

1 **Rise of clathrodictyid stromatoporoids during the Great Ordovician**

2 **Biodiversification Event: insights from the Upper Ordovician Xiazhen**

3 **Formation of South China**

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5 Juwan Jeon^{1,2}, Kun Liang^{1*}, Stephen Kershaw^{3,4}, Jino Park⁵, Mirinae Lee⁶ and Yuandong

6 Zhang^{1,2}

7

8 ¹State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and

9 Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy

10 of Sciences, Nanjing 210008, China

11 ²University of Chinese Academy of Sciences (UCAS), Beijing 100049, China

12 ³Department of Life Sciences, Brunel University, Kingston Lane, Uxbridge, UB8 3PH, UK

13 ⁴Earth Sciences Department, Natural History Museum, Cromwell Road, London, SW7 5BD,

14 UK

15 ⁵Department of Geology, Kangwon National University, Chuncheon, 24341, Republic of

16 Korea

17 ⁶Division of Polar Earth-System Sciences, Korea Polar Research Institute, Incheon, 21990,

18 Republic of Korea

19

20 E-mail: Juwan Jeon [jjeon@nigpas.ac.cn], Kun Liang [kliang@nigpas.ac.cn], Stephen
21 Kershaw [stephen.kershaw@brunel.ac.uk], Jino Park [jinopark@kangwon.ac.kr], Mirinae
22 Lee [mirinae.lee@kopri.re.kr], Yuandong Zhang [ydzhang@nigpas.ac.cn]

23

24 ***Corresponding author:** kliang@nigpas.ac.cn

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26 **Running Header:** Late Ordovician clathrodictyid stromatoporoids from South China

27

28 **Abstract.**—Clathrodictyids are the most abundant stromatoporoids in the Upper Ordovician
29 Xiazhen Formation (middle to upper Katian) of South China. A total of nine species
30 belonging to four clathrodictyid genera are identified in the formation, including
31 *Clathrodictyon idense* Webby and Banks, 1976, *Clathrodictyon* cf. *Cl. microundulatum*
32 Nestor, 1964, *Clathrodictyon* cf. *Cl. mammillatum* (Schmidt, 1858), *Clathrodictyon*
33 *megalamellatum* Jeon n. sp., *Clathrodictyon plicatum* Webby and Banks, 1976,
34 *Ecclimadictyon nestori* Webby, 1969, *Ecclimadictyon undatum* Webby and Banks, 1976,
35 *Camptodictyon amzassensis* (Khalfina, 1960) and *Labyrinthodictyon cascum* (Webby and
36 Morris, 1976). The clathrodictyid fauna in the Xiazhen Formation is very similar to those
37 from both New South Wales and Tasmania, although the latter two Australian regions do not
38 share any common clathrodictyid species during the Late Ordovician. The
39 paleobiogeographic pattern indicates that the northward drift of South China resulted in a
40 favorable environment for the migration of clathrodictyids from other peri-Gondwanan
41 terranes to South China. Also, these peri-Gondwanan clathrodictyid species hosted various
42 endobionts, representing a variety of paleoecological interactions. The high abundance and

43 species-level diversity of clathrodictyid species presumably increased the substrate
44 availability of suitable host taxa, judging from the diverse intergrowth associations between
45 clathrodictyids and other benthic organisms. These paleoecological interactions between
46 stromatoporoid and other organisms are known from the Late Ordovician and became more
47 abundant and widespread in the Siluro–Devonian. Overall, the Late Ordovician clathrodictyid
48 assemblage in South China demonstrates one of the highest species-level diversities among
49 all peri-Gondwanan terranes and represents a precursor of clathrodictyid-dominant complex
50 communities of metazoan reefs.

51

52 UUID: <http://zoobank.org/f99f2d55-7f61-4a83-99fe-abc33ec47f6b>

53

54 **Introduction**

55

56 Clathrodictyid stromatoporoids form the dominant stromatoporoid group that became
57 cosmopolitan during the Silurian, and were abundant until the end of the Devonian (Nestor,
58 1997; Nestor and Stock, 2001), surviving the Frasnian-Famennian extinction (Webby et al.,
59 2015, fig. 363). This group is characterized by weakly differentiated and inflected laminae
60 with short to superposed pillars (Nestor, 1997, 2015) and is regarded as one of the most
61 important early Paleozoic stromatoporoids involved in the establishment of mid-Paleozoic
62 coral-stromatoporoid metazoan reefs (Nestor, 1997; Copper, 2002, 2011; Stearn, 2015a).
63 Their early appearance was recorded in the middle Katian Stage of the Late Ordovician, and
64 by then they were already widely distributed (Bolton, 1988; Lin and Webby, 1988; Nestor et
65 al., 2010; Nestor and Webby, 2013; Stearn et al., 2015; Webby, 2015a), in accordance with
66 the wide distribution of Ordovician metazoan reefs (Webby, 2002; Stock et al., 2015). The

67 early diversification of clathrodictyid stromatoporoids involved four genera (i.e.,
68 *Clathrodictyon*, *Ecclimadictyon*, *Camptodictyon* and *Labyrinthodictyon*), which occurred in
69 the middle Katian in central New South Wales and spread to the Tasmanian Shelf and South
70 China (peri-Gondwanan terranes), as well as Laurentia and Baltica (Webby, 2004, 2015a;
71 Stock et al., 2015; Webby et al., 2015; Jeon et al., 2020a).

72 In South China, clathrodictyids are commonly recorded as significant reef components on
73 the northern margin of the Cathaysian landmass (e.g., Yu et al. 1992; Chen 1995, 1996; Bian
74 et al. 1996; Li et al. 2004; Zhang et al. 2007). The Jiangshan-Changshan-Yushan (JCY)
75 triangle, on the border between Jiangxi and Zhejiang provinces of south-eastern China (Fig.
76 1), is particularly well-known for the development of clathrodictyid-dominated reefs (Bian et
77 al., 1996; Li et al., 2004; Wang et al., 2012; Yu et al., 1992; Park et al. 2021). Recent
78 investigations of Late Ordovician stromatoporoids from the Xiazhen and coeval Sanqushan
79 formations of the JCY triangle (Jeon et al. 2020a, 2022) revealed that clathrodictyids played a
80 critical role in a relatively complex reef community. However, species-level taxonomic work
81 on clathrodictyids has not been conducted. This study therefore: 1) presents a new detailed
82 taxonomic description of clathrodictyid stromatoporoids from the Upper Ordovician Xiazhen
83 Formation at Zhuzhai, Jiangxi Province, China; 2) links taxonomy with paleoecological
84 features; and 3) applies this information towards understanding the global development of
85 stromatoporoids as part of the Great Ordovician Biodiversification Event (GOBE). The
86 results emphasize the importance of early fossil records of clathrodictyids in the development
87 of stromatoporoids in the Late Ordovician Period.

88

89 **Geological setting**

90 The Upper Ordovician Xiazhen Formation at Zhuzhai, Yushan County, Jiangxi Province is
91 among the most classic representatives of Upper Ordovician carbonate successions in South
92 China (Fig. 1). The formation is characterized by mixed carbonate–clastic deposits, situated
93 on the Zhe-Gan Platform along the northern margin of the Cathaysian landmass (Li et al.,
94 2004; Zhang et al., 2007; Park et al., 2021). The depositional environment is interpreted to be
95 a mixed siliciclastic–carbonate ramp-type platform (Park et al., 2021). The Zhuzhai section of
96 the formation can be divided into three partially correlated sub-sections ZU1, ZU2 and ZU3
97 (Lee et al., 2012; Figs. 1.3, 2), separated by Quaternary sedimentary deposits (Fig. 1.3). The
98 stratigraphy of the Zhuzhai section was revised and divided into three units: a lower
99 limestone member, a lower shale member, a middle-mixed lithology member, and an upper
100 shale member in stratigraphic ascending order (Lee et al. 2012; Fig. 2). Comprehensive
101 paleontological studies on many fossil groups from the formation covered algae, brachiopods,
102 bryozoans, cephalopods, corals and trilobites, but little information is available for
103 stromatoporoids (Chen et al., 1987; Bian and Zhou, 1990; Chen, 1995, 1996; Lee et al., 2012,
104 Kwon et al., 2012; Lee, 2013; Dai et al., 2015; Lee et al., 2016a, 2016b, 2019; Liang et al.,
105 2016; Sun et al., 2016; Zhang, 2016; Park et al., 2017; Zhang et al., 2018; Jeon et al., 2020a,
106 b). The Xiazhen Formation is roughly correlative to the Sanqushan and Changwu formations
107 judging from the fossil components such as brachiopods and corals, and was previously
108 estimated to be of middle to late Katian age (e.g., Zhan et al., 2002; Zhang et al., 2007). The
109 discovery of graptolite *Anticostia uniformis* (Mu and Lin in Mu et al., 1993) in the base of the
110 upper shale member confirmed that the upper part of the formation is within the
111 *Dicellograptus complanatus* to *Paraorthograptus pacificus* Biozone (*Diceratograptus mirus*
112 Subzone), indicating a late Katian age (Chen et al., 2016).

114 **Materials and methods**

115 Approximately 420 specimens were collected from the 18 stromatoporoid-bearing intervals
116 (Figs. 2, 3), of which over 300 belong to clathrodictyid stromatoporoids. In the lower
117 limestone member, only two clathrodictyid specimens were collected. No stromatoporoid was
118 found in the lower shale member, interpreted to be deposited below wave base (Park, 2017)
119 and beyond the threshold of stromatoporoid survival. The majority of specimens were
120 collected from the S2 to S9 intervals of sub-section ZU2 and the S9 to S18 intervals of sub-
121 section ZU1, while only a few fragmented clathrodictyid samples were collected from ZU3,
122 which is correlated to the upper part of ZU 1 (Figs. 2, 3; see Lee et al., 2012, figs. 8 and 9). In
123 this collection, 239 stromatoporoid samples were selected and 420 thin sections were made
124 for taxonomic studies. These include specimens used by Lee et al. (2016a) and Jeon et al.
125 (2020a, b). The suprageneric taxonomic assignment and terminology used in this study
126 follow those of Nestor (2015) and Webby (2015b).

