 0.21–0.73 mm (n=155, species average 0.39 mm). The marginal edge of cyst plates is obscure, because of silicified preservation. Distances between each pillars are 0.25–2.44 mm (n=155, species average 0.92 mm). Pillars are persistent, long, and vertically well-developed, although they are variably preserved as solid or hollow without any outlines. Pillars range 1.91–9.43 mm in height (n=70, species average 4.23 mm) and 0.21–0.52 mm in diameter (n=70, species average 0.36 mm).

Materials.—Three specimens including NIGP 175190–175192.

Remarks. *Labechiella regularis* (Yabe and Sugiyama, 1930) has the widest distribution among other Ordovician labechiid species. It occurs in many peri-Gondwanan regions, including North China (Yabe and Sugiyama, 1930; Ozaki, 1938; Jeon et al., 2017), South China (present study) and Australia (Webby, 1969, 1991), to Siberian Platform (Yavorsky, 1955) and Tuva (Bogoyavlenskaya, 1971) during the late Middle to Late Ordovician interval. Among them, the Xiazhen materials are particularly close to *Lblla. regularis* from the Upper Ordovician of the Stony Tunguska and Kotuy rivers (Yavorsky, 1955), central New South Wales (Webby, 1969) and Tasmania (Webby, 1991), whereas the materials from Tuva exhibit thinner pillar, ranging from 0.10–0.15 mm (Bogoyavlenskaya, 1971). *Lblla. regularis* from the Upper Ordovician strata of Mongolia, described by Bol'shakova and Ulitina (1985), is not consistent with the original description and illustration of Yabe and Sugiyama (1930). The Mongolian samples possess much thinner cysts and slender pillars compared to previously reported materials (see Bol'shakova and Ulitina, 1985, p. 48, pl. 2, fig. 1a, b), and it seems to be an independent species of *Labechiella*, rather than *Lblla. regularis*.

Family Stylostromatidae Webby, 1993

Genus *Stylostroma* Gorsky, 1938

Type species.—*Stylostroma crissum* Gorsky, 1938.

Stylostroma bubsense Webby, 1991

Figure 8.1, 8.2, 8.3, 8.4

1991 *Stylostroma bubsense* Webby: p. 204, figs. 6d−e, 7a−b.

2020 *Pachystylostroma* Jeon, Liang, Park, Choh and Lee: p. 200, fig. 5g.

Type specimen.—Holotype UTGD 94659 from the lower part of the Gordon Limestone at Bubs Hill, and one paratype UTGD 94660 from the Dogs Head Formation of the middle Chudleigh Subgroup between Overflow Creek and Sassafras Creek, 1.5 km northwestern way of Ugbrook (Webby, 1991, p. 204, figs. 6d−e and 7a−b); deposited in University of Tasmania, Australia.

Occurrence.—The S15 and S17 intervals of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeletons are distinctively well-mammillate with domical growth form, up to 40 cm high and 100 cm wide, but mostly less than 46 mm in height and 90 mm in width. The mamelon columns are regularly placed, up to 12.26 mm (species average 6.97 mm) apart, ranging from 6.14–26.35 mm in height (n=10, species average 13.06 mm) and 1.45–3.42 mm in diameter (n=22, species average 2.51 mm). A certain phase without any mamelon columns is also observed.

Cysts are variable in both size and shape, ranging from 0.20–3.44 mm (n=153, species average 1.08 mm) high and 0.57–10.40 mm (n=153, species average 3.17 mm) wide. Generally, it has moderate convexity, but elongated, flat or highly convex cyst plates also commonly occur, and cyst width/height ratio ranges 1.36–7.59 (n=153, species average 3.27). Cyst plates particularly in the area of inter-mamelon are rather more irregularly and widely placed than the non-mamelon skeletal phase.

Denticles are the most predominant vertical elements. Pillars are generally short and less continuous and range 0.27–2.70 mm in height (n=14, species average 1.21 mm) and 0.09–

0.23 mm (n=14, species average 0.17 mm) in diameter. Preservation is variable from solid, hollow, and spar-filled forms.

Materials.—Ten specimens, including NIGP 168776 and 175193–175201

Remarks. — The present Xiazhen specimens of *Stylostroma bubsense* Webby 1991 share close morphological similarity with the Tasmanian specimens (Webby, 1991). Both specimens exhibit elongate to moderately convex cyst plates. The distributions of pillars are also similarly intensively developed in mamelon columns, while sparsely distributed in other skeletal phases (Webby, 1991).

Stylostroma bubense is also comparable with *Pachystylostroma mammillatum* Webby, 1979. However, due to lack of key characteristics of the genus *Pachystylostroma* (i.e., cysts of variable size, with alternating gently wavy cyst plates with wall thickness ranging from thin to very thick; Nestor, 1964, Webby, 2015a), the former *Pachystylostroma mammillatum* has been revised as a species of *Stylostroma*, *Sty*. *mammillatum* (Webby, 1979) (see p. 201 in Webby, 1991). It differs in exhibiting more commonly developed pillars than the present specimens. In addition, its mamelons do not exhibit any vertical elements, i.e., denticles and pillars (Webby 1979).

