

# 1 The Jiwozhai patch reef: A palaeobiodiversity hotspot in middle Givetian (Devonian) of South 2 China

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## 26 Abstract

27  
28 This study is a detailed palaeontological and palaeoecological analysis of a middle Givetian  
29 (Middle Devonian) high-diversity patch reef located in a platform interior setting in South China. The  
30 location is Jiwozhai, Guizhou Province, in the Dushan Formation. A total of 83 species (including 23  
31 undetermined species) belonging to 44 genera of reef organisms were identified, based on a detailed  
32 statistical analysis from 28 quadrats on the vertical section of the patch reef. The main reef builders are  
33 laminar and encrusting-behaviour stromatoporoids, laminar tabulate corals, and laminar ~~or~~ **<<Do you  
34 mean “and”? “Laminar” is a growth shape, “encrusting” is a type of substrate relationship; they are  
35 not compatible, so it cannot be “or”.** encrusting chaetetids, forming coverstones to build the reef  
36 framework, while abundant massive and branching tabulate corals and solitary rugose corals are also  
37 important for the formation of the reef by filling the spaces between the components of the coverstones.  
38 Reef dwellers including brachiopods, bryozoans, tubeworms, calcified cyanobacteria and gastropods,  
39 are only scarcely distributed in the Jiwozhai patch reef, having little impact on the distribution pattern.  
40 Consistent with the densely distributed species at Jiwozhai, complex ecological relationships, including  
41 extensive encrustations, spatial competition, and symbiosis have also been found among different  
42 organisms. The high palaeobiodiversity level of the Jiwozhai patch reef in platform interior emphasizes  
43 that understanding of species richness and diversity of functional groups in different habitats is critical  
44 for Givetian reef ecosystem reconstruction. Location of the patch reef in a platform interior may be the  
45 reason for the high diversity biota. The results from the Jiwozhai patch reef are evidence for a stable  
46 reef structure with evenly distributed major reef-frame builders and complex ecological relationships.  
47 The high level of species diversity is a common feature in South China, as well localities of many other  
48 palaeocontinents during the Givetian Period.

49  
50 Key words: stromatoporoids, tabulate corals, biodiversity, ecological complexity, biotic interactions

## 51 52 1. Introduction

53 Devonian reefs are of great importance in understanding the evolutionary, palaeoecological and  
54 palaeogeographic patterns of marine animals in deep time (Kiessling et al., 2002). During the Middle

55 Devonian Givetian stage, metazoan reefs reached an acme of the entire Phanerozoic (Copper, 2002;  
56 Copper and Scotese, 2003; Huang et al., 2019), manifested by vast scales, diverse reef complexes, as  
57 well as their geographic expansion to higher northern (50°N) and southern latitudes (50°S) (Kiessling,  
58 2001; Copper, 2002; Jakubowicz et al., 2019). Middle Devonian reefs were particularly abundant,  
59 occupying large continental seaboard areas of carbonate platforms and vast inland epicontinental seas,  
60 including megareefs of the 1700-30 km long tracts of the Western Canada Sedimentary Basin, Canadian  
61 arctic (Innuitian platform), eastern Laurentia “Old Red Continent” (United Kingdom to Poland), eastern  
62 Russian Platform (northeast Laurentia), Ural “Fold Belt” (eastern slopes of Urals), Siberia, northwest  
63 Africa, and South China (Playford, 1980; Copper and Scotese, 2003). However, quantifying reef  
64 biodiversity has become a major concern, not only for understanding ancient analogues of modern reefs,  
65 but also for reconstruction of global diversity patterns and the relationships between environmental  
66 changes and biotic events.

67 As major reef-building organisms, Palaeozoic stromatoporoids and corals reached their highest  
68 diversity peak in the Middle Devonian Period during their entire evolutionary histories (Scrutton, 1997;  
69 Stearn, 2015), and have been the subject of extensive studies (e.g. Cook, 1999; Stadelmaier et al., 2005;  
70 Salerno, 2008; Kershaw et al., 2018). Also, chaetetids, bryozoans, ostracods, brachiopods, gastropods,  
71 crinoid and calcified cyanobacteria are common reef components in Givetian reefs, yet with less  
72 detailed work (May, 1991). Comprehensive studies of biodiversity and fossil compositions of Devonian  
73 reefs are essential for understanding Palaeozoic ecosystems. However, such works are relatively rare  
74 (e.g. Mistiaen, 1985; May, 1988, 1992; Geldsetzer et al., 1989; Hubert et al., 2007; Song et al., 1994;  
75 Kiessling, 2009), and most previous studies mainly focus on a single group of reef organisms.

76 In the South China Craton, Givetian reef complexes are widespread, with more than 60 reported  
77 reef sites across eastern Yunnan, southern Guizhou, Guangxi and Hunan provinces, forming a reef belt  
78 that extends over 1700 km (Wu et al., 2010). Although the biodiversity of Givetian reefs in South China  
79 is thought to be one of the highest worldwide, there have been few detailed studies on the reef organisms  
80 (e.g. Song et al., 1994; Liu et al., 2004). In this paper, we investigate the biodiversity of a Givetian patch  
81 reef at Jiwozhai, South China in detail, based on a quantitative quadrat survey. The aims of this study  
82 are: 1) to reveal species richness of a platform interior patch reef in the South China marginal sea; 2) to  
83 investigate the complex palaeoecological interactions between the reef organisms, thus improving our  
84 knowledge of Palaeozoic reefs during their maximum developments; and 3) to understand spatial  
85 structure and distributions of reef components in the Jiwozhai patch reef.

## 87 2. Geological setting

88 The South China Craton was located on the east of the Palaeo-Tethys Ocean and near the equator  
89 during the Givetian Period (Fig. 1A). The Guangxi (also known as Kwanghsian) Orogeny that occurred  
90 in the Late Ordovician Period resulted in large-scale uplift and expansion of lands during Silurian to  
91 the Early Devonian time (Chen et al., 2010). South China drifted away from north Gondwana during  
92 ~400-385 Ma (Xian et al., 2019), and marine settings gradually developed in the southern part of South  
93 China due to intensified rifting and basement subsidence. In Givetian time, a large marginal sea was  
94 developed, leading to growth of an extensive carbonate platform, although this has a patchy distribution  
95 because of the formation of deep-water inter-platform basins (Fig. 1B). Middle Devonian marine  
96 deposits in South China Craton were divided by Hou et al., (1988) into four types, namely Qujing type  
97 (paralic facies), Xiangzhou type (benthic facies), Nandan type (pelagic facies) and transitional facies of  
98 the platform margin to upper slope. Xiangzhou type, in particular, is dominated by shallow-marine  
99 carbonate rocks yielding a rich benthic fauna of brachiopods, corals and stromatoporoids (Qie et al.,  
100 2019), and characterized by diverse Givetian reefs that are widely distributed in platform margins and  
101 interiors (Wu et al., 2010; Fig. 1B).

102 The Jiwozhai patch reef (GPS 25°50'56.12"N, 107°34'32.74"E) developed in the lower part of the  
103 Jiwozhai (previously spelled Chiwochai) Member of the Dushan (previously Tushan) Formation in  
104 Dushan section, southern Guizhou (Fig. 1C, D). The Formation is subdivided into three members, the  
105 Jipao (previously Chipao), Songjiaqiao (previously Sunchiachiao) and Jiwozhai members in ascending  
106 order (Liao, 2003), and assigned to the Givetian Stage based on occurrence of brachiopod  
107 *Stringocephalus*, as well as the representative rugose coral *Endophyllum-Sunophyllum-Argutastrea*  
108 assemblage through this unit (Fig. 1D) (Liao, 2003). The Jiwozhai Member is composed mainly of

109 dark-grey to black medium- to thick-bedded calcareous mudstone, muddy limestone and reef limestone  
110 in the lower part. It possesses a rich benthic fauna, including stromatoporoids, tabulate corals, rugose  
111 corals and brachiopods and others, described below. It has been interpreted as representing a shallow-  
112 marine environment in the platform interior along the southern margin of the Yangtze oldland (Liao,  
113 2003). Previous palaeontological investigations concerned mainly stromatoporoids and rugose corals.  
114 Yang and Dong (1963) described 17 species of stromatoporoids, including widespread species, such as  
115 *Stachyodes radiata*, *Hermatostroma episcopale*, *Paramphipora blokhini*, *Trupetostroma*  
116 *sublamellosum*, *Trupetostroma dushanense*, and *Actinostroma undulatum* in the lower part of the  
117 Jiwozhai Member. Another systematic palaeontological work concerns rugose corals, and a total of 20  
118 species were reported in the lower and upper part of the Jiwozhai Member (Liao and Birenheide, 1984,  
119 1985; Birenheide and Liao, 1985). However, detailed and comprehensive studies on the Jiwozhai patch  
120 reefs are still lacking, except some pioneering work on the sedimentology, sequence stratigraphy, and  
121 general characteristics of the reefs (Wang et al., 2014; Wang, 2016).