127 Network analysis is applied to evaluate the global paleobiogeographic affinity of
128 Ordovician clathrodictyids, and presented as a diagram showing geographic relationships of
129 taxa. Occurrences of clathrodictyid species are organized as a binary dataset (i.e., terrane and
130 clathrodictyid species), processed with Gephi software, version 0.9.2 (Bastian et al., 2009) to
131 produce a network analysis diagram in which a source node (i.e., terrane) is connected to a
132 target node (i.e., clathrodictyid species) by a line (called an edge in Gephi terminology).
133 Endemic clathrodictyid species are revealed where a target node is linked to only a single
134 source node. Cosmopolitan species are indicated where several source nodes (terrane) are
135 connected to several target nodes (taxa) and the size of the nodes provides a visual
136 impression of the degree of cosmopolitanism. From the various display options within Gephi,
137 Force Atlas 2 was chosen to display the clathrodictyid data as the most appropriate for the

138 purposes of this study. The following parameters were involved in this study: scaling 10.0,
139 gravity 1.0, edge weight influence 1.0, number of threads 3, tolerance 1.0 and approximation
140 1.2.

141 The dataset of the Ordovician clathrodictyid stromatoporoids for the network analysis was
142 collected from previously published data as well as in this study, including 27 species from
143 South China (Lin and Webby, 1988; Jeon et al., 2022; this study), North China (Lin and
144 Webby, 1988), Qaidam (Lin and Webby, 1988), Tarim (Dong and Wang, 1984), New South
145 Wales (Webby, 1969; Webby and Morris, 1976; Pickett and Percival, 2001), Tasmania
146 (Webby and Banks, 1976), Altai-Sayan Fold Belt (Khalfina, 1960), Laurentia (Bolton, 1988;
147 Nestor et al. 2010) and Baltica (Nestor, 1964; Bogoyavlenskaya, 1973). A few previously
148 reported clathrodictyid species are not included (e.g., Bol'shakova and Ulitina, 1985;
149 Khromych, 2001; Jiang et al., 2011) because of their problematic taxonomic assignments or a
150 lack of detailed description and illustration.

151

152 *Repository and institutional abbreviation.*— All the clathrodictyid stromatoporoid specimens
153 from the Xiazhen Formation, are deposited in Nanjing Institute of Geology and
154 Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

155

156 **Systematic paleontology**

157

158 Phylum Porifera Grant, 1836

159 Class Stromatoporoidea Nicholson and Murie, 1878

160 Order Clathrodictyida Bogoyavlenskaya, 1969

161 Family Clathrodictyidae Kühn, 1939

162

163 *Clathrodictyon* Nicholson and Murie, 1878

164 *Type species.*—*Clathrodictyon vesiculosum* Nicholson and Murie, 1878.

165 *Clathrodictyon idense* Webby and Banks, 1976

166 Figure 4

167

168 1976 *Clathrodictyon idense* Webby and Banks, p. 130, pl. 1, figs. 1, 2

169

170 *Type specimen.*—Holotype UTGD 58125 from the Gordon Limestone Subgroup, southwest
171 of Ida Bay, Tasmania: precise stratigraphic horizon and location unknown (Webby and
172 Banks, 1976, p. 130, pl. 1, figs. 1, 2); deposited in University of Tasmania, Hobart, Australia.

173 *Occurrence.*—The S2–4, S7 and S9 intervals of the Xiazhen Formation (Upper Ordovician,
174 Katian) at Zhuzhai, Yushan County, Jiangxi Province, China (Figs. 2, 3).

175 *Description.*—Columnar to dendroid forms of skeletons (up to 100 mm high and 7 mm wide)
176 dominate; fragmented low domical and bulbous ones (up to 40 mm high and 50 mm wide)
177 are also common. Skeletons exhibit a variety of orientations. Astrorrhizae, latilaminae and
178 mamelons are not observed.

179 Laminae are continuous, moderately wavy, and regularly spaced, ranging 0.05–0.23 mm
180 thick (number of measured laminae=121, average 0.13 mm); 5–7 laminae per millimeter.

181 Pillars are short, stout, and rod-like. Galleries are commonly elongated and round, ranging
182 0.10–1.15 mm wide (number of measured galleries=121, average 0.42 mm).

183 In the axial part of the columnar and dendroid growth forms, zigzag-shaped cassiculate
184 skeletal structure is well-developed. The structure is sharply folded and radially upward-

185 arranged, which resembles the *Ecclimadictyon*-like cassiculate structure. During growth it
186 gradually changed to the normal laminae skeletal phase (Fig. 4.1, 4.3).

187 *Materials*.—27 specimens, including NIGP 159424, 159440, 159441, 177100–177113 from
188 the S2–S3 interval, NIGP 177114 and 177115 from the S7 interval, NIGP 177116–177123
189 from the S9 interval the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan
190 County, Jiangxi Province, China.

191 *Remarks*.—The present Xiazhen specimens show close morphological resemblances to those
192 of *Clathrodictyon idense* Webby and Banks, 1976 from the Gordon Limestone Subgroup,
193 southwest of Ida Bay, Tasmania. The Tasmanian specimens are similar to the present
194 specimens in features of laminae, exhibiting 10–12 laminae within 2 mm (Webby and Banks,
195 1976). However, the Tasmanian specimens are restricted to sheet-like growth forms (Webby
196 and Banks, 1976), in contrast to the present specimens, which show a much wider spectrum
197 of growth forms (Fig. 3).

198

199 *Clathrodictyon megalamellatum* Jeon new species

200 Figure 5

201

202 *Type specimen*.—Holotype with three thin sections, NIGP 177124-1–3 from the S18 interval
203 of the Xiazhen Formation at Zhuzhai, Yushan County, Jiangxi Province, China.

204 *Diagnosis*.—*Clathrodictyon* with laminae planar, continuous, laterally well-developed and
205 widely spaced, ranging 1.05–4.21 mm in thickness (2 to 3 per millimeter); pillars rod- to
206 funnel-like, and crumpled; galleries varying from slightly round to angular, ranging 0.17–
207 1.60 mm in width; microstructure compact.

208 *Occurrence*.—The S18 interval of the Xiazhen Formation (Upper Ordovician, Katian) at
209 Zhuzhai, Yushan County, Jiangxi Province, China (Figs. 2, 3).

210 *Description*.—Skeleton is low domical, up to 98 mm wide and 45 mm high. Astrorhizae and
211 latilaminae are not found, but mamelon-like upward-arching areas are common. Laminae are
212 continuous, planar, and notably widely spaced, ranging 1.05–4.21 mm in thickness (number
213 of measured laminae=92, average 2.62 mm), laminae spaced 2–4 per mm (mostly 3). Wavy
214 and slightly undulating laminae are rarely seen. In longitudinal section, pillars are well-
215 defined and commonly extend to inter-laminar space, varying from rod- to funnel-like shapes.
216 In tangential section, pillars range from round to elongate. Galleries vary from slightly round
217 to angular shapes, ranging 0.17–1.60 mm (number of measured galleries=88, average 0.53
218 mm) wide.

219 *Etymology*.—Combination of Greek, *mégas*, large and latin, *lamella*, thin plate or layer;
220 derivation from its morphological feature of widely spaced laminae with well-developed
221 pillars, clearly distinguishable from other previously known *Clathrodictyon* species found in
222 Late Ordovician strata.

223 *Material*.—One specimen of NIGP 177124-1–3 from the S18 interval of the Xiazhen
224 Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

225 *Remarks*.—~~This new species has the most widely spaced planar laminae, which is the most~~
226 ~~distinctive and distinguishable feature unlike other previously known *Clathrodictyon* species~~
227 ~~during the Ordovician.~~ One of the typical skeletal features of *Clathrodictyon* is irregularly
228 wrinkled laminae (Nestor 2015), but wavy laminae are less common in *Clathrodictyon*
229 *megalamellatum* Jeon n. sp. Its planar laminae (Fig 5.1, 5.2, 5.3, 5.4, 5.8) are rather similar to
230 that of the genus *Petridiostroma*, which is characterized by planar and continuous laminae
231 (Nestor, 2015). However, in terms of pillars, the present new species is closer to genus
232 *Clathrodictyon* in morphological features, possessing varying rod-, funnel to crumpled form
233 in both longitudinal and tangential sections (Fig. 5). *Petridiostroma* is first known in the early
234 Silurian (middle Llandovery), much later than the appearance of *Clathrodictyon* in the Late

235 Ordovician (middle Katian) (Webby et al., 2015; Stock et al., 2015). Although this new
 236 species possesses similar morphological features to both *Clathrodictyon* and *Petridiostroma*,
 237 here it is regarded as a species of *Clathrodictyon*, based on their similarity of pillars and
 238 stratigraphic occurrences.

239

240 *Clathrodictyon* cf. *Cl. mammillatum* (Schmidt, 1858)

241 Figure 6

242

243 cf. 1858 *Stromatopora mammillata* Schmidt: p. 232

244 cf. 1867 *Stromatopora mammillata* Schmidt; Rosen, p. 71, pl. 8, figs 1-5.

245 cf. 1964 *Clathrodictyon mammillatum* (Schmidt); Nestor, p. 42, pl. 13, figs 7-8 (cum syn)

246 1969 *Clathrodictyon* aff. *mammillatum* (Schmidt); Webby, p. 657, pl. 126, figs. 3–5.

247 non cf. 1980 *Clathrodictyon mammillatum* (Schmidt); Yang and Dong, p. 397, pl. 1, figs. 5–

248 6.

249 1988 *Clathrodictyon* cf. *mammillatum* (Schmidt); Lin and Webby, p. 242, fig. 5a–e.

250 2022 *Clathrodictyon* cf. *mammillatum* (Schmidt); Jeon, Li, Na, Liang and Zhang, p. 60, figs

251 2a, b, 3a, b, 4a, b.

252

253 *Occurrence*.—The S1, S3, S9, 11, 14–16 and S18 intervals of sub-sections ZU1 and ZU2,
 254 and the lower part of ZU3 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai,
 255 Yushan County, Jiangxi Province, China (Figs. 2, 3).

256 *Description*.— Growth form of skeletons varies from laminar, low domical, dendroid, to
 257 irregular, up to 80 mm wide and 50 mm high, and commonly fragmented. Mamelons range
 258 1.89–3.90 mm in diameter (number of measured mamelons=8, average 2.94 mm), and up to

259 5.35 mm apart from each other, generally around 3 mm. Astrorhizae and latilaminae are not
260 found.