Stylostroma ugbrookense Webby, 1991

Figure 8.5, 8.6

1991 *Stylostroma ugbrookense* Webby, p. 202, figs. 5a−e, 6a−c.

2020 *Stylostroma* Jeon, Liang, Park, Choh and Lee: p. 200, fig. 5f.

Type specimen.—Holotype UTGD 94648 and nine paratypes (UTGD 90521, 94649, 98500−98506) from the upper part of the Dogs Head Formation (Upper Ordovician, early

Katian) of the Gordon Group of Ugbrook in Mole Creek area and Gunns Plains of Tasmania, Australia (Webby, 1991, p. 202, figs. 5a−e and 6a−c); deposited in University of Tasmania, Australia.

Occurrence.—The S3, S5−6 intervals of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China. It occurs commonly in S6 interval with domical growth form up to 40 cm high and 100 cm wide, while it is rare in S3 and S5 with laminar growth form up to 5 cm high and 13 cm wide.

Description.—Skeletons are laminar to low domical growth forms, up to 40 cm high and 100 cm wide, and it has slightly to highly wavy laminar forms. Mamelons are generally slender, regularly spaced, up to 18 mm (but normally around 9 mm) apart, and vertically aligned, probably owing to geotrophic growth. Non-mamelon skeletal phase also occurs. Undulating sediment-filled spaces between mamelon columns are commonly observed, but do not have lateral continuity. Latilaminae are seen, up to 70 mm, but not common.

Cysts are generally small, ranging from 0.11–0.57 mm high (n=255, species average 0.27 mm) and 0.20–14.33 mm wide (n=255, species average 2.39 mm). Cyst plates have low to moderate convexity, ranging in cyst width/height ratio from 1.00 to 30.93 (n=255, species average 8.11). Cysts, in the area between two mamelon columns, are slightly to moderately larger than those that occur in mamelon columns and non-mamelon skeletal phases. Pillars are slender and well-developed through the skeleton, but also absent in some parts of the skeleton, which is composed of only cyst plates and denticles. Pillars are more dominantly developed with outward curved direction in mamelon columns. Pillars range 0.54–6.36 mm in height (n=132, species average 2.40 mm) and 0.13–0.39 mm in diameter (n=132, species average 0.21mm). In tangential sections, pillars show ‘distinctive stellate branching patterns’ (Webby, 1991), thus astrorhizae. Preservation is variable, even within a single skeleton, ranging from solid to hollow, with or without outlined walls, and spar-filled pillars.

Materials. —Twenty-three specimens, including NIGP 168775 and 175202–175223 from the S6 interval, NIGP 175224 from the S5 interval, NIGP 175225 from the S3 interval.

Remarks.—The materials from Tasmania exhibit cysts with variable size and shape ranging from 0.1–0.3 mm high and 0.6–1.2 mm wide, and well-developed pillars, ranging up to 12 mm high and 0.20 mm in diameter (Webby, 1991) which is closely similar to the present Xiazhen materials. However, in the present material, a skeletal phase without any vertical element, which is only composed of cyst plates, is also observed. This difference is considered as intraspecific variation.

Family Aulaceratidae Kühn, 1927

Genus *Thamnobeatricea* Raymond, 1931

Type species.—*Thamnobeatricea parallela* Raymond, 1931

Thamnobeatricea gouldi Webby, 1991

Figure 9.1, 9.2, 9.3, 9.4, 9.5, 9.6

1979 *Cryptophragmus*? sp. Webby: p. 97, fig. 5c.

1991 *Thamnobeatricea gouldi* Webby: p. 220, Figs. 14a–f, 16b

2020 *Aulacera* Jeon, Liang, Park, Choh and Lee: p. 200, fig. 5e.

Type specimen.—Holotype, deposited in University of Tasmania, Australia, UTGD 94654 and two paratypes (UTGD 81647, 98525) from the upper part of the Lower Limestone Member of the Benjamin Limestone (Gordon Group) in the Florentine Valley, Tasmania (Webby, 1991, p. 220, figs. 14a–f, 16b).

Occurrence.—The S2−S5 and S8 intervals of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

Description.—Skeletons are long, continuous, dominated by single columnar growth form, and up to 160 mm in height and 11 mm in width (commonly 8 to 10 mm). Branching form is rarely observed. They are preserved in a variety of orientations and mostly fragmented. Astrorhizae are not found.

Internal skeletal structure is composed of axial, lateral and outer recrystallized lateral zones, which can be distinguished by the presence and size of cyst plates. The axial zone occupies more than 50 percent of the diameter, composed of slightly overlapping large cyst plates. Cysts range from 1.58–5.79 mm in height (species average 2.96 mm, n=75) and 1.04–8.41 mm in width (species average 4.72 mm, n=75). Cyst plates have moderate to high convexity, and cyst width/height ratio ranges from 0.34–3.73 (n=75, species average 1.59). Lateral zone is composed of up to 5 cyst plates, ranging from 0.29–2.20 mm, mostly approximately 1 mm. Cysts in the lateral zone are smaller than those in the axial zone, ranges 0.12–1.30 mm in height (n=276, species average 0.26 mm) and 0.21–1.58 mm in width (n=276, species average 0.61 mm). Cyst plates have moderate convexity, and cyst width/height ratio ranges from 0.91–4.56 (n=276, species average 2.39). Denticles are rarely developed, and pillars are not found. Branches developed from the abnormally large cyst plates in the lateral zone (Fig. 9.5). Outer lateral zone, which does not exhibit any internal structure, composed of coarse calcite spar replacement, ranging from 0.54–2.82 mm, mostly around 1.50 mm, with distinctive nodular external surfaces. The outer surface is also characterized by sporadically developed denticles.

