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Earliest known spatial competition between stromatoporoids: evidence from the Upper Ordovician Xiazhen Formation of South China

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Abstract.—The earliest known interpreted spatial competition between two species of stromatoporoids, *Clathrodictyon* cf. *C. mammillatum* (Schmidt, 1858) and *Labechia* sp. is found in the Upper Ordovician Xiazhen Formation at Zhuzhai, South China. The interaction between these taxa was initiated by settlement of *Labechia* sp. on the surface of *C.* cf. *C. mammillatum*. Distortions of the intraskeletal elements of stromatoporoids represented by abnormally large, wide cysts and thick cyst plates in *Labechia* sp. are observed, along with zigzag crumpled distorted laminae and antagonistic behavior of the skeleton in *C.* cf. *C. mammillatum*, indicating syn-vivo interactions. The growth of *Labechia* sp. was terminated by the overgrowth of *C.* cf. *C. mammillatum*, possibly reflecting the ecological superiority of *C.* cf. *C. mammillatum* over *Labechia* sp. The observations are interpreted as competitive interaction between stromatoporoids and was most likely facultative, thus most likely occurring by chance, but the interaction allows assessment of different growth behaviors of the stromatoporoid species. Analysis of the interaction provides evidence to improve understanding of the paleoecology and growth behaviors of early stromatoporoids.

Introduction

Paleozoic stromatoporoids were one of the most abundant organisms in reef complexes and associated facies from the Ordovician to the Late Devonian (Kershaw, 2015; Stearn, 2015;

Kershaw et al., 2018). They lived in warm, shallow, tropical to subtropical marine environments, exhibiting a variety of growth forms (Stock et al., 2015; Webby et al., 2015) and are commonly found associated with other organisms, including many cases of intergrowth with other organisms such as tabulate and rugose corals, brachiopods, bryozoans and worm tubes in reef environments (e.g., Kershaw, 1987; Young and Noble, 1989; Zhen and West, 1997; Lin and Webby, 1998; Nestor et al., 2010; Da Silva et al., 2011; Vinn and Wilson, 2012; Vinn and Mõtus, 2014; Stearn, 2015; Lee et al., 2016; Kershaw et al., 2018).

Many associations between stromatoporoids and other organisms may be interpreted as spatial competition with, or predation by, the associated other organisms; some cases have been considered to be symbiotic interactions based on modification of the adjacent skeletal structure of the host stromatoporoid (Kershaw et al., 2018). The majority of intergrowth associations are known from Silurian and Devonian strata (e.g., Mori, 1970; Kershaw, 1987; Young and Noble, 1989; Nestor et al., 2010; Da Silva et al., 2011; Vinn and Wilson, 2012; Vinn and Mõtus, 2014; Vinn et al., 2015; Vinn, 2016a, b), with a few recorded from Ordovician rocks (e.g., Lin and Webby, 1998; Lee et al., 2016).

These symbiotic interactions resulting from the associated organisms caused interruption of stromatoporoid growth (Webby and Kershaw, 2015; Kershaw et al., 2018), which is important for understanding growth control of stromatoporoids (Kershaw et al., 2018). However, interactions between different stromatoporoids have rarely been described from the fossil record although intergrowth between the skeletons of two or more stromatoporoids frequently occurs in reefal environments (Stearn, 2015). Prosh and Stearn (1996) briefly mentioned the interaction between two Devonian species of stromatoporoids and interpreted their relationship as spatial competition. However, more detailed investigation of the interactions between two or more stromatoporoids is required to fully verify the nature of the relationship.

In this study, we document and interpret the inter-genera interactions between two species of Late Ordovician stromatoporoid, *Clathrodictyon* Nicholson and Murie, 1878 and *Labechia* Milne-Edwads and Haime, 1851 from the Upper Ordovician Xiazhen Formation at Zhuzhai, Jiangxi Province, China. The aim of study is to assess the nature of the earliest known spatial interaction between stromatoporoids, thus providing new information to understand the paleoecology and growth behaviors of early stromatoporoids.

Geological setting

The Jiangshan–Changshan–Yushan (JCY) triangle region of South China is located in the border area between Jiangxi and Zhejiang provinces (Fig. 1.1). The JCY triangle is a representative region for studying the Ordovician System in South China (Zhang et al., 2007). The Ordovician carbonate successions in the region were deposited on the Zhe-Gan Platform in the northern part of the Cathaysian landmass (Chen et al., 1987; Rong and Chen, 1987; Wu, 2003; Zhang et al., 2007; Zhan and Jin, 2007; Rong et al., 2010). The Upper Ordovician Xiazhen Formation at Zhuzhai, Yushan County is one of the best-exposed Ordovician carbonate successions in the region and is considered to be correlated to the Sanqushan and Changwu formations in Jiangshan and Changshan counties (Zhang et al., 2007). The stratigraphy of the 190 m thick formation has been revised on the basis of detailed lithological and paleontological data (Lee et al., 2012).

The depositional environments of the Xiazhen Formation are interpreted as shallow-marine deposits of an epicontinental sea north of the Cathaysian landmass of South China (Li et al., 2004; Lee et al., 2012). Based on fossils and correlation with the Sanqushan and Changwu Formation, the age of the Xiazhen Formation is estimated to be middle to late Katian (Zhang et al., 2007). In addition, the finding of the graptolite *Anticostia uniformis* in the upper shale member of the formation (Chen et al., 2016) indicates that the upper part of the Xiazhen Formation at Zhuzhai is within the range of the *Dicellograptus complanatus* (middle Katian) to *Normalograptus persculptus* (late Hirnantian) graptolite biozones (Chen et al., 2016).

Materials and methods

More than 400 stromatoporoid specimens were collected and examined by thin sections, but only one specimen shows clear interactions between two stromatoporoids. This studied rock sample is from the uppermost interval of the Xiazhen Formation, above the upper shale member (arrows in Fig. 1.2, 1.3). The interval, which is characterized by limestone–shale couplets in mudstone to packstone (Fig. 1.4), contains abundant patch reefs that are composed of mainly dendroid clathrodictyids in a variety of orientations and the tabulate corals *Agetolites*, *Catenipora*, *Heliolites* and *Plasmoporella*.

For a better observation of the stromatoporoid growth patterns, 20 serial sections of the specimens were prepared at intervals ranging from 1.0 to 1.2 mm. The taxonomic assignments of stromatoporoids follow Webby (2015b) and Nestor (2015).

Repository and institutional abbreviation.—All serial thin sections, used in this study are deposited in Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China as following specimen number; NIGP 169634-1–20.

