

Stromatoporoids from a Middle Devonian reef in South China and their palaeoecological implication

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Stromatoporoids are the major constructors of a Givetian (Middle Devonian) fossil reef in shallow marine facies, in the Jiwozhai Member of the Dushan Formation, at Dahekou, near Dushan, Guizhou Province, South China. Stromatoporoids, together with other reef building and dwelling components (rugose corals, tabulates, chaetetids and others), form a high diversity community, making the Jiwozhai reef a palaeobiodiversity hotspot. In this study 11 species belonging to nine genera and four orders are identified, including *Gerronostromaria grossum* (Clathrodictyida), *Pseudotruperostroma porosum*, and *Salairella buecheliensis* (Stromatoporida), *Clathrocoilona spissa*, *Stictostroma saginatum*, and *Synthetostroma actinostromoides* (Stromatoporellida) and ?*Habrostroma laminosum*, *Parallelopora* sp., *Stachyodes costulata*, *Stachyodes fasciculata* and *Stachyodes* sp. (Syringostromatida). Among them, *Clathrocoilona spissa* and *Gerronostromaria grossum* are the most abundant stromatoporoid taxa. Stromatoporoid growth form, size, substrate and growth interruption are considered to be key autecological parameters to evaluate their growth behaviour and contribution in reef formation. Skeletons of laminar *Clathrocoilona spissa* are commonly smaller (up to 40 mm in basal dimension and less than 2 mm in thickness) than other stromatoporoid taxa and frequently encrusted on other organisms. In contrast, *Gerronostromaria grossum* dominates the assemblage, with its larger laminar growth form (up to 500 mm in basal dimension and 40 mm in thickness) expanding both on bioclastic and clay-rich micritic substrate and shows repeated growth interruptions, altogether evidence that this taxon was resilient to environmental pressure and may have pioneered the reef development. The variation of growth preference among stromatoporoid taxa therefore indicates a different growth strategy of each stromatoporoid in this reef environment.

Key words: Stromatoporoidea, reef, morphology, palaeoecology, Givetian, Guizhou, South China Block.

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Introduction

Devonian shallow marine environments are exceptionally highlighted for the worldwide proliferation of reefs in Earth history (Kiessling et al. 1999; Copper 2002; Copper and Scotese 2003). Stromatoporoids were the major reef-building organisms that became highly diverse during the Middle Devonian (Stearn 2015a; Kershaw et al. 2018). The highest Palaeozoic stromatoporoid generic diversity was in the Eifelian (early Middle Devonian); this study focuses on

stromatoporoids of Givetian age (late Middle Devonian) with the second-highest diversity, represented in traditional taxonomy by seven orders and 45 genera (Stearn 2015a). As the main reef-building organism, stromatoporoids play a significant role during the colonisation stage of reef development (Jakubowicz et al. 2019) and constitute a large portion of metazoan frameworks especially in Middle to Late Devonian fossil reefs (Cockbain 1984; Cook 1999; Salerno 2008; Da Silva et al. 2011a, b; Wolniewicz 2021). On the South China Block, stromatoporoids achieved their

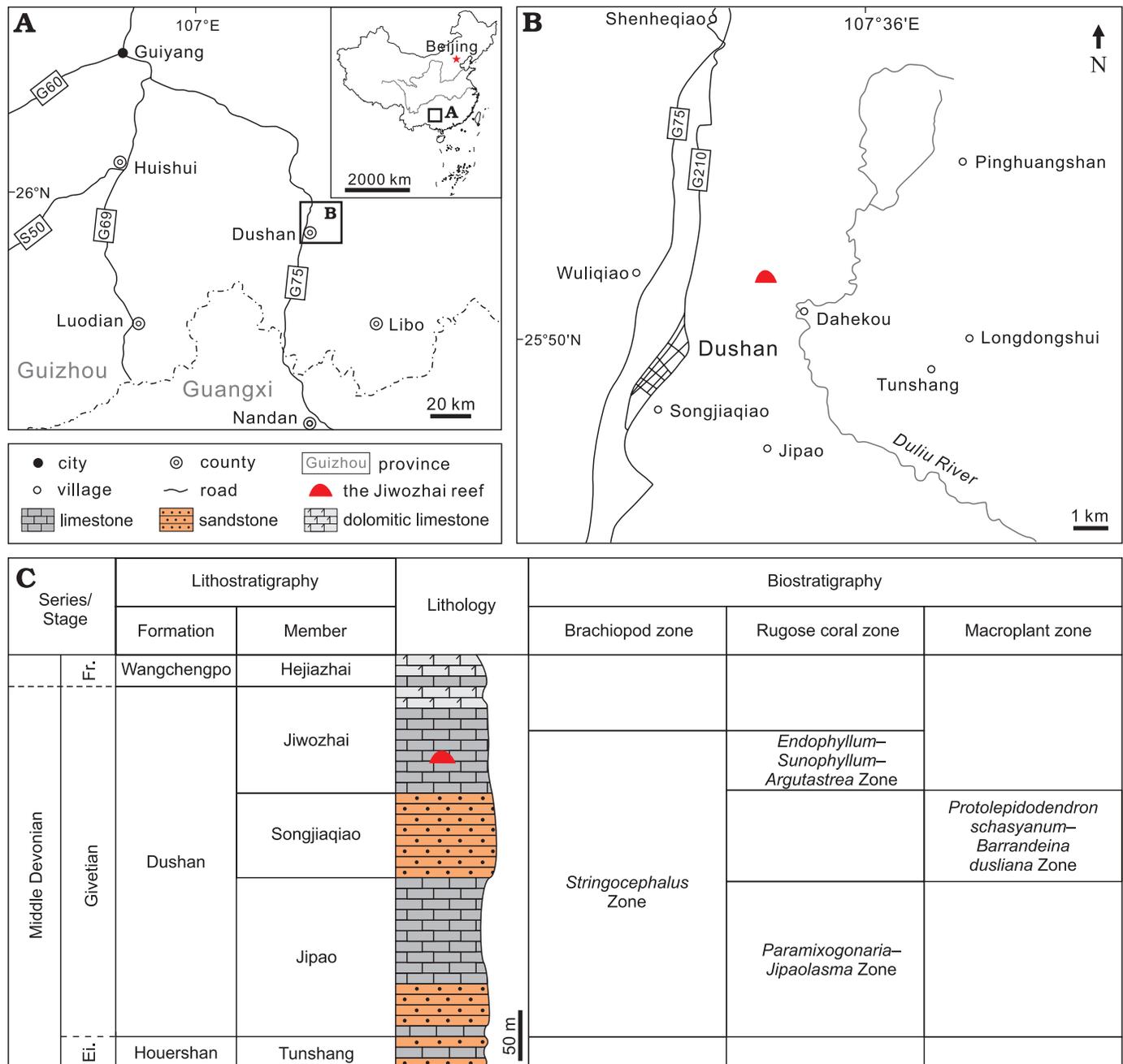


Fig. 1. Location and stratigraphy of the Jiwozhai reef in Dushan County, Guizhou, South China. A. Map showing southern Guizhou and northern Guangxi and the studied area in China. B. Locality of the Jiwozhai reef in Dushan County. C. Depositional successions and fossil assemblages of the supposed uppermost Eifelian to lowermost Frasnian in Dushan, Guizhou province (modified after Liao et al. 1979; Liao 2003). Abbreviations: Ei, Eifelian; Fr., Frasnian.

highest diversity (37 genera) and abundance during the Givetian (Dong 2001) and constructed a reef realm extending from eastern Yunnan to northern Guangdong provinces. Stromatoporoids attracted much attention of palaeontologists in South China for over 100 years, including some representative works in Guizhou, Guangxi, Hunan, and Yunnan provinces (e.g., Yabe and Hayasaka 1920; Chi 1940; Yabe and Sugiyama 1941; Yang and Dong 1963, 1979; Wang and Huang 1985; Dong and Liu 1992).

Although the studies of Givetian stromatoporoids in South China are numerous, most previous works were

poorly illustrated and written in Chinese, thus unfavourable for interpretation and a worldwide correlation. Many established taxa were limited to simple systematic descriptions with poorly preserved specimens (e.g., Yang and Dong 1979; Dong et al. 1989; Dong and Liu 1992). Also their palaeoecological implications in reef ecosystems were not fully exploited (e.g., Liu and Dong 1991; Dong and Song 1992), thereby limiting a precise reconstruction of the stromatoporoid biodiversity and reef-building habits in the various palaeoenvironments in which they occur.

A recent comprehensive study of the Jiwozhai reef in the

Dushan Formation, at Dahekou, Guizhou Province revealed that stromatoporoids are the main reef component (Huang et al. 2020). This study complements the previous work of Huang et al. (2020), providing details of stromatoporoid taxonomy and their palaeoenvironmental aspects in the reef formation. The aims of this study are (i) to provide a systematic treatment of the Chinese Givetian stromatoporoid fauna from Guizhou in relation to global occurrence; this includes revision of these Givetian stromatoporoids according to the updated taxonomic classification provided by Stearn (2015b); and (ii) to interpret the palaeoecological habits of stromatoporoids in this low-relief reef structure.

Institutional abbreviations.—NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Geological setting

During the Givetian Epoch, the South China Block was separated from north-eastern Gondwana and extended across the palaeoequator in the eastern Palaeo-Tethys Ocean (Xian et al. 2019). Many carbonate platforms and interplatform depressions formed within the interpreted heart-shaped sea across the South China Block, covering a large area of several provinces ranging from the present-day eastern Yunnan, southern Guizhou, Guangxi, middle-southern Hunan, to northwestern Guangdong (Jin and Ju 1998). Over 60 sites in South China preserve coral-stromatoporoid reefs, witnessing the Palaeozoic acme in reef development in the South China epicontinental sea (Huang et al. 2020), probably due to the suitable climate (related to palaeolatitude) and the ongoing transgression (Joachimski et al. 2009; Liao and Ma 2011).

The Dahekou section in Dushan, Guizhou Province, represents one of the most well-known shallow-water stratotype sections of the Devonian in South China (Fig. 1A, B). Palaeogeographically it was part of the Qian-Gui Platform interior, adjacent to the Yangtze landmass (Jin and Ju 1998). Dushan Formation cropping out therein can be divided into three lithological units in ascending order, the Jipao Member (mainly limestone), the Songjiaqiao Member (mainly sandstone) and the Jiwozhai Member (limestone) (Fig. 1C). The formation is generally consistent with the brachiopod *Stringocephalus* Zone, approximately corresponding to the Givetian Stage (Liao 2003). The Jiwozhai Member, consists mainly of reefal limestone, marly bedded limestone, is partially dolomitized; the member contains the rugose coral *Endophyllum*–*Sunophyllum*–*Argutastrea* assemblage (Liao 2003; Liao and Ma 2011) (Fig. 1C), which corroborates the Givetian age.

The Jiwozhai reef (GPS coordinates: 25°50'43.01" N, 107°34'46.51" E), located in the lower part of Jiwozhai Member, is orientated east-west, its exposure extending only 100 meters due to the limitation of a reverse fault in the east, and the strata slope gently towards the cliff in the

west (Fig. 2A). The reef is 4.5 m thick (Fig. 2B), with underlying massive argillaceous coral floatstone, mudstone and overlying bedded coral-stromatoporoid floatstone-rudstone (Fig. 2A). The reef is thus consistent with classification as a biostrome, but the limited outcrop means that this cannot be verified at present. A large number of benthic organisms was reported from the reef unit including stromatoporoids, rugose corals, tabulate corals, chaetetid sponges, brachiopods, bryozoans, tubeworms, calcified cyanobacteria, ostracods, gastropods, echinoderms and others (e.g., Huang et al. 2020). Among them, stromatoporoids occur as mainly laminar forms, and are the most significant organisms (Fig. 2B, C). Dendroid and bulbous forms played minor roles for reef building (Fig. 2D). Furthermore, complicated bio-ecological interactions, such as encrustation, spatial competition and endosymbiotic intergrowth, have been recognized among stromatoporoids, tabulates, rugose corals, chaetetid sponges and tubeworms (Huang et al. 2020).

Material and methods

All stromatoporoid samples were collected from the Jiwozhai reefal boundstone in the lower part of the Jiwozhai Member (Dushan Formation) in April 2018 (Fig. 2A). 28 quadrats (0.5×0.5 m for each one), occupying 7 m² altogether, were chosen from the vertically exposed outcrop of the reef unit (Fig. 2B) for quantitative statistics of abundance, diversity and ecological parameters of reef fauna (Huang et al. 2020). 15 to 45 samples per quadrat were randomly numbered and collected in situ, with detailed photographs showing sample locations (e.g., Fig. 2C). The growth form (including basal dimension and thickness) of each stromatoporoid was measured in the field, and details collected from polished blocks.

A total of 517 samples (some samples contain more than one stromatoporoid) of different sizes (10–150 mm in diameter) were collected from the Jiwozhai Member, and prepared into longitudinal and tangential thin sections for stromatoporoid taxonomy. Based on 1740 thin sections, 773 skeletons of stromatoporoids were identified, belonging to 11 species in nine genera and four orders. Latilaminae and associated substrates were preferentially observed with the thin sections. Well-preserved portions of stromatoporoid skeletons were measured for taxonomic identification. Considering that the skeletal thickness of many thin stromatoporoids is not more than 2 mm, the data of numbers of pachystromes (horizontal skeletal elements) per 2 mm were assembled to provide comparisons between samples and applied in palaeoecological interpretations. Growth form and skeletal terminologies in this paper follow the usage of Kershaw and Riding (1978) and Stearn (2015b), respectively.

Statistics of ecological information of the studied stromatoporoids are presented in the SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app67-Huang_et_al_SOM.pdf).

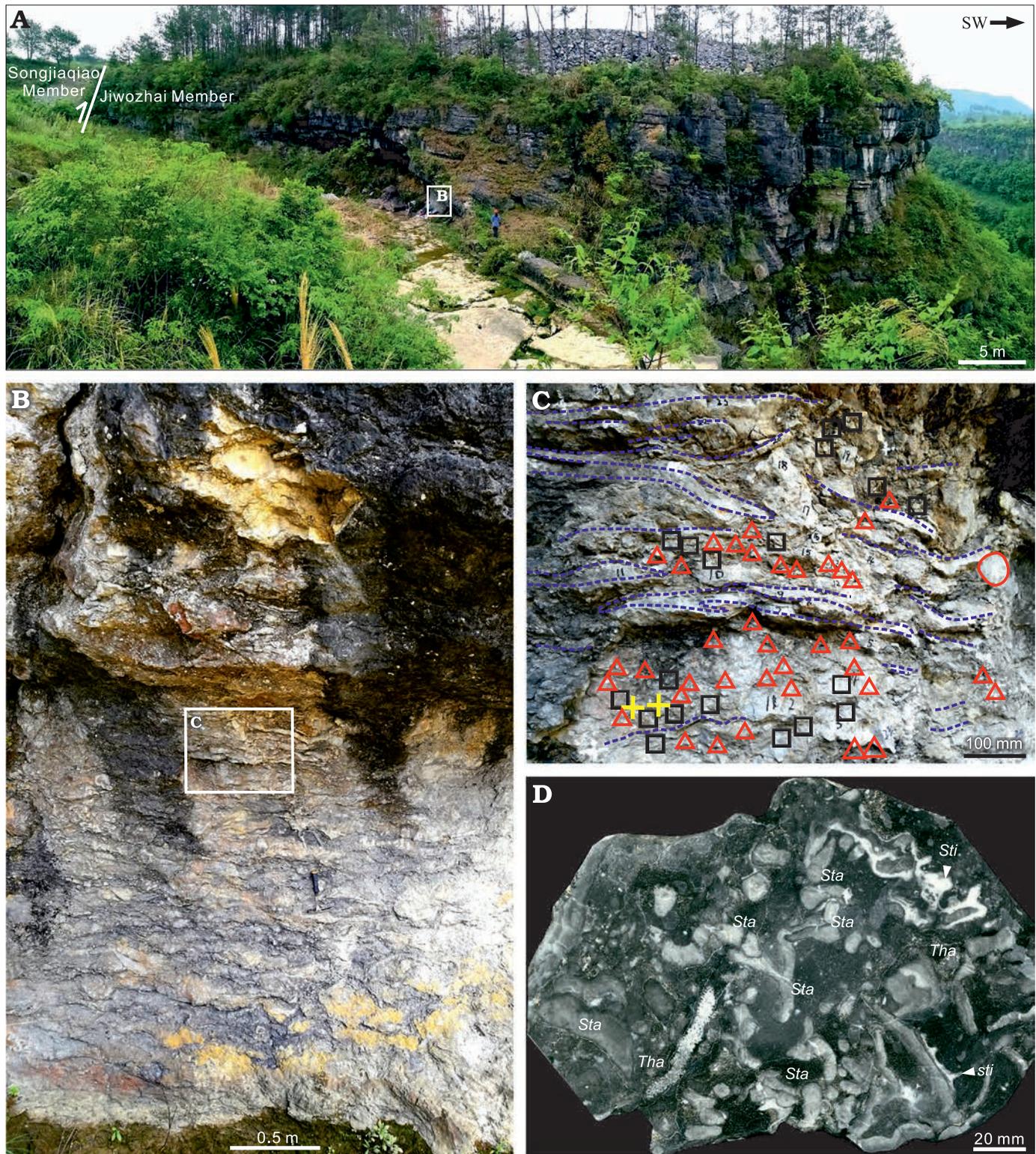


Fig. 2. Field photographs of the Jiwozhai reef. **A.** A panoramic view of the whole reef unit, with a white rectangle indicating the studied area. Note the reverse fault in the east. **B.** A general view shows the studied area of the reef unit. **C.** Enlarged field photo of the reef fragment marked in B, showing the thick or thin laminar stromatoporoids (undulating dashed line) covered on branching tabulate corals (triangles), solitary rugose corals (crosses), dendroid stromatoporoids (squares), bulbous stromatoporoid (circled line), and clay-rich micrites (fine grained sediments between the metazoan skeletons). **D.** An example of polished block of the Jiwozhai reef limestone showing toppled dendroid or laminar *Stachyodes fasciculata* Dong in Dong et al., 1989, and encrusting *Stictostroma saginatum* (Lecompte, 1951) in the upper area. Note the conspicuous digitation of mamelons of *Stictostroma saginatum* (Lecompte, 1951) in the lower right corner. *Sti.*, *Stictostroma saginatum* (Lecompte, 1951); *Sta.*, *Stachyodes fasciculata* Dong in Dong et al., 1989; *Tha.*, *Thamnopora cf. pansiensis* Tchi, 1966.

