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Disorientation of corals in Late Ordovician lime mudstone: A case for ephemeral, biodegradable substrate?

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ABSTRACT

Massive coralla representing the tabulate coral *Agetolites* occur on a lime mudstone bed in the Upper Ordovician Xiazhen Formation of southeastern China. Other fossils include solitary rugose corals, bryozoans, trilobites, and mollusks. In addition, abundant spicules and spicule networks suggest that sponges were widespread. The occurrence of intact, unabraded fossils in micritic matrix and the absence of high-energy sedimentary structures indicate deposition in low-energy conditions. Thin section analysis of disoriented specimens demonstrates that geopetal indicators are consistent with stratigraphic "up" and differ from the growth axes of the corals, implying that geopetal infillings formed after disorientation. The growth axes of coralla were not redirected during life, suggesting that the corals were either dead at the time of disorientation or died as a result of disorientation. An examination of cyclomorphism indicates that the corals died at different times, rather than during a single event. A close association between sponges and corals is suggested by the presence of spicule networks in calices and intracorallum spaces of *Agetolites*. It is hypothesized that disorientation of corals was related to growth on biodegradable substrates. We suggest that many coral larvae settled on sponges that formed "sponge meadows". Disorientation of the resulting corals may have occurred when (1) a host sponge could no longer support the weight of a coral and collapsed, (2) increasing weight or imbalance of a coral caused it to fall off the sponge, or (3) a coral became detached when the sponge died and decomposed. If the coral was alive, sudden deposition in a disoriented position within muddy sediment resulted in its death. Disorientation of massive skeletons, such as colonial coralla, is most commonly attributed to water energy. This study suggests that ephemeral substrates may have been involved in some cases.

1. Introduction

The orientation of fossils is a significant area of taphonomic study, providing important information regarding the palaeoecology of ancient organisms, palaeoenvironmental conditions, and processes of sedimentation (Toots, 1965a, 1965b; Kissling and Lineback, 1967; Nagle, 1967; Manten, 1971, p. 435, 437; Kobluk et al., 1977; Potter and Pettijohn, 1977, p. 44–47, 73–77; Potter et al., 1980, p. 65–68; Hodges and Roth, 1986; Elias et al., 1987, 1988; Dodd and Stanton Jr., 1990, p. 241–247; Fürsich and Oschmann, 1993). Most skeletonized organisms functioned as sedimentary particles after death or breakage, which might record depositional conditions including hydrodynamic regime, transportation, and palaeocurrent direction. Considerable attention has been paid to the orientation of mollusk shells such as those of cephalopods and gastropods, because their elongate and conical shapes indicate current direction (e.g. Nagle, 1967). However, less attention has been paid to the orientation of massive skeletons, including those of colonial corals (e.g. Kobluk et al., 1977).

During life, corals are known to generally grow upward from the substrate, to which they may be attached (Scrutton, 1998). However, coral skeletons are commonly disoriented or dislodged in both modern environments and ancient deposits. Disorientation of corals has most commonly been interpreted to be a direct result of water movement, such as during high-energy storms and hurricanes (Stoddart, 1962; Kobluk et al., 1977; Bries et al., 2004). Corals can also become disoriented if supporting sediment is removed by the scouring action of bottom currents (Abbott, 1974). Increasing size during growth of the coral itself may have caused instability (Kobluk et al., 1977). The effect

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of other organisms has also been considered, including reduced stability due to boring activity at the base of the coral skeleton (Scoffin, 1972; Tunnicliffe, 1981) or bioturbation of supporting sediment (Brett and Baird, 1986). Only a few previous studies have examined the disorientation of Palaeozoic tabulate corals (Kissling and Lineback, 1967; Manten, 1971; Philcox, 1971; Kobluk et al., 1977; Hodges and Roth, 1986; Baarli et al., 1992; Young and Elias, 1995). The principal cause of disorientation was interpreted to be water movement. In the present study, we provide an example suggesting that growth on ephemeral substrates may have resulted in disorientation in a low-energy environment.

Agetolitids are an extinct group of problematic corals from the Late Ordovician. They are characterized by a cerioid massive corallum with communicating mural pores and numerous tabulae in each corallite, which support an assignment to tabulate corals (Hill, 1981; Sun et al., 2014, 2016). Although the alternation of long and short septa in *Agetolites* is reminiscent of the arrangement in rugose corals, the insertion of septa in *Agetolites* does not clearly indicate an affinity with rugosans (Sun et al., 2014, 2016).