261 Laminae vary from slightly wrinkled, and laterally continuous well-developed, ranging 0.07–
262 0.45 mm (number of measured laminae=113, average 0.14 mm), and spacing 4–8 laminae per
263 millimeter (normally 5 laminae). Pillars are dominantly simple rod-like, and rarely branching
264 triangular wedge-shape. Galleries are round, elongated and slightly angular, ranging 0.12–
265 0.95 mm (number of measured galleries=0.96, average 0.34 mm) wide. In the axial part of the
266 dendroid form, laminae are more widely spaced than the normal phases, and radially arranged
267 with sharply folded zigzag *Ecclimadictyon*-like phases (Fig. 6.4).

268 *Material*.—20 specimens, including NIGP 177125, 177126 from the S1 interval, NIGP
269 177127–177130 from the S9 interval, NIGP 177131 from S11 interval, NIGP 177132 from
270 the S15 interval, NIGP 177133-1, 2 and 177313 from the S16 interval, NIGP 159423,
271 159430, 159433, 159442, 159445, 159447, 159448, 169634-1–20, 177134, 177135 from the
272 S18 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan
273 County, Jiangxi Province, China.

274 *Remarks*.—The present specimens of *Clathrodictyon* cf. *Cl. mammillatum* from the Xiazhen
275 Formation share close morphological features with those from Sanqushan, Changshan,
276 Zhejiang Province and New South Wales (Lin and Webby, 1988; Webby, 1969; Jeon et al.,
277 2022). Laminae in the latter specimens are spaced 6–9 laminae per 2 mm (Webby, 1969),
278 thicker than those of the Xiazhen Formation specimens, which is considered as intraspecific
279 variation.

280

281 *Clathrodictyon* cf. *Cl. microundulatum* Nestor, 1964

282

Figure 7

283

284 cf. 1964 *Clathrodictyon microundulatum* Nestor, p. 41, pl. 13, figs. 1–6
285 1969 *Clathrodictyon cf. microundulatum* Nestor; Webby, p. 657, pl. 126, fig. 6, pl. 127, figs
286 1–4.
287 1988 *Clathrodictyon cf. microundulatum* Nestor; Lin and Webby, p. 242, Fig. 6a, b.
288 2021 *Clathrodictyon cf. microundulatum* Nestor; Jeon, Li, Na, Liang and Zhang, p. 62, figs
289 2e, f, 4e, f.
290
291 *Occurrence.*—The S3, S13 and 15–18 intervals of sub-sections ZU1 and ZU2, and the upper
292 part of ZU3 of the of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan
293 County, Jiangxi Province, China (Figs. 2, 3).
294 *Description.*—Skeletons range from laminar, low to high domical, to irregular growth forms.
295 Large domical forms are commonly found in the S15 interval, up to 100 cm wide.
296 Latilaminae and mamelons are not observed. Astrorhizae rarely found (Fig. 7.4). Laminae,
297 which are similar to vesicular in morphology, are well-undulating, thickness ranges 0.16–
298 0.43 mm (number of measured laminae=96, average 0.30 mm) high, spaced 3–5 laminae per
299 millimeter. Pillars are persistently crumpled and funnel-like shaped. Galleries are round and
300 elongated, ranging 0.19–1.58 mm (number of measured galleries=88, average 0.67 mm)
301 width. Astrorhizae are approximately 0.3–0.4 mm in diameter and 2 mm high, with ragged
302 marginal contacts with laminae.
303 *Material.*—66 specimens, including NIGP 177136 and 177137 from the S3 interval, NIGP
304 177138 from the S9 interval, NIGP 159427, 159428, 159437, 159438, 177139–177179 from
305 the S15 interval, NIGP 159421, 177180–177185 from the S16 interval, NIGP 177186,
306 177187 from the S17 interval, NIGP 159420, 177188–177194 from the S18 interval NIGP
307 177195, 177196 from the upper part of the sub-section ZU3 of the Xiazhen Formation (Upper
308 Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

309 *Remarks.*—The Xiazhen specimens of *Clathrodictyon* cf. *Cl. microundulatum* show close
 310 skeletal resemblances to those from the Sanqushan Formation in Changshan, Zhejiang
 311 Province, China and from the New South Wales, Australia (Webby, 1969; Percival et al.,
 312 2006; Jeon et al., 2022). Astrorhizae have not been found in the Sanqushan specimens, but
 313 both the New South Wales and Xiazhen Formation specimens possess well-developed
 314 astrorhizae with ragged margins between laminae.

315 A vertically developed tube is developed in the present specimen (Fig. 7.3); the tube has
 316 the same compact microstructure as the stromatoporoid (similar example of fig. 18 in
 317 Kershaw et al., 2018). Parts of the tube are in open continuation with stromatoporoid galleries
 318 and may be part of the stromatoporoid skeletal structure. However, it remains possible that
 319 the tube is a bioclaustration (an intergrown organisms lacking its own shell). This vertical
 320 element is distinguishable from astrorhizae (Fig. 7.4, right-hand side) and intergrown tubes
 321 (Fig. 7.1, 4, 5). Astrorhizae have ragged marginal contact with laminae (Fig. 7.4).
 322 Stromatoporoid laminae also show concave or convex curving of laminae near the contact
 323 with intergrown corals (Fig. 7.4 upper left; also see both astrorhizae and intergrown *Bajgolia*
 324 in Fig. 16.1, 2). In contrast, the stromatoporoid laminae adjacent to the vertical tube in Fig.
 325 7.3 does not exhibit any skeletal distortions. Overall, the nature of this tube is not resolved
 326 and may require more samples to verify.

327

328 *Clathrodictyon plicatum* Webby and Banks, 1976

329 Figure 8

330 1976 *Clathrodictyon plicatum* Webby and Banks, p. 131, pl. 2, figs. 1–5

331 2021 *Clathrodictyon plicatum* Webby and Banks; Jeon, Li, Na, Liang and Zhang: p. 3, figs

332 2c, d, 3c.

333

334 *Type specimen.*—Holotype UTGD 94626 and paratypes UTGD 94623–94625, 94628–94629,
335 94631–94632 from the Upper Ordovician Den Formation of the uppermost Gordon
336 Limestone Subgroup, Tasmania (Webby and Banks, 1976, p. 131, pl. 2, figs. 1–5; see Burrett
337 et al., 1989 for the stratigraphic information); deposited in University of Tasmania, Hobart,
338 Australia.

339 *Occurrence.*—The S10–S12, S14–S18 intervals of sub-sections ZU1 and ZU2, and the upper
340 part of ZU3 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan
341 County, Jiangxi Province, China (Figs. 2, 3).

342 *Description.*—Skeletons vary from laminar, low to high domical, bulbous, dendroid, to
343 irregular or even digitate, up to 16 cm wide and 15 cm high. Astrorhizae and latilaminae are
344 not found. Mamelons are common, spacing 2.83–5.43 mm (number of measured distance
345 between two mamelons=13, average 4.28 mm), and up to 9.66 mm apart from each other,
346 generally 6 mm.

347 Laminae are laterally continuous and regularly spaced, ranging 0.08–0.25 mm (number of
348 measured laminae=86, average 0.15 mm), usually spaced from 6–8 per millimeter (average
349 7). Galleries are round and elongate, and of variable width, ranging 0.15–1.06 mm (number
350 of measured galleries=86, average 0.51 mm). In the axial part of columnar growth form,
351 widely-spaced laminae developed. These laminae are interlayered with crumpled laminae of
352 sharp, chevron-like folds, which are rather similar to cassiculate network in actinodictyids,
353 such as *Ecclimadictyon* and *Plexodictyon* (see Fig. 8 for folded-chevron like crumpled
354 laminae in *Clathrodactyon plicatum* and Figs. 9 and 10 for skeletal features of *Ecclimadictyon*
355 species).

356 *Materials.*—56 specimens, including NIGP 177197–177224 from the S10 interval, NIGP
357 177225–177228 from the S11 interval, NIGP 177229 from the S12 interval, NIGP 159429,
358 177230–177232 from S14 interval, NIGP 177233–177239 from the S15 interval, NIGP

359 177240 from the S16 interval, NIGP 168768, 177241–177246 from the S17 interval, NIGP
 360 177247–177250 from the S18 interval of the Xiazhen Formation (Upper Ordovician, Katian)
 361 at Zhuzhai, Yushan County, Jiangxi Province, China.

362 *Remarks.*—Both the specimens of *Clathrodictyon plicatum* Webby and Banks 1976 from the
 363 Upper Ordovician Den Formation of Tasmania (Webby and Banks, 1976) and from South
 364 China (Jeon et al., 2022; the present study) exhibit an abnormal skeletal phase, represented by
 365 ~~angularly~~ folded chevron-like crumpled laminae (‘a *Plexodictyon*-type structure’ in p. 131 of
 366 Webby and Banks 1976; ‘*Plexodictyon*-like abnormal phase’ in p. 5 of Jeon et al., 2022).
 367 This skeletal variation has been interpreted as an advanced growth strategy affected by
 368 environmental conditions (Jeon et al., 2022), and this species correspondingly shows the
 369 longest stratigraphic range in the Xiazhen Formation, representing a wide range of
 370 depositional environments.

371

372 Family Actinodictyidae Khalфина and Yavorsky, 1973

373

374 *Ecclimadictyon* Nestor, 1964

375 *Type species.*—*Clathrodictyon fastigiatum* Nicholson, 1887.

376 *Ecclimadictyon nestori* Webby, 1969

377 Figure 9

378 1969 *Ecclimadictyon nestori* Webby, p. 660, pl. 128, fig.1, pl. 129, figs. 1–6.

379 1988 *Ecclimadictyon* sp. A Lin and Webby, p. 239, fig. 3a–d.

380

381 *Type specimen.*—Holotype, SUP 28203 from the Upper Ordovician Vandon Limestone
 382 between Belubula River and Large Flat (Webby, 1969). One paratype, SUP 28256 from the
 383 upper part of the Upper Ordovician Belubula Limestone, and the others (SUP 26199–26202,

384 26204, 26209) from the Upper Ordovician Vandon Limestone of New South Wales (see
385 Webby, 1969, p. 660) in the Cliefden Caves Limestone Subgroup, New South Wales
386 (Webby, 1991, p. 660, pl. 128, fig.1, pl. 129, figs. 1–6; see Percival et al., 2011 for the
387 regional stratigraphic information); deposited in Australian Museum, Sydney, Australia.
388 *Occurrence.*—The S2–4, 10, 16, 18 intervals of sub-sections ZU1 and ZU2, and the upper
389 part of ZU3 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan
390 County, Jiangxi Province, China (Figs. 2, 3).