Results

Intergrown stromatoporoid species.—Stromatoporoids are common sessile organisms in the Xiazhen Formation. Three genera of clathrodictyids and eight genera of labechiids are recorded from the formation (Jeon et al., 2018). The stromatoporoid assemblage is characterized by the dominance by *Clathrodictyon*, which has the longest stratigraphic range throughout the formation of the diverse stromatoporoid fauna (Jeon et al., 2018). The two stromatoporoid species involved in the interaction are identified as *Clathrodictyon* cf. *C. mammillatum* (Schmidt, 1858) and *Labechia* sp.

Clathrodictyon is characterized by its continuous laminae, which are commonly irregularly wrinkled, with short funnel-shaped, rod-like or oblique pillars (Nestor, 2015). The *Clathrodictyon* species involved in the syn-vivo interaction is identified as *Clathrodictyon* cf. *C. mammillatum* (Schmidt, 1858; Fig. 2.1, 2.2). Based on longitudinal sections (Fig. 2.2), its laminae are well developed and continuous, showing slight undulations between rare short rod-like pillars. Lamina thickness ranges from 0.10 to 0.32 mm (mean = 0.19 mm, n = 50), and there are commonly 9 to 12 laminae in a vertical thickness of 2 mm (Fig. 2.2). Mamelon columns are common, although partially dissolved due to diagenesis. Pillars are short, rod-like and restricted to interlaminar spaces, forming irregular galleries. This species is also reported from the Sanjushan Formation at Yushan (Lin and Webby, 1988).

The other stromatoporoid species is characterized by well-developed upwardly convex cyst plates and pillars, which are diagnostic of labechiids (Webby, 2015b). Most cyst plates have an irregular outline in transverse view (Fig. 2.3), and some are moderately to highly convex in vertical section (Fig. 2.4). In transverse view, pillars are ellipsoidal to circular in shape, and most are preserved hollow and flanged, locally solid, with a thickness of 0.15–0.36 mm (mean = 0.24 mm, n = 45; Fig. 2.3). In longitudinal section, stout, round pillars are developed intermittently (Fig. 2.4). In this study the taxon is reasonably identified as *Labechia* sp. from the direct evidence of the morphological features, including convex cyst plates with round and stout pillars (Fig. 2.3, 2.4), which are characteristic of *Labechia* rather than *Labechiella*, and different from any other labechiid genera.

Ecological interactions between stromatoporoids.—In the Xiazhen Formation, *Clathrodictyon* and *Labechia* co-occur in four of the total 18 stromatoporoid-bearing intervals (Jeon et al., 2018), but their intergrowth is recognized only from the uppermost interval of the formation, which is interpreted as a patch reef environment. A single specimen (NIGP 169634) shows that the beginning of the intergrowth started with the settlement of *Labechia* sp. on the growth surface of *Clathrodictyon* cf. *C. mammillatum* (Figs. 2.4, 3, 4). Ecological interactions can be judged from the thicker-than-normal growth of the cyst plates of *Labechia* sp. (Figs. 2.4, 3.1–3.3, 4.6–4.8) and the highly distorted character of the interaction between the two stromatoporoids (Figs. 2.4, 3, 4). Subsequently, larger-sized, irregularly shaped cysts, which are indicative of rapid growth after initial settlement, appeared in the basal portion of *Labechia* sp. Such cyst malformations (abnormally thick cyst plates and large, irregular cysts) are commonly observed not only in the initial portion of the skeleton, but also in subsequent growth stages (Figs. 2.4, 3, 4).

Distorted skeletal structure in *Clathrodictyon* cf. *C. mammillatum* is commonly observed where its skeleton is in contact with *Labechia* sp. and also possibly by sediment interruptions (Figs. 2.4, 3, 4). The distortion in *C.* cf. *C. mammillatum* appears to be weaker than that in *Labechia* sp. The abnormal development of *C.* cf. *C. mammillatum* is manifest as zigzag crumpled distorted structure (Figs. 2.4, 3.3). It is necessary to note that even within one stromatoporoid specimen, the structure can vary significantly in relation to disturbing influences during its growth. In some instances, the laminae of *C.* cf. *C. mammillatum* occupy the cyst interspaces of *Labechia* sp., and its interskeletal structure exhibits distorted growth, which is considered to represent antagonistic behavior (aggressive and passive reactions; Figs. 2.4, 3.2, 4.7–4.8).

The occurrence of abnormal growth in both stromatoporoids indicates that their intergrowth occurred while both organisms were alive. Finally, their intergrowth ceased because *Clathrodictyon* cf. *C. mammillatum* overgrew *Labechia* sp. (Figs. 3, 4). It is apparent that the *C.* cf. *C. mammillatum* individual lived longer than the *Labechia* sp. individual and may have ultimately had a faster growth rate.

In addition to the interaction with *Labechia* sp., *Clathrodictyon* cf. *C. mammillatum* served as a host for various endobionts including the tabulate coral *Bajgolia* and the solitary rugose corals *Tryplasma* and *Streptelasma* (Fig. 5). However, there was no distortion of skeletal elements in *C.* cf. *C. mammillatum*, suggesting that the growth of the stromatoporoid was not greatly affected by the coral intergrowth, or that the stromatoporoid grew around pre-existing coral skeletons.

Discussion

Earliest known stromatoporoid spatial competition.—Intergrowth associations have previously been interpreted as an adaptation to seek shelter from adverse environmental conditions (e.g., competition, predation or depositional environments; Webby and Kershaw, 2015; Kershaw et al., 2018) or enhanced substrate stability (Vinn and Mõtus, 2014; Lee et al., 2016; Vinn et al., 2017). It has been proposed that stromatoporoids with well-developed laminae probably provided more favourable substrates for the settlement of tabulate corals than other stromatoporoids (Mori, 1970). This phenomenon applies particularly to Ordovician stromatoporoids, in which intergrowth commonly occurs between corals and stromatoporoids possessing well-developed laminae, such as the clathrodictyids (e.g., Lin and Webby, 1988; Lee et al., 2016). In this study, *Clathrodictyon* cf. *C. mammillatum* which possesses well-developed mamelon columns possibly provided a suitable substrate for the growth of *Labechia* sp. The serial sections demonstrate a competitive interaction between *Clathrodictyon* cf. *C. mammillatum* and *Labechia* sp, and that both stromatoporoids were significantly affected, as judged by the distorted skeletal structures. We speculate that the settlement of *Labechia* sp. caused a reduction in the feeding surface of *C.* cf. *C. mammillatum*. Therefore, the distortion (Figs. 2.4, 3, 4) and consequent change in growth habit produced distorted structures indicative of soft tissue reaction of *C.* cf. *C. mammillatum* (Fig. 6.1–6.3). In contrast, abundant apparent endobionts *Bajgolia* are associated with *Clathrodictyon*, especially around mamelon columns, but no distortion of skeletal structures is observed in *C.* cf. *C. mammillatum* in these cases (Fig. 5.3, 5.4). In addition, densely spaced *Bajgolia* are commonly observed to occupy a relatively large area of the centre of the mamelon columns of clathrodictyids (Lee et al., 2016, figs. 2h, 3c, 6). It is obvious that interaction with *Bajgolia* was not critical to the feeding of *C.* cf. *C. mammillatum*, whereas the settlement of *Labechia* sp. significantly affected the skeleton of *C.* cf. *C. mammillatum*. In the same horizon, not only *Bajgolia* also other tabulate corals including *Heliolites* and solitary rugose corals *Streptelasma* and *Tryplasma* occur. The solitary rugose corals have been reported and interpreted as endobionts in species of *Clathrodictyon* based on longitudinal sections (Lee et al., 2016, fig. 2; Fig. 5). It is noteworthy that none of the *Clathrodictyon* skeletons exhibit malformation from their coral endobionts. Therefore, this difference suggests that the modifications of *Clathrodictyon* cf. *C. mammillatum* and *Labechia* sp. are due to spatial competition between each other, rather than being an example of commensalism or parasitism, as reported from the endobiotic corals and other organisms (e.g., Lee et al., 2016; Vinn et al., 2015, 2017; Zapalski and Hubert, 2010). This is the earliest known interpreted spatial competition between stromatoporoids, occurring in the uppermost interval of Xiazhen Formation at Zhuzhai, South China, within the range of the