Cyst plates vary from sharp-leaf or pointed-top shapes to overlapping bubble-like forms as the skeleton grew (Fig. 9.3, 9.4). The lateral zone, which is composed of small cysts, is rudimentary in early growth, but the outer coarse-calcite-recrystallized lateral zone are persistent.

Materials.—Five specimens, including NIGP 175231–175235 from the S3 interval, six specimens, including 168774 and 175226–175230 from the S4 interval, NIGP 175249 from the S5 interval, and thirteen specimens, including NIGP 175236–175248 from the S8 interval.

Remarks.—The present specimens are similar to Tasmanian specimens in terms of both skeletal features and measurements. However, the Tasmanian specimens (particularly UTGD 90454; see fig. 16b in Webby 1991) commonly show branching form, which is rare in the specimens of the Xiazhen Formation. It seems to show intraspecific variation in different environmental conditions.

Genus *Sinabeatricea* Jeon new genus

Type species.—*Sinabeatricea luteolus* new genus new species

Diagnosis.—Branching columnar aulaceratid, composed of two skeletal zones; in the axial zone, an open radiating fibrously reticulate network occupying about 60 % of the diameter, surrounded by low to moderately convex cyst plates, and penetrated by short and stout pillars; round papillae well-developed, representing tops of individual pillars on the terminal growth surface; astrorhizae unknown.

Occurrence.— The S3 interval of the lower Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Etymology.—Latin, *Sina*, China. Billings (1857) did not state the derivation of his genus name *Beatricea*, which has been revised as a junior synonym of *Aulacera* Plummer, 1843. It probably derived from the Latin word *Beatrix*, bringer of happiness.

Remarks.— The internal structure of *Sinabeatricea* gen. nov. is divided into two skeletal zones: the central axial columnar zone and the outer surrounded lateral zone, which is a typical characteristic of aulaceratid stromatoporoids. Aulaceratid genera were reported from peri-Gondwana, Laurentia, and Siberia (i.e., *Aulacera* Plummer, 1843, *Thamnobeatricea* Raymond, 1931, *Sinodictyon* Yabe and Sugiyama, 1930, *Ludictyon* Ozaki, 1938, *Alleynodictyon* Webby, 1971, *Quasiaulacera* Copper, Stock and Jin, 2013), but not in Baltica. This group possesses large, convex-up, and widely spaced cyst plates with or without denticles in their axial zones. *Sinabeatricea* is differentiated from previous known aulaceratid genera by possession of the open reticulate skeletal elements in the axial column, while other genera possess large, convex, widely spaced overlapped cyst plates in the axial column (Webby, 2015c). This unique axial zone is surrounded by moderately convex cyst plates with continuous, stout, and short pillars, similar to other aulaceratid genera, possessing common skeletal characteristics *Labechia*.

The diversification of aulaceratid stromatoporoids occurred intensively in the Middle Ordovician interval, and their early diversification was epichroic (Stock et al., 2015; Nestor and Webby, 2013). Aulaceratid labechiids initially diversified only in North China, recorded by five genera, and none of them are known from the other contemporary terranes of late Darriwilian age (Stock et al., 2015; Nestor and Webby, 2013, Webby, 2015a). However, those North Chinese Darriwilian provincial aulaceratids are not known in the Upper Ordovician succession of North China. Together with the highest diversity peak of Ordovician stromatoporoids in the Katian, seven aulaceratid genera are known, mostly from Australia (Webby, 1971, 1991) and Laurentia (Cameron and Copper, 1994; Copper et al., 2013). This probably indicates that their subsequent diversification was related to worldwide dispersion during the Middle to Late Ordovician interval. It is postulated that aulaceratids were highly diverse in Laurentia and Siberia (Personal communication with Paul Copper, 2020), but only a few species have been reported (Copper et al., 2013). Recent studies reveal that Greenland (Harper et al., 2014) and Siberia (Dronov et al., 2016) are also promising for aulaceratid research, and further detailed study is needed.

Sinabeatricea luteolus Jeon new species

Figure 10.1, 10.2, 10.3, 10.4, 10.5

Type specimen.—Holotype NIGP 175250, paratypes 175251 and 175252.

Diagnosis.—A species of *Sinabeatricea* with open radiating reticulate network of 16–20 mm in diameter in the axial zone, occupying up to about 60 percent of the diameter of the fossil; the reticulate network surrounded by lateral zone, and composed of low to moderately convex cyst plates penetrated by short and stout pillars; cyst plates ranging from 0.19–0.69 mm high and 0.11–1.80 mm wide; pillars ranging from 1.04–3.75 mm high and 0.18–0.68 mm in diameter.