391 *Description.*—Skeletons are mostly laminar, and rarely low domical and irregular in growth
392 forms, up to 10 cm wide and 4 cm high. Astrorhizae, mamelons and latilaminae are not
393 found.

394 Skeletons consist of sharply folded chevron-like crumpled laminae, which are laterally
395 continuous, forming regular cassiculate networks. The thickness of laminae ranges 0.08–0.20
396 mm (number of measured laminae=92, average 0.12 mm), spaced 6–8 laminae per millimeter
397 (average 7 laminae). Pillars are poorly developed and confined to inter-laminar spaces.
398 Galleries are mostly rhomboid with sharp marginal areas. Sharply-crumpled laminae exhibit
399 isolated dots or appear to be linked with others.

400 *Materials.*—51 specimens, including NIGP 177251–177253 from the S2–S3 interval, NIGP
401 177254–177259 from the S4 interval, NIGP 177260–177263 from the S10 interval,
402 NIGP177264–177267 from the S15 interval, NIGP 177268–177271 from the S16 interval,
403 NIGP 177272, 177273 from the S17 interval, NIGP 159431, 159436, 159443, 159444,
404 159449, 168769, 177274–177294 from the S18 interval of the Xiazhen Formation (Upper
405 Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi Province, China.

406 *Remarks.*—The single specimen of *Ecclimadictyon* from the Sanqushan Formation, which
407 was described in Lin and Webby (1988), was designated as an independent species of
408 *Ecclimadictyon* in open nomenclature (*Ecclimadictyon* sp. A in p. 239 of Lin and Webby,

409 1988), judging from its more conspicuous latilaminae and larger astrorhizal canals than those
410 of *Ecclimadictyon nestori* (Lin and Webby, 1988). However, those differences cannot serve
411 as critical features to separate two independent stromatoporoid species, and should be
412 counted as skeletal variations of a single species. Both of them show identical sharply-folded,
413 zigzag-shaped crumpled laminae, forming angular galleries, as mostly spacing 7–8 laminae
414 per millimeter. Thus, in this study, *Ecclimadictyon* sp. A in Lin and Webby, 1988 is
415 synonymized with *Ecclimadictyon nestori* Webby, 1969, judging from their close skeletal
416 morphological resemblance.

417

418 *Ecclimadictyon undatum* Webby and Banks, 1976

419 Figure 10

420 1976 *Ecclimadictyon undatum* Webby and Banks, p. 132, pl. 2, figs. 1–3.

421

422 *Type specimen.*—Holotype (UTGD 94636) and three paratypes (UTGD 90917, 94637,
423 94638) from the Upper Ordovician Den Formation of the uppermost Gordon Limestone
424 Subgroup, Tasmania (Webby and Banks 1976, p. 132, pl. 2, figs. 1–3; see Burrett et al., 1989
425 for the regional stratigraphic information).

426 *Occurrence.*—The S11, S12 and S15 intervals of the Xiazhen Formation (Upper Ordovician,
427 Katian) at Zhuzhai, Yushan County, Jiangxi Province, China (Figs. 2, 3).

428 *Description.*—Skeleton is laminar in growth form, up to 14 cm wide and 3 cm high.

429 Mamelon, latilaminae and astrorhizae are not found. An unidentified endobiont (referred as
430 ‘*Eofletcheria*-like tubules’ in Lee et al., 2016a) occurs only in the current species (Fig. 10.5,
431 6).

432 The internal structure is variable, ranging from coarsely to finely structured laminae. In the
433 coarser skeletal phase, laminae are moderately crumpled, forming elongated and round

434 galleries (Fig. 10.1). In more finely structured portions of the skeleton, laminae are rather
 435 sharply-folded and galleries are more angular rhomboid (Fig. 10.2). The thickness of laminae
 436 ranges 0.13–0.39 mm (number of measured laminae=86, average 0.21), spaced 3–5 laminae
 437 per millimeter (average 4 laminae). Pillars are mostly indistinct.

438 *Materials*.—13 specimens, including NIGP 177295, 177296 from the S11 interval, NIGP
 439 177297 from the S12 interval, NIGP 159425, 159426, 177298–177307 from the S15 interval
 440 of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County, Jiangxi
 441 Province, China.

442 *Remarks*.—The specimens of *Ecclimadictyon undatum* from Tasmania show that laminae
 443 range 12–14 per two millimeters (Webby and Banks, 1976), slightly finer than those in the
 444 Xiazhen Formation specimens. These differences in laminae dimensions are considered to be
 445 an intraspecific variation. Astrorhizae are not found in either specimens. *E. undatum* Webby
 446 and Banks, 1976 exhibits widely spaced, less sharply folded laminae and coarser cassiculate
 447 structures than *E. nestori* Webby, 1969.

448

449 *Camptodictyon Nestor, Copper and Stock, 2010*

450 *Type species*.—*Camptodictyon penefastigiatum* Nestor, Copper and Stock, 2010.

451 *Camptodictyon amzassensis* (Khalfina, 1960)

452 **Figure 11**

453 1960 *Clathrodactyon(?) kirgismicum amzassensis* Khalfina, p. 370, pl. O–1, figs. 1–3.

454 1969 *Ecclimadictyon amzassensis* (Khalfina); Webby, p. 659, pl. 127, figs. 5–7, pl. 128, figs.
 455 1–5.

456 1984 *Ecclimadictyon crassilamellatum* Dong and Wang, p. 260, pl. 14, fig 2a, b

457 1984 *Ecclimadictyon xinjiangense* Dong and Wang, p. 261, pl. 14, fig 3a, b

458

459 *Type specimen.*—Holotype No. 537 with three thin sections from the Amzass Formation of
460 Gornaya Shoriya, Russia (Khalfina, 1960, p. 370, pl. O–1, figs. 1–3); deposited in Trofimuk
461 Institute of Petroleum Geology and Geophysics, Russian Academy of Sciences, Novosibirsk,
462 Russia.

463 *Occurrence.*—The S15, 17 intervals of the Xiazhen Formation (Upper Ordovician, Katian) at
464 Zhuzhai, Yushan County, Jiangxi Province, China (Figs. 2, 3).

465 *Description.*—Skeleton is laminar, about 20 mm high and 60 mm wide. Latilaminae and
466 mamelon columns are not found.

467 Laminae range from zigzag-shaped (also commonly referred as ‘chevron-like’; see Nestor et
468 al., 2010, p. 83 for the diagnosis of genus *Camptodictyon*), smoothly downward-folded to
469 undulating structures, spaced 5–7 per mm (average 6). Thickness of laminae is 0.06–0.22 mm
470 (number of measured laminae=55, average 0.13 mm). Pillars are short and commonly
471 indistinct, but may also reach the other laminae, 0.03–0.17 mm high (number of measured
472 laminae=70, average 0.08 mm). Galleries are round and elliptical in longitudinal section,
473 varying 0.32–1.61 mm in width (number of measured galleries=52, average 0.75 mm).
474 Astrorhizae are sporadically developed, represented by short and curved astrorhizal galleries
475 (Fig. 11.2).

476 *Materials.*— Three specimens, including NIGP 177308 from the S15 interval, NIGP 177309,
477 177310 from the S17 interval of the Xiazhen Formation (Upper Ordovician, Katian) at
478 Zhuzhai, Yushan County, Jiangxi Province, China.

479 *Remarks.*— The Xiazhen Formation specimens closely resemble specimens from Altai-Sayan
480 (Khalfina, 1960) and New South Wales (Webby, 1969), with 3–6 laminae per millimeter.

481 *Ecclimadictyon xinjiangense* (NIGP 70420) and *E. crassilamellatum* (NIGP 70421) from
482 Xinjiang, China develop cassiculate networks from downward folded to undulating laminae
483 (see pl. 14, fig 2a, b and pl. 14, fig 3a, b of Dong and Wang, 1984, respectively). These

484 skeletal characteristics are much closer to the generic concept of *Camptodictyon* (Nestor et
 485 al., 2010, p. 83; Nestor, 2015, p. 758) than to *Ecclimadictyon* (Nestor, 2015, p. 758). The
 486 skeletal differences in these two species (i.e., slightly thicker laminae, space of astrorhizal
 487 canals) are not considered to possess significant taxonomic value to justify them as
 488 independent species in Dong and Wang (1984) (Lin and Webby, 1988). The specimens from
 489 Xinjiang, China show similar morphological features with those in current material, thereby
 490 being regarded as junior synonyms of *Camptodictyon amzassensis* (Khalfina 1960).

491

492 *Labyrinthodictyon* Nestor, Copper and Stock, 2010

493 *Type species.*—*Labyrinthodictyon angulosum* Nestor, Copper and Stock, 2010.

494 *Labyrinthodictyon cascum* (Webby and Morris, 1976)

495 Figure 12

496

497 1976 *Plexodictyon? cascum* Webby and Morris, p. 132, fig. 5a–c, 5e.

498 2021 *Labyrinthodictyon cascum* (Webby and Morris 1976); Jeon, Li, Na, Liang and Zhang, p.

499 7, figs 2g, h, 3d, e.

500

501 *Type specimen.*—Holotype (SUP 78258), three paratypes (SUP 77277–77279) from the

502 Upper Ordovician Ballingool Limestone in upper part of the Bowan Park Limestone

503 Subgroup, New South Wales (Webby and Morris, 1976, p. 132, fig. 5a–c, 5e; see Percival et

504 al., 2011 for the regional stratigraphic information); deposited in the Australian Museum,

505 Sydney, Australia.

506 *Occurrence.*—The S15 interval of the Xiazhen Formation (Upper Ordovician, Katian) at

507 Zhuzhai, Yushan County, Jiangxi Province, China (Figs. 2, 3).

508 *Description.*—Skeletons are fragmented, but indicate a laminar growth form. Mamelons and
509 astrorhizae are not found. Skeletons consist of planar paralaminae, which are laterally
510 continuous. Thickness of paralaminae is 0.21 to 0.78 mm (number of measured
511 paralaminae=67, average 0.45 mm), regularly spaced 2 per millimeter (exceptionally 3
512 paralaminae are also seen). The inter-paralaminae exhibit cassiculate laminae, of variable
513 from irregularly crumpled to triangular-wedge shapes, spacing 2–3 crumpled laminae within
514 one paralamina. Galleries are angular and variable in both shape and size.