Dicellograptus complanatus (middle Katian) to *Normalograptus persculptus* (late Hirnantian) graptolite biozones (Chen et al., 2016).

Of the two stromatoporoids involved in the intergrowth, the skeleton of *Labechia* sp. possesses irregularly spaced, large cysts different from normal forms, whereas the skeleton of *C.* cf. *C. mammillatum* exhibits rather regularly spaced laminae, similar to the other skeletons of the species from this interval except for showing crumpled, distorted skeletal structure. This difference is possibly related to the different growth rates of the two species, as *C.* cf. *C. mammillatum* is likely to have grown faster than *Labechia* sp.

Very few previous studies concern the intergrowth between different stromatoporoids. The association between *Gerronostroma septentrionalis* Prosh and Stearn, 1996 and *Stromatopora polaris* (Stearn, 1983) was reported from Lower Devonian (Emsian) of Arctic Canada and their relationship is described as competitive (Prosh and Stearn, 1996). Based on the illustration, it is noteworthy that none of the distorted skeletal structures occurred by the interfingering contact (Prosh and Stearn, 1996, pl. 4, fig. 4), which is different from the present study. As little is known about the intergrowth between different stromatoporoids, further studies on other formations are necessary, in order to understand the growth behaviors of stromatoporoids.

Paleoecological implications.—Both *Clathrodictyon* and *Labechia* are widely distributed in Late Ordovician sedimentary sequences (Nestor and Webby, 2013; Stock et al., 2015). The labechiids appeared in the late Early Ordovician (Li et al., 2017) and initially diversified in the late Middle Ordovician (Webby, 2004; Nestor and Webby, 2013; Stock et al., 2015; Webby, 2015a), which was earlier than the clathrodictyids. The clathrodictyids, however, spread rapidly and achieved a circum-equatorial distribution in the Late Ordovician (Nestor and Webby, 2013). Later, they became a major cosmopolitan group after a rapid radiation in the Silurian, which was crucial to the evolution of Paleozoic stromatoporoids (Nestor, 1997).

A recent study on the intergrowth between stromatoporoids and the tabulate coral *Bajgolia* revealed that only two clathrodictyid genera (*Clathrodictyon* and *Ecclimadictyon*) contained various endobionts such as tetradiids, tabulate corals and solitary rugose corals (Lee et al., 2016). In addition, *Clathrodictyon* is the most abundant stromatoporoid genus in the Xiazhen Formation, occupying a long stratigraphic distribution and a wide range of lithofacies (Jeon et al., 2018). The long stratigraphic range of *Clathrodictyon* in the formation is a potential indication that clathrodictyids, especially *Clathrodictyon*, had broader ecological plasticity and more flexible growth strategies than did labechiids (Jeon et al., 2018). Correspondingly, the spatial competition between *Clathrodictyon* cf. *C. mammillatum* and *Labechia* sp. provides direct evidence that *Clathrodictyon* could outcompete *Labechia* as a result of its flexible growth behaviors (Fig. 6).

Compared with the coral-stromatoporoid association, the interaction between *Clathrodictyon* and *Labechia* occurs more rarely in the formation. Their relationship seems to be facultative rather than obligatory, which is similar to the coral-stromatoporoid and tabulate-rugose corals associations (Lee et al., 2016; Vinn et al., 2017). Due to lack of clear evidence, the nature of the relationship between various endobionts and the hosting stromatoporoids is difficult to explore, as very often there are no skeletal distortions among the organisms. The intergrowth between corals and stromatoporoids was commonly interpreted to be commensalism, as their growth seems unaffected (e.g., Mori, 1970; Kershaw, 1987; Vinn, 2016a), whereras tubeworm endobionts, including *Cornulites*, *Streptindytes*, and *Torquaysalpinx* seem to be more complex to evaluate (Vinn, 2016b). Based on the downbending-curved laminae of stromatoporoids in the vicinity of the symbiont tube, the *Torquaysalpinx*-stromatoporoid relationship is interpreted to be parasitism (Zapalski and Hubert, 2011). Downwardly or upwardly curved laminae near the contact with the endobionts has been considered as a criterion to judge whether it is positive or negative to the hosting stromatoporoids (Kershaw, 1987, 2013; Young and Noble, 1989; Lee et al., 2016). This study shows that evaluation of distorted structures in the intergrown organisms are also important for analysing their ecological relationship. In addition, the fact that spatial competition between different stromatoporoids in the reefs appeared as early as in the Late Ordovician suggests that spatial competition, which has been studied extensively in modern marine communities, deserves greater emphasis in the understanding of Paleozoic reef ecosystems.

Conclusions

We report the earliest known spatial competition between two species of stromatoporoids, *Clathrodictyon* cf. *C. mammillatum* and *Labechia* sp., from the Upper Ordovician Xiazhen Formation at Zhuzhai, South China. *Labechia* sp. exhibits large-sized and irregularly shaped cysts, indicative of rapid growth after initial settlement on the surface of *C.* cf. *C. mammillatum*. Alteration of the growth pattern of *C.* cf. *C. mammillatum* to produce crumpled distorted skeletal structure occurs during the interaction with *Labechia* sp. Intergrowth between *C.* cf. *C. mammillatum* and tabulate and solitary rugose corals suggests that corals did not significantly affect the growth of stromatoporoids and thus did not cause distortion of the stromatoporoid skeleton. Obviously distorted skeletal elements are present at the physical contact between the different stromatoporoids, indicating spatial competition between the organisms. This study of competitive interaction between stromatoporoids increases our understanding of the paleoecology and growth behaviors of early stromatoporoids. The spatial competition between *Clathrodictyon* cf. *C. mammillatum* and

Labechia sp. provides direct evidence that species of *Clathrodictyon* have more flexible growth behaviours than those of *Labechia*.