The Xiazhen Formation in southeastern China is a well-known Late Ordovician carbonate succession containing a highly diversified biota (Li et al., 2004; Lee et al., 2012; Fig. 1A–B). *Agetolites* is the most abundant genus of colonial corals in the formation; five species of this genus were recently re-described from the formation (Sun et al., 2016). The sizes and shapes of coralla are primarily considered species-specific features, but they are also partly related to lithofacies (Sun et al., 2016). On the bedding surfaces of some *Agetolites*-bearing units, coralla are preserved in various orientations from apparent upright growth position to toppled and overturned postures, possibly reflecting energy conditions of the environment (Sun et al., 2016; Fig. 2A–F). Sun et al. (2016, Table 1) tabulated the inferred relative energy level and the distribution and orientation of *Agetolites* coralla for each coral-bearing bed in the Xiazhen Formation. Interestingly, the lowermost bed ("A1 bed") was described as a low-energy deposit, while the coralla in it are mostly disoriented. In this lime mudstone-dominated bed, there are overturned coralla of *Agetolites* of various shapes and sizes, up to 50 cm in diameter and 40 cm high, without any abrasion (see interval A1 of Sun et al., 2016). In this paper, we investigate the taphonomy of coral heads in the A1 bed by combining field observation and petrographic analysis, and provide a new, plausible scenario explaining the unusual preservation dynamics of overturned *Agetolites* coralla in a low-energy deposit.

2. Geological setting and methods

The Late Ordovician Xiazhen Formation crops out in the JCY (Jiangshan-Changshan-Yushan) triangle area near the border between Jiangxi and Zhejiang provinces, located in the eastern part of the South China Plate (Zhang et al., 2007; Fig. 1A–B). The formation is up to 190 m thick and comprises carbonate-siliciclastic successions with numerous patch reefs and biostromes (Lee et al., 2012). The Xiazhen Formation is estimated to be Katian to Hirnantian in age based on the occurrence of the graptolite *Anticostia uniformis* in the upper shale member (Chen et al., 2016).

Specimens for this study were collected from the upper bedding surface, measuring 1.6 m by 3.5 m (Fig. 2A), of a fine-grained limestone bed (floatstone with mudstone to wackestone matrix; the "A1 bed" of Sun et al., 2016) in the lower limestone member, 59 to 60 m above the base of the formation (sub-section ZU 2 of Lee et al., 2012; Fig. 1C). This bed, which was previously described as coral floatstone (Lee et al., 2012) and calcareous mudstone (Sun et al., 2016), contains diverse fossils including tabulate and solitary rugose corals, mollusks, trilobites, bryozoans, sponge spicules, and unidentified shells. In total, 93 thin sections were prepared to analyze the types of organisms and the texture of carbonates surrounding them. All thin sections were obtained from the uppermost part of the bed and are perpendicular to bedding. For each specimen, the stratigraphic "up" direction was recorded from the outcrop, and orientations of the central growth axes of corals and geopetal structures within coralla were identified from each thin section. Image-processing software "ImageJ" (Schneider et al., 2012) was used for measurements and records of numerical values of the various organisms in the thin sections.

3. Results

3.1. Descriptions

The bed containing the disoriented coralla of *Agetolites* (the floatstone bed indicated by a black arrow in Fig. 1C) is as much as 0.5 m thick and consists of bioturbated light-gray floatstone with mudstone to wackestone matrix (Fig. 2A–F). Intact fossils of the solitary rugose coral *Tryplasma*, mollusks, trilobites, bryozoans, and unidentified shells are commonly scattered within the muddy matrix, and are partly surrounded by disarticulated sponge spicules (Figs. 2G–H, 3A–H). Burrows infilled with light-gray sediment and sponge relicts occur sporadically within the muddy matrix (Fig. 3A, I–K). High-energy sedimentation indicators, such as graded laminae or erosive surfaces, are absent in the studied bed as well as the rest of the lower limestone member of the Xiazhen Formation (Park et al., 2015).

Massive, low domical to hemispherical *Agetolites* coralla are conspicuous on the bed. They are intact and preserved in various orientations, ranging from the original upright growth orientation (Fig. 2B–C) to completely overturned (Figs. 2D–F, 4A–G). The diameter of agetolitids ranges from 2.5 cm to 47.1 cm on the bedding planes (avg. = 12.1 cm, n = 9). Of 27 coralla recognized in thin sections, 15 were disoriented (55.6%) and only one was definitely in growth