Occurrence.—The S3 interval of the lower Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai section, Yushan County, Jiangxi Province, China.

Description. Skeletons are restricted to columnar growth form, up to 40 mm in diameter. Height is indeterminable because the specimens are preserved as fragmented stems with a variety of orientations. Mamelons and astrorhizae are not found.

Internal skeletal structure is divided into two different skeletal zones, axial and lateral zones. Those skeletal zones are differentiated by open reticulate skeletal structure and cyst plates with well-developed pillars. The axial zone is composed of open radiating reticulate skeletal structure, ranging from 0.09–0.15 mm in thickness. The axial zone grades to the lateral zone, which is composed of cyst plates and continuous well-developed pillars. Cysts range from 0.19–0.69 mm high (n=43, species average 0.35 mm) and 0.11–1.80 mm wide (n=43, species average 0.73 mm). Cyst plates have low to moderate convexity, and cyst width/height ratio ranges from 0.42–5.04 (n=43, species average 2.12). Pillars, which are round and persistently well-developed, generally penetrate less than four cyst plates, ranging from 1.04–3.75 mm (n=58, species average 2.27 mm) high and 0.18–0.68 mm (n=99, species average 0.31 mm) in diameter. Preservation is solid and partially silicified.

Etymology.—*Sinabeatricea luteolus*: from Latin *lūteolus*, yellowish, in referring to its distinctive color.

Materials.—Five specimens including NIGP 175250–175254 from the S2 interval.

Remarks.—This species is distinguishable from other known aulaceratid species by a distinctive axial zone with open reticulate skeletal structure, surrounded by moderately convex cyst plates that are penetrated by short and stout pillars. This meshwork structure has not been observed in other aulaceratid species, nor other labechiid groups. The basal part of the skeleton has not been found, thus it is difficult to compare with other taxa and also to assess how this columnar species initially grew. A further study of better-preserved specimens is required to reveal its growth characteristics.

Paleobiogeographic pattern of Ordovician labechiid stromatoporoids

A total of 181 species is recorded in publications and this new study, which is a relatively large number of taxa, and may represent most, if not all, of the total stromatoporoid low-level taxa (species) of this part of the Ordovician record. However, this study cannot address the validity of this range of taxa, so the full complement of recorded taxa is used in analysis here. Thus the analyzed 181 species belong to 22 genera of labechiid stromatoporoids that occurred throughout 12 terranes. Most of the stromatoporoid species were endemic and occur only within a single terrane. Laurentia shows the highest species-level diversity among all terranes. However, in terms of generic level, 14 labechiid genera have been reported from peri-Gondwanan regions, particularly South China and Australian regions, possessing the highest genetic diversity level (compiled data from Webby in Stock et al., 2015, present study and other compiled references). The result of the network analysis (Fig. 11) shows that the Ordovician stromatoporoids can be grouped into two faunal provinces, the peri-Gondwana–Tarim–Siberia (GTS) and Laurentia–Baltica–Siberia (LBS), judging from the occurrences of characteristic genera (i.e., *Labechiella* and *Stromatocerium*) and co-occurring stromatoporoid species.

Peri-Gondwana–Tarim–Siberia (GTS) Province. —The GTS Province is characterized by the co-occurrences of *Rosenella woyuensis*, *Pseudostylodictyon poshanense*, *Labechia shanhsiensis*, *Lb. variabilis, Labechiella regularis* (Fig. 11). Their earliest reports are from the Middle Ordovician carbonates (upper Darriwilian) of North China (Yabe and Sugiyama, 1930; Ozaki, 1938; Dong, 1982). The North Chinese fauna reached its greatest diversity during the late Darriwilian. This stromatoporoid assemblage is initially provincial in North China during the Middle Ordovician but became widely distributed to adjacent regions during the Late Ordovician. This identifiable, successive stromatoporoid fauna is herein termed North China Darriwilian provincial assemblage. The GTS Province is also characterized by the wide distribution of *Labechiella*, comparable to that of *Stromatocerium* in Laurentia, Baltica, and a certain part of Siberia.

The occurrences of *Labechia altunensis* Dong and Wang, 1984 and *Stylostroma*-related species indicate that Tarim was close to South China and Tasmania in biogeographic relations during the Late Ordovician, as it has also been observed from other fossil groups (e.g., Han et al., 2009; Tang et al., 2017; Fang et al., 2019; Sproat and Zhan, 2019). Although the Mongolian species in Bol'shakova and Ulitina (1985) require further re-evaluation of taxonomy, species of *Labechiella*, *Lophiostroma* and *Ludictyon* occur in the Upper Ordovician strata of Mongolia, indicating that Mongolia had a close biogeographic affinity with peri-Gondwanan terranes (especially North China) and Siberia (Stock et al., 2015; Nestor and Webby, 2014).