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References

Chen, X., Rong, J.Y., Qiu, J.Y., Han, N.R., Li, L.Z., and Li, S. J., 1987, Preliminary stratigraphy, sedimentologic and environmental investigation of Zhuzhai section: Journal of Stratigraphy, v. 11, p. 23–34. [In Chinese with English abstract]

Chen, Z.Y., Kim, M.H., Choh, S.J., Lee, D.-J., and Chen, X., 2016, Discovery of *Anticostia uniformis* from the Xiazhen Formation at Zhuzhai, South China and its stratigraphic implication: Palaeoworld, v. 25, p. 356–361.

Da Silva, A.-C., Kershaw, S., and Boulvain, F., 2011, Stromatoporoid palaeoecology in the Frasnian (Upper Devonian) Belgian platform, and its applications in interpretation of carbonate platform of carbonate platform environments: Palaeontology, v. 54, p. 883–905.

Jeon, J., Liang, K., Park J., Choh, S.-J., and Lee, D.-J., 2018, Late Ordovician stromatoporoids from the Xiazhen Formation of South China: paleoecological and paleogeographical implications: Geological Journal, published online 14 December 2018, p. 1–13. https://doi.org/10.1002/gj.3401

Kershaw, S., 1987, Stromatoporoid–coral intergrowths in a Silurian biostrome: Lethaia, v. 20, p. 371–382.

Kershaw, S., 2015, Paleoecology of the Paleozoic Stromatoporoidea, *in* Selden, P.A., ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 631–651.

Kershaw, S., Munnecke, A., and Jarochowska, E., 2018, Understanding Palaeozoic stromatoporoid growth: Earth-Science Reviews, v. 187, p. 53–76.

Lee, D.-C., Park, J., Woo, J., Kwon, Y.K., Lee, J.-G., Guan, L., Sun, N., Lee, S.-B., Liang K., Liu, L., Rhee, C.-W., Choh, S.-J., Kim, B.-S., and Lee, D.-J., 2012, Revised stratigraphy of the Xiazhen Formation (Upper Ordovician) at Zhuzhai, South China, based on palaeontological and lithological data: Alcheringa, v. 36, p. 387–404.

Lee, M., Elias, R.J., Choh, S.-J., and Lee, D.-J., 2016, Insight from early coral–stromatoporoid intergrowth, Late Ordovician of China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 463, p. 192–204.

Li, Q., Li, Y., and Kiessling, W., 2017, The oldest labechiid stromatoporoids from intraskeletal crypts in lithistid sponge–*Calathium* reefs: Lethaia, v. 50, p. 140–148.

Li, Y., Kershaw, S., and Mu, X., 2004, Ordovician reef systems and settings in South China before the Late Ordovician mass extinction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 205, p. 235–254.

Lin, B.-Y., and Webby, B.D., 1988, Clathrodictyid stromatoporoids from the Ordovician of China: Alcheringa, v. 12, p. 233–247.

Milne-Edwards, H., and Haime, J., 1851, Monographie des Polypiers fossils des Terrainés Paleonzoiques, précédée d'un tableau general de la classification des Polypes: Archives du Muséum d'Histoire naturelle de Paris 5, 502 p.

Mori, K., 1970, Stromatoporoids from the Silurian of Gotland, Part 2: Stockholm Contributions in Geology 22, Stockholm, 152 p.

Nestor, H., 1997, Evolutionary history of the single-layered, laminate, clathrodictyid stromatoporoids: Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica, v. 91, p. 319–328.

Nestor, H., 2015. Clathrodictyida: Systematic descriptions, *in* Selden, P.A., ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 755–768.

Nestor, H., and Webby, B.D., 2013, Biogeography of the Ordovician and Silurian Stromatoporoidea, *in* Harper, D.A.T., and Servais, T. eds., Early Palaeozoic biogeography and palaeogeography: Geological Society of London, Memoir 38, London, p. 67–79.

Nestor, H., Copper, P., and Stock, C., 2010, Late Ordovician and Early Silurian Stromatoporoid Sponges from Anticosti Island, Eastern Canada: Crossing the O/S Mass Extinction Boundary: National Research Council Research Press, Ottawa, Canada, 152 p.

Nicholson, H.A., and Murie J., 1878, On the minute structure of Stromatopora and its allies: Zoological Journal of the Linnean Society, v. 14, p. 187–246.

Prosh, E.C., and Stearn, C.W., 1996, Stromatoporoids from the Emsian (Lower Devonian) of Arctic Canada: Bulletins of American Paleontology, v. 109, p. 1–66.

Rong, J.Y., and Chen, X., 1987, Faunal differentiation, biofacies and lithofacies patterns of the Late Ordovician (Ashgillian) in South China: Acta Palaeontologica Sinica, v. 26, p. 507–535. [In Chinese with English abstract]

Rong, J.Y., Zhan, R.B., Xu, H.G., Huang, B., and Yu, G.H., 2010, Expansion of the Cathaysian Oldland through the Ordovician-Silurian transition: emerging evidence and possible dynamics: Science China, Earth Science, v. 53, p. 1–17.

Schmidt, F., 1858, Untersuchungen über die Silurische Formation von Ehstland, Nord-Livland und Oesel: Archiv für die Naturkunde Liv-, Esth- und Kurlands, erster serie, Bd. II, 248 p.

Stearn, C.W., 1983, Stromatoporoids from the Blue Fiord Formation (Lower Devonian) of Ellesmere Island, Arctic Cananda: Journal of Paleontology, v. 57, p. 539–559.

Stearn, C.W., 2015, Internal morphology of the Paleozoic Stromatoporoidea, *in* Selden, P.A. ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 487–520.

Stock, C.W., Nestor, H., and Webby, B.D., 2015, Paleobiogeography of the Paleozoic Stromatoporoidea, *in* Selden, P.A. ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 653–689.

Vinn, O., 2016a, Symbiotic endobionts in Palaeozoic stromatoporoids: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 453, p. 146–153.

Vinn, O., 2016b, Tentaculitoid tubeworms as endobiotic symbionts of Paleozoic corals and sponges. Palaios, v. 31, p. 440–446

Vinn, O., and Mõtus, M.-A., 2014, Endobiotic Rugosan symbionts in stromatoporoids from the Sheinwoodian (Silurian) of Baltica: PLoS ONE 9: e90197. http://dx.doi.org/10.1371/journal.pone.0090197.

Vinn, O., and Wilson, M.A., 2012, Epi- and endobionts on the late Silurian (early Pridoli) stromatoporoids from Saaremaa Island, Estonia: Annales Societatis Geologorum Poloniae, v. 82, p. 195–200.