### 122 123 **3. Materials and methods**

124 The studied patch reef is revealed in an exposure orientated east-west and located in the Dushan  
125 Dahekou geopark. The reef is not fully exposed, the part that is accessible is about 4.5 m thick and  
126 nearly 100 m wide (Fig. 2A). The patch reef is rich in fossils, accounting for 60%-80% of the carbonates  
127 (Fig. 2B–F), while limestones surrounding the patch reef are composed of thick-bedded bioclastic  
128 limestone with sparse fossils of corals and stromatoporoids. This study is based on detailed  
129 measurements of the Jiwozhai patch reef, including field observations of lithologies and sedimentary  
130 structures and sampling for microfacies analysis. Twenty-eight quadrats (0.5 m × 0.5 m), occupying 7  
131 m<sup>2</sup> in total were selected from the vertical section of the patch reef (Figs. 2A, D; 3A, B) for quantitative  
132 analyses. The selected quadrats are representative of the entire patch reef structure. Fossil compositions  
133 of each quadrat were photographed and sampled in detail. Depending on fossil preservations in each  
134 quadrat, 15 to 45 samples per quadrat were collected to study the distribution patterns of reef  
135 components (Fig. 3C), and the sampled area was mapped in the field, with supporting photography. In  
136 total, 665 specimens were collected and analyzed. For a better identification of fossil species and  
137 investigation of microfacies, 2804 thin sections (including sets of serial sections), as well as eight  
138 polished slabs were also prepared for additional observations. The diversity and abundance of major  
139 fossil components, including stromatoporoids, rugose corals, tabulate corals, chaetetids, brachiopods,  
140 bryozoans, calcified cyanobacteria and tubeworms are counted based on the samples from the quadrats.  
141 For branching stromatoporoids and tabulate corals, we count only the relatively completed branches in  
142 an attempt to avoid an overestimation of the actual number. Nevertheless, we accept that branching  
143 stromatoporoids, as fragments, are difficult to quantify so our estimate of those components is less  
144 precise than non-branching forms. Distribution of the fossil components and reef structure is realized  
145 by detailed counting of the thin sections and slabs, as well as broad identification of fossil types from  
146 the field photos over the vertical section of the patch reef. Fossil components and diversity of each  
147 quadrat are illustrated in detail, and the variation among the quadrats is also evaluated by comparing  
148 the accumulating number of genera and species from the first quadrat to the last. All fossil specimens  
149 are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences,  
150 Nanjing, China.

### 151 152 **4. Fossil components of the patch reef**

153 The Jiwozhai patch reef represents a biodiversity hotspot in South China marginal sea near the  
154 palaeoequator during the Givetian Period, recording 83 species belonging to 44 genera of 8 phyla reef  
155 organisms that identified from the 28 quadrats of the Jiwozhai patch reef (Fig. 4A). Among them, rugose  
156 corals, tabulate corals, stromatoporoids, chaetetids, and brachiopods are relatively more abundant in  
157 number, while other benthic fossils such as bryozoans, calcified cyanobacteria, crinoids, gastropods,  
158 etc. are relatively scarce in the reef community. All the reef organisms identified in this study are  
159 described below according to their importance with respect to the reef-forming process.

#### 160 161 *4.1 Stromatoporoids*

162 Stromatoporoids, the most important reef-forming organisms in the Jiwozhai patch reef, are highly  
163 diversified in generic and specific level (10 genera, 16 species; N = 755; Fig. 4A, B). A great majority  
164 of the stromatoporoids range from 20 to 40 cm in width, but some much larger ones exceed 50 cm.  
165 Their sizes are on average, much larger than any other reef contributor in the Jiwozhai reefs. The most  
166 abundant genus is *Clathrocoilon* (N = 270; Fig. 4B). Next, *Trupetostroma* (N = 149), *Stachyodes* (N  
167 = 111), *Actinostroma* (N = 99), and *Stictostroma* (N = 98) are also quite common, while *Stromatopora*  
168 (N = 9), *Salirella* (N = 8), *Habrostroma* (N = 7), *Synthetostroma* (N = 3) and *Parallelopora* (N = 1)  
169 appear relatively sparsely (Fig. 4B). This distribution of taxa, with 2 or 3 taxa being very abundant, and  
170 others less so, is characteristic of stromatoporoid assemblages in the Palaeozoic (Kershaw et al., 2018).  
171 Stromatoporoids in the patch reef exhibit laminar and dendroid forms, and encrusting behaviours. As  
172 the main reef constructors, the ratio of width to height of laminar stromatoporoids is generally over 10.  
173 Among them, *Trupetostroma dushanense* (N = 128; Fig. 5G) and *Actinostroma undulatum* (N = 99; Fig.  
174 5A), both possessing long and continuous pillars much thicker than their laminae, are the most abundant  
175 species. Many of the laminar stromatoporoids show conspicuous latilaminae inside the skeletons (Fig.  
176 5A, B, G). The frequent sediment influx and settlement of calcified cyanobacteria on the surface of the  
177 stromatoporoid skeletons appear to be regular, and may be seasonal, indicating a higher depositional  
178 rates than the growth of the stromatoporoids which cause the cease of growth of the stromatoporoids.  
179 However, the laminar stromatoporoids recovered quickly and continued to grow (Fig. 5A, B, G). Also,  
180 the encrusting-behaviour stromatoporoids are important reef builders, often found to be associated with  
181 solitary rugose corals, tabulate corals, chaetetids and bryozoans (Fig. 5B, H). *Clathrocoilon* and  
182 *Stictostroma* are the most abundant encrusting-behaviour genera (Fig. 5B, C, E). In addition, dendroid  
183 stromatoporoids belonging to species of *Stachyodes* (Fig. 5E) occur in the patch reef in a variety of  
184 orientations, but are more common in the upper part. They are less important than the laminar and/or  
185 encrusting-behaviour stromatoporoids.

#### 186 4.2 Tabulate corals

187 As important reef builders, the tabulate corals show a diverse assemblage with 8 genera and 13  
188 species (N = 630; Fig. 4A, B) and possess various growth forms. *Thamnopora* (N = 303) is the most  
189 common one, followed by *Crassialveolites* (N = 101), *Cladopora* (N = 68), *Roseoporella* (N = 57),  
190 *Aulopora* (N = 42), and *Scoliopora* (N = 39), while *Alveolites* (N = 10) and *Syringopora* (N = 10) are  
191 relatively scarce (Fig. 4B). Branching tabulate corals are commonly 15–40 cm in height and 2–13 mm  
192 in diameter. *Thamnopora* cf. *pansiensis* (N = 236; Fig. 6H) and *Thamnopora compacta* (N = 50; Figs.  
193 6G) are predominant, while *Cladopora fistula* (N = 68; Fig. 6K, L) is less abundant. Most specimens  
194 of branching species are found to be toppled and fragmented, commonly distributed in the matrix  
195 between the reef frameworks, while some are encrusted by stromatoporoids or chaetetids (Fig. 5H, 6G),  
196 or served as hard grounds for growth of other organisms. Compared with branching tabulates, the  
197 massive tabulate corals, including species of *Alveolites* and *Crassialveolites* (Fig. 6I, J), *Roseoporella*  
198 all of which range from laminar to domical growth forms, are slightly less abundant in number. Other  
199 taxa that occur rarely in the Jiwozhai patch reef include tabulate corals with reptant growth style  
200 (whereby the coral tubes grew horizontally along the substrate) include species of *Aulopora* and the  
201 early growth stages of *Syringopora*. Species of *Aulopora* commonly used the surface of dead laminar  
202 stromatoporoids or chaetetids as substrate, while *Syringopora* began growth on surfaces of  
203 stromatoporoids assumed to have been alive when *Syringopora* settled. *Syringopora* tubes then became  
204 endosymbionts of stromatoporoids, in two taxa, *Stromatopora hüpschii* (Fig. 5F) and  
205 *Trupetostroma* cf. *colliculosum*. There is likely to have been a biological symbiotic relationship  
206 between *Syringopora* and those two stromatoporoid taxa. No free forms of *Syringopora* are observed  
207 in this reef.

#### 208 4.3 Chaetetid sponges

209 *Chaetetid sponges* are also important skeletal reef builders, but only one species, *Litophyllum*  
210 *inflatus* is found (N = 144; Fig. 4A, B), much less diversified than the corals and stromatoporoids in the  
211 Jiwozhai reefs. The species exhibit laminar to low domical growth forms of 1–4 mm in height (Fig. 5A,  
212  
213

214 I) or encrusting other organisms (Figs. 5H, 6G), forming the reef framework together with  
215 stromatoporoids and corals.