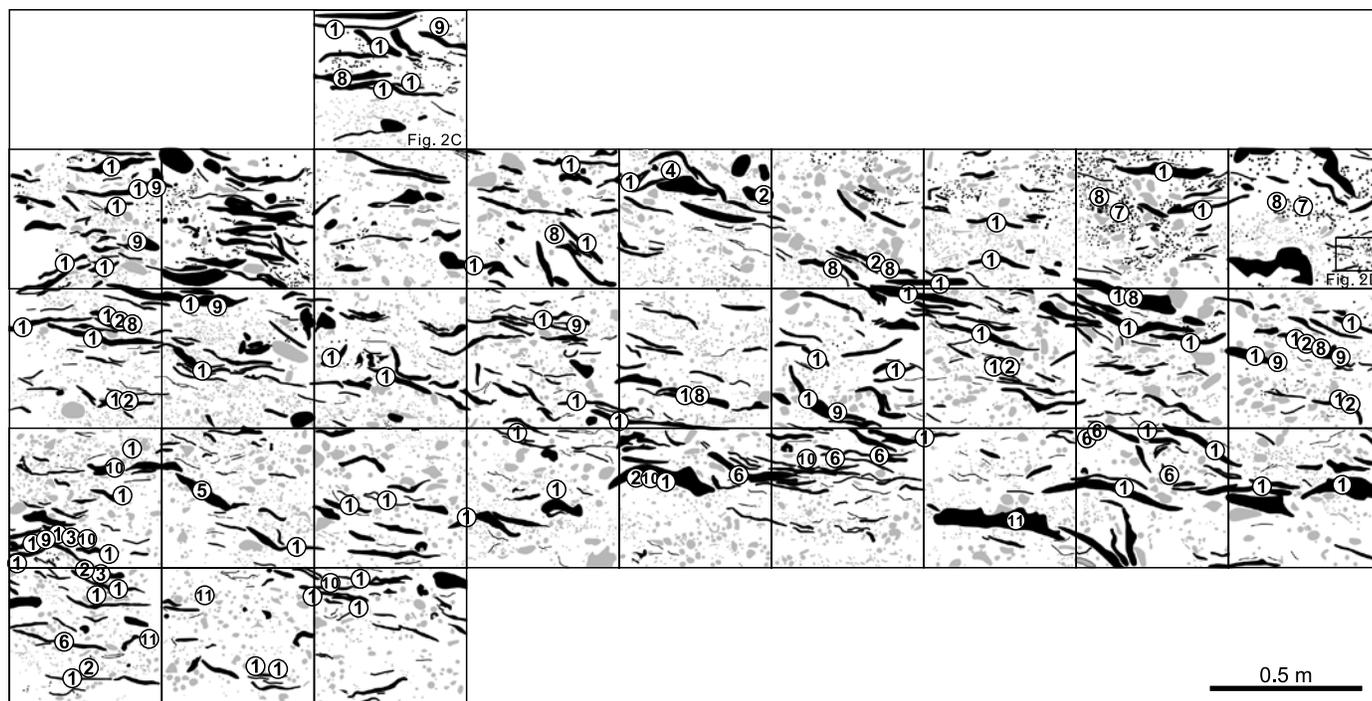


Fig. 3. Schematic vertical section of stromatoporoids in the Jiwozhai reef (Huang et al. 2020) showing the spatial distribution of different stromatoporoids, note the predominance of the *Gerronostromaria grossum* Dong, 1974, in the laminar form stromatoporoids. 1, *Gerronostromaria grossum* Dong, 1974; 2, *Clathrocoilona spissa* (Lecompte, 1951); 3, *Habrostroma laminosum* (Lecompte, 1952); 4, *Parallelopora* sp.; 5, *Pseudotrurpetostroma porosum* (Yang and Dong, 1979); 6, *Salirella buecheliensis* (Bargatzky, 1881); 7, *Stachyodes costulata* Lecompte, 1952; 8, *Stachyodes fasciculata* Dong in Dong et al., 1989; 9, *Stachyodes* sp.; 10, *Stictostroma saginatum* (Lecompte, 1951); 11, *Synthetostroma actinostromoides* Lecompte, 1951. Black, stromatoporoids; gray, other organisms between stromatoporoids.

Results

Stromatoporoid composition and spatial distribution.—

In total, 11 species belonging to nine genera are identified from the Jiwozhai reef, including *Clathrocoilona spissa* (Lecompte, 1951), *Gerronostromaria grossum* Dong, 1974, *Habrostroma laminosum* (Lecompte, 1952), *Parallelopora* sp., *Pseudotrurpetostroma porosum* (Yang and Dong, 1979), *Salirella buecheliensis* (Bargatzky, 1881), *Stachyodes costulata* Lecompte, 1952, *Stachyodes fasciculata* Dong in Dong et al., 1989, *Stachyodes* sp., *Stictostroma saginatum* (Lecompte, 1951), and *Synthetostroma actinostromoides* Lecompte, 1951. Stromatoporellids are the most abundant stromatoporoid group with three species in three genera. Among them, *Clathrocoilona spissa* is numerically the most common species, whereas *Stictostroma saginatum* and *Synthetostroma actinostromoides* are less common. Syringostromatids include five species of three genera. Species of *Stachyodes* are relatively common, especially in the upper part of the reef, with two fully identified species and one species in open nomenclature. *Habrostroma laminosum* and *Parallelopora* sp. are relatively rare. Only one clathrodictyid species, *Gerronostromaria grossum* is identified, and this species is also abundant. Stromatoporellids *Salirella buecheliensis* and *Pseudotrurpetostroma porosum* are identified, and these stromatoporoid species are relatively rare compared to the other stromatoporoid groups.

Among all these species, *Gerronostromaria grossum* is the most conspicuous and predominant stromatoporoid in almost all the quadrats of the reefal vertical outcrop (Fig. 3: 1). However, the most abundant species, *Clathrocoilona spissa* can hardly be distinguished in the field due to its small size (Fig. 3: 2). *Pseudotrurpetostroma porosum* (Fig. 3: 5), *Salirella buecheliensis* (Fig. 3: 6) and *Synthetostroma actinostromoides* (Fig. 3: 11) rarely occur in the lower part of the reef unit with their relatively large size. *Stachyodes costulata* (Fig. 3: 7) and *Stachyodes fasciculata* (Fig. 3: 8) can be easily identified especially in the upper part of the reefal outcrop owing to their distinctive external form. The other species, *Habrostroma laminosum* (Fig. 3: 3), *Parallelopora* sp. (Fig. 3: 4), *Stachyodes* sp. (Fig. 3: 9) and *Stictostroma saginatum* (Fig. 3: 10), are mostly recognized only in thin sections because of their rare occurrence or small sizes.

Palaeoecology of the stromatoporoid fauna.—Relationships between stromatoporoids, their associated organisms and sediments provide useful information for palaeoecological analysis in terms of external morphology, size, substrate, growth interruption and associated organisms. (e.g., Da Silva et al. 2011a, b; Kershaw et al. 2018; Wolniewicz 2021). We apply four attributes: (i) external morphology; (ii) size; (iii) substrate; (iv) growth interruption to statistically evaluate the palaeoecology of stromatoporoids (Fig. 4).

(i) External morphology. Laminar growth forms of stromatoporoids are most predominant in the Jiwozhai reef.

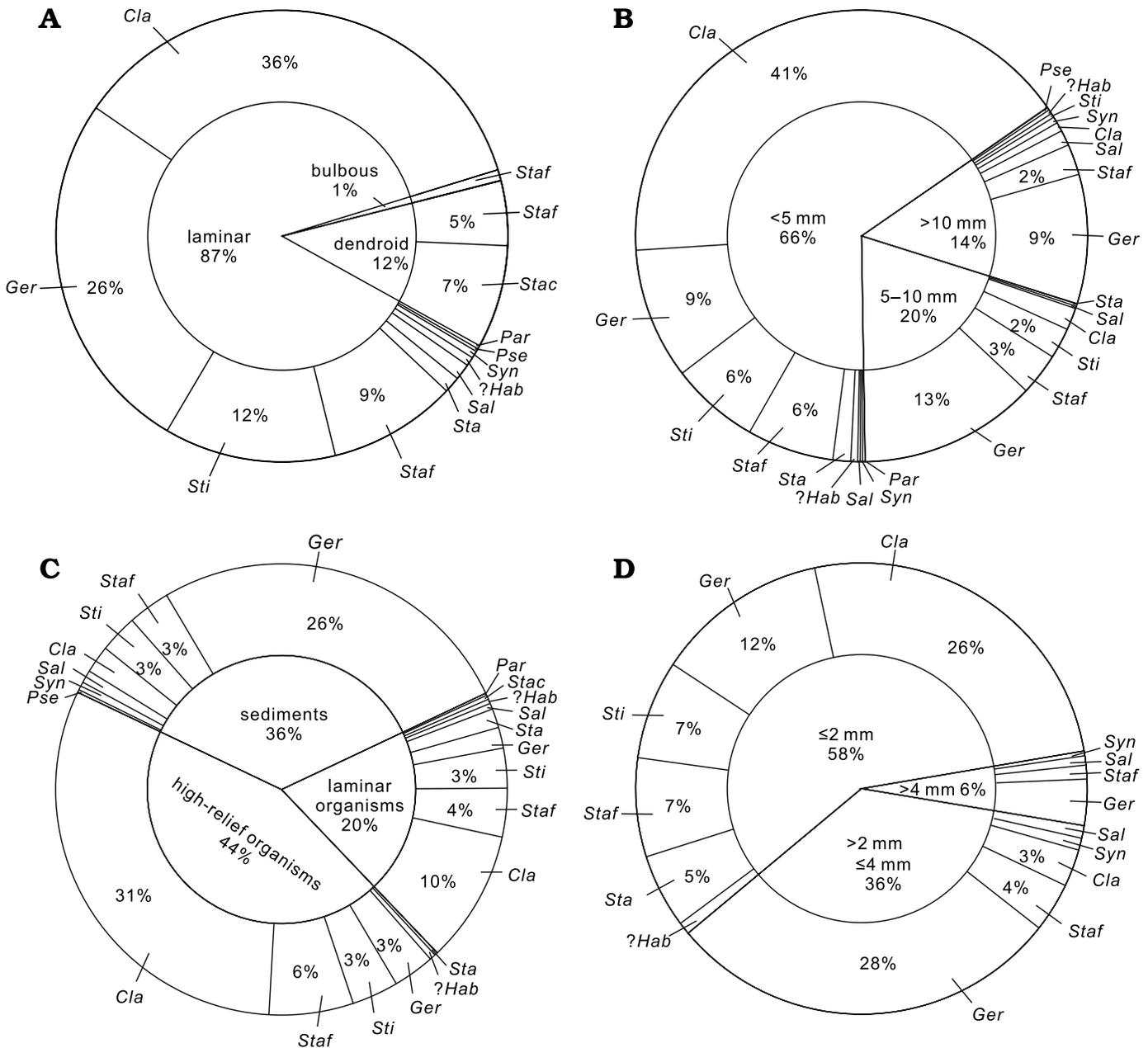


Fig. 4. Pie charts illustrating palaeoecological parameters of the stromatoporoid fauna. **A.** External morphology. **B.** Thickness. **C.** Substrate types. **D.** Thickness of growth interruption. Abbreviations: *Ger*, *Gerronostromaria grossum* Dong, 1974; *Cla*, *Clathrocoilona spissa* (Lecompte, 1951); *?Hab*, *?Habrostroma laminosum* (Lecompte, 1952); *Par*, *Parallelopora* sp.; *Pse*, *Pseudotruperostroma porosum* (Yang and Dong, 1979); *Sal*, *Salirella buecheliensis* (Bargatzky, 1881); *Sta*, *Stachyodes* sp.; *Stac*, *Stachyodes costulata* Lecompte, 1952; *Staf*, *Stachyodes fasciculata* Dong in Dong et al., 1989; *Sti*, *Stictostroma saginatum* (Lecompte, 1951); *Syn*, *Synthetostroma actinostromoides* Lecompte, 1951.

87% of the investigated stromatoporoids possess laminar growth forms (mostly in situ), and *Clathrocoilona spissa* is the most common taxa (Fig. 4A). *Gerronostromaria grossum*, *Stictostroma saginatum*, and *Stachyodes fasciculata* also possess laminar growth forms. Dendroid and bulbous growth forms also occur, but these morphologies are relatively rare (Fig. 4A). Only two *Stachyodes* species show dendroid growth forms, and are commonly preserved as fragments in a variety of orientations together with broken branching tabulates (e.g., *Thamnopora* cf. *pansiensis* Tchi, 1966, *Cladopora fistula* Tchi, 1975, solitary rugose corals).

Among these *Stachyodes* species, *S. fasciculata* Dong in Dong et al., 1989, rarely shows bulbous growth form, which is approximately 1% of all the investigated stromatoporoids.

(ii) Size. The sizes of stromatoporoids were investigated by measurement of basal dimension and maximum vertical thickness of stromatoporoid skeletons. The basal dimensions generally range 10–50 cm, with some more than 50 cm and even reaching 100 cm. Thickness of stromatoporoids was divided into three groups: (a) <5 mm, (b) 5–10 mm, and (c) >10 mm (Fig. 4B). Small sizes of the skeletons are characteristic of the entire stromatoporoid fauna, 66% of which present a thickness

below 5 mm, including the most common *Clathrocoilona spissa* and a small portion of *Gerronostromaria grossum*, *Stictostroma saginatum*, and laminar *Stachyodes fasciculata*. A small number of stromatoporoids range from mainly 5 mm to 10 mm in thickness, including *Gerronostromaria grossum* and laminar *Stachyodes fasciculata*. Very few stromatoporoids show relatively large thicknesses, with representative *Gerronostromaria grossum* exceeding 10 mm in thickness, rarely more than 20 mm.

(iii) Substrate. Three types of substrates are recognized in the Jiwozhai reef: (a) sediments, (b) growth surface of prior high-relief organism skeletons, and (c) prior to laminar organism skeletons (Fig. 4C). High-relief organisms (e.g., solitary rugose corals, branching and massive tabulate corals, dendroid stromatoporoids) are the most common substrates especially for the small thin laminar *Clathrocoilona spissa*. The relatively large skeletons of *Gerronostromaria grossum* generally show preference to cover a large area of sediment including bioclasts and clay-rich micrites after the initial settlement. In addition to encrusting on high-relief organisms, a number of stromatoporoids, such as *Clathrocoilona spissa*, overgrew different laminar organisms (e.g., chaetetids, tabulate corals or laminar stromatoporoids), and buried by sediments.