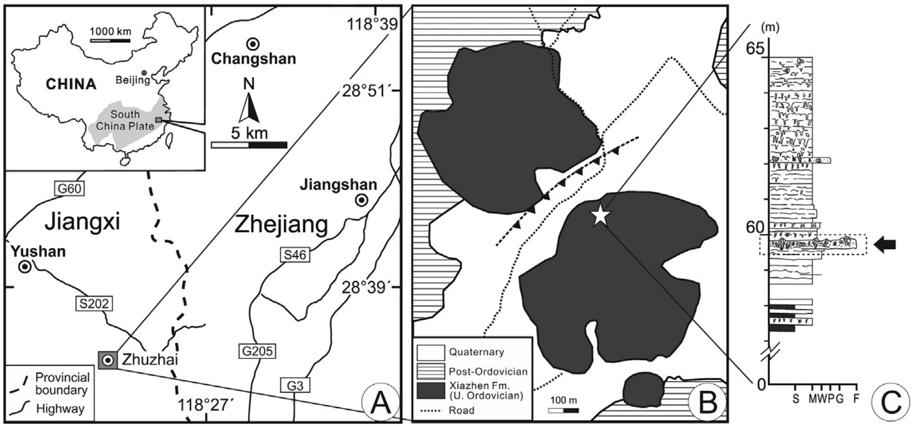

Fig. 1. (A) Index map of China (South China Plate shaded) and location of the study area. (B) Simplified geologic map of the Xiazhen Formation at Zhuzhai and location of the studied section (star). (C) Stratigraphic column of the upper part of the lower limestone member of the Xiazhen Formation; the studied bed containing numerous coralla of *Agetolites* and other fossils (Fig. 2) is indicated by an arrow. Modified after Lee et al. (2012).

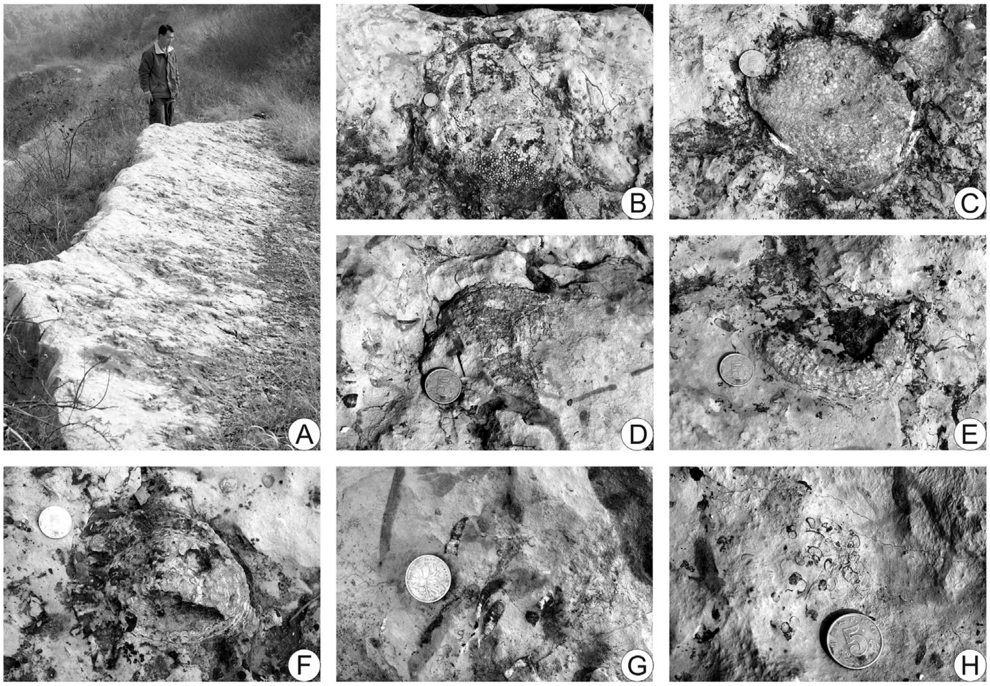

Fig. 2. Outcrop photographs of the studied bed and fossils exposed on the bedding surface. (A) Upper bedding surface of the micritic limestone. (B–F) Coralla of *Agetolites* as exposed on the upper bedding surface; some are preserved in upright life orientation (B–C), but many are disoriented (D–F). (G) Several coralla of the solitary rugose coral *Tryplasma*. (H) Gastropods with other shelly fossils. Diameter of the coin in B–H is 20.5 mm.

orientation (3.7%); the orientation of the other 11 coralla was undetermined because they were observed only in transverse sections lacking diagnostic features. The coralla show no evidence of breakage or abrasion. Most are surrounded by micrite, but some small coralla are attached to other organisms, such as mollusk shells (Fig. 3H). Overgrowth relationships among coralla of *Agetolites* are rare (Fig. 4G). The growth direction of each corallum is different. Basal growth surfaces of the coralla surrounded by micrite are usually concave or irregularly curved (Fig. 4A), whereas the coralla that grew on mollusk shells or each other have basal surfaces conforming to the substrate (Figs. 3H, 4G). The wall morphology at the base and in intracorallum parts of *Agetolites* are seemingly comparable (Fig. 4A).