216

#### 217 4.4 Rugose corals

218 At specific level, rugose corals are the most diverse reef organisms in the Jiwozhai patch reef (9  
219 genera, 29 species; N = 198; Fig. 4A, B). Among the genera, solitary rugose corals are predominant,  
220 including *Sinodisphyllum* (N = 67), *Pseudozaphrentis* (N = 35), *Temnophyllum* (N = 28), *Mictophyllum*  
221 (N = 26), *Sunophyllum* (N = 16), and *Cystiphyllodes* (N = 11), while fasciculate and cerioid rugose  
222 corals are rare, including *Disphyllum* (N = 11), *Arguastrea* (N = 2), and *Thamnophyllum* (N = 2; Fig.  
223 4B). The solitary rugose coral species are represented by *Sinodisphyllum simplex* (N = 25; Fig. 6B), *S.*  
224 *litvinovitshae* (N = 22), *S. variable* (N = 15), *Pseudozaphrentis hejiazhaiense* (N = 35; Fig. 6A),  
225 *Temnophyllum poshiense* (N = 10) and *Mictophyllum cf. shawoziense* (N = 15), of which the diameter  
226 ranges commonly from 1.2 to 2 cm. Large solitary rugose corals are extremely rare, represented by  
227 *Cystiphyllodes corneolum* (N = 2), which is up to 6 cm in diameter (Fig. 6F). A significant number of  
228 solitary rugose corals was encrusted or intergrown with stromatoporoids or chaetetid sponges (Fig. 6A;  
229 free-living solitary rugose corals are horn-shaped, mostly living on matrix between the reef frameworks.  
230 Apart from the abundant solitary rugose corals, fasciculate rugose corals, represented by *Disphyllum*  
231 *intermedium* (N = 9) and *Thamnophyllum sinense?* (N = 2), are found to be toppled and fragmented in  
232 most cases, while cerioid rugose corals, represented by *Argustarea thomasi* (N = 2; Fig. 6C) are in  
233 growth position. Although fasciculate and cerioid rugose corals are reef-frame builders, they are scarce  
234 and not significant for the reef-forming process of the Jiwozhai patch reef.

235

#### 236 4.5 Brachiopods

237 Brachiopods are highly diverse in both generic and specific levels (8 genera, 16 species; N = 84; Fig.  
238 4A, B). *Athyris* and *Emanuella*, each possessing 4 species, are more diversified than the other genera  
239 (Fig. 7C, D). The majority of the brachiopods in the patch reef are quite small-sized, with a width  
240 ranging from 5 to 10 mm. The most common species is *Leiorhynchus* sp. A (N = 51; Fig. 7A),  
241 followed by *Athyris* sp. A (N=8; Figs. 7C), *Howittia dushanensis* (N = 5; Figs. 7B), and *Ambothyris*  
242 sp. (N = 5). Some brachiopods grow on the surfaces of laminar stromatoporoids or tabulate corals, and  
243 were occasionally buried after death by growth of stromatoporoids (Fig. 8E). The typical Givetian  
244 brachiopod *Stringocephalus*, which is a giant brachiopod that occurs commonly in the Dushan  
245 Formation, has not been found in the Jiwozhai patch reef, suggesting unfavourable habitats for these  
246 large-sized brachiopods.

247

#### 248 4.6 Bryozoans

249 Bryozoans in the Jiwozhai patch reef are of low-diversity and rare (4 genera, 4 species; N = 19;  
250 Fig. 4A, B). They are variable in growth forms, ranging from domical, laminar to branching.  
251 *Fistuliporella hemispherioidea* is the most common species (N = 16), often encrusting other organisms  
252 (Fig. 8F). The domical bryozoans have a width up to 40 mm (Fig. 7E), while small branching ones are  
253 only 1 mm in diameter, dwelling on the soft substrate in the reef matrix, and often found to be  
254 fragmented.

255

#### 256 4.7 Tubeworms

257 One species of tubeworms, *Torquaysalpinx sokolovi* (N = 42; Fig. 4A, B), is frequently found  
258 embedded in the skeletons of stromatoporoids, tabulate corals and chaetetids (Figs. 5I, 7G, H), yet no  
259 free-living ones are found, suggesting an endosymbiotic relationship. *Torquaysalpinx sokolovi* is  
260 usually round or elliptical in transverse view, with diameters ranging from 1 to 2 mm. The tube walls  
261 are relatively thick and spiraling-shaped upward (Fig. 7G), comparable to those described by Zapalski  
262 and Hubert (2011). Dissepiments are occasionally observed inside the tubes (Fig. 7H). Judging from  
263 the non-curved growth band near the tubeworms (i.e. laminae in stromatoporoid, tabulae in chaetetid),  
264 the growth of stromatoporoids and chaetetids was generally not affected by the species, similar to the  
265 endobiont corals.

266

#### 267 4.8 Calcified cyanobacteria

268 Calcified cyanobacteria are of low-diversity, rare and not significant in the Jiwozhai patch reef.  
269 We recognized three different taxa (N = 24; Figs. 4A, B; 7J, K); Fig. 7J shows a thin layer of  
270 *Rothpletzella*-like microbe, and Fig. 7K more closely resembles *Hedstroemia*, which is fan-shaped or  
271 hand-shape illustrated containing continuously bifurcated filaments of 50 to 80  $\mu\text{m}$  in diameter (Fig.  
272 7K), is identified from the patch reef. The specimens have much larger filaments than those reported  
273 from the Silurian of Gotland (Wood, 1948), but similar to those of the Upper Devonian strata of Russia  
274 (Zatoń and Jarochowska, 2018). Besides, a few specimens of *Girvanella* are also found to occur, but  
275 only from one quadrat, evidence of limited distributions of the organism. The calcified cyanobacteria  
276 commonly grew on the surface of stromatoporoid skeletons, indicating growth interruption of the  
277 stromatoporoids. Ordovician calcimicrobe associations in Tarim Basin were interpreted by Liu et al.  
278 (2016), to be common in environments that are partly restricted, such as lagoonal and back-reef facies,  
279 discussed later.

280

#### 281 4.9 Other fossils

282 Ostracods, gastropods, nautiloids, echinoderms occurred sporadically in the patch reef (Fig. 7F, I,  
283 L). Under the microscope, the ostracods (Fig. 7L) are about 0.7 mm in length and commonly co-occur  
284 with gastropods. They are reef-dwelling organisms of the reef community. Only one nautiloid fragment  
285 (Fig. 7F) is observed in quadrat 14. In addition, plenty of crinoid stems fragments are also found to  
286 occur, indicating the existence of these reef-dwelling organisms in the Jiwozhai reef.

287

### 288 5. Ecological complexity

289 Prior to the Frasnian-Famennian mass extinction, metazoan reefs are composed of ecologically  
290 interacting species and characterized by various types of symbiotic interactions between different  
291 organisms during Early and Middle Devonian time (Vinn, 2016; 2017). Although the Jiwozhai reef  
292 represents a small patch reef that existed in the platform interior along the Yangtze oldland, which is  
293 generally considered to be a relatively unfavourable habitat with high turbidity and soft substrate,  
294 complex ecological relationships are found to occur in all 28 quadrats. The biotic interactions between  
295 different reef contributors are mainly manifested as extensive encrustations, spatial competition, and  
296 symbiosis. The abundance of fossils and the complexity of interactions identified in this study are  
297 evidence that the environment was favourable to the organisms found as fossils.

298 The most conspicuous ecological feature in the Jiwozhai patch reef is the extensive encrustation  
299 by species of stromatoporoids *Clathrocoilon crassitexta*, *C. obliterated*, *C. spissa*, *Stictostroma*  
300 *saginatam*, and chaetetids *Litophyllum inflatus*, occurring in a total of 716 cases observed in the majority  
301 of collected samples. These encrusting-behaviour stromatoporoids and chaetetids have flexible growth  
302 strategies, and their growth forms vary greatly from one species to another and flexibly changed under  
303 different environmental conditions. The encrusting behaviour is more or less opportunistic, commonly  
304 over dead skeletons (Figs. 5B, E, G; 6A, G; 8A, B, F), but there is evidence in Fig. 8C, D that  
305 stromatoporoids could grow over living organisms. A growth sequence of multiple encrustations by  
306 stromatoporoids, tabulate corals, and/or chaetetid is commonly observed (Figs. 5H; 6J; 8A, D, F),  
307 forming rigid boundstones important for the formation of reef frameworks.

308 Due to the densely packed skeletons, competition for growth space is commonly found to occur,  
309 between: different stromatoporoid taxa; stromatoporoids and corals; stromatoporoids and chaetetids;  
310 stromatoporoids and bryozoa; and chaetetids and corals. A total of 35 cases of competition was observed  
311 in the suite of 2804 thin sections (Table 1). Live-live competitive behaviour is demonstrated by the  
312 growth deformity of the organisms and their direct contacts (Fig. 8C, D). Competitive intergrowths  
313 between these co-occurring species possibly indicate competition for favorable substrates between the  
314 benthic organisms. It is estimated that the actual spatial competition between the reef organisms must  
315 be much more than the counted number. The fact that all the observed cases involve either  
316 stromatoporoids or chaetetids, or both, is interpreted here as evidence that hypercalcified sponges are  
317 more active in occupying spaces in the patch reef.