(iv) Growth interruption. Growth interruptions are common in the stromatoporoids, represented by latilaminae (prominent tangential sets of horizontal elements of the skeleton bounded by prominent lines representing growth interruptions). The thickness of latilaminae is subdivided into three grades herein: (a) ≤ 2 mm, (b) > 2 mm and ≤ 4 mm, and (c) > 4 mm (Fig. 4D). More than half of latilaminae (58%) are less than 2 mm, 36% of them ranges 2–4 mm, and remaining 6% of them are over 4 mm in thickness. The thickness and numbers of latilaminae are considered to be evidence that *Gerronostromaria grossum* and *Synthetostroma actinostromoides* were exceedingly resilient and recovered quickly after interruptions (which were most likely caused by sediment deposition). However, *Clathrocoilona spissa*, *Stictostroma saginatum* and laminar *Stachyodes fasciculata*, which frequently encrusted high-relief organisms, were presumably vulnerable to the interruption triggered by sedimentation and/or sporadic high-energy currents and could hardly keep overgrowing.

Systematic palaeontology

Phylum Porifera Grant, 1836

Class Stromatoporoidea Nicholson and Murie, 1878

Order Clathrodictyida Bogoyavlenskaya, 1969

Family Gerronostromatidae Bogoyavlenskaya, 1969

Genus *Gerronostromaria* Nestor, 2011

Type species: Gerronostroma elegans Yavorsky, 1931; Middle Devonian of Kuznetsk Basin, Russia.

Gerronostromaria grossum Dong, 1974

Fig. 5A.

1974 *Gerronostroma grossum* sp. nov.; Dong 1974: 221, pl. 102: 5, 6.
1979 *Gerronostroma grossum* Dong, 1974; Yang and Dong 1979: 39,
pl. 14: 3, 4.

1982 *Gerronostroma grossum* Dong, 1974; Dong and Wang 1982: 13,
pl. 4: 3, 4.

1992 *Parallelopora ostiolata* Bargatzky, 1881; Dong and Song 1992:
32, pl. 4: 2a.

2020 *Actinostroma undulatum* Yang and Dong, 1963; Huang et al.
2020: 7, text-fig. 5A.

2020 *Trupetostroma dushanense* Yang and Dong, 1963; Huang et al.
2020: 11, text-fig. 7G, H, 8B.

Material.—202 specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with one specimen (NIGP 177047) illustrated.

Description.—Skeletons are laminar, with thickness generally between 5–25 mm, occasionally exceeding 25 mm and up to 40 mm. Growth surface features are not visible because stromatoporoids are cemented into limestone surfaces, thus not visible. In longitudinal section, regular networks are formed by continuous laminae and pillars (Fig. 5A₁), commonly with regularly spaced latilaminae (Fig. 5A₁), ranging 1–6 mm in thickness. Pillars are thick, post-like or occasionally upward spreading, vertically superposed through a number of laminae (up to 22 counted), spacing 7–10 per 2 mm, ranging 0.05–0.2 mm in thickness. Laminae are thin or locally thickening, laterally extensive, slightly undulose, spacing 12–16 per 2 mm, ranging 0.02–0.05 mm in thickness. Galleries are horizontal elongate, or round. Mamelons are conspicuous, 4–6 mm wide. Dissepiments are abundant in the astrorhizal canals and occasionally common in the galleries. Spiral tubes are frequently observed. In tangential section, pillars are isolated and round (Fig. 5A₂). Laminae are present as concentric circles in tangential section are due to curvature of laminae in the longitudinal plane. Astrorhizae are prominent, ranging 2–6 mm in diameter, at a distance of 4–6 mm from one to another, with central astrorhizal canals. The microstructure is essentially compact, but occasionally clinoreticular probably due to diagenetic alteration (Fig. 5A₃, A₄).

Remarks.—The present species was previously assigned to *Actinostroma undulatum* Yang and Dong, 1963, by Huang et al. (2020) due to the suspected colliculi and regular network, but it essentially resembles *Gerronostromaria grossum* Dong, 1974, described by Dong and Wang (1982) in relation to the dense laminae and thick pillars. Also it was formerly classified as *Trupetostroma dushanense* Yang and Dong, 1963, by Huang et al. (2020) according to the regular network formed by thin laminae and superposed pillars, but *Trupetostroma* Parks, 1936, possesses tripartite laminae that are not present in *Gerronostromaria* Nestor, 2011. Dong and Song (1992) identified this species as *Parallelopora ostiolata* Bargatzky, 1881, by the appearance of unclear microreticulate microstructure, but the regular networks formed by continuous laminae and pillars in longitudinal sections of

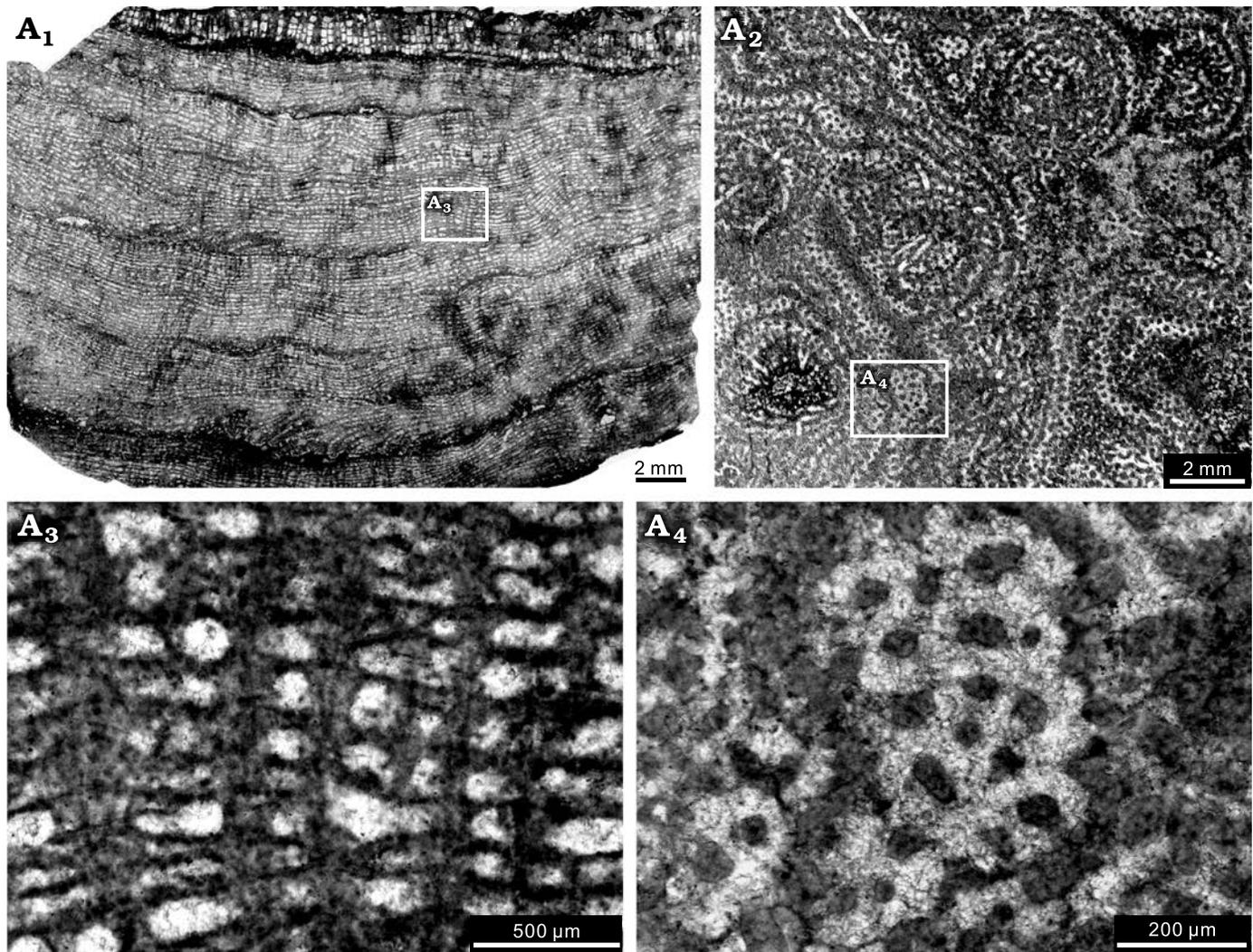


Fig. 5. Stromatoporoid *Gerronostromaria grossum* Dong, 1974, NIGP 177047, from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. A₁, longitudinal section, note the well differentiated network constructed by thin laminae and pillars; A₂, tangential section showing the distinct mamelons; A₃, enlargement of A₁, illustrating the common occurrence of the diagenetic “clinoreticular” microstructure inside the continuous pillars; A₄, enlargement of A₂, showing the isolated pillars.

Gerronostromaria grossum Dong, 1974, are totally different from the dominant pachysteles of *Parallelopora* Bargatzky, 1881, and the supposed microreticulate microstructure may not represent the original structure.

Stratigraphic and geographic range.—Givetian (Middle Devonian) of Yunnan, Guizhou, Guangxi, and Hunan provinces, South China.

Order Stromatoporellida Stearn, 1980

Family Stromatoporellidae Lecompte, 1951

Genus *Clathrocoilona* Yavorsky, 1931

Type species: *Clathrocoilona abeona* Yavorsky, 1931; Middle Devonian of Kuznetsk Basin, Russia.

Clathrocoilona spissa (Lecompte, 1951)

Fig. 6.

1951 *Stromatoporella spissa* sp. nov.; Lecompte 1951: 187, pl. 27: 1–4.

1968 *Stromatoporella spissa* Lecompte, 1951; Flügel and Flügel-Kahler 1968: 399.

1971 *Stromatopora spissa* (Lecompte, 1951); Kaźmierczak 1971: 92, pl. 21: 2.

1971 *Clathrocoilona spissa* (Lecompte, 1951); Zúkalová 1971: 56, pl. 15: 1, 2.

1974 *Clathrocoilona spissa* (Lecompte, 1951); Flügel 1974: 165, pl. 24, 26, 27.

1980 *Clathrocoilona spissa* (Lecompte, 1951); Mistiaen 1980: 196, pl. 7: 3–9.

1984 *Clathrocoilona spissa* (Lecompte, 1951); Cockbain 1984: 25, pl. 11: 1–4.

1985 *Clathrocoilona spissa* (Lecompte, 1951); Mistiaen 1985: 96, pl. 6: 6–8.

1988 *Clathrocoilona spissa* (Lecompte, 1951); Mistiaen 1988: 174.

1993 *Clathrocoilona (Clathrocoilona) solidula spissa* (Lecompte, 1951); May 1993: 38, pl. 7: 2; pl. 8: 1, 2.

1999 *Clathrocoilona (Clathrocoilona) solidula spissa* (Lecompte, 1951); May 1999: 127.

1999 *Clathrocoilona spissa* (Lecompte, 1951); Cook 1999: 507, text-fig. 28C, 29.

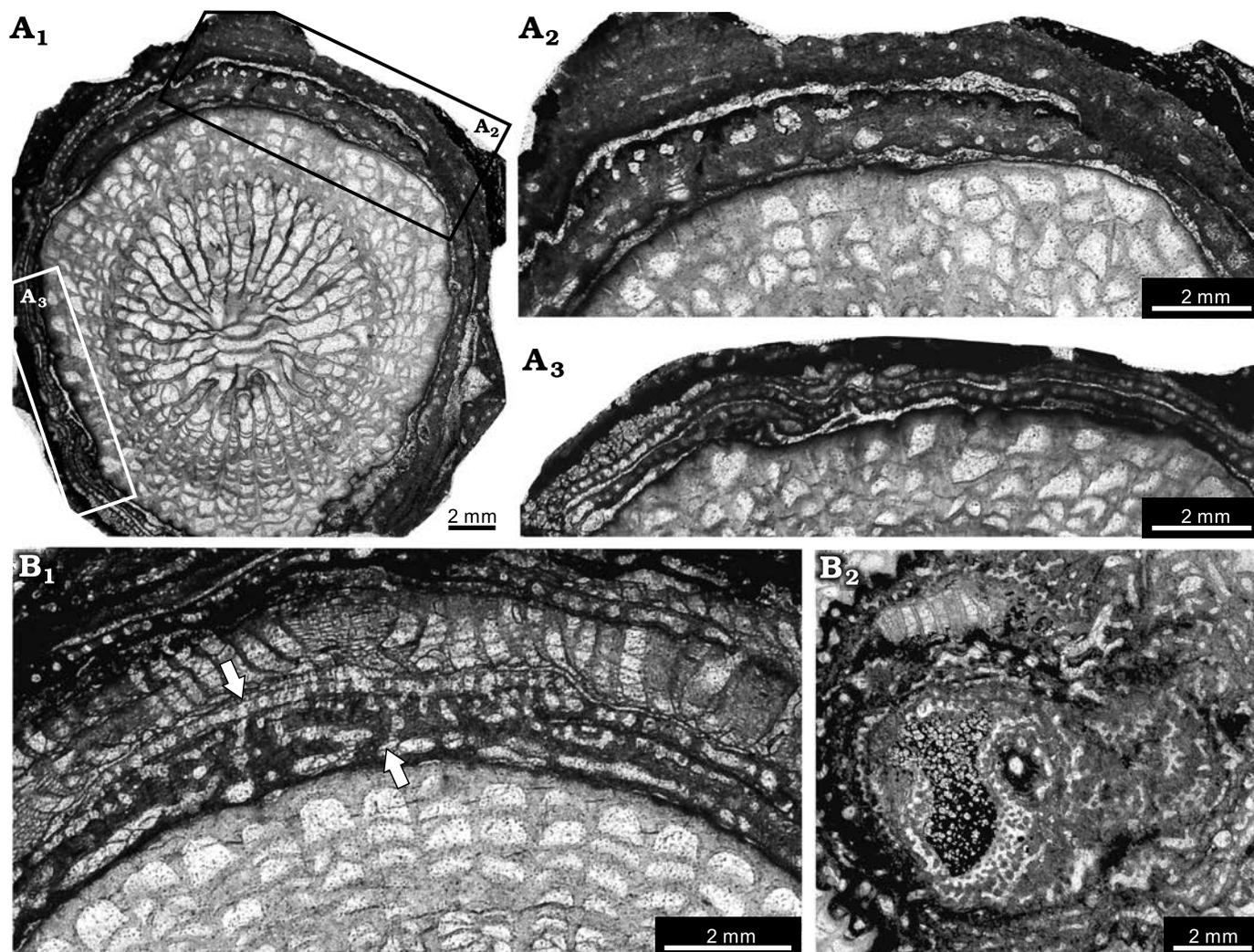


Fig. 6. Stromatoporoid *Clathrocoilona spissa* (Lecompte, 1951), from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. **A.** NIGP 177048; A₁, longitudinal section showing the contemporarily encrusting layers, with black and white rectangles illustrating details; A₂, A₃, enlargement of A₁, note the obvious discrepancy between different areas in the same stromatoporoid: the condensed skeletons of A₂ are similar to *Clathrocoilona spissa* (Lecompte, 1951) and thin laminae of A₃ are consistent with *Clathrocoilona obliterata* (Lecompte, 1951). **B.** NIGP 177049; B₁, longitudinal section, note the intra-specific variations (white arrows) of the lower irregular layers similar to *Clathrocoilona crassitexta* (Lecompte, 1951) and the upper regular layers identical to *Clathrocoilona obliterata* (Lecompte, 1951); B₂, tangential section.

2005 *Clathrocoilona* (*Clathrocoilona*) *solidula spissa* (Lecompte, 1951); May 2005: 180, pl. 13: 2, 3.

2008 *Clathrocoilona spissa* (Lecompte, 1951); Salerno 2008: 74, pl. 11: 2.

2020 *Clathrocoilona spissa* (Lecompte); Huang et al. 2020: 7, text-fig. 5B; 11, text-fig. 8C, F.

2020 *Clathrocoilona crassitexta* (Lecompte); Huang et al. 2020: 8, text-fig. 6A, G, I, 11, text-fig. 8A, D, F.

2020 *Clathrocoilona obliterata* (Lecompte); Huang et al. 2020: 11, text-fig. 8F.

Material.—275 specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with two representative specimens (NIGP 177048 and NIGP 177049) illustrated.