Corallites of *Agetolites* are mostly filled with calcite cement, but some intertabularial spaces are partly to completely filled with peloidal or micritic sediment (Figs. 4A–G, 5A–I). The infilling sediment occupies as much as 4.6% of the intraskeletal area below the calices in each *Agetolites* corallum in transverse thin section. Although the *Agetolites* coralla seem virtually intact, some delicate tabulae have perforations, especially at the bases of calices (Fig. 5F–G), and these corals produced mural pores between corallites during growth (Figs. 4G, 5D), most of which are corner pores (Figs. 4B, 5C). Small openings such as these probably allowed sediment to be deposited in intraskeletal spaces. Scattered sponge spicules or well-preserved spicule networks occur within some intertabularial spaces (Figs. 4C, E–G, 5B–G). Circular to oval-shaped peloids are common within the *Agetolites* coralla and mollusk shells (Figs. 3A, 4C, G, 5B, F, H). There are numerous geopetal structures within the *Agetolites* coralla, formed by micrite, aggregated peloidal masses, and sponge spicules. Regardless of the composition, all geopetal structures within a single corallum generally indicate the stratigraphic “up” direction, as inferred from the lines of intersection of upper geopetal surfaces with the plane of the stratigraphically oriented thin section of the corallum (Fig. 4A–G). However, these geopetal orientations usually deviate from the growth direction of *Agetolites*, by about 15 degrees to 180 degrees (average = 91 degrees, n = 7 coralla; Figs. 4A–G, 5B, E–F).

3.2. Constituents

3.2.1. Corals

The colonial coral *Agetolites* has a cerioid growth form with densely packed corallites (Fig. 4A–G). In transverse sections, corallites have variable polygonal shapes, usually hexagonal to octagonal with 8 to 20 alternating long and short septa (Figs. 4B, 5C). In longitudinal sections, flat and slightly concave tabulae are very common (8 to 18 tabulae per cm; Fig. 4C–F). Spacing of tabulae varies within *Agetolites* coralla, forming alternating dense and sparse cyclomorphic growth bands (Fig. 4D–F). Terminal growth stages of these corals vary among specimens; some coralla were terminated in bands with densely spaced tabulae (Fig. 4E), whereas others apparently died in sparse bands (Fig. 4G). The calice of each corallite is deep and filled with micritic sediment and/or bioclasts (Fig. 4A, G). Some coralla exhibit partial mortality, with corallites possibly terminated by deposition of sediment (Fig. 5A). Subsequent colony rejuvenation involved the generation of new corallites by lateral increase, but the overall growth axis of the corallum remained unchanged. In such cases, new corallites grew on the sediment and/or sponge remains infilling and covering the terminated calices (Fig. 5A–B). Coralla of *Agetolites* record little evidence of changes in growth direction during life (Fig. 4A–F).

Of the five species of *Agetolites* described from the Xiazhen Formation (Sun et al., 2016), *A. oculiporoides* Lin, 1960 and *A. maxima* (Lin and Chow, 1977) occur in the studied bed. *Agetolites maxima* (Figs. 4B–G, 5C, E–H) is restricted to the lower part of the Xiazhen Formation, whereas *A. oculiporoides* (Figs. 4A, 5A–B, D, I) occurs throughout the formation (Sun et al., 2016). In general, *A. maxima* is characterized by large, subpolygonal to polygonal corallites with short septa, whereas *A. oculiporoides* tends to have smaller, polygonal corallites with long septa and crenulated walls (Sun et al., 2016). Maximum sizes of corallites of these two species are characteristically larger than in other *Agetolites* species occurring in the formation (Sun et al., 2016, Table 6). Among the collected specimens from the studied bed, *A. maxima* (n = 20) predominates over *A. oculiporoides* (n = 7).