Laurentia–Baltica–Siberia (LBS) Province. —The LBS Province represents the highest diversity species level of labechiid stromatoporoids and only a few species shared among Laurentia, Baltica, and Siberia. LBS province is also characterized by the occurrence of *Stromatocerium* (e.g., Galloway, 1957; Galloway and St. Jean, 1961; Bogoyavlenskaya, 1973; Nestor, 1976; Bolton, 1988; Khromykh, 2001). Baltica has distinctively low species-level diversity, which is possibly due to the late arrival of early labechiid stromatoporoids. In addition, columnar aulaceratid stromatoporoids were not found to occur in Baltica, but they have been reported from both Laurentia and Siberia (e.g., Yavorsky, 1955; Galloway, 1957; Galloway and St. Jean, 1961; Bolton, 1988; Copper et al., 2013).

In Siberia, the labechiid assemblage is characterized by a mixture of both Laurentian and peri-Gondwanan species, judging from the occurrence of *Stromatocerium*, gigantic *Aulacera*, and *Labechiella* (particularly *Labechiella regularis*), and other co-occurring labechiids such as *Rosenella woyuensis*, *Labechia huronensis*, *Lb*. *macrostyla*, *Stromatocerium australe*, *Aulacera undulata* (Fig. 11.1). This reflects the bilateral migration patterns from both peri-Gondwana and Laurentia, which corresponds to the study of possible oceanic currents during the Middle to Late Ordovician interval (e.g., Servais et al., 2014; Pohl et al., 2016).

Discussion

Stromatoporoids indicate shallow, tropical to subtropical waters (Nestor and Webby, 2013; Stock et al., 2015). Ordovician labechiid stromatoporoids are specifically regarded as temperature-sensitive and thermophilic (Nestor and Stock, 2001; Webby, 2004). In the past several decades, the paleobiogeographic study of Ordovician stromatoporoids in both regional and global scales provided the basis for understanding their distribution patterns and biogeographic affinities among different terranes (e.g., Lin and Webby, 1989; Nestor and Webby, 2013; Stock et al., 2015; Webby, 1980, 1992). However, these studies did not pay enough attention to South China, due to a lack of sufficient investigation of stromatoporoids from this terrane, as only few genera have been reported from South China before (e.g., Lin and Webby, 1989; Nestor and Webby, 2013; Stock et al., 2015). Recent investigation (Jeon et al., 2020) revealed a diverse stromatoporoid fauna in the Xiazhen Formation, indicating that South China was also a favorable region for the diversification of stromatoporoids similar to other peri-Gondwanan regions. As many as 19 genera of labechiid stromatoporoids globally occurred in the Katian, attaining the highest generic diversity level during the entire evolutionary history of labechiids (Webby, 2004; Stock et al., 2015). In geographic ranges, they also attained the widest circum-equatorial distribution (Webby, 2004). Due to the obvious higher generic diversity level, the peri-Gondwanan regions, including Australia and South China and some other terranes, has been proposed to be the diversification center for Late Ordovician stromatoporoids (Stock et al., 2015, Nestor and Webby, 2013, Jeon et al., 2020a).

Pseudostylodictyon poshanense, *Labechia shanhsiensis*, *Lb. variabilis*, and *Labechiella regularis* are found in the Xiazhen Formation. These species occurred first in the upper Darriwilian of North China, which possessed the most diverse and distinctive Darriwilian labechiid fauna, including 24 species in 9 genera (Yabe and Sugiyama, 1930a, b; Endo, 1932; Ozaki, 1938; Sugiyama, 1941; Dong, 1982; Kano et al., 1994; Jeon et al., 2017, 2019), and are herein defined as North China Darriwilian provincial species. Among these early North Chinese species, *Rosenella woyuensis* and *Lb. variabilis* also occur in the coeval succession of Sibumasu (Unit J of the Lower Setul Limestone of the Langkawi Islands, Malaysia;

Webby et al., 1985), reflecting the close paleogeographic distance between North China and Sibumasu during the Ordovician (Burrett et al., 2014, 2017). The subsequent occurrences of those particular species in South China and Australian regions indicate that the North China provincial species dispersed among the peri-Gondwana regions during the late Middle Ordovician to Late Ordovician interval. Of these species, *Lbllla. regularis* significantly shows the widest geographic distribution (Fig. 11.1), occurring in North China (Darriwilian of the Middle Ordovician; Yabe and Sugiyama, 1930; Ozaki, 1938 Kano et al., 1994; Jeon et al., 2017), Australian terranes (including New South Wales and Tasmania; Katian of Upper Ordovician; Webby, 1969; Webby, 1991), Kazakh terranes (Katian of Upper Ordovician; Karimova and Lesovaya, 2007) and Siberia (Katian of Upper Ordovician; Bogoyavlenskaya, 1971; Yavorsky, 1955; Khromych, 2001). The dispersal pattern of other North China Darriwilian provincial labechiids, including *Rosenella woyuensis*, *Pseudostylodictyon poshanense*, *Labechia variabilis*, and *Lb. shanhsiensis*, are fairly similar to that of *Lbllla. regularis* (Fig. 11.1). The distribution and dispersal pattern of North China provincial species show that co-occurring species of stromatoporoids occur more commonly in terranes which are geographically close together, thus evaluation of co-occurring stromatoporoid species can be useful for the criterion for establishment of the biogeographic realm of terranes (Fig. 11).