Vinn, O., Toom, U., and Mõtus, M.-A., 2015, Earliest known rugosan-stromatoporoid symbiosis from the Llandovery of Estonia (Baltica): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 431, p. 1–5.

Vinn, O., Liang, K., and Toom, U., 2017, Endobiotic rugose coral symbionts in Silurian tabulate corals from Estonia (Baltica): Palaios, v. 32, p. 158–165.

Webby, B.D., 2004, Stromatoporoids, *in* Webby, B. D., Paris, F., Droser, M. L., and Percival, I. G., eds., The Great Ordovician Biodiversification Event: Columbia University Press, New York, p. 112–118.

Webby, B.D., 2015a, Early evolution of the Paleozoic Stromatoporoidea, *in* Selden, P.A. ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 575–592.

Webby, B.D., 2015b, Labechiida: Systematic descriptions, *in* Selden, P.A. ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 709–754.

Webby, B.D., and Kershaw, S., 2015, External morphology of the Paleozoic Stromatoporoidea: Shapes and growth habits, *in* Selden, P.A. ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 417–486.

Webby, B.D., Stearn, C.W., and Nestor, H., 2015, Biostratigraphy of the Paleozoic Stromatoporoidea, *in* Selden P.A., ed., Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, Vol. 4–5: The University of Kansas Paleontological Institute, Lawrence, Kansas, p. 613–630.

Wu, H., 2003, Tectonopalaeogeographic analysis of the geologic problems related to ophiolitic belt in northeastern Jiangxi Province: Journal of Palaeogeography, v. 5, p. 328–342. [In Chinese with English abstract]

Young, G.A., and Noble, J.P.A., 1989, Variation and growth in syringoporid symbiont species in stromatoporoids from the Silurian of eastern Canada: Australasian Association of Palaeontologists Memoir, v. 8, p. 91–98.

Zapalski, M.K., and Hubert, B.L., 2011, First fossil record of parasitism in Devonian calcareous sponges (stromatoporoids): Parasitology, v. 138, p. 132–138.

Zhan, R.B., and Jin, J.S., 2007, Ordovician–Early Silurian (Llandovery) Stratigraphy and Palaeontology of the Upper Yangtze Platform, South China: Science Press, Beijing, 169 p.

Zhang, Y.D., Chen, X., Yu, G.H., Dan, G.D., and Liu, X., 2007, Ordovician and Silurian rocks of northwest Zhejiang and northeast Jiangxi provinces, SE China: University of Science and Technology of China Press, Hefei, 189 p.

Zhen, Y.-Y., and West, R.R., 1997, Symbionts in a stromatoporoid–chaetetid association from the Middle Devonian Burdekin Basin, north Queensland. Alcheringa, v. 21, p. 271–280.

FIGURE CAPTIONS

Figure 1. **(1)** Map of China and enlargement of the location of the border area between Jiangxi and Zhejiang provinces. **(2)** Geological map of the Xiazhen Formation near the town

of Zhuzhai. The locality from which the specimen NIGP169634 was collected is indicated by the white arrow. **(3)** Stratigraphic columns of the upper part of the Xiazhen Formation; S = shale, M = mudstone, W= wackestone, P = packstone, G = grainstone, F= floatstone. All figure parts are modified after Lee et al. (2012). **(4)** Field photograph of outcrop showing limestone–shale couplets in mudstone to packstone. Pen for scale is 12.5 cm in length.

Figure 2. (1–3) Thin section photomicrographs showing normal skeletal elements, NIGP 169634-4. **(1)** Transverse view of *Clathrodictyon* cf. *C. mammillatum* showing small circular to elliptical pillars. **(2)** Longitudinal view of *C.* cf. *C. mammillatum* characterized by continuous and slightly undulating laminae. **(3)** Transverse view of *Labechia* sp. characterized by well-developed flanged and hollow pillars with ellipsoidal to circular shapes. **(4)** Vertical view of the relationship between two species of stromatoporoids. Note short, stout and round pillars of *Labechia* sp. in the vertical view. Note large-sized and irregular-shaped cysts of *Labechia* sp. (black arrows), distortions of *C.* cf. *C. mammillatum* (white arrow) within the cyst interspaces of *Labechia* sp., and crumpled laminae of *C.* cf. *C. mammillatum* (yellow arrow), NIGP 169634-18.

Figure 3. Typical distorted structures of *Clathrodictyon* cf. *C. mammillatum* and *Labechia* sp. during their interactions with schematic drawings. **(1)** Abnormal large cyst of *Labechia* sp. (black arrow) and distorted laminae of zigzag-crumpled shapes in *C.* cf. *C. mammillatum*, by the settlement of *Labechia* sp. (right yellow arrow), and also possibly by sediment interruption (left yellow arrow), NIGP 169634-14. **(2)** Enlarged photograph of the rectangular area in (1). Note antagonistic behavior indicated by the distorted laminae of *C.* cf. *C. mammillatum* (white arrow) in the cyst interspaces of *Labechia* sp., and abnormal large cysts of *Labechia* sp. (black arrow) near their physical contacts. **(3)** Enlarged photograph of the

rectangular areas in (1) showing the physical contact between *C.* cf. *C. mammillatum* and *Labechia* sp. Skeletal malformation of *Labechia* sp. is manifest by uneven-thickened cyst plate and abnormal large cysts (black arrows), and zigzag crumpled laminae (yellow arrow) in *C.* cf. *C. mammillatum* near the physical contacts of the two stromatoporoids. **(4–9)** Schematic drawing to illustrate the process of ecological interactions between two stromatoporoids in (1).

Figure 4. (1–5) Transverse serial sections showing distorted skeletal elements in *Labechia* sp. and *C.* cf. *C. mammillatum* during their ecological interactions, each interval ranging from 1.0 to 1.2 mm, respectively, exhibiting upward growth of the studied specimen, NIGP 169634-8–12. **(6)** Enlargement of the left rectangular area in (2). **(7)** Enlargement of the right rectangular area in (2). **(8)** Enlargement of the right rectangular area in (3). Space occupation of the laminae of *C.* cf. *C. mammillatum* is reflected by their skeletal distortions (white arrows in 7 and 8) in the cyst interspaces of *Labechia* sp. Large-sized and irregular-shaped cysts of *Labechia* sp. are indicated by black arrows, while crumpled laminae of *C.* cf. *C. mammillatum* are indicated by yellow arrows.