The solitary rugosan *Tryplasma* is another common coral in the bed (Figs. 2G, 3B–D). Coralla of *Tryplasma* are conical to cylindrical in form, as much as 7 mm in diameter and 24 mm in length. In transverse section, the coralla are circular to elliptical with short septal spines. In

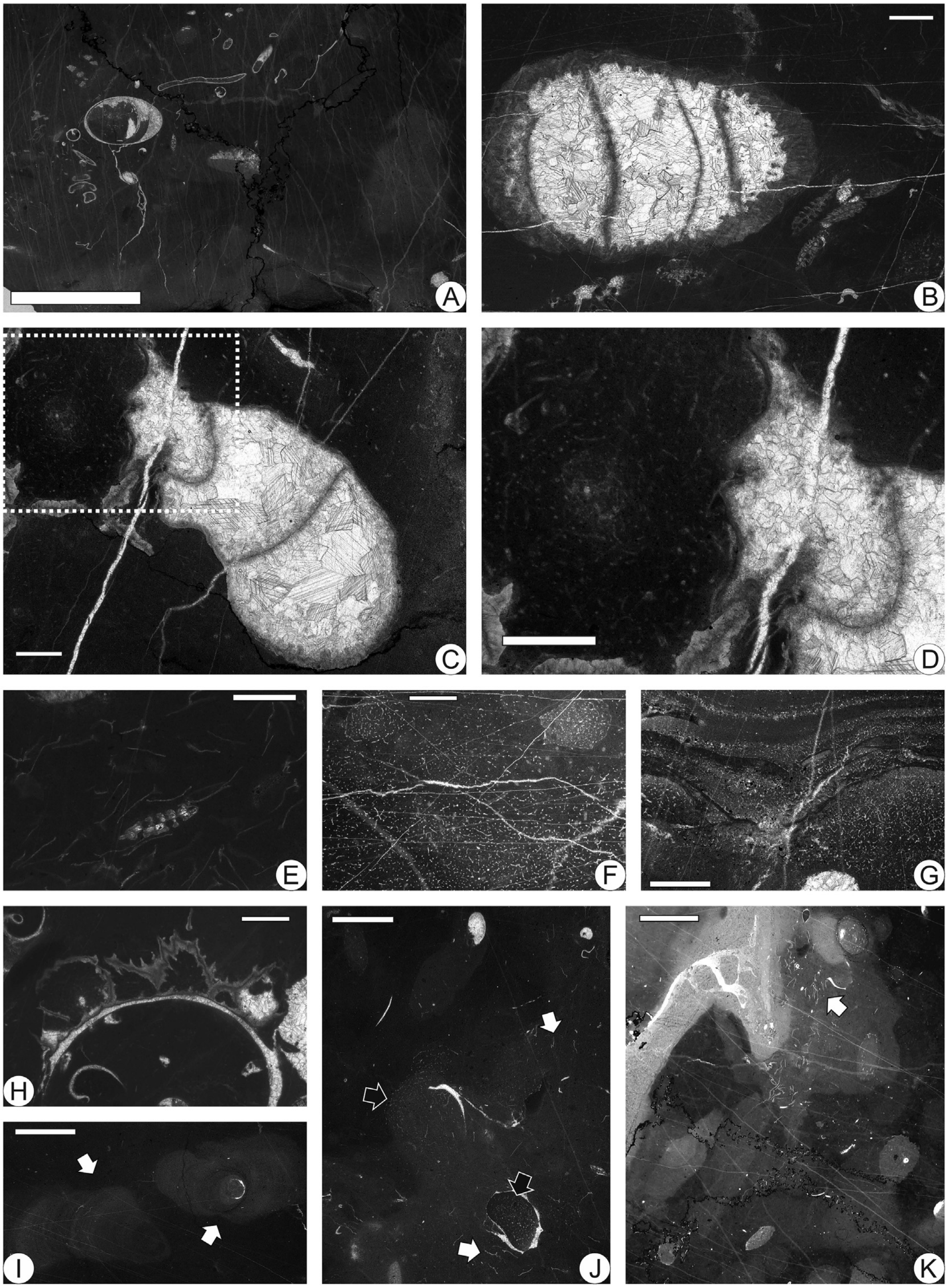

Fig. 3. Photomicrographs of fossils and other components in the studied bed. (A) Mollusks (gastropods and cephalopod), bryozoans, trilobite fragments, and shelly fossils in bioturbated micrite. Scale bar = 10 mm. (B) *Tryplasma* and bryozoans surrounded by well-preserved to poorly preserved sponge spicule networks. Scale bar = 1 mm. (C) Holdfast of *Tryplasma* attached to spicule networks. Scale bar = 1 mm. (D) Enlargement of dotted rectangle in C, showing the nature of spicule networks. Scale bar = 1 mm. (E) Long-ray spicules and a bryozoan in micrite. Scale bar = 1 mm. (F–G) Spicule networks of short rays with homogeneous micrite in interstices of networks. Scale bars in F and G = 2 mm. (H) *Agetolites* attached to a mollusk shell. Scale bar = 5 mm. (I) Two burrows (arrows) occurring within micrite. Scale bar = 2 mm. (J) Scattered long-ray spicules (white arrows), poorly preserved short-ray spicule networks (black arrows), and cylindrical burrows within micrite; note that some sponge remains occur inside a shell. Scale bar = 2 mm. (K) Overprinted burrows in micrite; note that some long-ray spicules occur in burrows (arrow). Scale bar = 5 mm.