318 Endosymbiotic intergrowth occurs between tabulate coral *Syringopora* and stromatoporoid  
319 *Stromatopora hüpschii* (N = 9; Fig. 5F) and *Trupetostroma cf. colliculosum* (N = 1); no free-living  
320 *Syringopora* is observed, suggesting the growth of syringoporoid corals relies on stromatoporoids.  
321 Another symbiotic relationship involves tubeworms (N = 48; Figs. 5I, 7G, 7H) embedded within the

322 skeletons of stromatoporoids *Actinostroma undulatum*, *Stromatopora hüpschii*, and *Trupetostroma*  
323 *dushanense*, tabulate coral *Roseoporella* sp. A, *Roseoporella* sp. B, *Scoliopora* sp., and *Alveolites*  
324 *stenoporides*, and chaetetids *Litophyllum inflatus*. In contrast to syringoporoids, the tubeworms have  
325 been interpreted as parasites to the host organisms (Tapanila, 2005; Zapalski and Hubert, 2011). In  
326 addition, rare brachiopod shells of unknown species are found to be associated with the stromatoporoid  
327 *Stromatopora*, and there may have been syn-vivo interactions between the two organisms (Fig. 8E),  
328 although this is difficult to prove. These cases suggest that symbiotic relationships or syn-vivo  
329 interactions occur commonly due to the high density and diversity of benthic organisms.

330

## 331 6. Spatial distributions of the reef community

332 From detailed mapping of components of the Jiwozhai patch reef (Fig. 9), it is clear that the patch  
333 reef is slightly inclined towards its margin, containing abundant stromatoporoids, tabulate corals, and  
334 chaetetids, and rugose corals that are densely packed as the main reef builders. For major reef-frame  
335 builders, the Jiwozhai patch reef is characterized as *Actinostroma-Clathrocoilona-Thamnopora-*  
336 *Crassialveolites* ecological community. Following the classification of reef limestones by Flügel (2010),  
337 the framework of Jiwozhai patch reef is predominantly composed of coverstones, framestones and  
338 bafflestones (Figs. 2B–D; 3B, 9). The coverstones are carbonate rocks dominated by in-situ tabular or  
339 lamellar organisms covering, protecting and stabilizing broken debris, and was included by Embry and  
340 Klovan (1971) as a part of bindstone category. The coverstones in the present study are composed of  
341 abundant laminar (several to tens centimeters in basal length) stromatoporoids, tabulate corals,  
342 chaetetids that are mostly in growth positions, covering smaller bioclasts and matrixes and stabilizing  
343 unconsolidated sediment on the seafloor (Fig. 2B–F). These laminar fossils usually have undulated  
344 bottoms; although their width and thickness are highly variable, the ratio of width to thickness is  
345 commonly more than 10. In general, they are distributed unevenly among the 28 quadrats and more  
346 abundant in the upper part of the patch reef (Fig. 9). Less abundant in the number of occurrences, massive  
347 tabulate corals and branching tabulate corals, and solitary rugose corals densely filled the spaces  
348 between the coverstones, forming framestones and bafflestone to build the patch reef (Fig. 9). The  
349 massive tabulate corals that filled the spaces are mostly in growth position, while branching tabulate  
350 corals and solitary rugose corals are in a variety of orientations, and more common in the lower part of  
351 the patch reef (Fig. 9). The branches of tabulate corals are potentially wave-resistant, supplying spaces  
352 for depositions of smaller intraclasts. Also, the matrix between the coverstones is composed of  
353 dolomitic lime-muds and micro-calcite<<do you mean “micrite”? If not then please state clearly what  
354 is micro-calcite. containing various reef dwellers including brachiopods, gastropods, nautiloids,  
355 echinoderms, etc.

356 Although the generic and specific level diversities of reef organisms fluctuate among different  
357 quadrats, the major reef frame builders, including stromatoporoids, tabulate corals, and chaetetids are  
358 quite evenly distributed (Fig. 10A, C), as there are no distinct diversity changes by accumulating the  
359 genera and species numbers of the 28 quadrats (Fig. 10B, D). Stromatoporoids *Actinostroma undulatum*,  
360 *Trupetostroma dushanense*, *Clathrocoilona crassitexta*, *C. obliterated*, *C. spissa*, *Stachyodes costulata*,  
361 *S. radiata*, *Stictostroma saginatum* and tabulate corals *Crassialveolites dushanensis*, *Thamnopora* cf.  
362 *pansiensis*, *Cladopora fistula*, *Scoliopora* sp., *Roseoporella* sp. A, *Aulopora* cf. *compacta* are common  
363 reef constructing species that occur in all quadrats. The distributions of rugose corals and brachiopods,  
364 however, changes significantly among the quadrats, as judged by the obvious increase of generic and  
365 specific level diversity by accumulating the quadrats (Fig. 10B, D). Brachiopods occur more commonly  
366 in the middle and upper part of the patch reef, while rugose corals are more abundant in the lower part,  
367 serving as hard grounds for the growth of reef-frame building organisms. Other fossil groups, including  
368 tubeworms, bryozoans, calcified cyanobacteria and gastropods, are only sparsely distributed in the  
369 Jiwozhai patch reef. They do not have impacts on the distribution pattern due to low species richness  
370 and abundances.

371 Thus, distribution of components of the Jiwozhai patch reef (Fig. 9), using quadrat measurements  
372 to assemble data, gives evidence for a relatively stable reef structure, with laminar and encrusting-  
373 behaviour stromatoporoids and chaetetids, and laminar to low domical tabulate corals as main reef-  
374 frame builders, while massive tabulate corals, branching tabulate corals, solitary rugose corals, and  
375 other subordinate organisms filled the spaces between the coverstones. Such a mode is also found in

376 the other patch reefs of the Dushan Formation at Jiwozhai (Fig. 2B-D). In addition, the reef-frame  
377 builders are evenly distributed, while significant variations occur among the subordinate reef builders  
378 and reef dwellers.

379

### 380 **7. Comparisons with other Givetian reefs**

381 A number of Givetian reefs occur in South China Craton, such as the platform-margin reefs from  
382 Buzhai, Maoying of Guizhou Province and Liuzhai, Beishan and Yanshan from Guangxi Province,  
383 biostromes of the Qiziqiao Formation from Hunan Province (Dong et al., 1989; Liu and Dong, 1991;  
384 Mao and Wu, 1995; Shen and Yu, 1996; Liu et al., 2000; Liu et al., 2004). The platform-margin reef  
385 complexes at Buzhai and Liuzhai are all of large size, and 604, 129.5, 667 meters in thickness,  
386 respectively, much thicker than the Jiwozhai patch reef. They are built mainly by stromatoporoids  
387 *Actinostroma*, *Stromatopora*, *Clathrocoilona*, *Trupetostroma* and *Ferestromatopora*, and tabulate  
388 corals *Thamnopora*, *Alveolites*, and *Crassialveolites*, more or less similar to the major reef constructors  
389 of the Jiwozhai patch reef. However, the stromatoporoids in these platform-margin reefs are mostly  
390 domical forms (Liu and Dong, 1991; Liu et al., 2004), forming reef frameworks directly against high-  
391 energy environments. In addition, fasciculate and cerioid rugose corals, and brachiopod  
392 *Stringocephalus* are also more abundant in these reefs, but the diversity of solitary rugose corals is  
393 considerably less than that of the Jiwozhai patch reef. It is noteworthy that species of *Amphipora* are  
394 commonly found in the lagoon facies of these reef complexes, yet not a single skeleton is observed in  
395 the Jiwozhai patch reef. Liu et al. (2016) noted that calcimicrobe associations including *Rothpletzella*  
396 and *Hedstroemia* taxa (present in the Jiwozhai samples) are indicative of some measure of restricted  
397 environments, that might apply to the Jiwozhai reef setting. The lack of the stromatoporoid taxon  
398 *Amphipora* in Jiwozhai is unusual. *Amphipora* is ubiquitous in Devonian reef systems and its absence  
399 in Jiwozhai may reflect some environmental differences compared to platform margin reefs in other  
400 Devonian examples.

401 Compared with the platform-margin reefs of South China, the Jiwozhai patch reef possesses more  
402 diverse rugose and tabulate corals in both genus and species level, but similar in the diversity level of  
403 stromatoporoids. 15 species that occur both in the platform-margin reefs and the present patch reef are  
404 stromatoporoids *Clathrocoilona crassitexta*, *Clathrocoilona obliterated*, *Synthetostroma*  
405 *actinostromoides*, *Stromatopora hüpschii*, *Habrostroma laminosum*, *Parallelopore ostiolata*,  
406 *Stachyodes costulata*, *Stachyodes radiata*, tabulate corals *Thamnopora cf. pansiensis*, *Cladopora fistula*,  
407 rugose corals *Temnophyllum waltheri*, *Temnophyllum poshiense*, *Sinodisphyllum simplex*,  
408 *Sinodisphyllum variable*, *Sunophyllum typicum*, whereas most other species are restricted to more open  
409 environment (e.g. *Stringocephalus*).