Together with those North China Darriwilian provincial labechiid species, other species also support a close paleobiogeographic affinity with Australia. It has been proposed that South China and Australia (including New South Wales and Tasmania) may have close paleobiogeographic relationships, judging from the occurrences of a few clathrodictyid species (Stock et al. 2015). Our network analysis shows that South China shares many common labechiid species with those of central New South Wales and Tasmania (Fig. 11.1), including *Labechiella gondwanense* sp. nov., *Lbllla. regularis*, *Stylostroma bubsense*, *Sty. ugbrookense* and *Thamnobeatricea gouldi*. *Labechiella gondwanense* sp. nov. occurs widely in North China (formerly *Cystistroma donnellii* in Jiang et al., 2011), South China, New South Wales (formerly *Labechia variabilis* in Webby 1969), and Tasmania (formerly *Labechiella variabilis* in Webby 1991) during the Katian. Until now, Tasmanian stromatoporoids fauna were thought to be closely related to those from Laurentia, judging from the shared occurrences of the labechiid genera *Thamnobeatricea*, *Pachystylostroma,* and *Aulacera* (Stock et al. 2015; Lin and Webby 1989; Webby 1991; Webby et al., 2000). However, the finding of co-occurring labechiid species, including *Stylostroma bubsense*, *Sty. ugbrookense* and *Thamnobeatricea gouldi* in both South China and Tasmania (Webby, 1991 and the present study) indicates that the Tasmanian Shelf had a much closer palaeobiogeographic affinity with peri-Gondwanan regions than with Laurentia. It is noteworthy that New South Wales had a quite different labechiid assemblage from that of Tasmania (Nestor and Webby, 2013, Webby et al., 2000), although they were geographically close to each other during the Late Ordovician. In the case of the Tasmanian labechiids, species of *Pachystylostroma*, *Aulacera,* and *Thamnobeatricea* are found but these are not known from coeval successions of New South Wales. A species of *Cystistroma* was found to occur in New South Wales (Webby, 1969) instead of Tasmania and South China. In contrast, *Alleynodictyon* commonly occurs in both Tasmania and New South Wales (Webby, 1971, 1991, Webby et al., 2000), whereas it is not found in South China.

Although the exact location of Tarim during the Late Ordovician is still controversial, the paleobiogeographic studies of various fossil groups consistently show that Tarim and other peri-Gondwanan terranes share faunal affinities (Webby et al., 2000; Stock et al., 2015; Tang et al., 2017; Han et al., 2017; Sproat and Zhan, 2019). In terms of stromatoporoids, judging from the occurrence of *Labechia altunensis* Dong and Wang 1984 in South China and Tarim, *Stylostroma* in Tasmania (Webby, 1991), South China, and *Stylostroma*-related species in Tarim (formerly classified as *Pseudolabechia* in Dong and Wang, 1984; ranges from probably late Darriwilian to early Sandbian; Webby et al., 2000), those two terranes are closely related. This close biogeographic affinity is correspondingly supported by other fossil groups, including brachiopods (Sproat and Zhan, 2019), distinctive conodonts *Tasmanognathus* (Zhen et al., 2010) and *Serratognathus* (Wang et al., 2007; Zhen et al., 2009), chitinozoans (Tang et al., 2017), and corals (Han et al., 2017). However, it should be noted that North China Darriwilian provincial species (e.g., *Rosenella woyuensis, Pseudostylodictyon poshanense*, *Labechiella regularis* and *Lblla*. *variabilis*) occurred in many peri-Gondwanan regions (particularly South China and Australia) but not in Tarim, indicating a relatively large distance between North China and Tarim.

Rhynchonelliform brachiopods, which were one of the most common invertebrate fossil groups during the Great Ordovician Biodiversification Event, exhibit similar biogeographic patterns to that of the labechiid stromatoporoids. The South China rhynchonelliform brachiopods were generally composed of cosmopolitan species, having faunal similarity with the Kazakh terranes in the Sandbian (Harper et al., 2013, Cocks and Torsvik, 2020). During the middle to late Katian, the South China brachiopods exhibited a close relationship with those of the eastern Gondwanan (particularly, New South Wales) fauna, reflecting the northern path via South China (Torsvik and Cocks, 2017), and this pattern became more evident by the middle to late Katian as South China likely intersected migration pathways defined by surface currents (Harper et al., 2013). This is rather similar to the biogeographic pattern of Late Ordovician labechiid stromatoporoids in that South China shares a number of co-occurring species with eastern Gondwanan regions (including New South Wales and Tasmania). A recently-proposed new term 'Cathay-Tasman Province' (Cocks and Torsvik, 2020) correspondingly shows similar recognition of a faunal province, judging from the studies of brachiopods and trilobites. However, it differs from the current GTS Province, as the former does not include Siberia, Altai-Sayan Fold Belt, and Mongolia (see fig. 6 and corresponding text in Cocks and Torsvik, 2020). Graptolites and cephalopods, which are mobile organisms reached a high diversity level in the Late Ordovician, exhibiting generally increasing endemism throughout the Katian, apparently different from the above-mentioned benthic sessile organisms (Goldman et al., 2013; Fang et al., 2019). During the Late Ordovician, the cephalopod assemblage of South China had biogeographic affinities with those from small terranes of peri-Gondwana (i.e., Sibumasu, Lhasa, Himalaya) located between South China and Australia, but it is remarkably different from that of Australia (Fang et al., 2019). The pattern of cephalopod distribution is somewhat different from that of of labechiid stromatoporoids, which is likely due to different modes of living strategies.