Description.—Skeletons are thin laminar in growth form, commonly below 2 mm in thickness, with only a few exceeding 5 or 10 mm, in almost all samples encrusting high-relief

organisms, such as tabulate corals (e.g., *Thamnopora* cf. *pansiensis* Tchi, 1966), solitary rugose corals (e.g., *Mictrophyllum* cf. *shawoziense* He, 1978), or other laminar organisms, such as bryozoans (e.g., *Fistuliporella hemispheroidea* Yang, 1954), and other species of stromatoporoids. Surface features cannot be viewed because the stromatoporoids are enclosed in cemented limestone. Latilaminae are conspicuous, ranging 0.2–6 mm in thickness, mostly within 2 mm. In longitudinal section, the skeletons show distinct skeletal variations (Fig. 6A). In some areas, the structures are generally amalgamated, with laminae and pillars being hardly differentiated (Fig. 6A₂). Laminae and pillars are irregularly thick with regard to both their thickness and width; they range, respectively, from 0.2 to 0.4 mm thickness, and spacing is 4–6 per 2 mm. Gallery shapes are variable, round or irregular, with or without abundant dissepiments. In the other areas, skeletons are constructed by regular laminae

and pillars (Fig. 6A₃), such as the terminal part of latilaminae (Fig. 6B₁). Laminae are continuous, formed by the lighter axial zone and the coated dark layer, spacing 8–14 per 2 mm, 0.02–0.06 mm in thickness, with frequent single layers in a thickness of 0.2 mm (Fig. 6A₃). Pillars are spool-shaped, confined to the interlaminar spaces, with thinner ones 0.02–0.04 mm in thickness, thicker ones 0.1–0.2 mm in thickness, spacing 8–12 per 2 mm. In tangential section of the regular areas, pillars appear isolated, 0.05–0.1 mm in thickness (Fig. 6B₂). Laminae are occasionally tripartite with conspicuously light axial zone in regular area.

Remarks.—The present species resembles *Clathrocoilona crassitexta* (Lecompte, 1951), *C. obliterated* (Lecompte, 1951), and *C. spissa* (Lecompte, 1951) from the Dinant Basin, southern Belgium. Thus, this species was preliminarily assigned to *Clathrocoilona crassitexta*, *C. obliterated* and *C. spissa*, respectively, in Huang et al. (2020) using different samples. However, detailed study reveals intra-specific variations in specimens of the Jiwozhai reef. The irregular areas show close similarity to *Clathrocoilona crassitexta* because of their densely irregular skeletons, and the regular areas retain a high degree of consistency with *C. obliterated* in terms of prominent tripartite structure and regular thin laminae and short pillars. Therefore, all these characteristics are present within the same specimens, and this may indicate that *Clathrocoilona spissa*, *C. obliterated*, and *C. crassitexta* are synonymous species with intra-specific variations. Here, we temporarily assign this species to *Clathrocoilona spissa* due to the dominant irregular skeletons.

Stratigraphic and geographic range.—Lower Givetian (Middle Devonian) of Eifel, Germany, and central Bohemia, Czech Republic; lower to middle Givetian (Middle Devonian) of Guangxi and Guizhou provinces, South China, and Queensland, Australia; Givetian to Frasnian (Middle–Upper Devonian) of Avesnois and Boulonnais, France, Dinant Basin, Belgium, Holy Cross Mountains, Poland; lower Frasnian (Upper Devonian) of Moravian Karst, Czech Republic; Frasnian (Upper Devonian) of Canning Basin, Australia.

Genus *Stictostroma* Parks, 1936

Type species. *Stictostroma gorriense* Stearn, 1995; Emsian (Lower Devonian) of Gorrie, Ontario, Canada.

Stictostroma saginatum (Lecompte, 1951)

Fig. 7A, B.

- 1951 *Stromatoporella saginata* sp. nov.; Lecompte 1951: 171, pl. 22: 5–7; pl. 23: 1–3.
 1968 *Clathrocoilona saginata* (Lecompte, 1951); Flügel and Flügel-Kahler 1968: 373.
 1983 *Clathrocoilona* cf. *saginata* (Lecompte, 1951); Stearn 1983: 549, text-fig. 5G–H.
 1984 *Clathrocoilona saginata* (Lecompte, 1951); Cockbain 1984: 25, pl. 10: A–D.
 1985 *Stictostroma saginatum* (Lecompte, 1951); Mistiaen 1985: 115, pl. 8: 6–11.
 1988 *Stictostroma saginatum* (Lecompte, 1951); Mistiaen 1988: 176, pl. 21: 5–9.

- 1999 *Stictostroma saginatum* (Lecompte, 1951); Mistiaen 1999: 36, pl. 3: 9–12; pl. 4: 1, 2.
 2000 *Stictostroma saginatum* (Lecompte, 1951); Mistiaen and Gholamalain 2000: 83, pl. 6: 6–8.
 2008 *Stictostroma saginatum* (Lecompte, 1951); Salerno 2008: 82, pl. 12: 2.
 2020 *Stictostroma saginatum* (Lecompte, 1951); Huang et al. 2020: 7, text-fig. 5C.

Material.—95 specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with two typical specimens (NIGP 177050 and NIGP 177051) illustrated.

Description.—Skeletons are laminar, with common prominent digitation of mamelons forming columns (a maximum of 25 mm in height) (Figs. 2D, 7A), occasionally encrusting on solitary rugose corals or branching tabulate corals (e.g., *Thamnopora* sp., solitary rugose corals) (Fig. 7B). In longitudinal section, the skeleton consists of extensive laminae and restricted pillars. Laminae are extensive, gently undulating but sharply increased around the mamelons, spacing 8–12 per 2 mm and 0.05–0.2 mm in thickness. Pillars are spool-shaped, commonly confined to one interlaminar space, irregularly spacing about 7–10 in 2 mm and 0.05–0.2 mm in thickness. Galleries are circular, oval, or horizontally elongate. Mamelons are protruding, with central astrorhizal canals, generally 2–20 mm in height. In tangential section, individual pillars form round dots, 0.05–0.1 mm in diameter; laminae present as concentric circles. Mamelons are distinct, showing a round central astrorhizal canals, with separated by distances of 2–4 mm (Fig. 7A₁). The microstructures are compact or ordinicellular (Fig. 7A₃).

Remarks.—The skeletal structures of this species are exactly the same as *Stromatoporella saginata* Lecompte, 1951, and *Stictostroma saginatum* described by Mistiaen (1988: 176–179, pl. 21: 8, 9). Although *Stictostroma* Parks, 1936, is highly similar to *Stromatoporella* Nicholson, 1886, in relation to extensive laminae, confined pillars, and ordinicellular microstructure, the latter genus is characterized by abundant ring pillars. In the absence of ring pillars, the species was assigned to *Clathrocoilona* Yavorsky, 1931 (Flügel and Flügel-Kahler 1968; Stearn 1983; Cockbain 1984) or *Stictostroma* (Mistiaen 1985, 1988, 1999; Salerno 2008). It closely resembles *Clathrocoilona* in terms of laterally continuous laminae and confined pillars, but they are different in microstructure. Here, we assign this species to *Stictostroma* due to the coarsely ordinicellular microstructure.

Stratigraphic and geographic range.—?Emsian (Lower Devonian) of Ellesmere Island, Canada; Givetian (Middle Devonian) of Eifel, Germany and Guizhou Province, South China; lower Frasnian (Upper Devonian) of Central Mountains, Afghanistan; middle Frasnian (Upper Devonian) of Boulonnais and Avesnois, France; upper Frasnian (Upper Devonian) of Dinant and Namur basins, Belgium; Frasnian (Upper Devonian) of Kerman and Esfahan provinces, Iran, and Canning Basin, Australia (Mistiaen and Gholamalain 2000).

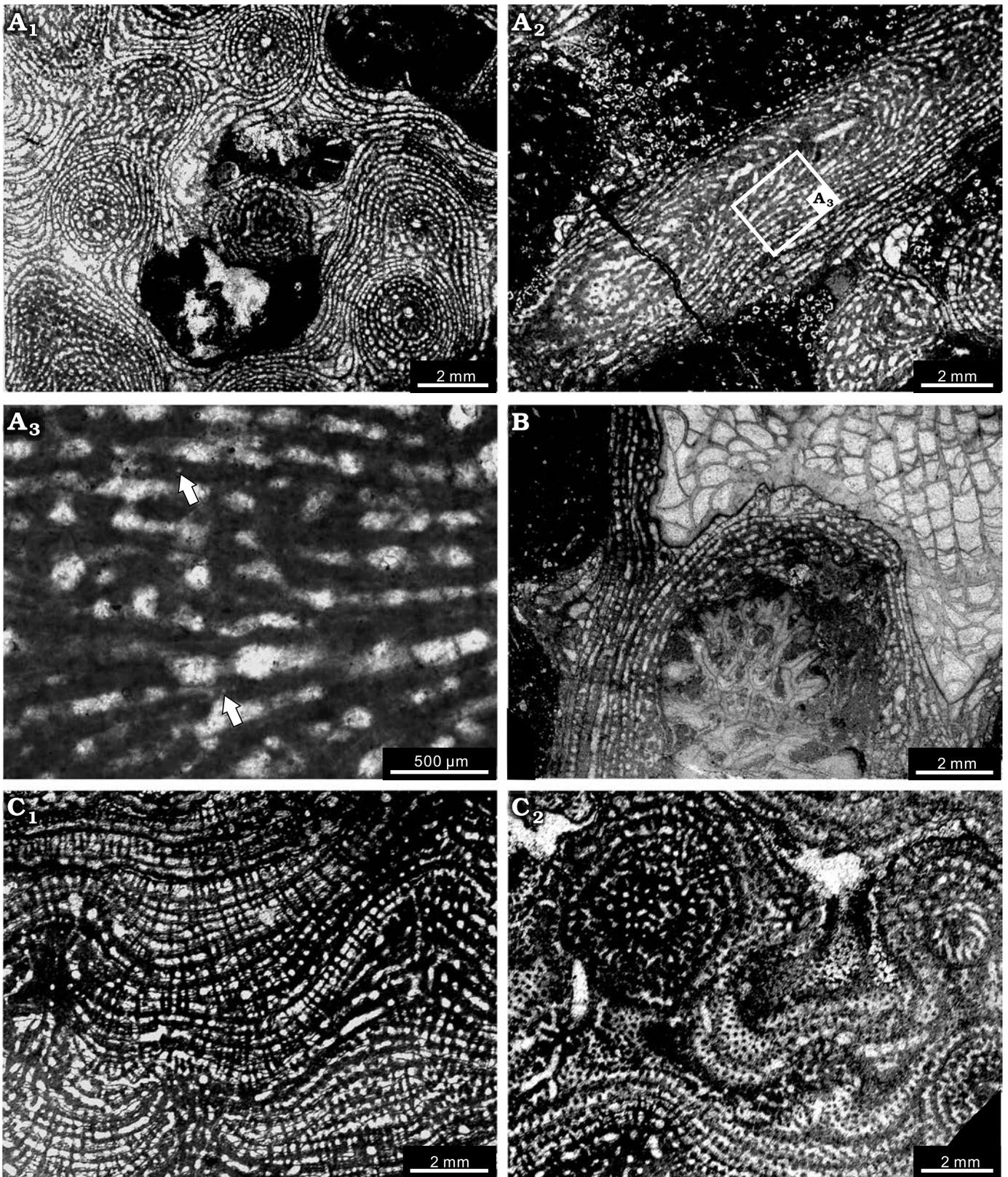


Fig. 7. Stromatoporoids from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. **A, B.** *Stictostroma saginatum* (Lecompte, 1951) **A.** NIGP 177050; A₁, tangential section showing the isolated pillars and locally irregular skeleton; A₂, longitudinal section, note the prominently vertically erected mamelon; A₃, enlargement of A₂, note the coarsely ordnicellular microstructure (arrows). **B.** NIGP 177051; longitudinal section, note the encrusting skeleton over *Thamnopora* sp. debris and a solitary rugose coral. **C.** *Synthetostroma actinos-tromoides* Lecompte, 1951, NIGP 177052; C₁, longitudinal section; C₂, tangential section.

Genus *Synthetostroma* Lecompte, 1951

Type species: Synthetostroma actinostromoides Lecompte, 1951; Givetian (Middle Devonian) of Surice, Belgium.

Synthetostroma actinostromoides Lecompte, 1951

Fig. 7C.

- 1951 *Synthetostroma actinostromoides* sp. nov.; Lecompte 1951: 194, pl. 20: 3, 4.
 1968 *Synthetostroma actinostromoides* Lecompte, 1951; Flügel and Flügel-Kahler 1968: 18.
 1971 *Synthetostroma actinostromoides* Lecompte, 1951; Zúkalová 1971: 53, pl. 12: 1–5.
 1978 *Synthetostroma actinostromoides* Lecompte, 1951; Huang 1978: 33, pl. 6: 4.
 ?1978 *Synthetostroma actinostromoides* Lecompte, 1951; Wang 1978: 35, pl. 18: 1.
 1980 *Synthetostroma* cf. *actinostromoides* Lecompte, 1951; Mistiaen 1980: 196, pl. 9: 3–6.
 1982 *Trupetostroma doupenglingense* Yang and Dong, 1979; Dong and Wang 1982: 14, pl. 5: 7, 8.
 1982 *Pseudoactinodictyon* cf. *distanum* Yang and Dong, 1979; Dong and Wang 1982: 16, pl. 7: 7, 8.
 ?1988 *Synthetostroma actinostromoides* Lecompte, 1951; Wang 1988: pl. 15: 1.
 1992 *Synthetostroma actinostromoides* Lecompte, 1951; Dong and Song 1992: 29, pl. 2: 3.
 1992 *Trupetostroma assumptum* Yang and Dong, 1979; Dong and Liu 1992: 167, pl. 1: 1.
 1992 *Clathrocoilona* cf. *variabilis* Yang and Dong, 1979; Dong and Liu 1992: 169, pl. 3: 4.
 1993 *Clathrocoilona* (*Synthetostroma*) *actinostromoides* (Lecompte, 1951); May 1993: 40, pl. 10: 1.
 2008 *Synthetostroma actinostromoides* Lecompte, 1951; Salerno 2008: 79, pl. 11: 1.
 2020 *Synthetostroma actinostromoides* Lecompte, 1951; Huang et al. 2020: 7, text-fig. 5D.

Material.—Four specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with one specimen (NIGP 177052) illustrated.

Description.—Skeletons are commonly laminar. Among the four specimens, two small ones preserved as fragments, 3–5 mm in thickness. The largest one shows a thickness up to 50 mm (Fig. 3). Latilaminae exist, each latilamina is 2–6 mm thick. In longitudinal section, the skeletons consist of multilamellar laminae and slender pillars (Fig. 7C₁). Laminae are continuous, undulating, integrated by multiple microlaminae and abundant imbricating dissepiments, spacing 5–7 per 2 mm and 0.05–0.2 mm in thickness. Pillars are post-like, confined to interlaminar spaces but systematically superposed, penetrating 3–4 laminae, spacing 7–10 per 2 mm and 0.05–0.15 mm in thickness. The galleries are variable, rectangular to subcircular. Mamelons are conspicuous, with a height of 4–6 mm (Fig. 7C₁). Astrorhizal canals and interlaminar spaces are often pervaded by dissepiments. In tangential section, isolated pillars are rounded or locally irregular in form, in diameter of 0.1–0.2 mm. Laminae show concentric circles around mamelon. Mamelons are 2–3 mm in width, with a distance of 4–8 mm from one to another (Fig. 7C₂). The microstructure is compact.

Remarks.—The present specimens from Jiwozhai reef share high morphological similarities with the holotype of *Synthetostroma actinostromoides* Lecompte, 1951, and show well-preserved mamelons. Although *Synthetostroma actinostromoides* once was regarded as a junior synonym of *Clathrocoilona* by Kosareva (1976), the presence of superposed pillars and frequent microlaminae is not matched with the generic concept of *Clathrocoilona* (laminae thick, tripartite; pillars confined to the interlaminar spaces, not systematically superposed). *Trupetostroma doupenglingense* Yang and Dong, 1979, *Pseudoactinodictyon* cf. *distanum* Yang and Dong, 1979, described by Dong and Wang (1982) and *Trupetostroma assumptum* Yang and Dong, 1979, *Clathrocoilona* cf. *variabilis* Yang and Dong, 1979, described by Dong and Liu (1992) seem to be similar to the Jiwozhai reef specimens in terms of tripartite laminae and abundant dissepiments, thus further re-evaluation of these species is required.

Stratigraphic and geographic range.—Lower Givetian (Middle Devonian) of Eifel and Sauerland, Germany; middle Givetian (Middle Devonian) of Boulonnais, France; Guizhou, Hunan, and Yunnan provinces, South China, and Dinant Basin, Belgium; ?upper Givetian to lower Frasnian (Middle–Late Devonian) of Moravian Karst, Czech Republic.