410 In central Hunan, Liu et al. (2000) reported six types of reef assemblages in the Givetian biostromes  
411 of the Qiziqiao Formation by differences of the major reef-frame builders, including a) irregular forms  
412 of stromatoporoids *Actinostroma*, *Stromatopora*, *Clathrodictyon*, *Stromatoporella* and massive rugose  
413 coral *Argutastrea*; b) domical corals *Argutastrea* and *Endophyllum* and stromatoporoids *Stromatopora*,  
414 *Gerronostroma*, and *Parallelopore*, c) branching tabulate corals *Thamnopora* and encrusting-behavior  
415 stromatoporoids *Clathrocoilona*, d) small and high domical stromatoporoids *Trupetostroma*,  
416 *Actinostroma*, and *Clathrocoilona*, and tabulate corals *Alveolites* and *Thamnopora*, e) thin laminar  
417 stromatoporoids *Clathrocoilona*, *Trupetostroma*, and *Stromatopora*, and f) biostromes built by calcified  
418 cyanobacteria. Compared with the biostromes of the Qiziqiao Formation, the Jiwozhai patch reef is a  
419 combination of types C and E of the types recognized by Liu et al. (2000), and reef organisms are more  
420 densely packed, with very few domical stromatoporoids, and the calcified cyanobacteria are not  
421 significant reef builders. The differences among the reef types are mainly controlled by the different  
422 depositional environments (Liu et al., 2000). Similar classifications of the types of Middle Devonian  
423 reefs have also been described in Europe (Burchette, 1981; Fernandez-Martinez et al., 1994), suggesting  
424 cosmopolitan features in Middle Devonian reefs. The Jiwozhai patch reef is located within the platform  
425 interior, with muddy substrates and periodical high-energy environments, resulting in the dominance of  
426 laminar stromatoporoids, tabulate corals, and chaetetids as main reef constructors. Zapalski *et al.* (2017)  
427 noted the dominance of platy tabulate and rugose corals in two Middle Devonian localities in the Holy  
428 Cross Mountains, Poland and interpreted photosymbiosis in those corals. In the Jiwozhai patch reef, not  
429 only tabulate corals, but abundant stromatoporoids and chaetetids exhibit platy growth habits similar to



430 those of the corals, and their growth forms may be affected by light availability, as well as the influence  
431 of soft substrates and periodical high energy events such as storms. The biodiversity level and intensive  
432 biotic interactions in the Jiwozhai patch reef are higher than previously reported reefs in South China,  
433 which is interpreted here to indicate that the platform interior reef was a biodiversity hotspot for the  
434 reef organisms.

435 We repeat a key point made earlier in this study, that the Devonian Period witnessed the most  
436 remarkable reef-building episode in the Phanerozoic, and particularly, stromatoporoid-coral reefs  
437 reached a climax during the early to middle Givetian (Copper, 2002), and distributed globally in low  
438 latitudes, extending even to higher latitudes (Kiessling, 2001; Jakubowicz et al., 2019). Metazoan reefs  
439 built mainly by stromatoporoids and tabulate and rugose corals were quite common in many other  
440 localities around the world, such as the lower Givetian coral limestones of Rhenish Massif (35 species  
441 of 33 genera, major reef builders include stromatoporoid *Stictostroma*, *Clathrocoilon* and tabulate  
442 coral *Alveolites*; May, 1992), Horn Plateau reefs in Canada (76 species, major reef builders include  
443 tabulate coral *Alveolites*, *Favosites*, *Thamnopora*, rugose coral *Atelophyllum*, *Australophyllum*,  
444 *Hexagonaria*, and stromatoporoid *Trupetostroma*, *Stromatopora*; Vopni and Lerbekmo, 1972), and  
445 Aferdou el Mrakib reefs in Morocco (46 species of 36 genera, major reef builder tabulate coral  
446 *Heliolites*, *Favosites*, rugose corals *Phillipsastrea*, *Endophyllum*, *Thamnophyllum*, and stromatoporoid  
447 *Stromatoporella*, *Actinostroma*; Jakubowicz et al., 2019). Although the reef-building organisms varied  
448 among different reef sites, it is apparent that the laminar growth forms of reef-building organisms  
449 including stromatoporoids and tabulate corals are a common feature of the Givetian communities and  
450 widespread on different palaeocontinents. On the other hand, biotic interactions, including encrustations,  
451 spatial competition, and various forms of symbiosis among these metazoan reefs are a common feature  
452 and occur frequently (May, 1992; Zhen and West, 1997), which plays an important role in the reef-  
453 forming process. The frequency of biotic interactions seems to reach a climax as well, in accordance  
454 with the magnificent scale of the Givetian reefs.

455 Detailed mapping of the Jiwozhai patch reef reveals remarkably high species-level biodiversity,  
456 adding to information about the complexity of reef ecological relationships, resulting in a stable reef  
457 ecosystem that is widespread in South China as well as many other localities of the world during the  
458 Givetian times. More detailed studies in terms of fossil components and ecological relationships on  
459 other reefs from South China as well as other palaeocontinents are necessary, for a better understanding  
460 of the biodiversity level and evolution of reef in deep time.

461 The reef system appears to have reached a mid-Palaeozoic maximum in the Middle Devonian  
462 Period, with cumulative thicknesses and sizes expanding in the late Eifelian and peaking especially in  
463 early to middle Givetian time (Copper, 2002). The major metazoan reef builders, including  
464 stromatoporoids, tabulate corals and rugose corals, attained their maximum genus-level diversity during  
465 the Eifelian (Scrutton, 1997; Stearn, 2015). However, in species-level diversity, the scenario might be  
466 different, as has been shown in the Devonian of Ardennes (Belgium), where maximum diversity appears  
467 in the Givetian (Zapalski *et al.*, 2007). Mega-reef belts over 1000 km were widespread to a global scale  
468 in Middle Devonian and the Givetian marks the peak of Devonian reef distribution and carbonate  
469 platform growth, following progressive expansion of metazoan reef from the Emsian onward (Copper  
470 and Scotese, 2003), which corresponds to the increasing diversity level of major reef building organisms.  
471 This study on the Jiwozhai patch reef adds to the evidence that high species diversity level and complex  
472 ecological relationships between reef organisms is a common feature of Middle Devonian reefs and  
473 closely related to the development of the vast-scale reef belts.

## 474 475 **8. Conclusions**

476 1. A total of 83 species (including undetermined species) belonging to 44 genera of eight different  
477 reef organisms were identified in Jiwozhai reef, Dushan Formation, South China, representing a high  
478 level of species biodiversity. Among them, rugose corals are the most diverse in specific level (29  
479 species of 9 genera), followed by stromatoporoids (16 species of 10 genera), brachiopods (16 species  
480 of 8 genera), tabulate corals (13 species of 8 genera), bryozoans (4 species of 4 genera), calcified  
481 cyanobacterias (3 species of 3 genera), chaetetids (1 species of 1 genus) and worms (1 species of 1  
482 genus). The order of abundance of reef organisms is stromatoporoids, tabulate corals and chaetetids,

483 followed by rugose corals and brachiopods, while bryozoans, calcified cyanobacterias and tubeworms  
484 are relatively scarce.

485 2. The Jiwozhai patch reef is characterized by coverstones as the main type of reef frame,  
486 containing rich laminar and encrusting-behaviour stromatoporoids and chaetetids, and laminar tabulate  
487 corals. Abundant massive and branching tabulate corals and solitary rugose corals are the main  
488 organisms to form framestones and bafflestones that fill the spaces between the coverstones. Reef  
489 dwellers including brachiopods, ostracods, bryozoans, gastropods, nautiloids, calcified cyanobacteria  
490 and tubeworms, which add to the reef biodiversity, but they are relatively scarce and not significant in  
491 forming the patch reef. The distribution of reef-frame builders is quite even, but significant variations  
492 occur among the subordinate reef builder and reef dwellers. In the Jiwozhai patch reef the major reef-  
493 framer building organisms form a group, here recognised as the *Actinostroma-Clathrocoilona-*  
494 *Thamnopora-Crassialveolites* ecological community.

495 3. Consistent with the densely packed and highly diverse species at Jiwozhai, complex ecological  
496 relationships, including extensive encrustation, spatial competition, and symbiosis have also been found  
497 among different organisms. The ecological relationships between the reef organisms are important for  
498 the formation of the patch reef.

499 4. Compared with the previously reported reefs in South China, the Jiwozhai patch reef, which is  
500 located in the platform interior, has a higher species diversity, indicating a biodiversity hotspot for the  
501 reef organisms, and is evidence that platform interiors are favourable places for reef growth. Coral-  
502 stromatoporoid reefs are widespread globally in Givetian times, and growth forms vary according to  
503 different depositional environments. The reef-frame builders of laminar and encrusting-behaviour  
504 stromatoporoids and tabulate corals, with extensive biotic interactions, are a common feature found in  
505 many other reefs as well.