longitudinal and oblique sections, tabulae are complete and apparently flat to concave. Most coralla of *Tryplasma* in the bed are surrounded by dark-coloured homogeneous micrite and filled with calcite cement. In contrast to most coralla of *Agetolites*, skeletons of *Tryplasma* do not exhibit geopetal structures composed of sediment or sponges within their intraskeletal space. One *Tryplasma* corallum has a root-like holdfast structure attached to spicule networks within the tabularium area of *Agetolites* (Fig. 3C–D). The base of another *Tryplasma* corallum occupies the calice of a terminated *Agetolites* corallite (Fig. 4E).

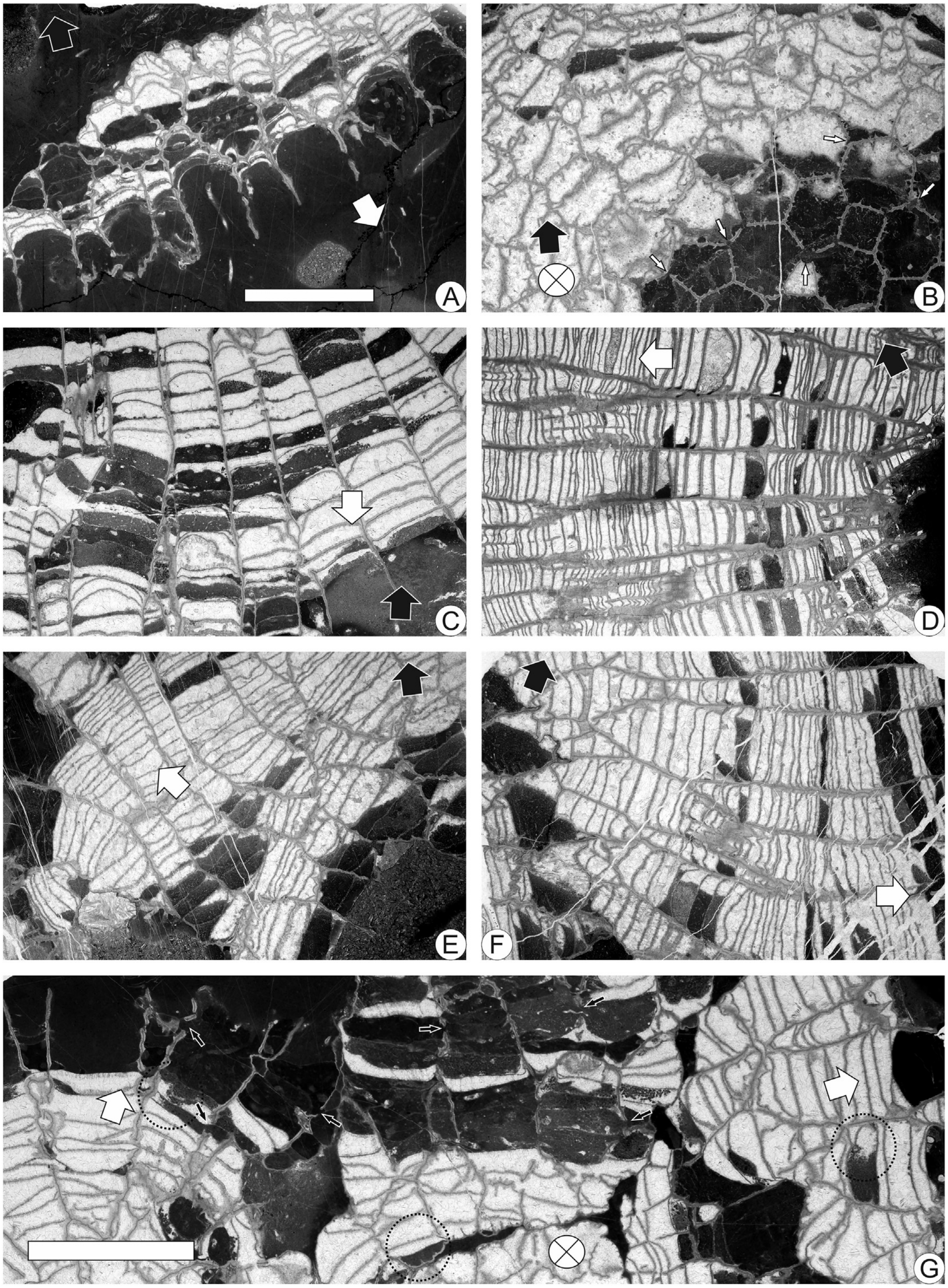

Fig. 4. Photomicrographs of *Agetolites* (A, *A. oculiporoides*; B–G, *A. maxima*) in the studied bed; stratigraphic "up" is toward the top of each photomicrograph. (A–G) Coralla of *Agetolites* with geopetal structures comprised of micrite, peloids, and sponge spicules. Note the preserved orientation of the *Agetolites* growth axis (large white arrow or symbol; the symbol ⊗ means the photomicrograph is approximately perpendicular to the growth axis) and the stratigraphic "up" direction indicated by geopetal structures (large black arrow); in A and C, the growth axis is opposite the stratigraphic "up" direction, whereas in B, D, and F, the growth axis is approximately parallel to bedding. The "up" directions indicated by geopetal structures are consistent with the stratigraphic "up" direction measured in the field, but do not match the growth axes of these disoriented coralla. In the upper left corner of E, *Tryplasma* is attached to a terminated corallite of *Agetolites*. (G) Several coralla have different growth directions (large white arrows and a symbol), but relatively uniform geopetal orientations (black dotted circles). Mural pores (small black arrows in G) and corner pores (small white arrows in B) are present between corallites. Scale bars in A (also applicable in B–F) and in G = 10 mm.

3.2.2. *Sponges*

Micritic aggregations with anastomosing networks of filamentous calcite microstructures are very common in the studied bed (Figs. 3B, E–G, J–K, 5B–I). Such fabrics are commonly described in early Palaeozoic limestones (e.g. Hong et al., 2012, 2014; Park et al., 2015, 2017) and have been interpreted as sponge remains (Luo and Reitner, 2014, 2016; Park et al., 2015, 2017). Although the filamentous structures in the Xiazhen Formation are calcitic, their original composition may have been different (Park et al., 2015). Sponge remains in the A1 bed typically appear as irregular patchy shapes comprising spicules,