Order Stromatoporida Stearn, 1980

Family Stromatoporidae Winchell, 1867

Genus *Pseudotruperetostroma* Khalфина and Yavorsky, 1971

Type species: Stromatopora pellucida artyschtsensis Yavorsky, 1955; Givetian (Middle Devonian) of Kuznetsk Basin, Russia.

Pseudotruperetostroma porosum (Yang and Dong, 1979)

Fig. 8A.

- 1979 *Hermatostroma porosum* sp. nov.; Yang and Dong 1979: 68, pl. 38: 7, 8.
 1980 *Hermatostroma parksi* Lecompte, 1952; Mistiaen 1980: 202: pl. 9: 7–9; pl. 10: 1, 2.
 1982 *Trupetostroma cellulolum* Lecompte, 1952; Dong and Wang 1982: 13, pl. 5: 1, 2.
 1982 *Hermatostroma porosum* Yang and Dong, 1979; Dong and Wang 1982: 22, pl. 13: 1, 2.
 1999 *Hermatostroma maculatum* Yang and Dong, 1979; Cook 1999: 511, text-fig. 32A–C; 33A–D.
 2008 *Pseudotruperetostroma cellulolum* (Lecompte, 1952); Salerno 2008: 92, pl. 15: 1–3.
 2020 *Trupetostroma* cf. *colliculosum* Khalфина, 1960; Huang et al. 2020: 6.

Material.—Two specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with one specimen (NIGP 177053) illustrated.

Description.—Skeletons are laminar, up to 50 mm in thickness (Fig. 3). Surface features are not visible in cemented limestone. In longitudinal section the skeleton between astrorhizae forms a regular network (Fig. 8A₁). Pachystromes

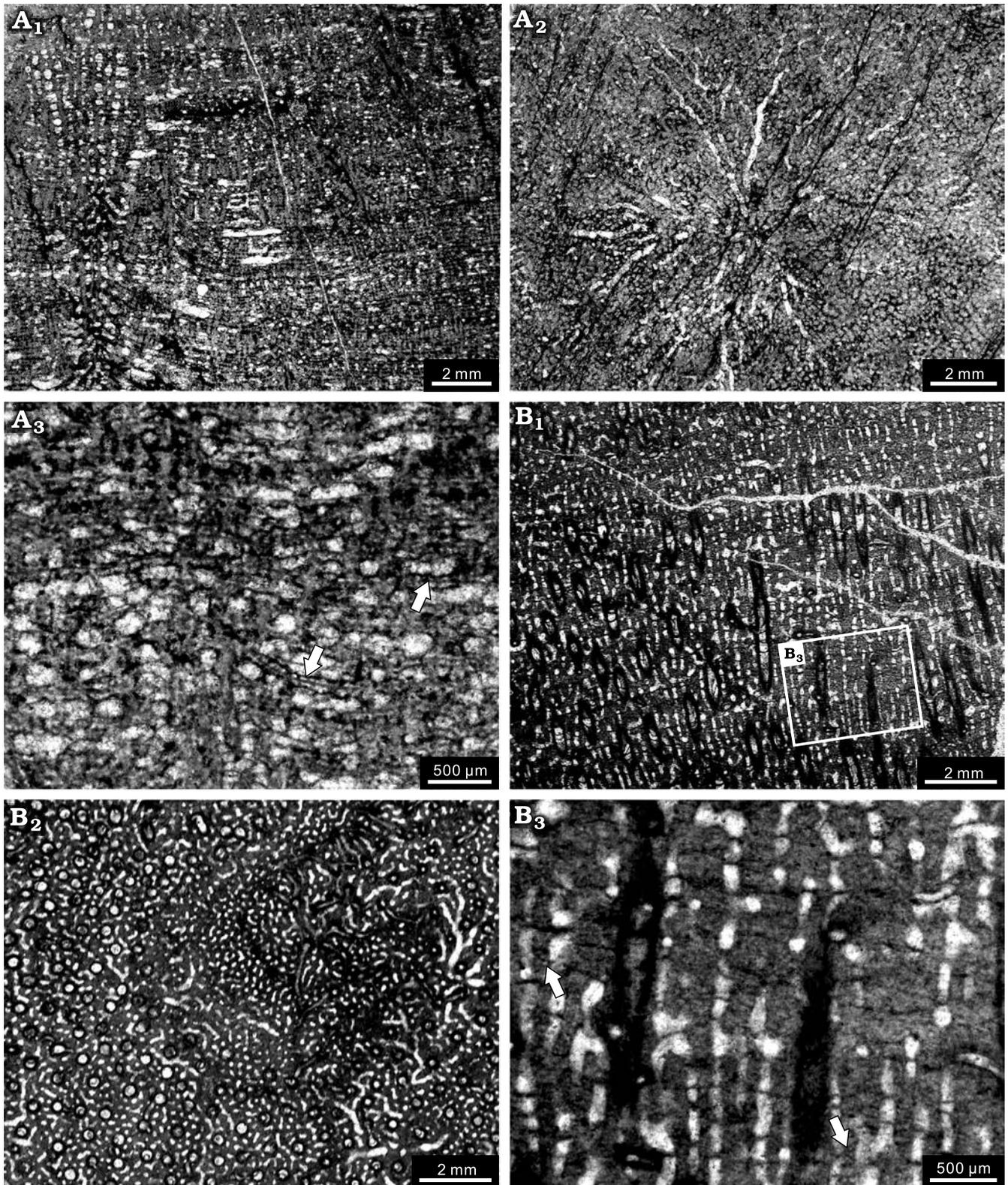


Fig. 8. Stromatoporoids from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. **A.** *Pseudotrurpetostroma porosum* (Yang and Dong, 1979), NIGP 177053; A₁, longitudinal section; A₂, tangential section; A₃, enlargement of longitudinal section showing coarsely cellular microstructure coated tangential elements (arrows). **B.** *Salirella buecheliensis* (Bargatzky, 1881), NIGP 177054; B₁, longitudinal section, note the predominance of the pachysteles in the right standard area and amalgamated structure in the left oblique orientation of the thin section; B₂, tangential section, note the autotubes in the upper middle area; B₃, enlargement of B₁ showing coarsely cellular microstructure (arrows) partially transformed into melanospheric microstructure; such features demonstrate the likely diagenetic character of these microstructures and therefore their unreliability as taxonomic discriminators.

are laterally continuous, occasionally undulose, spacing 8–12 per 2 mm, and of 0.1 mm in thickness. Pachysteles are vertically extensive, closely spaced, spacing 6–8 per 2 mm, 0.1–0.2 mm in thickness. In the upper part of the mamelons, the skeletons are dominated by continuously thick pachysteles, with 6 per 2 mm, 0.2 mm in thickness. Pachystromes weakly occur (Fig. 8A₁). Galleries are variable in sizes, 0.1–0.3 mm in diameter. Mamelons are conspicuous, horizontally extensive, with a height of 15–20 mm. Astrorhizal canals commonly contain abundant dissepiments. In tangential section, skeletons are densely compact with irregular networks or rare isolated pachysteles. Astrorhizae are predominant, up to 15 mm in diameter, with over 10 branching canals (Fig. 8A₂). The microstructure was mostly affected by the alteration of diagenesis, which possesses coarsely cellular-like structure (Fig. 8A₃).

Remarks.—This species was previously assigned to *Trupetostroma* cf. *colliculosum* Khalfina, 1960, but the specimens from Jiwozhai reef are quite different from *Trupetostroma* Parks, 1936, in terms of the atypical regular network of pachystromes and pachysteles. It closely resembles the *Pseudotrupetostroma cellulorum* (Lecompte, 1952) documented by Salerno (2008: 93–96, pl. 15: 3) with respect to structures near the mamelons, but the holotype of *Trupetostroma cellulorum* Lecompte, 1952, shows apparently confined inter-laminar pillars and different thin laminae.

Stratigraphic and geographic range.—Lower Givetian (Middle Devonian) of Eifel, Germany; lower to middle Givetian (Middle Devonian) of Guangxi, Yunnan, and Guizhou provinces, South China, and Queensland, Australia; middle Givetian (Middle Devonian) of Boulonnais, France.

Family Syringostromellidae Stearn, 1980

Genus *Salairella* Khalfina, 1961

Type species: *Salairella multicea* Khalfina, 1961; Eifelian (Middle Devonian) of Salair, Russia.

Remarks.—Genera of Stromatoporida and Syringostromatida were confused with each other for over 150 years until Stearn (1993) revised Stromatoporida in detail. The dominance of pachysteles was traditionally regarded as the diagnostic feature of the first named stromatoporoid *Stromatopora* Goldfuss, 1826 (e.g., Nicholson 1886; Galloway 1957; Dong 2001). Also some species belonging to *Salairella* were erroneously assigned to *Stromatopora* (e.g., Dong and Song 1992). Stearn (1993) elaborated the relationships between typical *Stromatopora* and its similar genera. He reaffirmed that presence of cassiculate structure is the key morphological feature of the holotype of *Stromatopora* from Germany. Therefore, although *Salairella* closely resembles *Stromatopora* in having tangentially amalgamated network, they are totally different in morphology of vertical sections of the skeleton.

Salairella buecheliensis (Bargatzky, 1881)

Fig. 8B.

1881 *Caunopora buecheliensis* sp. nov.; Bargatzky 1881: 290.

- 1952 *Parallelopora buecheliensis* (Bargatzky, 1881); Lecompte 1952: 290, pl. 50: 3, 4.
 1968 *Caunopora buecheliensis* Bargatzky, 1881; Flügel and Flügel-Kahler 1968: 53.
 1978 *Stromatopora hüpschii* (Bargatzky, 1881); Wang 1978: 27, pl. 13: 1.
 1980 *Stromatopora* cf. *buecheliensis* (Bargatzky, 1881); Mistiaen 1980: 210, pl. 13: 7–9; pl. 14: 1–3.
 1985 *Salairella buecheliensis* (Bargatzky, 1881); Mistiaen 1985: 145, pl. 12: 10–12; pl. 13: 1.
 1992 *Stromatopora hüpschii* (Bargatzky, 1881); Dong and Song 1992: 30, pl. 3: 1a, b.
 1999 *Salairella buecheliensis* (Bargatzky, 1881); May 1999: 129, pl. 1: 6.
 1999 *Salairella buecheliensis* (Bargatzky, 1881); Cook 1999: 525, text-fig. 45A–E.
 2005 *Salairella buecheliensis* (Bargatzky, 1881); May 2005: 204, pl. 21: 1, 2; pl. 30: 2, 3; pl. 31: 1; pl. 32: 1.
 2008 *Salairella buecheliensis* (Bargatzky, 1881); Salerno 2005: 97, pl. 14: 2.
 2020 *Stromatopora huepschii* (Bargatzky, 1881); Huang et al. 2020: 7, text-fig. 5F.

Material.—10 specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with one representative specimen (NIGP 177054) illustrated.

Description.—Skeletons are laminar in growth form, up to 20 mm in thickness and 500 mm in basal dimension (Fig. 3). The longitudinal section is dominated by pachysteles, partly with coarsely amalgamated networks or atypical cassiculate structures. Pachysteles are vertically continuous, commonly joining and dividing in oblique thin section (Fig. 8B₁), spacing 5–8 per 2 mm, 0.1–0.2 mm in thickness. Pachystromes are not clear, oblique or horizontal. Galleries are vertically elongate or occasionally irregular, crossed by flat or oblique dissepiments, at the same width as the pachysteles. Syringopodid symbionts are abundant, with a width of 0.2–0.3 mm, spacing 2–3 per 2 mm. The tangential section shows a closed network with dominantly circular autotubes between the astrorhizae (Fig. 8B₂). Width of the skeletal elements and autotubes 0.1–0.2 mm. Astrorhizae are conspicuous, generally bifurcated, 0.1–0.25 mm in diameter. Microstructure is normally cellular, 0.02 mm in diameter, but in some cases is melanospheric due to the diagenesis (Fig. 8B₃).

Remarks.—The predominance of vertically elongate pachysteles was also regarded as the main diagnostic characteristics of *Stromatopora* Goldfuss, 1826, for many years (e.g., Yang and Dong 1979; Dong 2001). Therefore, the samples in Jiwozhai reef were previously assigned to *Stromatopora huepschii* (Bargatzky, 1881) due to the rare existence of inconspicuous cassiculate structure probably caused by intraspecific variation, but the dominance of vertical elongate pachysteles justifies the designation as *Salairella buecheliensis*.

Stratigraphic and geographic range.—Eifelian to Givetian (Middle Devonian) of Dinant Basin, Belgium; lower Givetian (Middle Devonian) of Eifel, Germany, and Bohemia,

Czech Republic; lower to middle Givetian (Middle Devonian) of Boulonnais, France, Queensland, Australia, Central Mountains, Afghanistan, and Hunan and Guizhou provinces, South China.

Order Syringostromatida Bogoyavlenskaya, 1969

Family Coenostromatidae Waagen and Wentzel, 1887

Genus *Habrostroma* Fagerstrom, 1982

Type species: Stromatopora proxilaminata Fagerstrom, 1961; Middle Devonian of Ontario, Canada.

?*Habrostroma laminosum* (Lecompte, 1952)

Fig. 9A, B.

1952 *Stromatopora laminosa* sp. nov.; Lecompte 1952: 276, pl. 55: 3; pl. 56: 1, 2.

1968 *Stromatopora laminosa* Lecompte, 1952; Flügel and Flügel-Kahler 1968: 235.

1968 *Parallelopora laminosa* (Lecompte, 1952); Mallett 1968: 225, pl. 26: 1–6.

1978 *Stromatopora laminosa* Lecompte, 1952; Wang 1978: 29, pl. 14: 3.

1979 *Stromatopora* cf. *laminosa* Lecompte, 1952; Yang and Dong 1979: 55, pl. 27: 5, 6.

1982 *Stromatopora laminosa* Lecompte, 1952; Dong and Wang 1982: 37, pl. 9: 5, 6.

1993 *Habrostroma laminosum* (Lecompte, 1952); Stearn 1993: 222.

1995 *Stromatopora laminosa* Lecompte, 1952; Krebedünkel 1995: 110, pl. 14: 7, 8.

2005 *Habrostroma laminosum* (Lecompte, 1952); Stadelmaier et al. 2005: 24, pl. 9: 3.

2008 *Habrostroma laminosum* (Lecompte, 1952); Salerno 2008: 101, pl. 15: 4, 5.

2020 *Habrostroma laminosum* (Lecompte, 1952); Huang et al. 2020: 14.

Material.—Five specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with two specimens (NIGP 177055 and NIGP 177056) illustrated.

Description.—Skeletons are laminar to high domical, overgrowing on tabulate corals, solitary rugose corals, or other stromatoporoids, commonly 1–3 mm in thickness, with a maximum of 15 mm. Surface features are not visible in cemented limestone. Latilaminae are common, with individual latilaminae in a thickness of 1–3 mm. In longitudinal section, the skeletons are extremely dense (Fig. 9A, B₁), composed of thin laminae and thick pillars. Laminae are continuous, sharply undulose near the mamelons, spacing 8–14 mm per 2 mm, commonly with thickness of 0.02 mm (Fig. 9A). Pillars are short and thick, spool-shaped, laterally interconnected to account for the dense structure, spacing 7–10 per 2 mm, 0.1–0.2 mm in thickness. Galleries are tiny, smaller than the pillars, round or rarely elongate, commonly 0.05–0.15 mm in diameter. Mamelons conspicuous, with height of 2–5 mm, with central and branching astrorhizal canals. Dissepiments are distinct in the astrorhizal canals. The central areas of high domical specimens show indistinctive microreticulate structure formed by melanospheres multi-microlaminae (Fig. 9B₁). In tangential section, the skeletons are also

densely packed and can hardly be differentiated (Fig. 9B₂). The microstructure locally appears to be melanospheric or striated (Fig. 9B₂, B₃), probably due to diagenetic alteration.

Remarks.—The present specimens resemble *Stromatopora laminosa* Lecompte, 1952 due to the indistinctive microreticulate structure and diagenetically melanospheric or striated microstructure. This species was assigned by many palaeontologists to *Stromatopora* Goldfuss, 1826, for over four decades, but it does not have the typical cassiculate structure. Stearn (1993) revised *Stromatopora laminosa* into *Habrostroma laminosum* and we agree with this decision. Although Webby and Zhen (2008), Stearn (2015b), and Stock and Burry-Stock (2019) generally use pachystele and pachystrome to describe the skeleton of *Habrostroma* Fagerstrom, 1982, the holotype presented by Fagerstrom (1982) apparently shows isolated longitudinal elements, which are totally different from the vertically interconnected pachyestes. Therefore, we tend to use “laminae” and “pillars” to describe the skeleton of this genus. However, rare specimens in Jiwozhai reef show poor preservation of tangential section, so are not reliably assigned to *Habrostroma laminosum*.