Figure 5. Thin section photographs of coral endobionts within the skeleton of *Clathrodictyon* cf. *C. mammillatum*. **(1)** Oblique-cut of three solitary rugose coral *Tryplasma* (white arrows) and a solitary rugose coral *Streptelasma* (black arrow) surrounded by *C.* cf. *C. mammillatum*, NIGP 169634-8. **(2)** Two solitary rugose coral *Tryplasma* (white arrows) near the mamelon column of *C.* cf. *C. mammillatum*, NIGP 169634-11. **(3–4)** Transverse views of mamelon columns of *C.* cf. *C. mammillatum* and the neighboring endobiont tabulate coral *Bajgolia* (yellow arrows). Note that no distortion of *C.* cf. *C. mammillatum* is observed near the contacts with diverse endobionts, NIGP 169634-7, 6, respectively.

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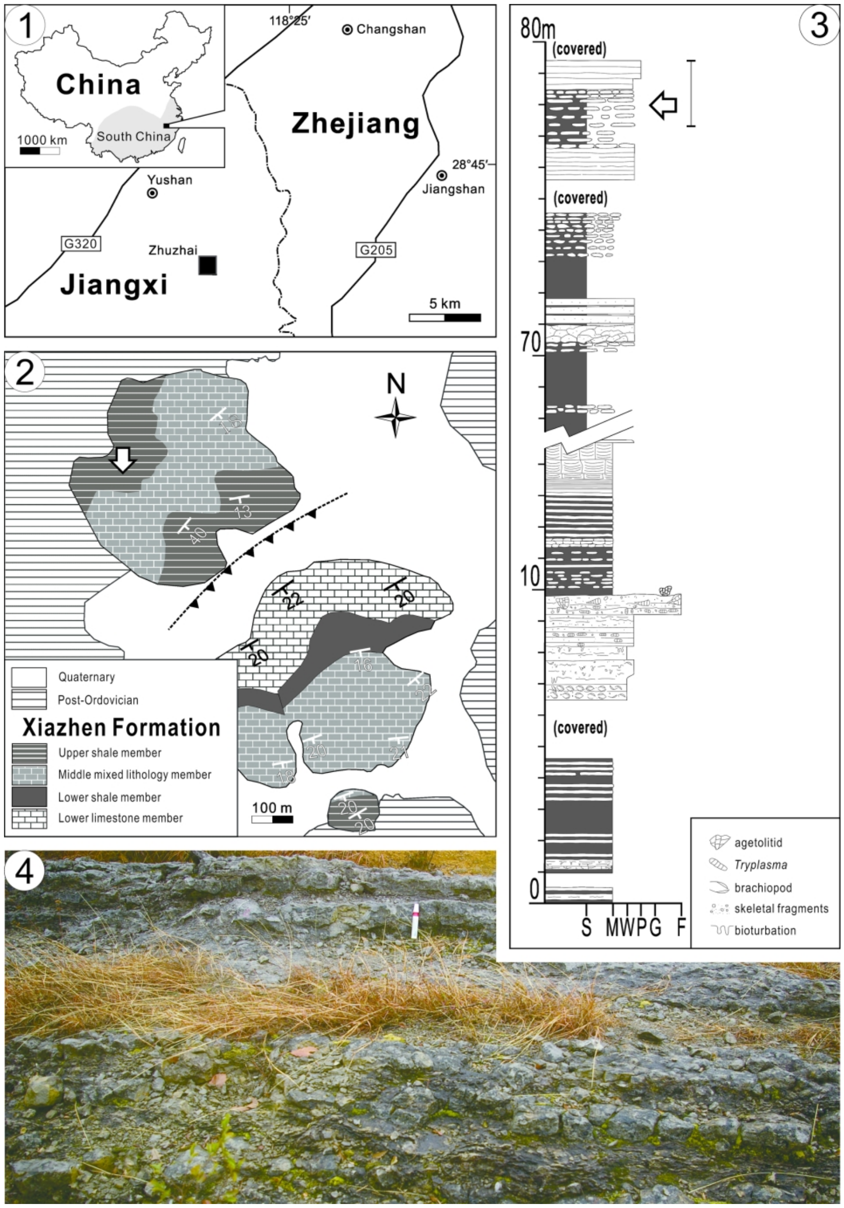

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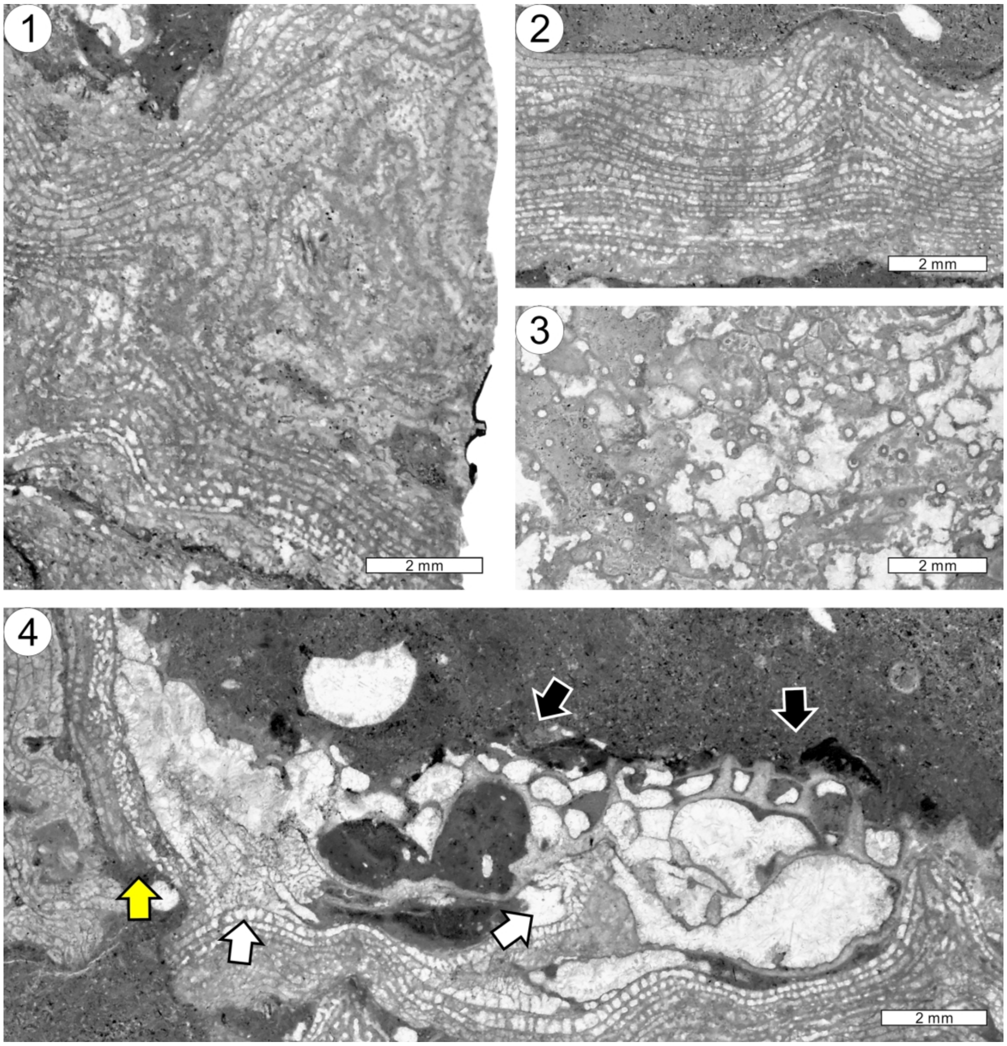