506

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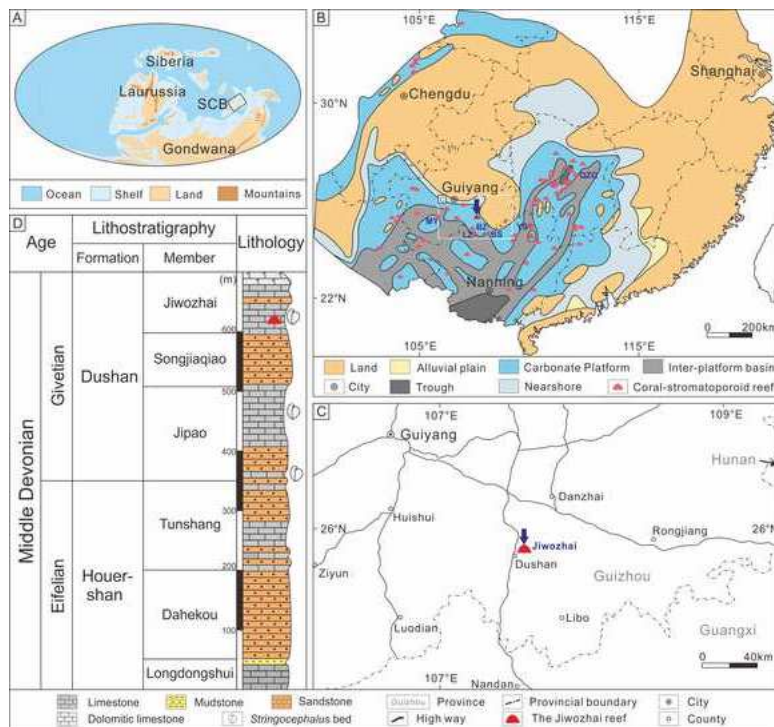
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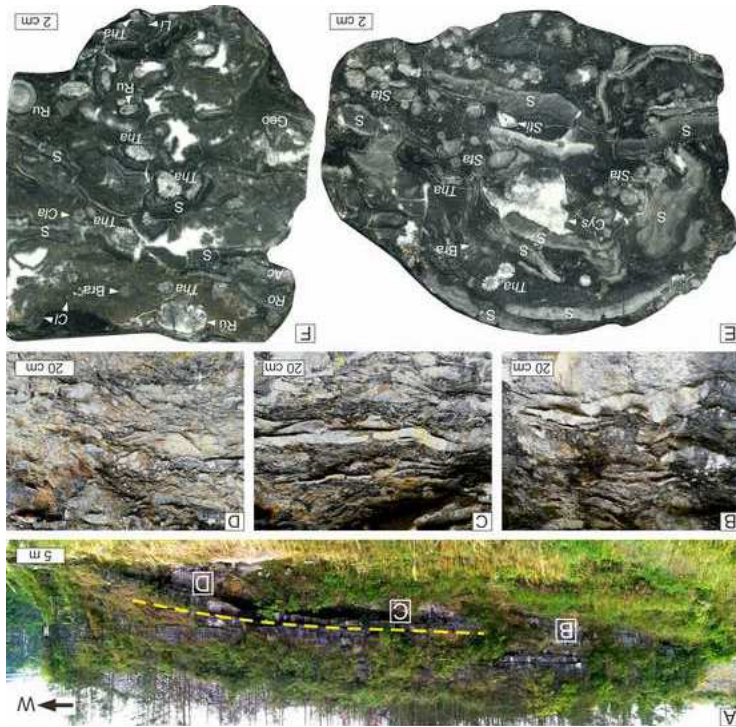
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653 **Table and Figure captions**

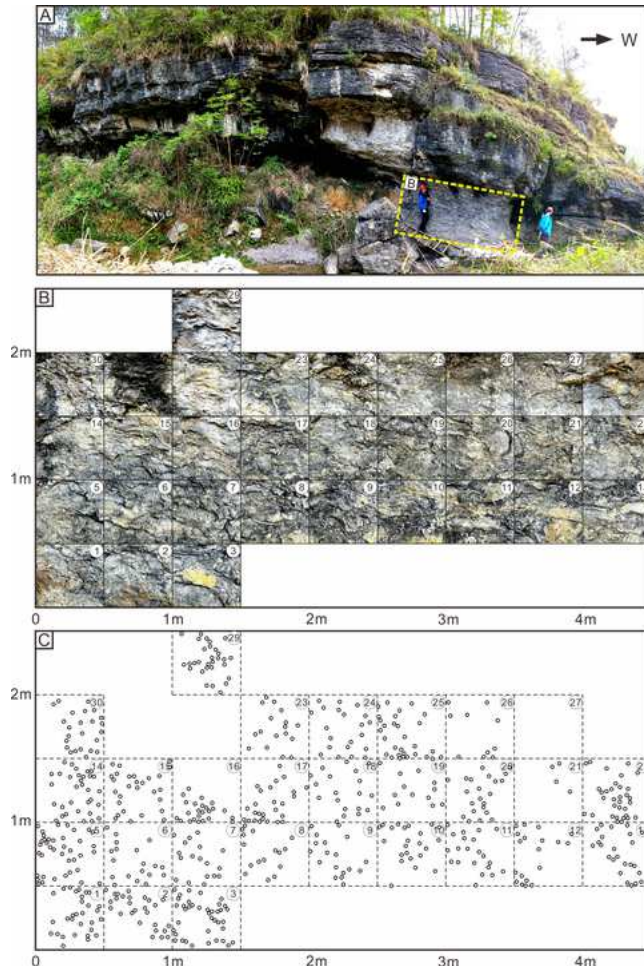
654 Table 1. 35 cases of spatial competition between the reef organisms.  
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658 Fig. 1. (A) Global palaeogeography during the Givetian Epoch (Middle Devonian) (After Golonka,  
659 2002), with a black rectangle indicating the South China Craton. (B) Palaeogeography of South China  
660 Block during the Givetian Epoch (modified after Jin and Ju, 1998), with red symbols marking the  
661 previously reported Givetian reefs in South China Craton (modified after Wu *et al.*, 2010). Maoying  
662 reef (MY), Buzhai reef (BZ), Liuzhai reef (LZ), Beishan reef (BS) and Yanshan reef (YS) are noted in  
663 this study. (C) Map of the studied area, with a red symbol showing the location of the Jiwozhai reefs.  
664 (D) Middle Devonian stratigraphic framework of Dushan County, Guizhou, South China (After Liao *et*  
665 *al.*, 1979; Liao, 2003).  
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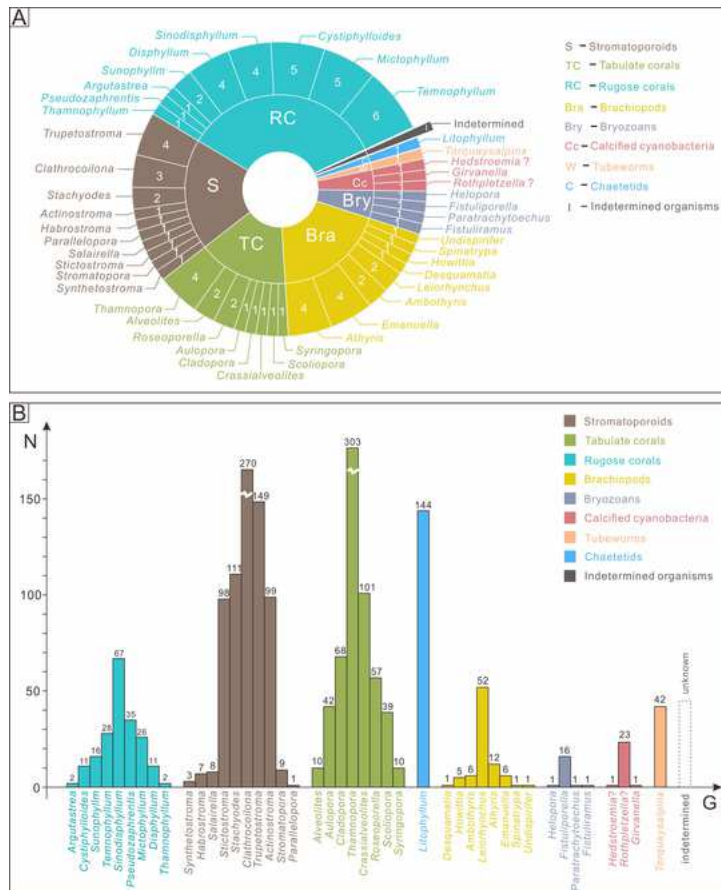