Stratigraphic and geographic range.—Lower Givetian (Middle Devonian) of Eifel Germany, and Guizhou Province, South China; lower to middle Givetian (Middle Devonian) of Queensland, Australia; Givetian to Frasnian (Middle–Late Devonian) of Dinant Basin, Belgium.

Family Parallelostromatidae Bogoyavlenskaya, 1984

Genus *Parallelopora* Bargatzky, 1881

Type species: Parallelopora ostiolata Bargatzky, 1881; Middle Devonian of Eifel, Germany.

Parallelopora sp.

Fig. 9C.

2020 *Parallelopora ostiolata* Bargatzky, 1881; Huang et al. 2020: 3.

Material.—One fragmental skeleton (NIGP 177057) from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China.

Description.—Skeleton appears to be laminar. Surface features are not visible in cemented limestone. In longitudinal section, the skeleton is made up of conspicuous pachyestes and indistinct pachyestromes (Fig. 9C₁). Pachyestes are slender, vertically straight, densely distributed, spacing 15–16 per 2 mm, 0.05–0.075 mm in thickness. Pachyestromes are thin, rarely exist, commonly replaced by dissepiments. Galleries are extremely narrow, with a width of 0.025–0.075 mm, infilled with concave dissepiments. In tangential section, the pachyestes interconnect, forming a closed network enclosing autotubes (Fig. 9C₂). Autotubes are circular, 0.025–0.05 mm in diameter. The microstructure is coarsely orthoreticulate.

Remarks.—The present species was preliminarily assigned to *Parallelopora ostiolata* Bargatzky, 1881, by Huang et al. (2020) according to the coarsely orthoreticulate microstructure, but the latter shows more thick and sparsely distributed

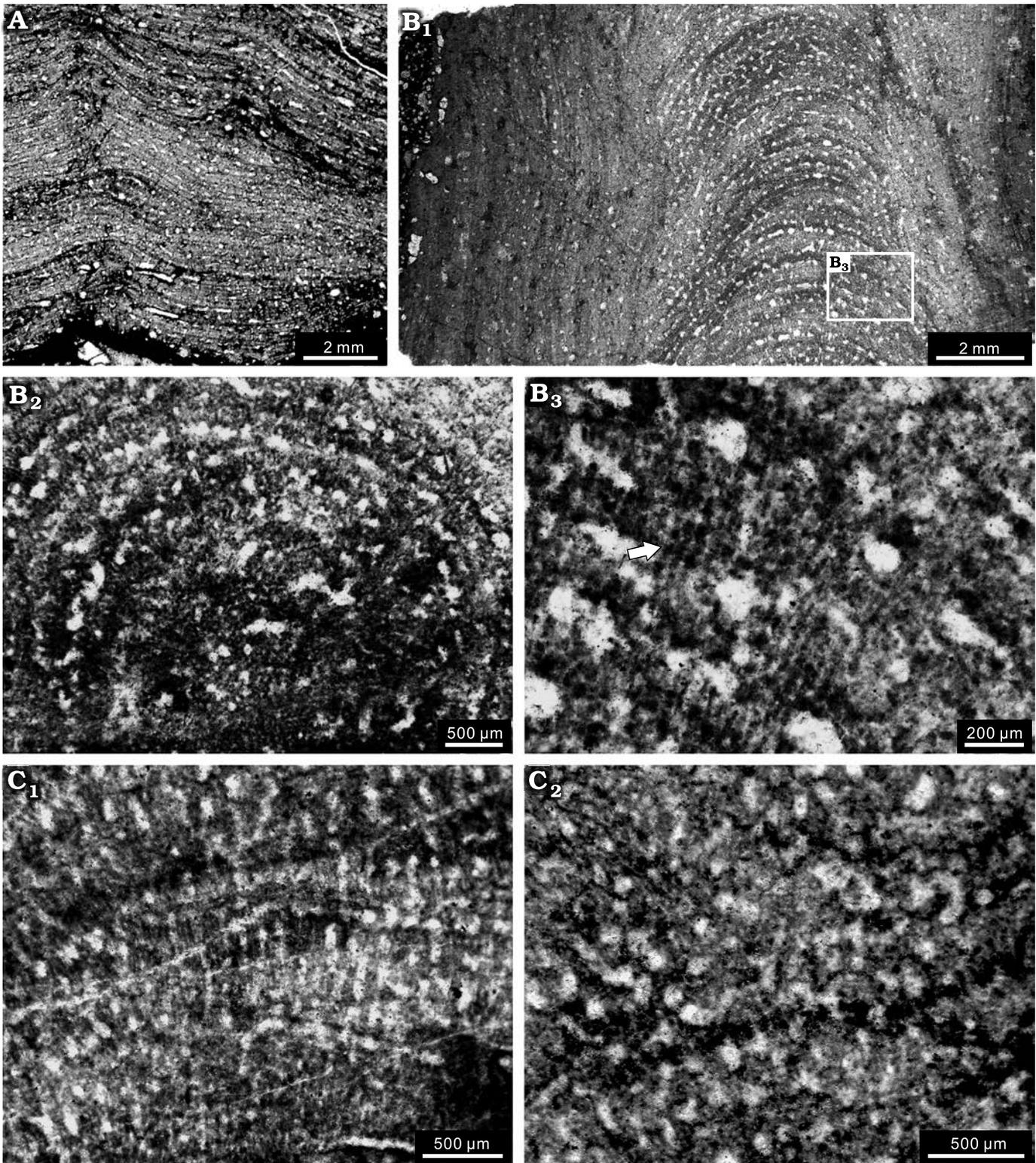
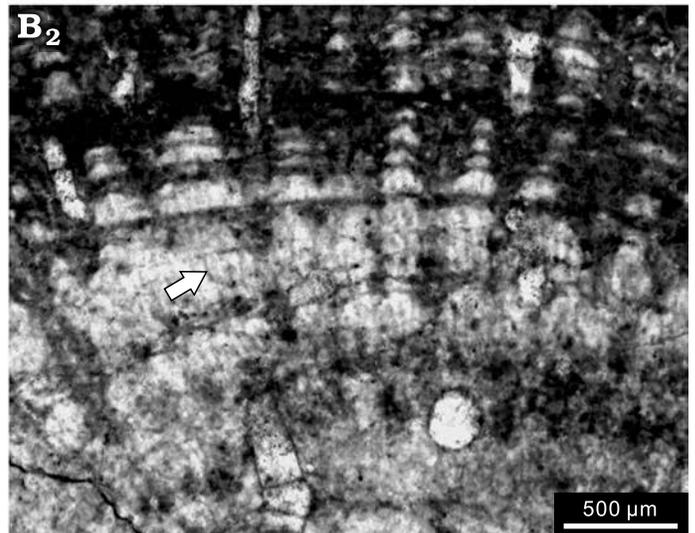
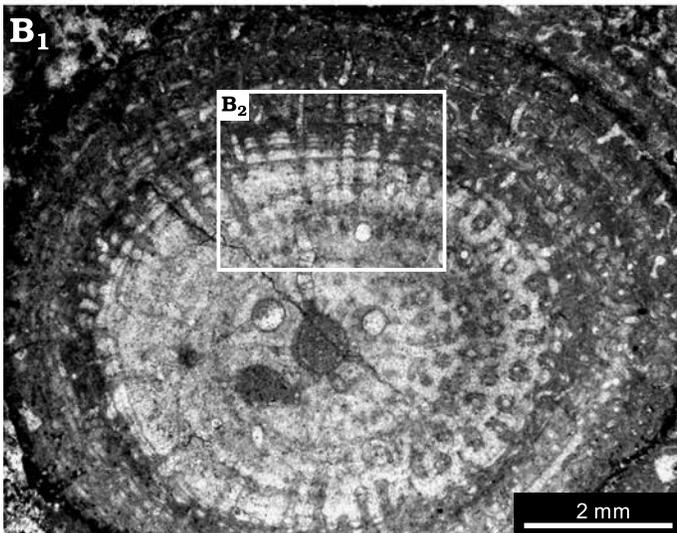
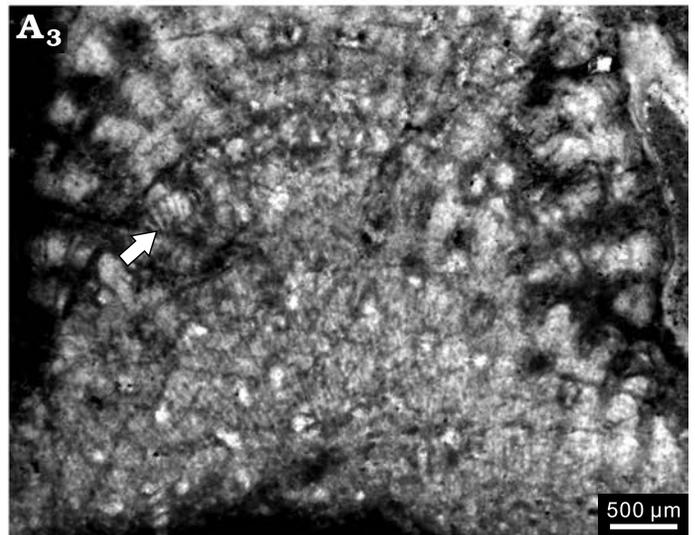
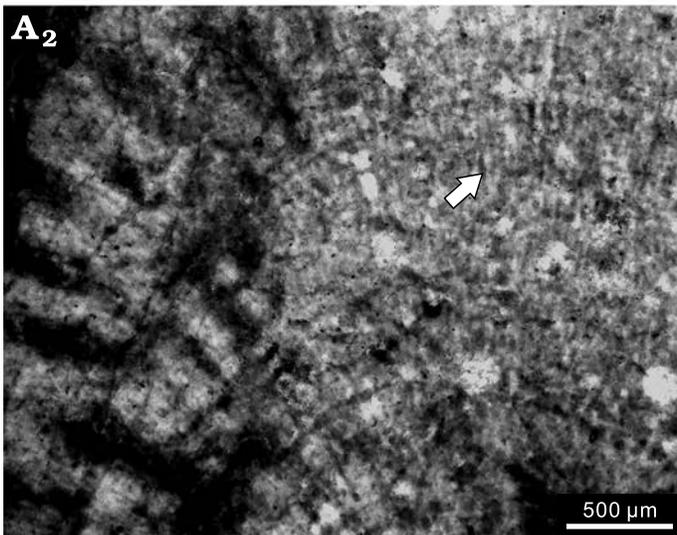
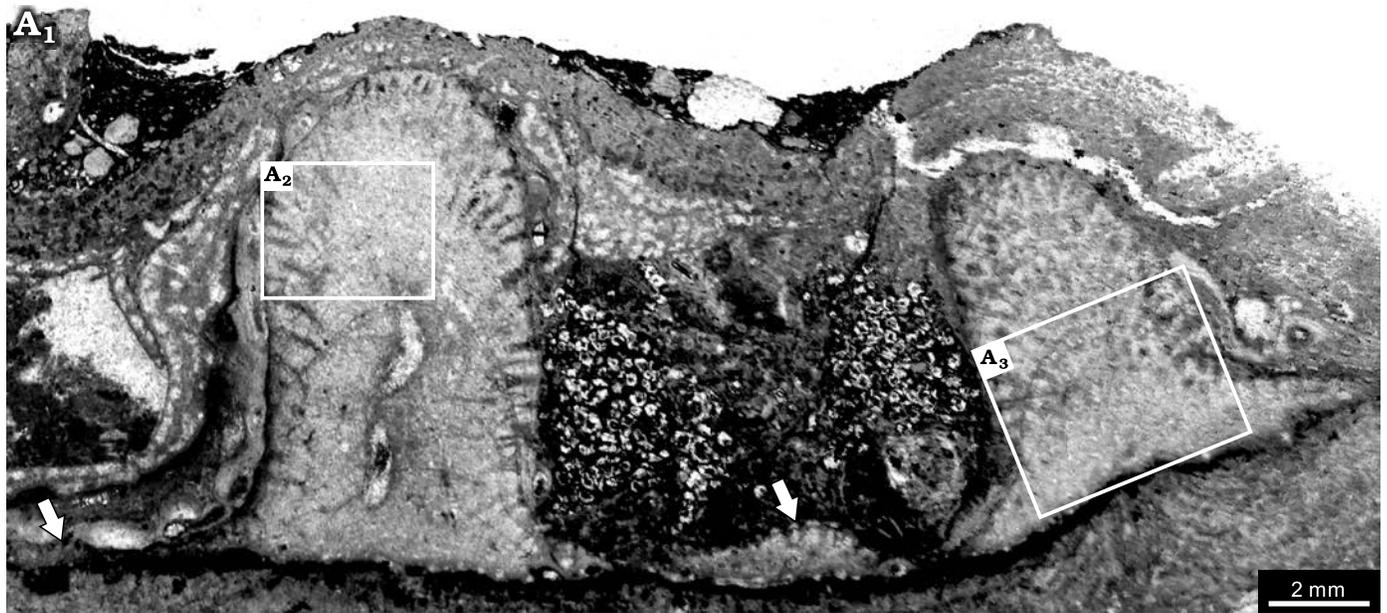


Fig. 9. Stromatoporoids from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. **A, B.** *?Habrostroma laminosum* (Lecompte, 1952) **A.** NIGP 177055; longitudinal section of the laminar form; **B.** NIGP 177056; **B₁**, longitudinal section of the high domical form; **B₂**, poor preservation of tangential section showing the dense structure; **B₃**, enlargement of **B₁**, showing possible microreticulate microstructure (arrow). **C.** *Parallelopora* sp., NIGP 177057; **C₁**, longitudinal section, note the microreticulate microstructure; **C₂**, tangential section showing the autotubes.

Fig. 10. Stromatoporoid *Stachyodes costulata* Lecompte, 1952, from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. **A.** NIGP 177058; **A₁**, longitudinal section of the whole thin section showing the columnar skeleton interconnected through →



laminar skeleton in the bottom (arrows); A₂, enlargement of A₁, note the striated microstructure (arrow); A₃, enlargement of A₁, showing autotubes and striated microstructure (arrow). **B.** NIGP 177059; B₁, tangential section showing the regular autotubes; B₂, enlargement of B₁, note the striated microstructure (arrow).

pachysteles, commonly spacing 5–6, or 8–10 per 2 mm, and with a width of 0.07–0.18 mm (Lecompte 1952; Galloway and St. Jean 1957; Galloway 1960). However, the poorly preserved single specimen cannot justify the assignment to a new species.

Family Stachyoditidae Khromykh, 1967

Genus *Stachyodes* Bargatzky, 1881

Type species: Stachyodes verticillata (M'Coy, 1850); Middle Devonian of Eifel, Germany.

Stachyodes costulata Lecompte, 1952

Fig. 10.

- 1952 *Stachyodes costulata* sp. nov.; Lecompte 1952: 309, pl. 64: 3; pl. 65: 1–4.
 1959 *Stachyodes costulata* Lecompte, 1952; Gogolezyk 1959: 372, pl. 4: 3; pl. 5: 1–3.
 1963 *Stachyodes costulata* Lecompte, 1952; Stearn 1963: 660, pl. 86: 4, 5.
 1966 *Stachyodes costulata* Lecompte, 1952; Klován 1966: 31, pl. 9: 1–6.
 1970 *Stachyodes costulata* Lecompte, 1952; Stearn and Mehrotra 1970: 18, pl. 4: 3, 4.
 1971 *Stachyodes costulata* Lecompte, 1952; Zúkalová 1971: 101, pl. 34: 5, 6.
 1974 *Stachyodes costulata* Lecompte, 1952; Khromykh 1974: 62, pl. 16: 1; pl. 17: 2.
 1979 *Stachyodes costulata* Lecompte, 1952; Yang and Dong 1979: 81, pl. 46: 9, 10.
 1984 *Stachyodes costulata* Lecompte, 1952; Cockbain 1984: 28, pl. 19: a–d; pl. 20: a.
 1984 *Stachyodes costulata* Lecompte, 1952; Dong and Wang 1984: 268, pl. 20: 3a, b.
 1988 *Stachyodes costulata* Lecompte, 1952; Khromykh and Hung 1988: 34, pl. 16: 6.
 1989 *Stachyodes costulata* Lecompte, 1952; Dong in Dong et al. 1989: 174, pl. 2: 3a–d.
 1992 *Stachyodes costulata* Lecompte, 1952; Dong and Liu 1992: 172, pl. 4: 5a, b.
 1999 *Stachyodes costulata* Lecompte, 1952; Mistiaen 1999: 39.
 2020 *Stachyodes costulata* Lecompte, 1952; Huang et al. 2020: 7, text-fig. 5E.