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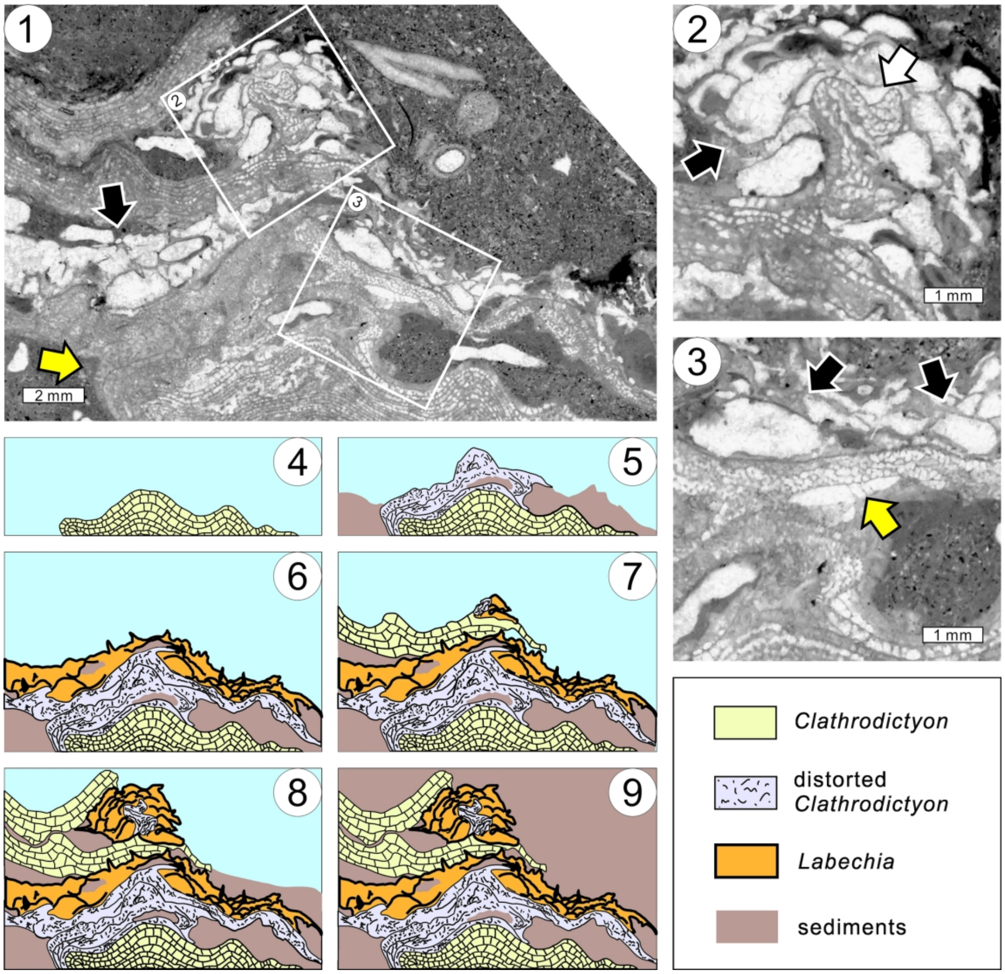

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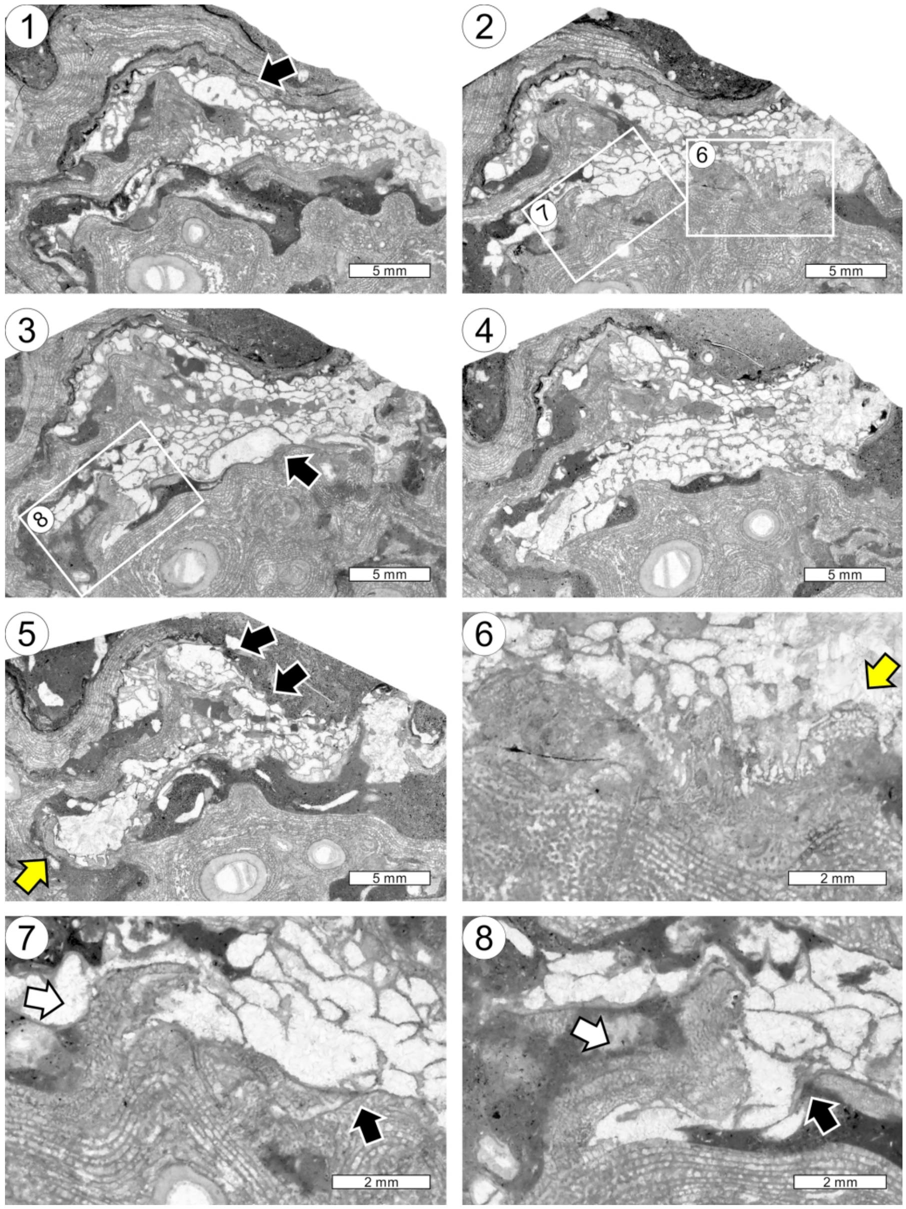