Overall, the Xiazhen labechiid assemblage is influenced by the northward rifting of South China along peri-Gondwana, forming a more favorable environmental condition for the development of stromatoporoids, judging from combination of the succeeding North China Darriwilian provincial species and Australian (especially Tasmania) faunas. This labechiid assemblage reflects the idea that South China was likely the locus for the intersectional migrations of North Chinese Darriwilian and Australian labechiid species during the Late Ordovician. The high diversity level in these peri-Gondwanan terranes is possibly due to the strong dispersal ability and rapid speciation rate of the labechiid stromatoporoids during their early evolutionary history.

Conclusions

(1) A diverse fauna of labechiid stromatoporoids is recorded from the Upper Ordovician Xiazhen Formation of South China, which represents one of the highest diversity levels among the terranes of the Late Ordovician. A total of 16 labechiid species belonging to eight genera are identified, including one new genus and four new species.

(2) The assemblage is characterized by a mixture of South China endemic species and North China Darriwilian provincial species (*Ps. poshanense*, *Lb. shanhsiensis*, *Lblla. regularis* and *Lblla. variabilis*), which were also commonly found in the other coeval peri-Gondwanan terranes, especially New South Wales and Tasmania of Australia. The dispersal of North China Darriwilian labechiid provincial species through the Late Ordovician of peri-Gondwanan terranes shows that endemism declined as stromatoporoids achieved their widest Ordovician circum-equatorial distribution. Moreover, the finding of *Sty. ugbrookense* and *Tha. gouldi* from both South China and the Tasmanian Shelf indicates that those two regions had a closer biogeographic affinity during Late Ordovician than previously thought.
(3) The northward shift of South China near to north-eastern Gondwanan terranes provided migration pathways of early labechiid stromatoporoids, resulting in a highly diverse Xiazhen labechiid assemblage that shared strong affinities to those of North China and Australian regions (especially Tasmania) during the Late Ordovician.

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FIGURE CAPTIONS

Figure 1. (1) Geographic map of China showing South China. **(2)** Enlargement of the study area near the border area between Jiangxi and Zhejiang provinces. The Zhuzhai section is indicated by the white square. **(3)** Geological map of the Xiazhen Formation, which is divided into three sub-sections, ZU 1, ZU 2, and ZU3.

Figure 2. Stratigraphic column of the Xiazhen Formation with 18 stromatoporoid-bearing intervals. The red-colored intervals indicate where labechiid stromatoporoids were found mostly together with clathrodictyids except S6 and S8 intervals. The black-colored intervals indicate where only clathrodictyid stromatoporoids were found C= claystone; M = mudstone or lime mudstone; W = wackestone; P = packstone; G = grainstone, F = floatstone or framestone; R = rudstone. LLM = lower limestone member; LSM = lower shale member; MMM = middle mixed-lithology member; USM = upper shale member. Modified after Lee et al. (2012) and Park et al. (2021). A large size version of this

figures is presented in Supplementary Data 1. ~~Full size of the column is presented in the Supplementary Data 1.~~

Figure 3. Lithofacies, interpreted energy-level and distributions of labechiid stromatoporoids and growth forms from the each stromatoporoid-bearing interval of the Xiazhen Fomation; SBI = stromatoporoid-bearing interval; M = mudstone, W = wackestone, P = packstone, G = grainstone, L–S couplets = limestone–shale couplets; L = low-energy depositional environment; M = medium-energy depositional environment; H = high-energy depositional environment; 1 = *Rosenella* sp.; 2 = *Cystostroma* sp.; 3 = *Pseudostylodictyon poshanense*; 4 = *Pseudostylodictyon* sp.; 5 = *Labechia altunensis*; 6 = *Labechia shanhsiensis*; 7 = *Labechia variabilis*; 8 = *Labechia zhuzhainus* sp. nov.; 9 = *Labechia* sp.; 10 = *Labechiella beluatus* sp. nov.; 11 = *Labechiella gondwanense* sp. nov.; 12 = *Labechiella regularis*; 13 = *Stylostroma bubsense*; 14 = *Stylostroma ugbrookense*; 15 = *Thamnobeatricea gouldi*; 16 = *Sinabeatricea luteolus* gen. et sp. nov.

Figure 4. (1–3) *Cystostroma* sp. from the S2 interval of the formation. **(1)** Longitudinal section showing *Cystostroma* sp. encrusted on shelly skeletal fragments, NIGP 168771-1. **(2)** Enlarged photograph noted in white rectangular area in **(1)**. **(3)** Longitudinal section of *Cystostroma* sp. with variable size of cysts, NIGP 175160. **(4–6)** Longitudinal and tangential sections of *Rosenella* sp. from the S11 interval, NIGP 168772. **(7, 8)** *Pseudostylodictyon poshanense* Ozaki 1938 from the upper part of rudstone interval of ZU 3, NIGP 175161. **(7)** Longitudinal section showing skeletal phase without mamelon columns. **(8)** Longitudinal section showing skeletal phase with mamelon with vertically punctuating vertical skeletal structure, seems to be pillars (white arrows). **(9)** Longitudinal section of selectively silicified *Pseudostylodictyon* sp. from the S15 interval. Note the white arrows indicating the vertically punctuating stout vertical skeletal structures that seem to be pillars, NIGP 168773.