515 *Materials.*—Three specimens, including NIGP 168770, 177311, 177312 from the S15
516 interval of the Xiazhen Formation (Upper Ordovician, Katian) at Zhuzhai, Yushan County,
517 Jiangxi Province, China.

518 *Remarks.*—The Xiazhen specimens have regularly spaced planar paralaminae, closely similar
519 to the specimens from New South Wales (Webby and Morris, 1976) and those from the
520 coeval Sanqushan Formation of South China (Jeon et al., 2022). All the specimens from
521 China and Australia show about 2 paralaminae per millimeter (Webby and Morris, 1976;
522 Jeon et al., 2022). No abnormal skeletal phases have been observed in the Xiazhen Formation
523 specimens, while abnormal *Ecclimadictyon*-like phases occur in the Sanqushan Formation
524 specimens (see fig. 3d, e of Jeon et al., 2022).

525

526 **Intergrowth association between clathrodictyid stromatoporoids and other sessile** 527 **organisms**

528 In the Xiazhen Formation, intergrowth associations between clathrodictyid stromatoporoids
529 and other sessile organisms are commonly found (Figs. 13–17, Table 1). The intergrowth
530 associations occur both in reef and non-reef environments, but are much more common in
531 reefs due to the high diversity and density of reef-building organisms. Lee et al. (2016) found

532 that only *Clathrodictyon* and *Ecclimadictyon* acted as host stromatoporoids. No intergrown
533 organisms were found within skeletons of *Camptodictyon* and *Labyrinthodictyon*. The
534 stratigraphic distribution of intergrowth associations between clathrodictyid stromatoporoids
535 and other sessile organisms in the Xiazhen Formation is listed in Table 1. The intergrowth
536 associations include seven host clathrodictyid species and various intergrown benthic
537 organisms. Among those intergrown benthic organisms, tabulate corals include *Agetolites*,
538 *Bajgolia*, *Catenipora* and *Heliolites* (Figs. 13–17), with the auloporid *Bajgolia* the most
539 common intergrown coral (Figs. 14–16; see figures in Lee et al., 2016a). Species of
540 *Agetolites* are found to envelop dendroid forms of *Clathrodictyon idense* particularly in the
541 S3 interval (Fig. 13.5, 13.6). Solitary-form rugose corals, *Streptelasma* and *Tryplasma* are
542 also found as endobionts. Other fossil groups, including *Rhabdotetradium* (see fig. 2b in Lee
543 et al., 2016a), unidentified *Eofletcheria*-like tubules (Fig. 10.6, 14.3; see fig. 2f of Lee et al.,
544 2016a), labechiid stromatoporoids (Fig. 14.6; see figures of Jeon et al., 2020b) and bryozoans
545 (Fig. 14.2) also intergrew within clathrodictyid stromatoporoids.

546 We interpret the intergrowth associations between clathrodictyid stromatoporoids and
547 other sessile organisms to have occurred by chance rather than an obligate association,
548 judging from the presence of both free-living and intergrown growth modes (Lee et al.,
549 2016a; Jeon et al., 2020b). The laminae of clathrodictyids are concavely or convexly curved
550 near the contact with the intergrown corals, which possibly show the different growth rates of
551 host clathrodictyids and intergrown organisms (Fig. 15). It can be inferred that most of the
552 endobionts had little to no impact on most of the host clathrodictyids, and some endobionts
553 even encrusted or grew near the astrorhizae of the host stromatoporoid (Fig. 16.1, 16.2).
554 However, in some cases, the host clathrodictyids show evidence of having been affected by
555 the intergrown organisms, judging from a narrow range of columnar to dendritic growth
556 forms (Fig. 16.3–16.7), abnormally spaced laminae (Fig. 16.8), and skeletal distortions (Fig.

557 14.6; see figs. 2.4, 3, 4 in Jeon et al., 2020b). Host stromatoporoids that contain intergrown
558 *Bajgolia* are often restricted to the branching dendroid forms (Fig. 16.3–16.7; Lee et al.,
559 2016a), which indicates that the growth direction and orientation of intergrown organism
560 could affect the growth of the host stromatoporoid in some cases. Skeletal deformation with
561 zigzag, crumpled distorted laminae of the host clathrodictyid is also observed near the
562 physical contacts with intergrown labechiids, indicating spatial competition between these
563 two stromatoporoids (compare Figs. 13–17 and figs. 2.4, 3, 4 in Jeon et al., 2020b).

564

565 **Paleobiogeographic pattern of Ordovician clathrodictyid stromatoporoids**

566

567 Ordovician clathrodictyid stromatoporoids rapidly reached a global distribution concurrently
568 with their earliest appearance in the middle Katian of the Late Ordovician (Stock et al.,
569 2015). A total of 27 clathrodictyid species were reported in the Late Ordovician interval
570 (middle Katian to Hirnantian). The wide range of skeletal variation in clathrodictyids may
571 confuse discrimination of lowest-level taxa and lead to over-splitting, but resolving this issue
572 requires examination of published materials, which is outside the scope of this study.

573 Nevertheless, the clathrodictyid species examined here belong to four genera

574 (*Clathrodictyon*, *Ecclimadictyon*, *Camptodictyon* and *Labyrinthodictyon*) and have been

575 recorded from nine terranes (Fig. 18). Many species were endemic and occurred within a

576 single terrane. Peri-Gondwanan terranes, including North China, Australia, South China and

577 other terranes (e.g., Tarim) share more clathrodictyid species in common than the other

578 terranes. In general, the network analysis diagram shows three independent clathrodictyid

579 faunal provinces (peri-Gondwana–Tarim–Altai, Laurentia and Baltica) (Fig. 18).

580

581 *Peri-Gondwana–Tarim–Altai Province*. —Peri-Gondwanan terranes, particularly Australia
582 and South China, show diverse clathrodictyids and share many common species of
583 *Clathrodictyon*, *Ecclimadictyon*, *Camptodictyon* and *Labyrinthodictyon*. It is noteworthy that
584 New South Wales and Tasmania do not share any common clathrodictyid species although
585 they were paleogeographically close to each other (Webby, 1969; Webby and Banks, 1976;
586 Webby and Morris, 1976; Webby et al., 2000).

587 *Camptodictyon amzassensis* (Khalfina, 1960) is an important species for defining this
588 faunal province in that it shows the widest paleobiogeographic distributions (Fig. 18),
589 occurring in New South Wales (Webby, 1969), South China (present study), Tarim (Dong
590 and Wang, 1984), and Altai-Sayan Fold Belt (Khalfina, 1960). This species had not yet been
591 found in North China, and only a single clathrodictyid species (*Clathrodictyon* cf. *Cl.*
592 *microundulatum* Nestor, 1964) occurs in both North China and the other peri-Gondwanan
593 terranes (i.e., South China and New South Wales). In addition to this species, two other
594 species: *Clathrodictyon?* sp., possessing distinctive skeletal features, and *Ecclimadictyon* sp.
595 B (Lin and Webby, 1988) have been reported only from North China.

596 No detailed taxonomic work on clathrodictyids from the Ordovician of Qaidam has been
597 undertaken, unfortunately, and thus our analysis is based on the few records in the literatures.
598 *Ecclimadictyon* cf. *E. koigense* Nestor, 1964 is the only clathrodictyid species known from
599 Qaidam (Lin and Webby, 1988). Occurrence of the tabulate coral *Agetolites* species and
600 labechiid stromatoporoids in Qaidam indicates a close paleobiogeographic relationship with
601 South China (Li and Lin, 1982), presumably indicating the two blocks belong to the same
602 clathrodictyid paleobiogeographic unit. Accordingly, we include Qaidam in the GTA
603 Province in this study.

604

605 *Laurentia Province.*— *Clathrodictyon* cf. *Cl. kudnavzevi* Riabinin, 1951, *Clathrodictyon* sp.
606 3 (Bolton, 1988), *Labyrinthodictyon angulosum* Nestor, Copper and Stock, 2010,
607 *Ecclimadictyon anticostiense* Nestor, Copper and Stock, 2010 and *Ecclimadictyon* sp.
608 (Bolton, 1988) are known to occur in this province. Of these, *Ecclimadictyon* sp. and
609 *Clathrodictyon* sp. 3 in Bolton (1988) are from the Portage Chute and Red River formations
610 of Manitoba, respectively, while the other three species are from the Ellis Bay Formation of
611 Anticosti Island (Nestor et al., 2010).

612

613 *Baltic Province.*— This province contains *Clathrodictyon microundulatum* Nestor, 1964,
614 *Clathrodictyon vormsiense* Riabinin, 1951, *Clathrodictyon gregale* Nestor, 1964,
615 *Clathrodictyon zonatum* Nestor, 1964, *Ecclimadictyon geniculatum* Bogoyavlenskaya, 1973,
616 *Ecclimadictyon porkuni* (Riabinin, 1951) and *Ecclimadictyon koigiense* Nestor, 1964. Among
617 them, *Clathrodictyon microundulatum*, *Clathrodictyon vormsiense* and *Ecclimadictyon*
618 *geniculatum* are from the Katian Stage (including Vormsi and Pirgu regional stages), while
619 the other four species are from the Hirnantian Stage (Porkuni Regional Stage) (Nestor, 1964).

620

621 **Discussion**

622

623 *Occurrence of clathrodictyid stromatoporoids and their paleobiogeographic implication.*—
624 South China was postulated to have been close to the other peri-Gondwana terranes (e.g.,
625 Australia), judging from the co-occurrence of some *Clathrodictyon* species and characteristic
626 agetolitid corals from the Sanqushan Formation (Webby, 1980; Lin and Webby, 1988, 1989).