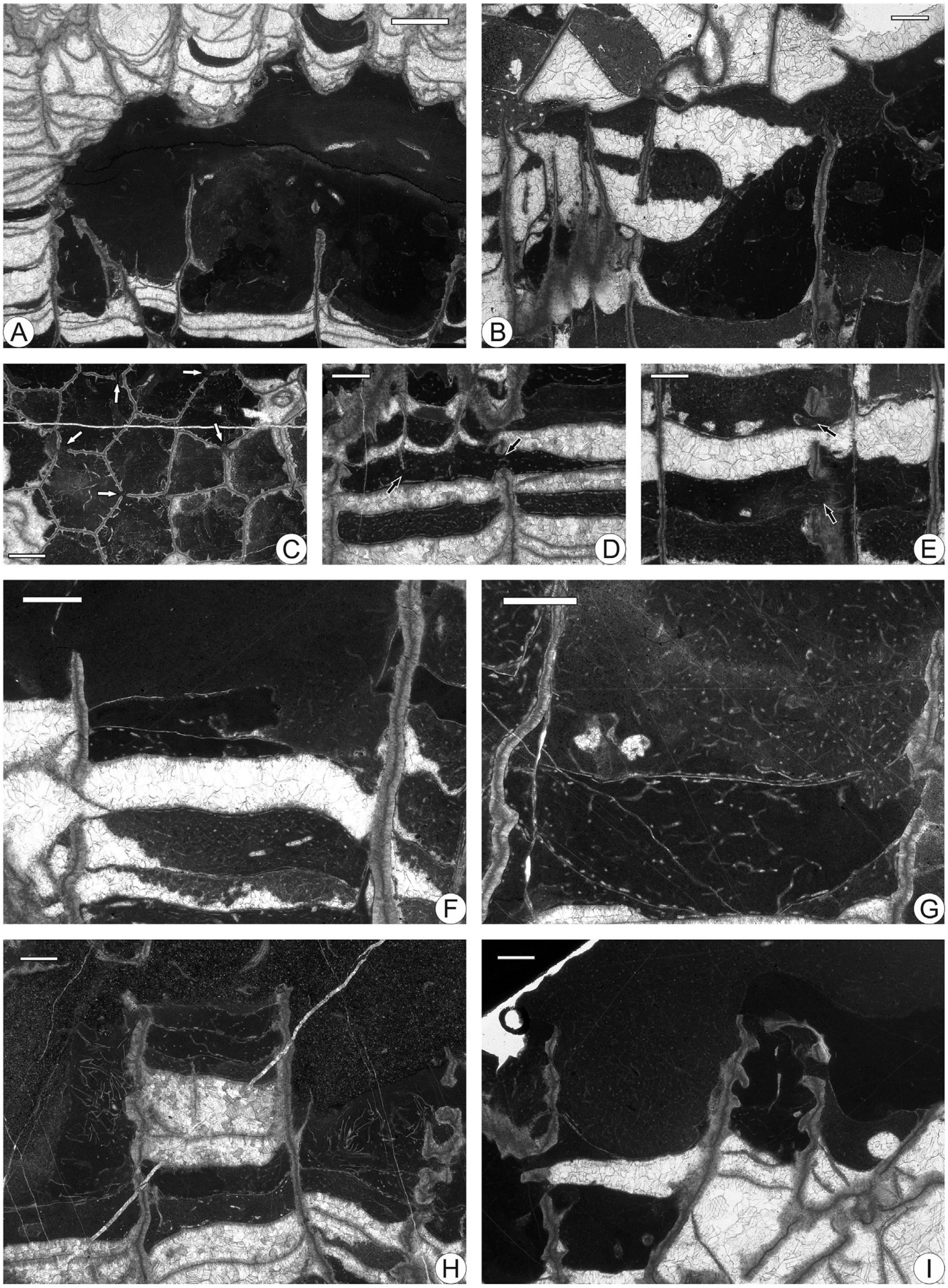

Fig. 5. Photomicrographs of *Agetolites* (A–B, D, I, *A. oculiporoides*; C, E–H, *A. maxima*) in the studied bed; stratigraphic "up" direction is toward the top of each photomicrograph. (A–B) Rejuvenation following partial mortality of *Agetolites*, with new corallites overgrowing micrite that filled and covered calices of terminated corallites. Note some patches of micrite with spicules; the sponge remains in B are attached to the basal part of the rejuvenated corallum. Scale bars in A = 2 mm and in B = 1 mm. (C–E) Sponge remains comprised of spicule networks are laterally continuous from one intertabularial area to another via corner pores (white arrows in C) and mural pores (black arrows in D and E). Scale bars in C = 2 mm and in D–E = 1 mm. (F–G) Sponge remains are vertically continuous from the calice (F) and upper intertabularial spaces (G) to lower spaces. Scale bars in F and G = 1 mm. (H) Numerous long-ray spicules within calices; note other sponge remains preserved in intertabularial spaces of the corallum. Scale bar = 1 mm. (I) Homogeneous micrite containing numerous sponge spicules within calices appears to encrust an area of micrite lacking spicules. Scale bar = 1 mm.

and commonly occur as spicule-bearing irregular tabular forms and mound-like structures cemented by calcite (Figs. 3F, G, 5B–G). These sponge spicules probably represent two groups based on their different spicule shapes. The first group consists of aggregated sponge spicules that do not form a distinct spicule network (Figs. 3E, J–K, 4A, 5H). These dissociated spicules