Material.—57 specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with two typical specimens (NIGP 177058 and NIGP 177059) illustrated.

Description.—Skeletons are dendroid, with some in situ specimens growing from laminar into erect columnar (Fig. 10A₁), but preserved as fragmented branches in most specimens. The branches are commonly 4–5 mm in diameter, up to 14 mm. In longitudinal section, the skeleton consists of dark thin pachystromes and thick pachysteles (Fig. 10A). In the central zone, the structure is relatively undifferentiated, with astrorhizal canal, 0.4 mm in diameter (Fig. 10A₁). In the peripheral zone, the structure is well differentiated. Pachysteles radiate from the central area and emerge perpendicularly to the surface, with a width of 0.2 mm. Pachystromes distributed as arches, spacing 7–8 per 2 mm, 0.02 mm in thickness

(Fig. 10A₂, A₃). Galleries are circular, perpendicular to the surface, 0.1–0.2 mm in diameter (Fig. 10A₃). In tangential section, pachysteles interconnect to form a regular closed network in the central zone, and gradually radiate to the peripheral zone (Fig. 10B₁). In the marginal zone, pachystromes distributed as concentric circles. The microstructure is apparently striated (Fig. 10A₂, A₃, B₂).

Remarks.—The present species is consistent with *Stachyodes costulata* Lecompte, 1952, due to the dense distributed of pachysteles. It differs from *Stachyodes radiata* Lecompte, 1952, in having a relatively undifferentiated structure in the central zone.

Stratigraphic and geographic range.—Givetian (Middle Devonian) of Queensland, Australia and Yukon, Canada; Givetian to lower Frasnian (Middle–Upper Devonian) of the Holy Cross Mountains, Poland; Givetian to Frasnian (Middle–Upper Devonian) of Yunnan, Guangxi, and Guizhou provinces, South China and Central Mountains, Afghanistan; Middle–Upper Devonian of Alberta, Canada; lower Frasnian (Upper Devonian) of Moravian Karst, Czech Republic; upper Frasnian (Upper Devonian) of the Dinant Basin, Belgium; Frasnian (Upper Devonian) of Namur Basin, Belgium; Frasnian (Upper Devonian) of Omolon, Russia; Frasnian (Upper Devonian) of Kerman Province, Iran, Canning Basin, Australia; Upper Devonian of northern and central Vietnam and Ulaçhan Mountains, Russia (Mistiaen 1999).

Stachyodes fasciculata Dong in Dong et al., 1989

Fig. 11.

- 1989 *Stachyodes fasciculata* sp. nov.; Dong in Dong et al. 1989: 273, pl. 17: 2a, b.
 1989 *Stachyodes bifurca* (Stearn, 1962); Dong et al. 1989: 275, pl. 16: 1a–c.
 1992 *Stachyodes fasciculata* Dong in Dong et al., 1989; Dong and Liu 1992: 172, pl. 4: 4a, b.
 2020 *Stachyodes radiata* Lecompte, 1952; Huang et al. 2020: 13.

Material.—112 specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with three specimens (NIGP 177060–62) illustrated.

Diagnosis.—Skeleton dendroid, laminar, and bulbous, formed by extremely well differentiated pachystromes and pachysteles. Pachystromes thin, in a thickness of 0.02 mm. Pachysteles thick, radiated from the central zones of the skeleton, interconnected to build the closed networks. Axial canal prominent in the dendroid forms, but branching canals common in laminar and bulbous forms.

Description.—Skeletons are dendroid, laminar, or rarely bulbous, but fragmented or overturned in most specimens (Fig. 11A). The dendroid branches are commonly 3–5 mm in diameter, sporadically up to 15 mm (Fig. 11A). The laminar forms 3–20 mm in thickness (Fig. 11B). The bulbous one shows a height of 40 mm and width of 30 mm (Fig. 11C₁). In longitudinal section, the skeleton consists of

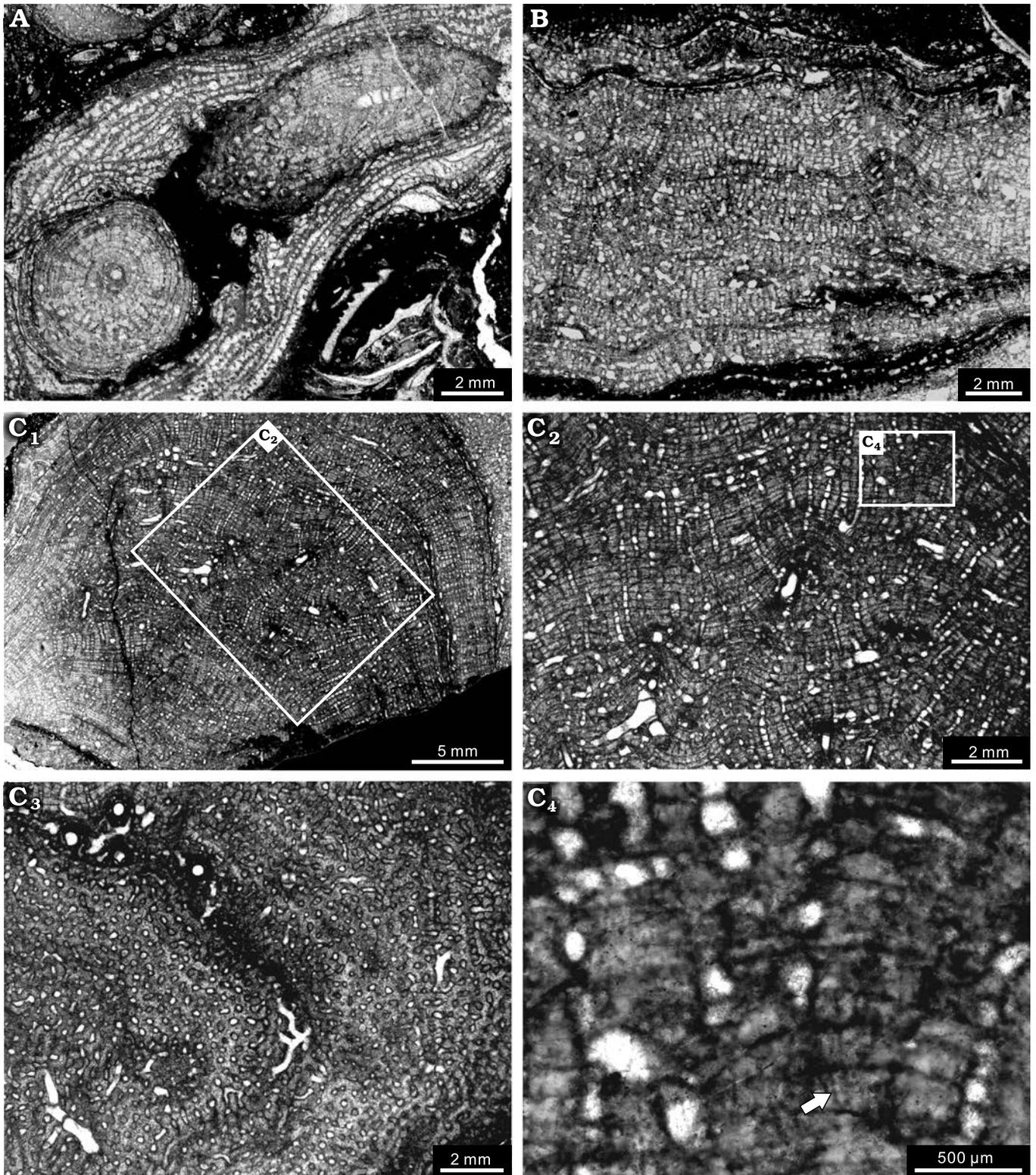


Fig. 11. Stromatoporoid *Stachyodes fasciculata* Dong in Dong et al., 1989, from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. **A.** NIGP 177060; longitudinal section and tangential section of the dendroid form. **B.** NIGP 177061; longitudinal section showing the thick pachyστελες and thin pachyστερομας. **C.** NIGP 177062; C₁, longitudinal section of the bulbous form; C₂, enlargement of C₁, illustrating regular skeleton; C₃, tangential section showing the autotubes and astrorhizal canals; C₄, enlargement of C₂, showing the coarsely striated microstructure (arrow).

conspicuous pachyστερομας and pachyστελες (Fig. 11A, B, C₁). Pachyστερομας are thin, parabolic in the dendroid forms,

relatively closely spaced, spacing 10–13 per 2 mm, 0.02 mm in thickness. Pachyστελες formed a closed network in the

skeleton surface, 0.2 mm thick. The galleries are divided by the thin pachystromes, with a width of 0.2 mm. Axial canal is prominent in the dendroid forms, 0.4–0.5 mm in diameter, infilled with dissepiments, while branching canals are more common in the laminar and bulbous forms (Fig. 11C₁–C₃). In tangential section, axial canal is circular, pachystyles clearly radiate from the axial to peripheral zone and pachystromes distributed as concentric circles in the dendroid forms (Fig. 11A). Pachystyles apparently interconnect to form a closed network in the bulbous forms (Fig. 11C₃). The microstructure is coarsely striated (Fig. 11C₄).

Remarks.—The dendroid forms of the present species were preliminarily assigned to *Stachyodes radiata* Lecompte, 1952, by Huang et al. (2020), but the latter shows more irregular and thicker pachystyles. Further study indicates the species is compatible with both *Stachyodes bifurca* (Stearn, 1962) and *Stachyodes fasciculata* as defined by Dong in Dong et al. (1989), and thus determination is problematic. Although the two samples are different in size, the close similarity of the skeleton morphology justifies the assignment to the same species. However, the relationships between *Syringostroma bifurcum* Stearn, 1962, and *Stachyodes bifurca* (Stearn, 1962) are not fully clear due to the preservation quality of the samples from Canada. Here, we assign these specimens to *Stachyodes fasciculata* Dong in Dong et al., 1989, in relation to the high consistency of the skeleton. The laminar forms of *Stachyodes* are not common in the Devonian, e.g., *Stachyodes australe* (Wray, 1967) and *Stachyodes jonelrayi* Stearn, 1975. The difference between the three species lies in the absence of two layers in the present species. The laminar forms of this species were partly assigned to *Salirella hybridina* Yang and Dong, 1979, by Huang et al. (2020) according to the closed network in the tangential section, but they are totally different in relation to microstructure and laterally extensive thin pachystromes in longitudinal section. Moreover, some of the laminar forms were assigned to *Trupetostroma dushanense* Yang and Dong, 1963, *T. regulamellatum* Yang and Dong, 1963, or *T. sublamellatum* Lecompte, 1952, in terms of thin pachystromes and closed network formed by pachystyles, but *Trupetostroma* Parks, 1936, is fundamentally featured by isolated pillars rather than interconnected pachystyles, thus these species do not belong to *Trupetostroma*.

Stratigraphic and geographic range.—Givetian (Middle Devonian) of Guizhou, Guangxi, and Hunan provinces, South China.

Stachyodes sp.

Fig. 12A.

Material.—Nine specimens from the Givetian (Middle Devonian) Jiwozhai reef, Dushan Formation, Dushan, Guizhou, South China, with one best preserved specimen (NIGP 177063) illustrated.

Description.—Skeletons are laminar forms, with a height up to 4 mm, commonly covering the other stromatoporoids. Latilaminae are exceptionally conspicuous and laterally un-

dulating, 1.5–2 mm in thickness. In longitudinal section, the skeleton consists of two zones (Fig. 12A₁). In the basal zone, the structure is weakly differentiated, with branching astrorhizal canals irregularly distributed, 0.1–0.4 mm in diameter. In the upper zone, short pachystyles are dominant, spacing 10 per 2 mm, 0.1 mm in thickness (Fig. 12A₁). Pachystromes cannot be recognized clearly. Mamelons are not apparent. In tangential section, the skeleton shows tight network formed by the interconnected pachystyles (Fig. 12A₂). Astrorhizal canals conspicuous, common with two branching canals (Fig. 12A₁, A₂). The microstructure is striated (Fig. 12A₃–A₅).

Remarks.—This species apparently differs from the other dendroid species and it corresponds very well to the laminar *Stachyodes* species demonstrated by Wolniewicz (2021: fig. 9G) in the Frasnian of Poland. It differs from the laminar *Stachyodes australe* (Wray, 1967) in terms of the two special different zones and lacking crescent growth zone in the basal layer. There is some similarity with a key species from Alberta, *Stachyodes jonelrayi* Stearn, 1975, that is characterised by possessing a basal layer in the skeleton; this taxon also shows basal layers in the lower portions of successive individual latilaminae after growth interruptions. Nevertheless we are not confident that the species from Jiwozhai reef is necessarily the same as *Stachyodes jonelrayi* and prefer to leave it in open nomenclature in this study. Further work may be able to finalise the species-level taxon.

Discussion

Reef-building implications of stromatoporoids.—Laminar stromatoporoid fossils are common in shallow marine carbonates as well as reef environments (Kershaw 2015) and presumably contributed to stabilize soft, muddy substrates (Jakubowicz et al. 2019). The interactions between stromatoporoids and their substrates can be divided into two patterns: (i) ambitopic growth pattern that expanded on unconsolidated substrates after initial settlement, and (ii) encrusting growth on hard substrates during their entire life without lateral expansion (Webby and Kershaw 2015: fig. 305). A few Devonian stromatoporoids adopted encrusting habits, such as *Clathrocoilona spissa* (Cook 1999; Wolniewicz 2021), while many Devonian stromatoporoids show ambitopic lifestyles through most of their life history (Webby and Kershaw 2015).

In the Jiwozhai reef, *Clathrocoilona spissa*, with thickness 0.5–5.0 mm, is the most abundant laminar stromatoporoid. Its initial growth stages commonly encrusted on hard surfaces of high-relief organisms forming a spherical skeleton. Only a few examples show ambitopic habits. It seems that *Clathrocoilona spissa* rarely sustained itself to grow large or expand laterally, and could hardly further stabilize the substrates. In contrast, *Gerronostromaria grossum* generally presents thick and wide skeletons (Fig. 3), possibly reflecting vertically and laterally growth abilities,

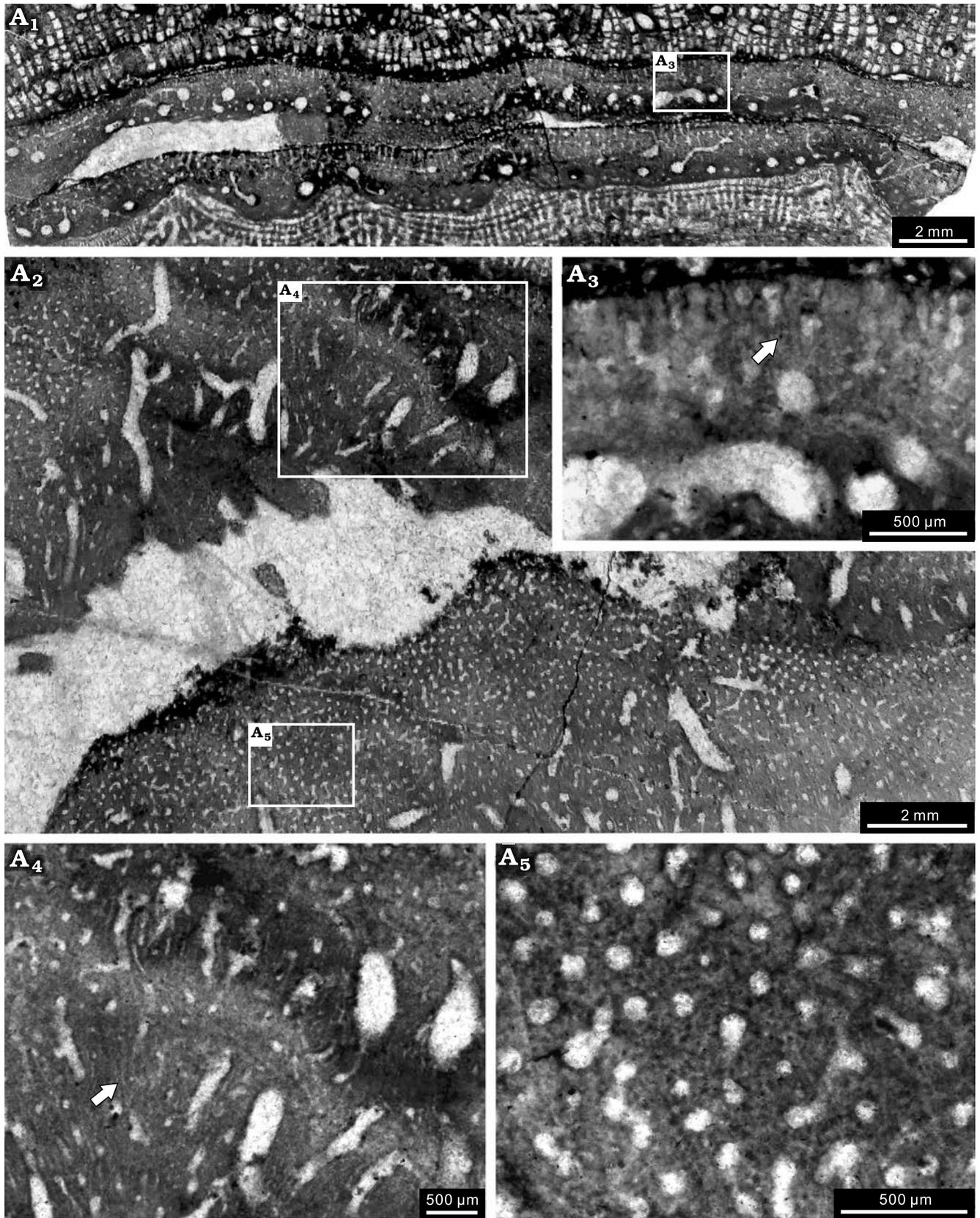


Fig. 12. Stromatoporoid *Stachyodes* sp. NIGP 177063, from the Jiwozhai reef, Jiwozhai Member, Dushan Formation, Givetian, Middle Devonian; Dushan, Guizhou, South China. A₁, longitudinal section; A₂, tangential section, note the autotubes and conspicuous astrorhizal canals; A₃, enlargement of A₁, note the coarsely striated microstructure (arrow); A₄, enlargement of the upper middle part of A₂, note the probably striated microstructure (arrow); A₅, enlargement of the lower left part of A₂, note the black dots in the tangential section.