627 A recent study of clathrodictyids from the Sanqushan Formation (Jeon et al., 2022), and the
628 present analysis, correspondingly show that South China has close faunal affinity to New
629 South Wales and Tasmania. It is noteworthy that New South Wales and Tasmania do not
630 share any common clathrodictyid species with each other despite their close paleogeographic
631 distance (Webby, 1969; Webby and Banks, 1976; Webby and Morris, 1976; Webby et al.,
632 2000). Similar to the clathrodictyid stromatoporoids, Percival et al. (2011) noted that the
633 brachiopods of New South Wales and Tasmania share surprisingly few faunal taxa. This
634 pattern was interpreted to be due to a deep ocean basin swept by strong currents, which
635 separated the benthic organisms of the two regions (Webby et al., 2000). If true, this strong
636 oceanic current may have also affected the migration of those Australian clathrodictyid
637 species to South China, judging from high faunal similarity of clathrodictyids between South
638 China and those two Australian regions.

639 The analysis presented here indicates that North China had the clathrodictyids had little
640 faunal similarity with the other peri-Gondwanan terranes (i.e., South China, Australia),
641 although this contrasts the paleobiogeographic pattern of labechiid stromatoporoids, which
642 show North and South China have faunal similarities (Jeon et al., 2021); the implication is
643 that these different taxa groups of stromatoporoids were under different controls with respect
644 to their dispersal. Only one species (*Clathrodictyon* cf. *Cl. microundulatum*) occurs in North
645 China, South China and New South Wales of peri-Gondwanan terranes. It should be noted
646 that none of the *Camptodictyon* species have been found in North China, despite the wide
647 distribution of *Camptodictyon amzassensis* during the Late Ordovician (Fig. 18), ranging
648 from the Altai-Sayan Fold Belt (Khalfina, 1960), Tarim (Dong and Wang, 1984), South
649 China (present study, Jeon et al., 2022) to New South Wales (Webby, 1969). However, Late
650 Ordovician stromatoporoids have not been well-studied from North China and other adjacent
651 terranes (i.e., Qaidam, Mongolia and Central Asia). Further studies are required for a

652 comprehensive evaluation of stromatoporoids and paleobiogeographic patterns of these
653 terranes.

654 The Peri-Gondwana–Tarim–Altai Province of clathrodictyid stromatoporoids corresponds
655 well with the recently proposed brachiopod benthic faunal province, named ‘Cathay-Tasman
656 Province’ by Cocks and Torsvik (2020). However, the Alati-Sayan Fold Belt is not included
657 in Cocks and Torsvik’s faunal provinces, which is the only difference from the present
658 clathrodictyid faunal provinces. The accurate paleogeographic location of Tarim continues to
659 be controversial, but consistent in the paleobiogeographic analyses among different fossil
660 groups (compare Fig. 18 and fig. 6 of Cocks and Torsvik, 2020). The occurrence of
661 brachiopod *Altaethyrella-Schachriomonina* assemblage in Tarim provided useful evidence,
662 indicating a close paleobiogeographic connection with South China (Sproat and Zhan, 2019),
663 which corresponds with the occurrence of *Cam. amzassensis* in Tarim and South China.

664 Laurentia, Baltica, and Siberia do not share any common clathrodictyid species. The species-
665 level diversity of clathrodictyids in these terranes is much lower than those of labechiids
666 (Jeon et al., 2021). The limited dispersal of clathrodictyid species in these faunal provinces is
667 possibly due to the later appearance of clathrodictyid stromatoporoids than labechiids, so
668 there was insufficient time for dispersal of clathrodictyids through terranes before the Late
669 Ordovician glaciation.

670

671 *Role of clathrodictyid stromatoporoids in intergrowth associations and implications in*
672 *relation to the Great Ordovician Biodiversification Event.*— During the Ordovician, in
673 conjunction with spectacular diversity increases of marine invertebrate organisms, the rise of
674 the Paleozoic Evolutionary Fauna is well-known to possess a much expanded ecospace and
675 greater ecological complexity than in the earlier Cambrian period (Zhang et al., 2010; Servais

676 et al., 2010). These complexities include better developed food webs and increased
677 competition between taxa (Zhang et al., 2010; Servais et al., 2010), which have been
678 interpreted to be major controlling factors of this magnificent evolutionary event (Harper et
679 al., 2004). Accordingly, the fossil record of paleoecological interactions remarkably increased
680 during the Ordovician and multiplied in subsequent periods, together with the increase of
681 predation pressure (Huntley and Kowalewski, 2007; Zhang et al., 2010). It is considered that
682 there were various modes of the paleoecological associations (e.g., mutualism,
683 commensalism, parasitism, competition) during the Ordovician (e.g., Young and Xu, 2002;
684 Tapanila and Holmer, 2006; Lee et al., 2016a; Jeon et al., 2020b), but it may have been
685 underestimated in the development of Ordovician marine ecosystems (Zhang et al., 2010);
686 such associations may have played critical roles in community organization and evolution
687 through deep time (Young and Xu, 2002).

688 Almost coinciding with the appearance and development of massive calcareous skeletal
689 organisms (e.g., bryozoans, corals, stromatoporoids) during the Great Ordovician
690 Biodiversification Event (GOBE), a new symbiotic growth mode occurred during the
691 Ordovician, which is well-known as an intergrowth association (also commonly referred to as
692 an endosymbiotic association). Before the Ordovician, a facultative simple attachment of one
693 skeleton to another is dominant in paleoecological associations (e.g., Topper et al., 2015,
694 Zhang et al., 2020), an association referred to as ‘ectosymbiotic’. Vinn (2017) interpreted
695 Cambrian epibionts to have simply benefited from a suspension feeding strategy. One of the
696 representative example of this ectosymbiotic interaction is *Wiwaxia* sp. and *Nisusia* sp. in the
697 Cambrian Burgess Shale of Canada (Topper et al., 2015). The earliest known intergrowth
698 association involved the early bryozoan *Orbiramus* and diverse sclerobionts were reported
699 from the Early Ordovician of South China (Ma et al., 2021). Bryozoans commonly hosted
700 various endobionts, such as cornulariid tubeworms and rugose corals in the subsequent stages

701 of the Ordovician (e.g., Vinn and Mõtus, 2012; Vinn et al., 2014, 2016, 2017, 2018a, b, 2019)
702 and later (e.g., Plusquellec and Bigey, 2019; Sendino et al., 2019). In contrast, early
703 stromatoporoids (i.e., labechiids) seemingly did not involve intergrowth associations during
704 the late Early to early Late Ordovician interval. The growth surface of those labechiid
705 stromatoporoids with superposed vertical skeletal elements (i.e., pillars, papillae) has been
706 interpreted as an unfavorable substrate for the settlement of endobionts' larvae (Mori, 1970),
707 which may explain the lack of endobionts during the entire evolutionary history of labechiids.

708 Along with the appearance of clathrodictyid stromatoporoids during the middle Late
709 Ordovician, diverse endobionts have been found within the skeletons of clathrodictyids
710 (Table 2). Endobionts were first described from the middle Katian strata (Upper Ordovician)
711 of New South Wales (Webby, 1969; Webby and Morris, 1976), including three clathrodictyid
712 species and three different types of endobiont coral *Bajgolia* (formerly described as *Propora*
713 in p. 657 of Webby, 1969), tubeworms and unidentified tabular organisms (Webby, 1969;
714 Webby and Morris, 1976). Other records are from the Upper Ordovician successions of
715 Tasmania (Webby and Banks, 1976) and South China (Lin and Webby, 1988; Young and Xu,
716 2002; Lee et al., 2016a; Jeon et al., 2020b). In particular, diverse endobionts are found in
717 diverse clathrodictyid species from the Xiazhen Formation of South China (Table 1), which
718 may correspond with the high biodiversity in South China during the GOBE (Rong et al.,
719 2006). Few examples of the intergrowth association between stromatoporoids and other
720 organisms are known from peri-Gondwanan regions of Late Ordovician (e.g., Lin and
721 Webby, 1988; Lee et al., 2016a; Jeon et al., 2020b; Table 2), while much more examples
722 have been reported world-widely in Silurian and Devonian limestones (e.g., Da Silva et al.,
723 2011; Kershaw, 1987; Kershaw et al., 2018; Mori, 1970; Nestor et al., 2010; Stearn, 2015b;
724 Vinn, 2016; Vinn and Mõtus, 2014; Vinn and Wilson, 2010; Young and Noble, 1989; Zhen
725 and West, 1997).

726 Reef-forming organisms (i.e., bryozoans, corals and sponges) diversified during the late
727 Middle to the Late Ordovician, with their biodiversity peaks in the Katian (Carrera and
728 Rigby, 2004; Ernst, 2017; Servais and Harper, 2018; Webby, 2004) and it is apparent that the
729 GOBE likely underpins the establishment of complex reef communities (Servais and Harper,
730 2018). For benthic sessile organisms, their occupation of higher substrate elevated by
731 encrusting other skeletal organisms was more promising for suspension feeding efficiency
732 than direct settlement on seafloor (Vinn and Wilson, 2010; Lee et al., 2016a; Vinn et al.,
733 2015; Vinn, 2016; Jeon et al., 2020b). The intergrowth associations may have offered
734 protection for the endobionts from water turbulence and benefited suspension feeding as well
735 (e.g., Kershaw, 1987; Vinn and Wilson, 2010; Vinn et al., 2018a). Some cases of specificity
736 between endobionts and particular host stromatoporoids may reflect complex biological
737 interactions (see Fig. 10.6; Kershaw et al., 2018).

738 Understanding intergrowth association between stromatoporoids and associated endobionts
739 provides valuable information about not only paleoecological interactions but also
740 paleobiological features on growth characteristics of associated organisms (Kershaw et al.,
741 2018). Bending laminae (including both up- and down-bending) in host stromatoporoids has
742 been proposed as an indicator for judging the paleoecological relationships between host
743 stromatoporoid and endobionts (e.g., Zapalski and Hubert, 2010). Down-bending of
744 stromatoporoid laminae is common in the vicinity of the endobionts (black arrows in Fig.
745 15.1–5), and up-bending laminae are commonly developed as well, even inside the same
746 stromatoporoid skeleton (white arrows in Fig. 15.1, 3, 6). The deflection of host
747 stromatoporoid laminae near endobiont tubes is variably developed during Siluro–Devonian
748 depending on host stromatoporoid species and intergrown organisms (e.g. Da Silva et al.,
749 2011; Kershaw, 2013; Kershaw et al., 2018; Vinn 2016). This is interpreted to indicate
750 variation of growth rates between each host stromatoporoid and intergrown organisms during

751 their syn-vivo interactions (Fig. 15.7–17). It is difficult to determine whether the interaction
752 strategy is commensalism or mutualism due to lack of critical evidence (Zapalski, 2011), but
753 it seems unlikely that such interactions are results of hostile actions, judging from the absence
754 of skeletal distortion.