Figure 5. (1, 2) Longitudinal and tangential sections of *Labechia altunensis* Dong and Wang, 1984 from the S15 interval, NIGP 175164-1. **(3–5)** Longitudinal and tangential sections of *Lb. variabilis* Yabe and Sugiyama, 1930 from the S17 interval, NIGP 168778-1, 5, 3, respectively. Branching and slender pillars are also seen in **(5)**. **(6–7)** Longitudinal and tangential sections of *Lb. shanhsiensis* Yabe and Sugiyama, 1930 from the S 18 interval, NIGP 175165-1, 3, respectively. The white arrow indicates a curved pillar in **(6)**, perhaps due to geotropic growth.

Figure 6. (1, 2) Longitudinal and tangential sections of *Labechia zhuzhainus* Jeon sp. nov. from the S18 interval, holotype NIGP 175169. **(3, 4)** Longitudinal and tangential sections of of *Lb. zhuzhainus* sp. nov. from the S18 interval, paratype NIGP 168777. Note the skeletal variation in **(3)**. **(5)** Longitudinal sections showing *Lb. zhuzhainus* sp. nov. encrusted on tabulate coral *Catenipora* from the S18 interval, paratype NIGP 175170. Note that the coral and stromatoporoid were not in a symbiotic intergrowth association. **(6, 7)** Longitudinal and tangential sections of *Labechia* sp. from the S18 interval, NIGP 175184 and NIGP 175185-1, respectively.

Figure 7. (1–3) Longitudinal and tangential sections of *Labechiella beluatus* Jeon sp. nov. from the S15 interval, holotype NIGP 175187-1, 2, respectively. Note very large, well-developed and persistent pillars. **(4)** Gradual skeletal change from longitudinal to tangential view of *Lblla. beluatus* sp. nov. from the S15 interval, paratype NIGP 175188-1. Note the existence of multi-branching pillars. **(5–7)** Longitudinal and tangential sections of *Lblla. gondwanense* Jeon sp. nov. from the S17 interval, holotype NIGP 175186-1, 2, 14, respectively. White arrow in **(6)** indicates a branching pillar developed in mamelon-like up-growth of the skeleton. **(8)** Longitudinal view of selectively silicified *Lblla. regularis* (Yabe and Sugiyama, 1930) from the rudstone interval of upper ZU 3, NIGP 175190.

Figure 8. (1, 2) Longitudinal and tangential sections of *Stylostroma bubsense* Webby 1991 from the S15 interval, NIGP 175193-1, 5, respectively. Note well-developed, but also sporadically developed, mamelon columns in **(1)**. **(3, 4)** A variety of longitudinal skeletal phases of *Sty. bubsense* from the S17 interval, NIGP 175194 and 175195, respectively. **(5, 6)** Longitudinal and tangential sections of *Sty. ugbrookense* Webby 1991 from the S6 and S3 intervals, NIGP 175202 and 175225-1 respectively. Note variable preservation of pillars, ranging from hollow (white arrows) and solid (black arrow) pillars in **(5)**.

Figure 9. (1–6) Longitudinal and tangential sections of *Thamnobeatricea gouldi* Webby 1991. Note the ontogenetic variation of cyst plates. **(3, 4)** Black arrows indicate the sharp marginal top of cyst plates in the early growth stage and white arrows indicate mature round cyst plates. **(5)** The occurrence of unusual large cyst plates (white arrows) in the later zone results in branching skeletons. **(1)** NIGP 175236-1 from the S8 interval, **(2)** NIGP 175237 from the S8 interval, **(3)** NIGP 175232 from the S3 interval, **(4)** NIGP 175233 from the S3 interval, **(5)** NIGP 175238 from the S8 interval, **(6)** NIGP 175249 from the S5 interval.

Figure 10. (1–3) Holotype NIGP 175250 of the longitudinal section of *Sinabeatricea luteolus* Jeon gen. et sp. nov. from the S3 interval of the Xiazhen Formation. **(2)** enlarged photograph in the rectangular area of **(1)** with typical skeletal characteristics of labechiids. **(3)** Tangential section of the lateral zone. **(4, 5)** Skeletal variations from the open reticulate network in the axial zone to cyst with pillars in the lateral zone from the S3 interval, paratypes NIGP 175251 and 175252, respectively.

Figure 11. (1) Network analysis diagram of Ordovician labechiid stromatoporoids using the layout Force Atlas 2 in Gephi version 0.9.2 (also see text) during the Ordovician. The

listed species are co-occurring labechiids between two or more terranes. North China Darriwilian provincial species are indicated with an asterisk mark (*). **(2)** Two major faunal provinces of labechiid stromatoporoid distribution during the Ordovician. Paleogeographic reconstruction modified from Cocks and Torsvik (2020). Note that the global stromatoporoid distribution is restricted to tropical to subtropical climatic zones.