which were conducive to preventing sediment winnowing by episodic water currents, thus further stabilizing substrates. *Pseudotrumpetostroma porosum*, *Salairella buecheliensis*, and *Synthetostroma actinostromoides* are quantitatively less than the other stromatoporoids, but their laterally extensive and vertically thick skeletons account for their abilities in covering sediments (Fig. 3). Dendroid but fragmented *Stachyodes costulata* and *Stachyodes fasciculata* presumably form hard substrates for the settlement of laminar taxa.

Individual thin laminar stromatoporoids (e.g., *Clathrocoilona spissa*) are interpreted to have been extremely vulnerable under episodic or sudden environmental pressures, and developed complex overgrowth skeletons, attached by other stromatoporoids, tabulate corals, chaetetids, bryozoans and calcified cyanobacteria (Figs. 6B₁, 10A₁, 12A₁). Such features are common in the Jiwozhai reef facies (Huang et al. 2020); they are significant for stabilization of the underlying substrates (dendroid stromatoporoids, massive and branching tabulate corals, solitary rugose corals, brachiopods, and micrites) and further development of the reef framework.

Comparisons with other laminar stromatoporoid communities.—Laminar stromatoporoid-dominated patch reefs, biostromes or mud mounds are common in shallow marine environments from the Eifelian to Frasnian in Europe, North America, North Africa, and Australia (Cook 1999; Mabilbe and Boulvain 2007; Da Silva et al. 2011a, b; MacNeil and Jones 2016), especially in the initial stage of reef formation (Cook 1995; Boulvain et al. 2009; Jakubowicz et al. 2019).

A Givetian barrier reef tract, which extended from Glageon of North France to Hotton of South Belgium, was initiated by laminar stromatoporoids, solitary and fasciculate rugose corals, branching and massive tabulate corals over the crinoidal mats (Boulvain et al. 2009). Although the systematic palaeontology and diversity of the stromatoporoids was studied by Lecompte (1951, 1952) and Hubert (2008), detailed palaeoecological studies of the laminar stromatoporoids and their reef-building habits are not well-developed. According to Hubert (2008), laminar stromatoporoids in the reef facies of Trois-Fontaines Formation in Glageon were identified as *Clathrocoilona spissa*, *Stictostroma saginatum*, *Stictostroma* sp. 2, *Hermaporella* sp. 4 and *Stromatoporella granulata*. This stromatoporoid assemblage is similar to the Jiwozhai reef with common occurrence of *Clathrocoilona spissa* and *Stictostroma saginatum*, but the dominant stromatoporoid taxa are unclear.

A series of Givetian biostromes, reefs and reef complexes have been reported from the Fanning River Group, north Queensland, Australia (Cook 1995, 1999). Reefs in the Fletcherview–Burdekin Downs area were constructed mainly by the *Gerronostromaria hendersoni*–*Hermapostroma maculatum* stromatoporoid community (Cook 1999). This community is characterized by *Gerronostromaria hendersoni*, *Hermapostroma maculatum* (constructors), *Stachyodes costulata* (bafflers), with minor role of *Clathrocoilona abeona* (encrusters), *Salairella buecheliensis* and some other stro-

matoporoids and corals. The common occurrence of coverstone in patch reefs is presumed to have resulted from fast growth expansion of laminar stromatoporoids upon muddy substrate for support (Cook 1999). A few stromatoporoids show extremely thin forms in the lagoonal pavements, in width of 20 to 80 cm and below a height of 10 cm (Cook 1999: fig. 3b). Also compound skeletons, formed by stromatoporoids and other organisms, are notable in the nearshore, fringing biostromes, probably indicating environmental stress under periodical depositional events or salinity variations (Cook 1999). The Givetian reef-building stromatoporoids in eastern Australia closely resemble the Jiwozhai reef stromatoporoids in terms of growth forms (thin laminar dominated), taxonomic compositions (*Gerronostromaria*, *Stachyodes*, *Salairella*) and lateral growth habit for the formation of reefal coverstone.

Laminar stromatoporoid biostromes also occur in Frasnian limestone of southern Belgium (e.g., Da Silva et al. 2011b; Poty and Chevalier 2007). The middle Frasnian laminar stromatoporoid biostromes mainly in the outer intermediate zone of the Tailfer and Villers sections are dominated by species of *Stachyodes*, *Stictostroma*, with few encrusting *Clathrocoilona*. Species of *Stictostroma* occur mostly in carbonate mudstone and *Stachyodes australe* (Wray, 1967) commonly grew on carbonate mud substrates, shells or encrusted by other stromatoporoids (Da Silva et al. 2011b). Moreover, three middle Frasnian carbonate mud mounds with laminar stromatoporoids were also described in La Boverie–Rochefort quarry of southern Belgium (Da Silva et al. 2011a). Laminar stromatoporoids were documented in the base of core mound, mound flank and adjacent level-bottom environments, and were featured by species of *Stictostroma*, *Stachyodes* and *Salairella*, similar to the stromatoporoid fauna in the Tailfer and Villers sections. Species of *Stictostroma* and *Salairella* mostly grew on mud and *Stachyodes australe* (Wray, 1967) also occurred on mud, shells or encrusted other stromatoporoids (Da Silva et al. 2011a). The laminar stromatoporoid fauna in the Frasnian of Belgium is slightly different from the Givetian Jiwozhai reef due to the special occurrence of *Stachyodes australe* (Wray, 1967) and differences in the most abundant stromatoporoid taxa; nevertheless their ecological implications for the stabilization of substrate are similar.

The middle Frasnian Alexandra Reef System, situated in the Northwest Territories, Canada, displays well-preserved stromatoporoids in different reef-related facies (MacNeil and Jones 2016). A large number of in situ laminar and anastomosing laminar stromatoporoids are concentrated in the reef front, including the species of *Stachyodes*, *Actinostroma* and some other stromatoporoids *Stromatopora*, *Hermapostroma*, and *Clathrocoilona*. These laminar stromatoporoids were interpreted to live in a water depth of 20–25 m, and generally associated with sediment, or encrusted by microbial organisms (MacNeil and Jones 2016). Compared with the stromatoporoid accumulation in relatively deeper setting of the Alexandra Reef System, laminar stromatoporoid framestones

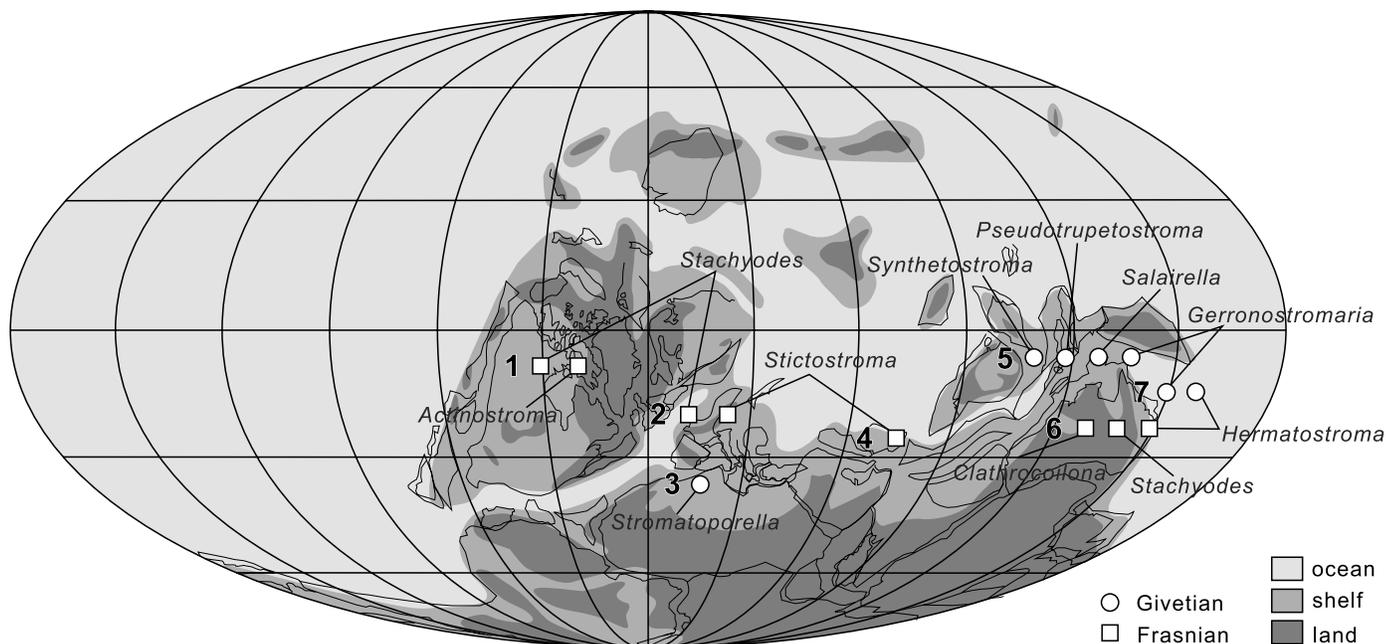


Fig. 13. Palaeogeographic distribution of the reef-building laminar stromatoporoid genera during the Givetian and Frasnian (Middle–Late Devonian). Localities: 1, Northwest Territories, Canada (MacNeil and Jones 2016); 2, Dinant Basin, southern Belgium (Da Silva et al. 2011a, b); 3, Anti-Atlas, Morocco (Jakubowicz et al. 2019); 4, Esfahan, central Iran (Mistiaen and Gholamalian 2000); 5, Guizhou, South China; 6, Canning Basin, western Australia (Cockbain 1984); 7, Queensland, eastern Australia (Cook 1999). Palaeogeographic map is based on Golonka (2002).

constructed by species of *Stromatopora* are also common in the shallow belt. Species of *Stromatopora* show intensive lateral and vertical growth habits to encrust the underlying stromatoporoids and further contributed to the thick framestone (MacNeil and Jones 2016). The Frasnian large reef complex in Canada shows distinctive ecological difference of the stromatoporoid assemblages, which are manifested by the species of thin laminar *Stachyodes* and *Actinostroma* in the deeper water coverstone and thick laminar *Stromatopora* in the shallow water framestone. Compared with the large reef complex, the small Givetian Jiwozhai reef was particularly characterized by the thin laminar *Gerronostromaria grossum* Dong, 1974, in the stromatoporoid fauna of this particular palaeoenvironment.

Therefore, the Jiwozhai stromatoporoid reef shows similarities to the Givetian and Frasnian reefs in South Belgium, North America, and East Australia in terms of stromatoporoid assemblages and depositional environment (Cook 1995, 1999; Boulvain et al. 2009; Da Silva et al. 2011a, b; MacNeil and Jones 2016). These stromatoporoid faunas are mainly characterized by species of *Stictostroma*, *Clathrocoelona*, *Salairrella*, laminar *Stachyodes*, and dendroid *Stachyodes*, but their most abundant taxa possibly vary between different time periods and various geographical positions (Fig. 13) (Cockbain 1984; Cook 1999; Mistiaen and Gholamalian 2000; Da Silva et al. 2011a, b; MacNeil and Jones 2016; Jakubowicz et al. 2019). In this study, *Gerronostromaria grossum* chiefly accounts for the formation of the Jiwozhai reef, noting that *Gerronostromaria hendersoni*–*Hermatostroma maculatum* dominated the laminar communities of the Givetian reefs in East Australia. However, laminar species of *Stachyodes*

characterized the laminar communities of the Frasnian reefs and mud mounds in North America and South Belgium. The laminar species of *Stictostroma* and *Salairrella*, which mostly grew on muddy substrate in the mid-Frasnian platform of South Belgium, also show high abundance in the development of biostromes. These thin laminar stromatoporoids generally show strong abilities stabilizing the soft, muddy substrate. Therefore, although *Clathrocoelona spissa* in the Jiwozhai reef commonly encrusted on high-relief organisms, it does not present the same positive effect on the construction of the reef as the laterally extensive *Gerronostromaria grossum*.

Overall, stromatoporoids in the Jiwozhai reef tend to show paleoecological preferences in terms of growth form indicating different growth strategies of stromatoporoid taxa, which corresponds with other previous studies (e.g., May 1993; Salerno 2008; Da Silva et al. 2011a, b; Wolniewicz 2021). Although the stromatoporoid taxa vary depending on the palaeogeographic distribution through the continents and time, it should be noted that low profile (i.e., laminar) stromatoporoids likely acted as important sediment stabilizers, thus triggering expansion of the carbonate factory (Da Silva et al. 2011b). Similarly, extensive development of Middle Devonian reefs and carbonate platforms throughout South China, which were favourable environments for benthic organisms including stromatoporoids, was presumably pioneered by growth variability of diverse stromatoporoid taxa. A combination of taxonomic investigation and palaeoenvironmental interpretation, as performed in this study, allow developments in interpretations of stromatoporoid biology and aids understanding of carbonate platform development in South China.

Conclusions

- Revision of the stromatoporoids from Jiwozhai reef, Dushan, Guizhou, South China documents 11 species belonging to nine genera. The stromatoporoid assemblage is characterized by diverse syringostromatids, abundant stromatoporellids and clathrodictyids, and a small number of other stromatoporoids.
- The stromatoporoid fauna was dominated by laminar stromatoporoids (*Clathrocoilona spissa*, *Gerronostromaria grossum*, *Stictostroma saginatum*, *Synthetostroma actinostromoides*, *Pseudotruperostroma porosum*, *Salairella buecheliensis*, *Habrostroma laminosum*, *Parallelopora* sp., *Stachyodes fasciculata* and *Stachyodes* sp.), which pioneered the formation of the reef coverstone by stabilizing large bioclasts and micrite sediment. Dendroid stromatoporoids (*Stachyodes costulata* and *Stachyodes fasciculata*) are also common, but generally present fragmented skeletons mixed in the matrix. Bulbous forms (*Stachyodes fasciculata*) are rare. The variation of stromatoporoid growth form indicates different growth strategies of stromatoporoid taxa.
- The morphology, substrate, size and minimal growth interruption features indicate that *Gerronostromaria grossum* is the main reef-building stromatoporoid in relation to its absolute predominance of growth advantage in stabilizing sediments. By contrast, *Clathrocoilona spissa* contributed less to the formation of the Jiwozhai reef. Advantages of these laminar stromatoporoids are manifested by sediment stability that presumably pioneered development of Middle Devonian carbonate platform in South China.
- Devonian laminar stromatoporoid communities are widespread in Europe, North America, North Africa, Australia, and South China. The laminar stromatoporoid faunas generally show similarities in relation to stromatoporoid composition, but the dominating species vary among different localities and periods.

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