755 Overall, the increasingly diverse examples of the intergrowth association during the GOBE
756 may be regarded as an evidence for early development of complex reef ecosystems. The new
757 growth strategy of syn-vivo association reflects increased competition for food and space in
758 response to the dynamic increase of marine biodiversity. For stromatoporoids, the
759 intergrowth association seems to have been facultative, depending on the emergence of the
760 clathrodictyids as a new group of stromatoporoids. Those host clathrodictyids represent high
761 skeletal density, compared to the earlier labechiids (Mistiaen, 1994; Vinn, 2016). The
762 laminate structure of clathrodictyid stromatoporoids seemingly contributed to development of
763 a complex reef ecosystem during the GOBE by providing stable substrate, enabling an
764 increased substrate availability by suitable host clathrodictyid taxa (Fig. 17). As a result, the
765 examples of intergrowth association between host clathrodictyid stromatoporoids and other
766 intergrown organisms in the Xiazhen Formation reflect the highly complex paleoecological
767 interactions of organisms in benthic communities during the Great Ordovician
768 Biodiversification Event.

769

770 **Conclusions**

771 Clathrodictyid stromatoporoids are abundant and rich fossils in the Upper Ordovician
772 Xiazhen Formation of South China. A total of nine species belonging to four genera of
773 clathrodictyids are identified, including *Clathrodictyon idense* Webby and Banks, 1976, *Cl.*

774 *megalamellatum* Jeon n. sp., *Cl.* cf. *Cl. mammillatum* (Schmidt, 1858), *Cl.* cf. *Cl.*
775 *microundulatum* Nestor, 1964 *Ecclimadictyon nestori* Webby, 1969, *E. undatum* Webby and
776 Banks, 1976, *Camptodictyon amzassensis* (Khalfina, 1960) and *Labyrinthodictyon cascum*
777 (Webby and Morris, 1976). This clathrodicthyid assemblage is characterized by a combination
778 of taxa recorded in New South Wales and Tasmania, although these two Australian regions
779 themselves do not show any faunal affinity in terms of clathrodicthyid stromatoporoids. The
780 occurrence of the Xiazhen Formation clathrodicthyid assemblage may have resulted from
781 independent faunal migration between South China and these two Australian regions. The
782 northward shift of South China in northeastern peri-Gondwanan region during the Middle to
783 Late Ordovician may have facilitated the development of a favorable environment for the
784 migration of clathrodicthyid stromatoporoids among peri-Gondwanan terranes. Frequent
785 intergrowth associations of these diverse clathrodicthyid species with other sessile organisms
786 are interpreted as evidence of increasing paleoecological interactions, which is critical for the
787 development of complex benthic communities. The emergence of clathrodicthyids in late
788 Ordovician time increased the paleoecological complexity and benthic community stability of
789 reef environments during the Great Ordovician Biodiversification Event.

790

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792

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814

815 **References**

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1176

1177 **Figure Captions**

1178

- 1179 **Figure 1. (1)** Locality of the study area in China. **(2)** Location of the Zhuzhai section, Yushan
1180 County, Jiangxi Province near the border with Zhejiang Province. **(3)** Geological map of
1181 the Xiazhen Formation at Zhuzhai section, which is divided into three partly coeval sub-
1182 sections, ZU1, ZU2, and ZU3. Modified after Lee et al. (2012).

1183 **Figure 2.** Stratigraphic column of the Xiazhen Formation with the 18 stromatoporoid-bearing
 1184 intervals. The red-colored intervals (i.e., S1–S5, S7, S9–S18, lower and upper part of
 1185 sub-section ZU3) indicate where clathrodictyid stromatoporoids were found. The black-
 1186 colored intervals (i.e., S6 and S8) indicate where only labechiid stromatoporoids occur.
 1187 C= claystone; M = mudstone or lime mudstone; W = wackestone; P = packstone; G =
 1188 grainstone, F = floatstone or framestone; R = rudstone. LLM = lower limestone member;
 1189 LSM = lower shale member; MMM = middle mixed-lithology member; USM = upper
 1190 shale member. Modified after Lee et al. (2012) and Park et al. (2021). A large size
 1191 version of this figure is presented in Supplementary Data 1.

1192 **Figure 3.** Lithology, interpreted depositional energy-level, stratigraphic distributions of
 1193 clathrodictyid stromatoporoids and their growth forms from each stromatoporoid-
 1194 bearing intervals of the Xiazhen Formation; SBI = stromatoporoid-bearing interval; M =
 1195 mudstone, W = wackestone, P = packstone, G = grainstone, L–S couplets = limestone–
 1196 shale couplets in wackestone to packstone, F = floatstone, Fr = framestone, R =
 1197 rudstone; L = low-energy depositional environment; M = medium-energy depositional
 1198 environment; H = high-energy depositional environment; *Cl. id.* = *Clathrodictyon*
 1199 *idense*; *Cl. cf. mml.* = *Clathrodictyon cf. Cl. mammillatum*; *Cl. cf. mc.* = *Clathrodictyon*
 1200 *cf. Cl. microundulatum*; *Cl. mglm.* = *Clathrodictyon megalamellatum* Jeon n. sp.; *Cl. pl.*
 1201 = *Clathrodictyon plicatum*; *E. nst.* = *Ecclimadictyon nestori*; *E. und.* = *Ecclimadictyon*
 1202 *undatum*; *Cam. amz.* = *Camptodictyon amzassensis*; *L. csc.* = *Labyrinthodictyon*
 1203 *cascum*.

1204 **Figure 4.** Thin-section photographs of *Clathrodictyon idense* Webby and Banks 1976 from
 1205 the S3 interval. (1) Longitudinal section of dendroid growth form of *Clathrodictyon*
 1206 *idense*, NIGP 177104-1. (2, 3) Enlargement of the rectangular area in (1), showing
 1207 longitudinal section and axial part. Note sharply folded, crumpled laminae in the axial

1208 part of (3). (4) Tangential section, NIGP 177103. (5) Tangential section of single (left)
 1209 and branching (right) dendroid forms of *Clathrodictyon idense*, NIGP 177106. Note that
 1210 a thin laminar form encrusted on the branching dendroid form (right).

1211 **Figure 5.** Holotype specimen of *Clathrodictyon megalamellatum* Jeon n. sp. from the S18
 1212 interval. (1, 3, 4) Longitudinal sections of *Clathrodictyon megalamellatum* Jeon n. sp.,
 1213 showing widely-spaced laminae and well-developed pillars; (1) NIGP 177124-1, (3, 4)
 1214 NIGP 177124-2, respectively. (2) Enlargement of the rectangular area in (1). (5–7)
 1215 Tangential sections of *Clathrodictyon megalamellatum* Jeon n. sp., showing irregularly
 1216 developed pillars with some circular structure, particularly in (3); (5, 6) NIGP 177124-1,
 1217 (7) 177124-2, respectively. (8) Enlargement of the rectangular area in (4), showing
 1218 astrorhizae-like structures in the mamelon-like up-growth areas.

1219 **Figure 6.** (1) Longitudinal to tangential view of *Clathrodictyon* cf. *Cl. mammillatum* from the
 1220 S18 interval, NIGP 169634. (2) Longitudinal section from the S18 interval, NIGP
 1221 177134. (3) Enlargement of the rectangular area in (2). (4) Longitudinal section of
 1222 dendroid form, showing sharply-folded, crumpled *Ecclimadictyon*-like laminae in the
 1223 axial part from the S9 interval, NIGP 177127-1. (5) Tangential section from the S9
 1224 interval, NIGP 177130.

1225 **Figure 7.** (1) Longitudinal section of *Clathrodictyon* cf. *Cl. microundulatum* from the S18
 1226 interval, NIGP 177194-4 (2) Enlargement of the rectangular area in (1). (3) Enlargement
 1227 of the rectangular area in (1), showing longitudinal section of a vertically developed
 1228 skeletal structural tube. (4) Astrorhizal structure of *Clathrodictyon* cf. *Cl.*
 1229 *microundulatum* from the S18 interval, NIGP 177194-13. (5) Tangential section of
 1230 *Clathrodictyon* cf. *Cl. microundulatum* with intergrown *Bajgolia* from the S18 interval,
 1231 NIGP 177194-4.

1232 **Figure 8.** Thin-section photographs of *Clathrodictyon plicatum* from the S10 interval. (1)
 1233 Longitudinal section of *Clathrodictyon plicatum*, showing skeletal variation from the
 1234 axial to lateral part NIGP 177200-3. Note the variation from the normal phase in the
 1235 lateral phrase of (2) and the sharply-folded, crumpled *Ecclimadictyon*-like axial part of
 1236 (3). (4, 5) Longitudinal and tangential sections of *Clathrodictyon plicatum*, respectively,
 1237 NIGP 177204. (6) Sharply folded, crumpled *Ecclimadictyon*-like structure in the axial
 1238 part in *Clathrodictyon plicatum* NIGP 177205. (7) Tangential section of *Clathrodictyon*
 1239 *plicatum*, showing well-developed mamelons, NIGP 177213-1.

1240 **Figure 9.** (1–3) Thin-section photographs of *Ecclimadictyon nestori* from the S18 interval.
 1241 (1, 2) Longitudinal section, NIGP 177286, 177287, respectively. (3) Tangential section,
 1242 NIGP 177288.

1243 **Figure 10.** (1–2) Longitudinal section of *Ecclimadictyon undatum* from the S15 interval,
 1244 NIGP 177302-1 and 177305, respectively. (3, 4) Tangential section from the S15
 1245 interval, NIGP 177302-7 and 177302-8, respectively. (5) Intergrown ‘*Eofletcheria*-like
 1246 tubulates’ in *Ecclimadictyon undatum*, NIGP 177299. (6) Enlargement of the rectangular
 1247 area in (5). Note that the endobionts are vertically grown, while free-living grown
 1248 tabulates have varying orientations in the matrix under the *Ecclimadictyon* skeleton.

1249 **Figure 11.** (1–3) Longitudinal sections of *Camptodictyon amzassensis* from the S15 interval,
 1250 (1, 2) NIGP177308-1; (3) NIGP 177308-2. (4) Tangential section of *Camptodictyon*
 1251 *amzassensis* from the S15 interval, NIGP 177308-1.