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 668 Fig. 2. Field photographs and polished slabs of the Jiwozhai patch reefs. (A) A general view of the patch  
 669 reef (dash line) and the overlying beddings. (B–D) Enlarged field photos of the patch reefs in (A),  
 670 showing the reef boundstones composed of coverstones, framestones, and bafflestones, note the densely  
 671 packed reef organisms. (E, F) Polished slabs showing the contents of the coverstone, note laminar  
 672 stromatoporoids encrusting rugose coral *Cystiphyllodes* in (E) and the tabulate coral *Thamnopora* in  
 673 (F). *Ac*: *Actinotroma*, *Sti*: *Stictostroma*, *Sta*: *Stachyodes*, *Cys*: *Cystiphyllodes*, *Tha*: *Thamnopora*, *Cl*:  
 674 *Clathrocoilona*, *Cl*: *Cladopora*, *Ro*: *Roseoporella*, *Li*: *Litophyllum*, *Ru*: rugose coral, *S*:  
 675 stromatoporoids, *Bra*: unknown brachiopod, *Geo*: geopetal structure.  
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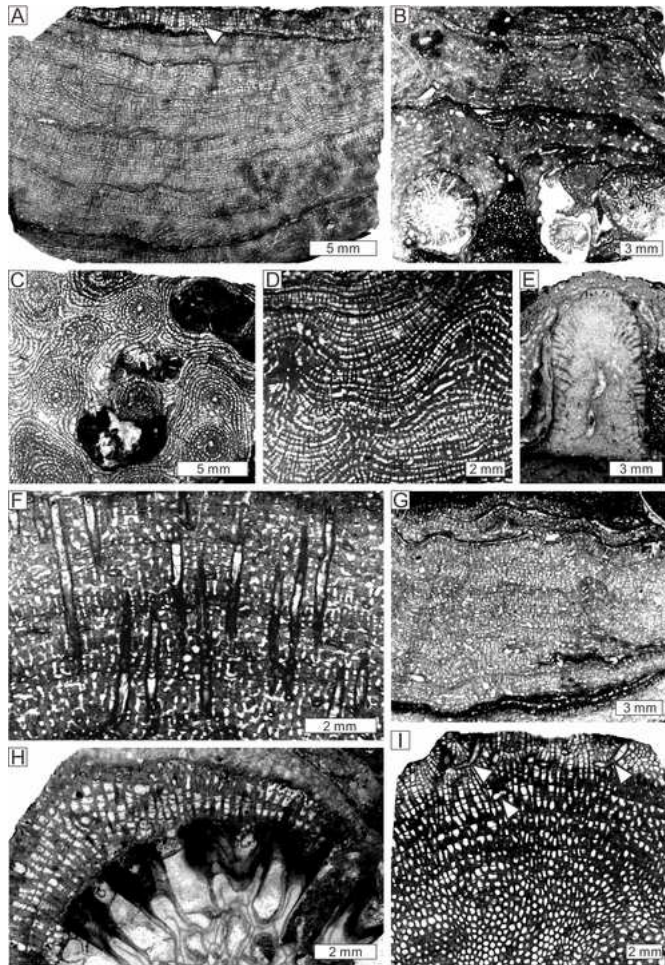
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Fig. 3. Field photographs and division of the quadrats in the studied patch reef, with divisions of the 28 quadrats. (A) A general view of the patch reef, with a yellow rectangle showing the studied patch reef. (B) Enlarged field photo of the rectangular area in (A), showing the divisions of the quadrats. (C) Sample collection positions from each of the 28 quadrats, each point representing a sample.



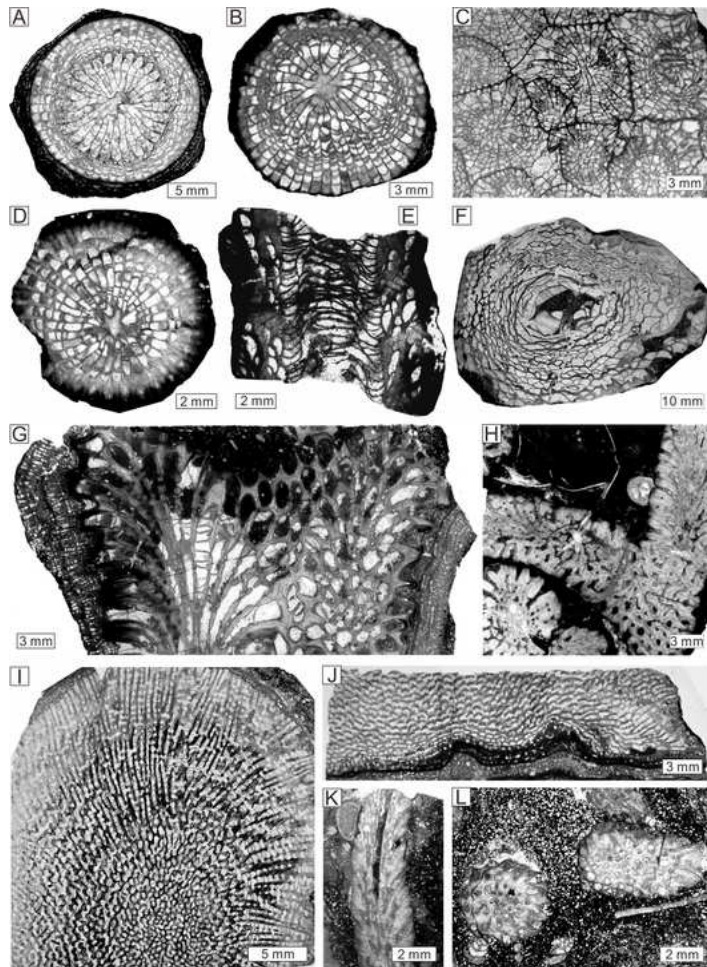
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 684 Fig. 4. (A) Diversity of reef organisms in the studied Jiwozhai reef, with numbers indicating species  
 685 richness, and percentages showing the abundance of species among the reef organisms. (B) Distribution  
 686 of abundance of genera of reef organisms in the 28 quadrats. N: number of occurrences  
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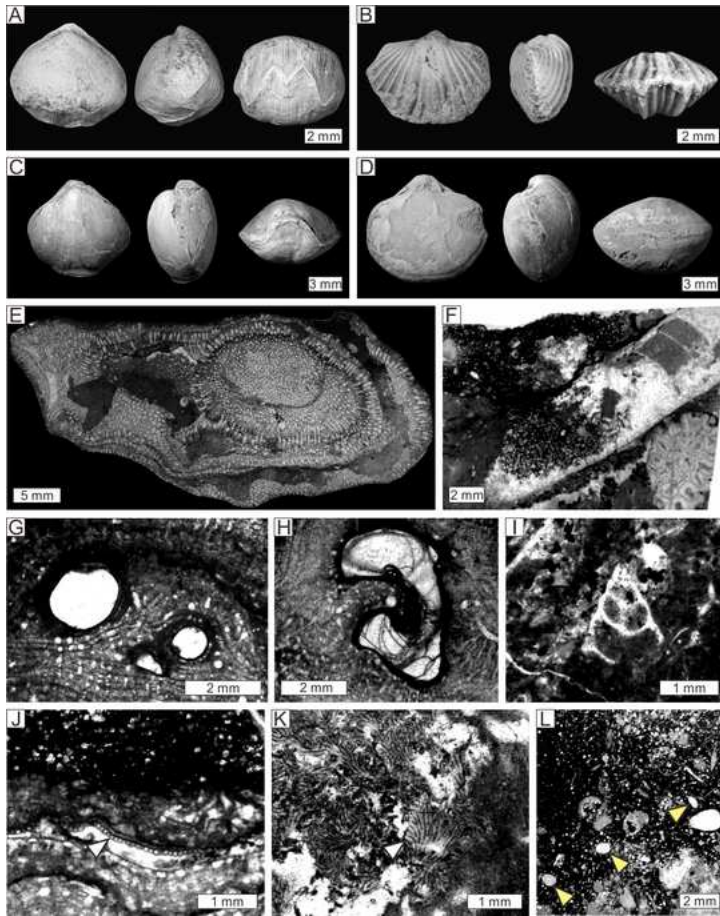


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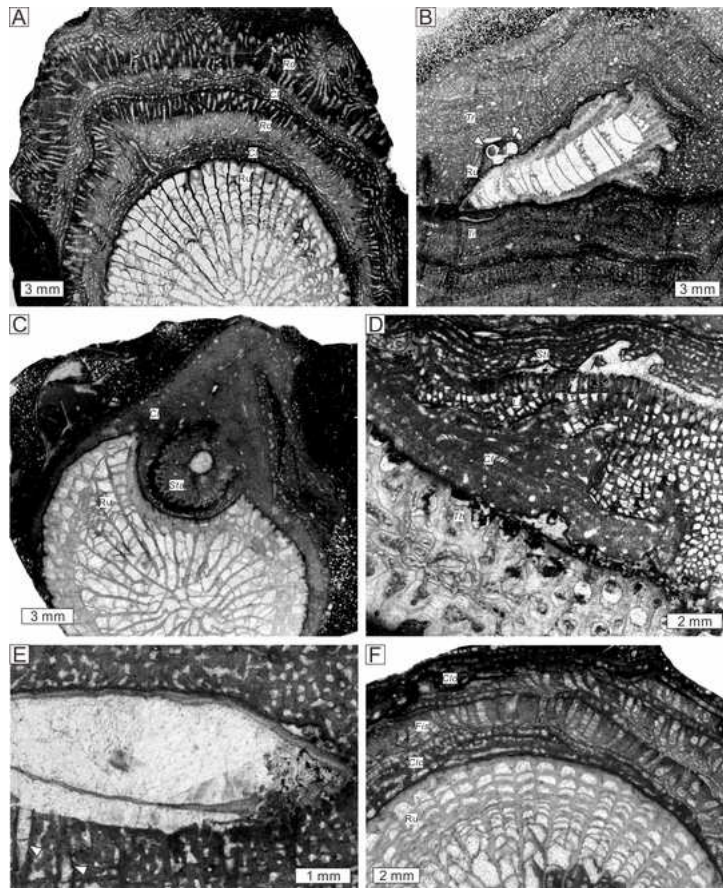
Fig. 5. Stromatoporoids and chaetetids in the studied Jiwozhai patch reef. (A) Longitudinal section showing *Actinostroma undulatum*, with a white arrow indicating the superposition of chaetetid *Litophyllum inflatus*, note the presence of latilaminae in the stromatoporoid. (B) *Clathrocoilona spissa* encrusting tabulate coral *Scoliopora*, note the presence of latilaminae in the stromatoporoid. (C) Transverse sections showing stromatoporoid *Stictostroma saginatum*. (D) Longitudinal section showing stromatoporoid *Synthetostroma actinostromoides*. (E) Stromatoporoid *Stachyodes costulata* encrusted by stromatoporoid *Stictostroma saginatum*, note the attachment of tabulate coral *Aulopora* cf. *compacta*. (F) Endosymbiotic *Syringopora* inside the skeleton of stromatoporoid *Stomatopora hüpschii*. (G) Longitudinal section of *Trupetostroma dushanense*, note the presence of latilaminae. (H) Chaetetid *Litophyllum inflatus* encrusting tabulate coral *Thamnopora compacta*. (I) Endosymbiotic tubeworms (white arrows) within *Litophyllum inflatus*.