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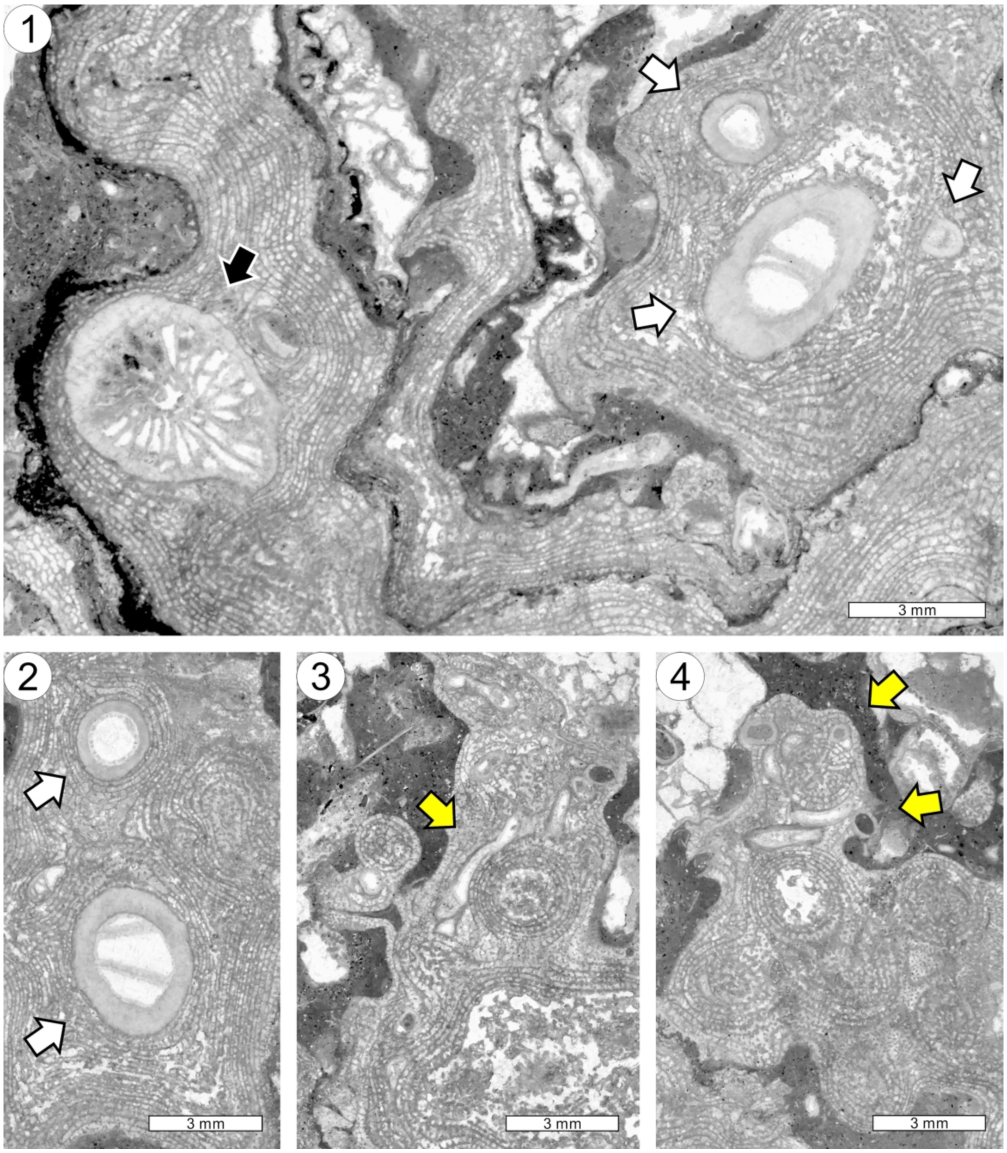

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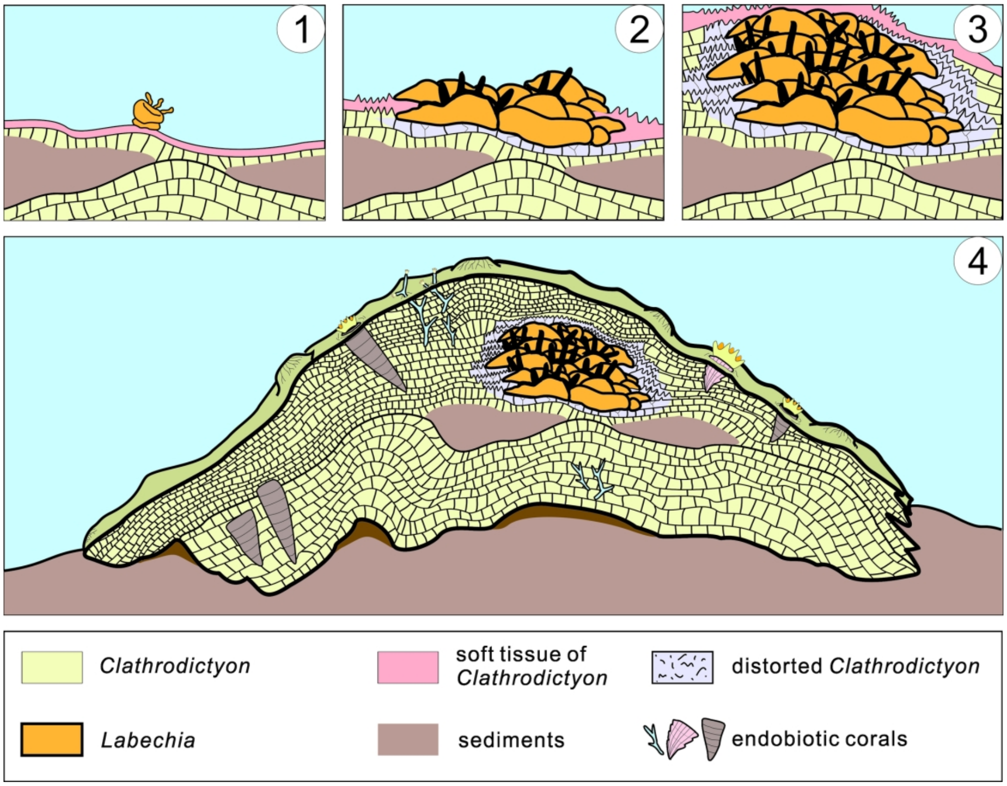

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