1252 **Figure 12.** (1–4) Longitudinal section of *Labyrinthodictyon cascum* from the S15 interval,
 1253 (1–3) NIGP 177311-1; (4) 177312-1. (5) Tangential section of *Labyrinthodictyon*
 1254 *cascum* from the S15 interval, NIGP 177312-2.

1255 **Figure 13.** Diverse paleoecological interactions among stromatoporoid and other organisms.
 1256 (1) Field photograph of dendroid growth form of *Clathrodictyon idense* Webby and

1257 Banks 1976 and intergrown solitary rugose coral *Tryplasma*. (2–3) Longitudinal and
 1258 tangential section of *Clathrodictyon* cf. *Cl. microundulatum* and intergrown tabulate
 1259 coral *Catenipora*, NIGP 177149-1, NIGP 177190, respectively. (4) Encrustation and
 1260 intergrowth association among *Clathrodictyon* cf. *Cl. mammillatum* and tabulate corals
 1261 *Agetolites* and *Heliolites*, NIGP 177313. Note irregular physical contacts between
 1262 tabulates and stromatoporoid. Upper right is a single tube with a flat base, encrusted and
 1263 partly embedded in the stromatoporoid surface. (5) *Clathrodictyon idense* and
 1264 intergrown *Tryplasma* and encrusted *Agetolites*, NIGP 177112-10. (6) Multi-intergrowth
 1265 association among *Agetolites*, *Clathrodictyon idense* and *Tryplasma*, NIGP 177101. (7)
 1266 Intergrowth association between *Clathrodictyon megalamellatum* Jeon n. sp. and
 1267 *Tryplasma*.

1268 **Figure 14.** Diverse paleoecological interactions among stromatoporoid and other organisms.

1269 (1) Longitudinal section of *Clathrodictyon* cf. *Cl. microundulatum* showing *Bajgolia*
 1270 were clustered along the growth surface of the stromatoporoid, and finally encrusted by
 1271 *Clathrodictyon* cf. *Cl. microundulatum*, NIGP 177194-6. (2) Poorly-preserved
 1272 clathrodictyid stromatoporoid and interlayering bryozoan *Rhombotrypa*, NIGP 177314.
 1273 It is difficult to distinguish whether bryozoan grew on a partially dead or living growth
 1274 surface of stromatoporoid, but the growth of bryozoan was terminated by the overgrown
 1275 host stromatoporoid. Note the difference in preservation between bryozoan and
 1276 stromatoporoid, likely indicating different original mineralogy of bryozoan and
 1277 stromatoporoid. (3) Unidentified tubular ‘*Eofletcheria*-like organism’ in the skeleton of
 1278 *Ecclimadictyon undatum*, NIGP 177303. Note that this endobiont is only found in
 1279 *Ecclimadictyon undatum*. (4) Crinoid stem and encrusting *Clathrodictyon plicatum* with
 1280 intergrown *Bajgolia* and *Tryplasma*, NIGP 177250-4. (5) Oblique section of micrite-
 1281 filled, enigmatic borings in the skeleton of *Ecclimadictyon nestori*, NIGP 177263. (6)

1282 Paleoecological interaction between *Clathrodictyon* cf. *Cl. mammillatum* and *Labechia*
 1283 sp., interpreted as spatial competition judging from their skeletal distortion (Jeon et al.,
 1284 2020b), NIGP 169634-14.

1285 **Figure 15. (1–6)** Thin-section examples of down- and up-bending of clathrodictyid
 1286 stromatoporoid laminae, caused by the intergrown corals. Black arrows indicate down-
 1287 bending laminae and white arrows indicate up-bending laminae; **(1)** NIGP 177179-14;
 1288 **(2)** NIGP 177194-4; **(3)** NIGP 177194-11; **(4)** NIGP 159437; **(5)** NIGP 176515; **(6)**
 1289 NIGP 177289. Down-bending laminae of *Clathrodictyon* cf. *Cl. microundulatum* occur
 1290 near *Bajgolia* in **(1–4)**, while the up-bending laminae are in the vicinity of intergrown
 1291 *Tryplasma* **(1, 3)**. **(5)** Down-bending laminae of *Clathrodictyon plicatum* occur near the
 1292 sharp irregularly shaped outer wall of *Bajgolia* (see also figures and corresponding text
 1293 in Jeon et al., in press). **(6)** Up-bending laminae of *Ecclimadictyon nestori* occur around
 1294 intergrown *Bajgolia*. **(7–17)** Schematic drawings to illustrate the process of forming
 1295 bending stromatoporoid laminae in the vicinity of endobiont. **(7–8)** Initial stage of
 1296 settlement of endobionts on the growth surface of clathrodictyid species. **(9–11)** With
 1297 the faster growth rate of clathrodictyid species than the endobionts, down-bending
 1298 laminae developed near the endobionts. The endobionts were commonly killed by the
 1299 overgrowth of clathrodictyid. **(12–14)** Process of up-bending laminae caused by the
 1300 faster growth rate of endobionts than host clathrodictyid species, commonly terminated
 1301 by sediment interruption. **(15–17)** Process of both up- and down-bending laminae
 1302 around endobionts. Up-bending laminae formed by encrustment of re-existed encrusting
 1303 endobiont in **(15)**. Faster growth of host clathrodictyid species reached up to same
 1304 growth level of endobiont, and caused down-bending laminae in **(16, 17)**.

1305 **Figure 16. (1–2)** Longitudinal section of astrophorizae (black arrows) of *Clathrodictyon* cf. *Cl.*
 1306 *microundulatum* with encrusted intergrown *Bajgolia*. Note that none of the distorted

1307 skeletal structures occurs near the contacts with endobionts, NIGP 177196-4 and 12,
 1308 respectively from the S18 interval. (3) Field photograph of feather-like growth form of
 1309 clathrodictyid (probably *Ecclimadictyon*) and intergrown *Bajgolia* cluster from the S17
 1310 interval. (4–7) Thin-section photographs of feather-like growth form of clathrodictyids
 1311 and intergrown *Bajgolia* clusters. (4) Dendroid *Ecclimadictyon nestori* with intergrown
 1312 *Bajgolia*, NIGP 159443 from the S18 interval. (5) Dendroid *Clathrodictyon* cf. *Cl.*
 1313 *mammillatum* with intergrown *Bajgolia*, NIGP 175173 from the S18 interval. (6)
 1314 Dendroid *Clathrodictyon plicatum* with intergrown *Bajgolia* NIGP 159448 from the S18
 1315 interval. (7) Branching dendroid *Clathrodictyon plicatum* with intergrown *Bajgolia*,
 1316 NIGP 159447 from the S18 interval. Specimens NIGP 159443, 159447 and 159448 in
 1317 (4, 6, 7) were also illustrated in Lee et al. (2016). (8) Abnormally widely spaced laminae
 1318 of *Clathrodictyon* cf. *Cl. microundulatum*, NIGP 159446 from the S18 interval.

1319 **Figure 17. (1–5)** Encrustation of diverse sessile organisms on the growth surface of
 1320 clathrodictyid species. (1) Encrusted and vertically grown *Tryplasma* on the growth
 1321 surface of *Clathrodictyon plicatum*, NIGP 177245 from S17 interval. (2) Encrusted
 1322 *Heliolites* on the growth surface of *Clathrodictyon* cf. *Cl. microundulatum*, showing
 1323 possible spatial competition judging from their irregular physical contact, NIGP 179198
 1324 from S15 interval. (3) *Syn-vivo* interaction between microbe and *Clathrodictyon idense*,
 1325 showing their twisted growth direction, NIGP 177107-1 from S3 interval. (4) Structure
 1326 interpreted as a spiculate sponge encrusted on *Clathrodictyon plicatum* from the S17
 1327 interval, NIGP 177243. (5) Multiple encrustations of tabulate coral, calcimicrobes and
 1328 bryozoans on the growth surface of *Clathrodictyon* cf. *Cl. mammillatum*, NIGP 177135
 1329 from S18 interval. (6) Schematic reconstruction to show a variety of paleoecological
 1330 interactions between clathrodictyid stromatoporoids and intergrown sessile organisms,
 1331 including labechiid stromatoporoid, rugose and tabulate corals.

1332

1333 **Figure 18. (1)** Network analysis diagram of Ordovician clathrodictyid stromatoporoid during
 1334 the Late Ordovician. These listed species are clathrodictyids shared between two or
 1335 more paleo-continents. **(2)** Three major faunal provinces of clathrodictyid
 1336 stromatoporoid distribution during the Late Ordovician. Red question marks on
 1337 Mongolia and Kazakh terranes indicate uncertain provinces to be included in peri-
 1338 Gondwana-Tarim-Altai faunal province due to insufficient investigation of
 1339 clathrodictyid stromatoporoid faunas. Paleogeographic reconstruction modified from
 1340 Cocks and Torsvik (2020). Note that this faunal province has a high similarity with the
 1341 ‘Cathay-Tasman Province’ proposed by Cocks and Torsvik (2020).

1342

1343 **Table Captions**

1344

1345 **Table 1.** Stratigraphic distribution of host clathrodictyid stromatoporoids and endobionts in
 1346 the Xiazhen Formation. The gray-colored intervals are occupied by labechiids
 1347 (*Stylostroma* and *Thamnobeatricea*, respectively) without any clathrodictyid species. 1,
 1348 *Clathrodictyon* cf. *Cl. mammillatum*; 2, *Clathrodictyon* cf. *Cl. microundulatum*; 3,
 1349 *Clathrodictyon idense*; 4, *Clathrodictyon megalamellatum* Jeon n. sp.; 5, *Clathrodictyon*
 1350 *plicatum*; 6, *Ecclimadictyon nestori*; 7, *Ecclimadictyon undatum*. Question mark
 1351 indicates unidentified poorly preserved clathrodictyid stromatoporoid.

1352

1353 **Table 2.** All reported occurrences of intergrowth associations between stromatoporoids and
 1354 other organisms in the Ordovician are compiled by age and locality. Note that the Katian
 1355 occurrences are all from peri-Gondwanan terranes, together with the earliest known

- 1356 appearances of clathrodictyids; (T), tabulate coral; (U), uncertain; (SR), solitary rugose
1357 coral; (St), stromatoporoid; (B), bryozoan; (TW), tubeworm.