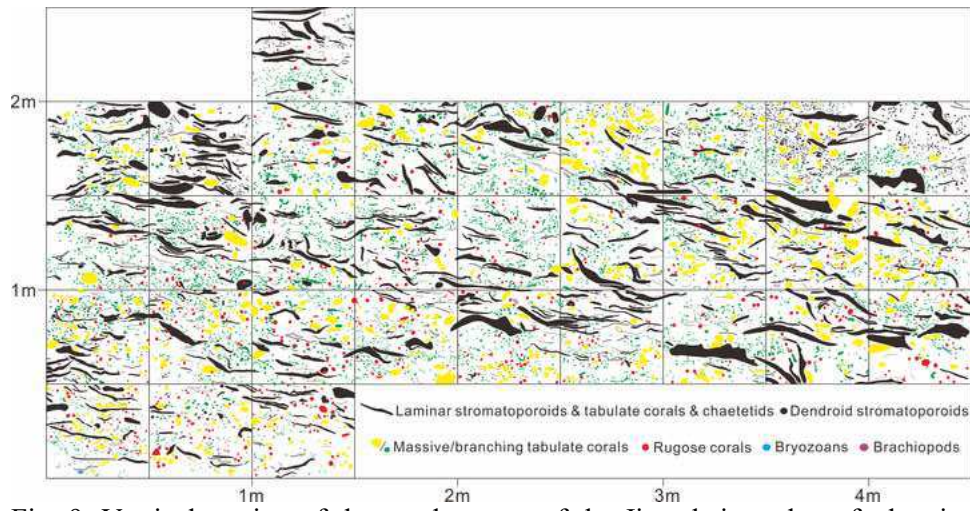
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 702 Fig. 6. Common rugose and tabulate corals in the Jiwozhai patch reef. (A) Transverse section showing  
 703 solitary rugose coral *Pseudozaphrentis hejiazhaiense* encrusted by stromatoporoid *Clathrocoilona*  
 704 *crassitexta*. (B) Transverse section showing solitary rugose coral *Sinodisphyllum simplex*. (C)  
 705 Transverse sections showing cerioid rugose coral *Argustarea thomasi*. (D) Transverse sections showing  
 706 solitary rugose coral *Sunophyllum typicum*. (E) Longitudinal section of solitary rugose coral  
 707 *Sunophyllum typicum*. (F) Transverse section showing solitary rugose coral *Cystiphyllodes corneolum*.  
 708 (G) Tabulate corals *Thamnopora compacta* encrusted by chaetetid *Litophyllum inflatus* (left) and  
 709 stromatoporoid *Clathrocoilona* (right). (H) Branching tabulate coral *Thamnopora* cf. *pansiensis*. (I)  
 710 Domicial tabulate coral *Crassialveolites dushanensis*. (J) Laminar tabulate coral *Alveolites fornicatus*  
 711 grow on the skeletons of stromatoporoid *Clathrocoilona*. (K) Longitudinal view of branching tabulate  
 712 coral *Cladopora fistula*. (L) Transverse section of *Cladopora fistula*.  
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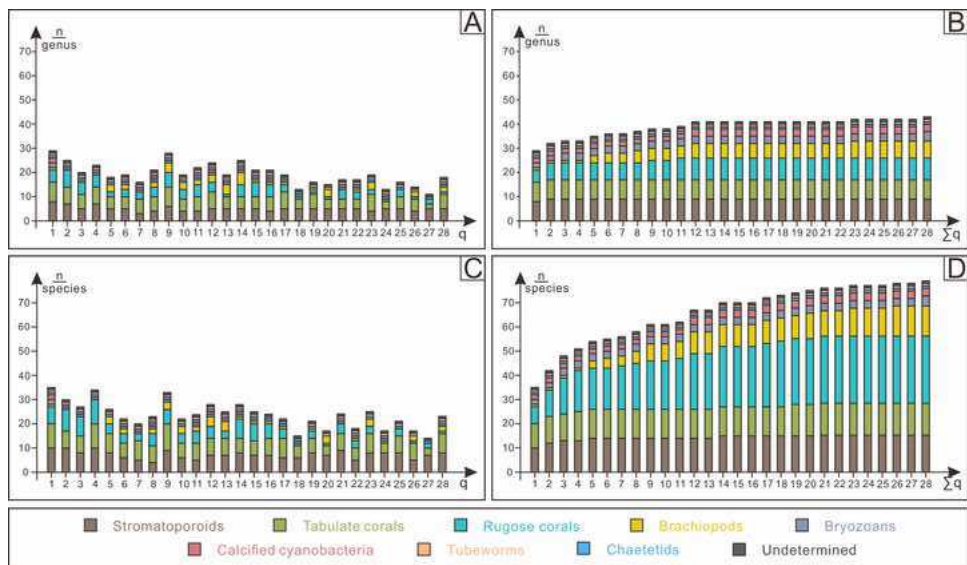
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 715 Fig. 7. Reef dwellers in the studied Jiwozhai patch reef. (A) Brachiopod *Leiorhynchus* sp. A, showing  
 716 dorsal, lateral and anterior views from left to right. (B) Brachiopod *Howittia dushanensis*, showing  
 717 dorsal, lateral and anterior views from left to right. (C) Brachiopod *Athyris* sp. A, showing dorsal, lateral  
 718 and anterior views from left to right. (D) Brachiopod *Emanuella plicata*, showing dorsal, lateral and  
 719 anterior views from left to right. (E) Bryozoan *Fistuliramus* sp. (F) Nautiloid of unknown species. (G)  
 720 Longitudinal section showing tubeworm *Torquaysalpinx sokolovi* within the stromatoporoid  
 721 *Trupetostroma dushanense*. (H) Tubeworm *Torquaysalpinx sokolovi* within the skeleton of  
 722 stromatoporoid *Trupetostroma dushanense*, note the present of dissepiments inside the tube. (I) A small  
 723 gastropod of unknown species. (J) Calcified cyanobacteria *Rothpletzella*? (K) Transverse view of  
 724 another calcimicrobe, possibly *Hedstroemia*?, with a white arrow showing the continuously bifurcated  
 725 filaments. (L) Ostracods (yellow arrows) found from the matrix of the patch reef.  
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 728 Fig. 8. Biotic interactions among the reef organisms in the studied Jiwozhai patch reef. (A) Alternations  
 729 of encrusting stromatoporoid *Clathrocoilona* (*Cl*) and tabulate coral *Roseoporella* (*Ro*) over a solitary  
 730 rugose coral (*Ru*), forming a growth sequence of multiple encrustations. (B) A solitary rugose coral  
 731 (*Ru*) that grew on the skeleton of stromatoporoid *Trupetostroma* (*Tr*) was encrusted by another skeleton  
 732 of *Trupetostroma* (*Tr*), note unknown shells attached on the rugose coral (arrows). (C) Syn-vivo  
 733 interactions between stromatoporoid *Clathrocoilona* (*Cl*) and a solitary rugose coral (*Ru*), note the  
 734 irregular shape of the corallum and a possible dead skeleton of stromatoporoid *Stachyodes* (*Sta*) inside  
 735 the skeleton of *Clathrocoilona*. (D) Spatial competition between stromatoporoid *Clathrocoilona* (*Cl*)  
 736 and chaetetid *Litophyllum inflatus* (*Li*), showing interfinger-marginal contacts, note the hard substrate  
 737 provided by a possible dead skeleton of tabulate coral *Thamnopora* (*Th*). (E) Brachiopod shells  
 738 embedded inside the stromatoporoid *Stomatopora* (*St*) skeleton, note endosymbiotic tabulate coral  
 739 *Syringopora* below (arrows). (F) Complex encrustations between stromatoporoid *Clathrocoilona*  
 740 *crassitexta* (*Clc*), *Clathrocoilona obliterated* (*Clo*), and bryozoan *Fistuliporella hemispherioidea* (*Fis*)  
 741 over rugose coral *Sinodisphyllum* (*Ru*), forming a growth sequence.  
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 744 Fig. 9. Vertical section of the quadrat area of the Jiwozhai patch reef, showing distribution of reef  
 745 organisms, based on extensive sampling and field photos of the 28 quadrats.  
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 748 Fig. 10. (A) Generic level occurrences of the reef organisms in each quadrat of the Jiwozhai reef. (B)  
 749 The accumulation of generic level occurrences of reef organisms from the first quadrat to the last. (C)  
 750 Specific level occurrences of reef organisms each quadrat of the Jiwozhai reef. (D) The accumulation  
 751 of specific level occurrences of reef organisms from the first quadrat to the last.  
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