have relatively clear outlines with uniform diameter, with a long ray ranging from 42 to 97 μm in length and as much as 9 μm in diameter, and two to four short rod-like rays at the tip of the long ray ranging from 5 to 20 μm in length. The long ray is commonly straight, slightly curved or undulating. Some of these appear to be needle-like without short rays at their tips, and occur as circular forms of various diameters in transverse section. The other group usually has smaller spicules, a few micrometers in length and diameter (Figs. 3B, F–G, J, 5A–G, I). These sponge spicules from the lower limestone member of the Xiazhen Formation at Zhuzhai were interpreted to represent "non-lithistid demosponges" by Park et al. (2015, 2017). These reticulated to slightly curved spicules either bifurcate or trifurcate. The spicule networks, which may usually represent partially preserved sponge bodies, transition gradually from well-preserved spicule networks into peloidal fabrics with micrite (Figs. 3G, 5A–B, E–F). Although the outlines of such spicule networks are obscured, some spicules occur within homogeneous micritic clumps. The interstices of spicule networks are filled with lighter-coloured micrite and common pyrite, and the networks are enclosed by darker-coloured micrite (Figs. 3F, J, 5A–G).

Sponge remains also occur commonly in calices of *Agetolites* and *Tryplasma*, and in intraskeletal spaces of *Agetolites*, gastropods, and cephalopods (Figs. 3C, J, 4A–C, E–G, 5A–I; as noted by Park et al., 2017). The intertabularial spaces of *Agetolites* are commonly occupied by sponge spicules. Well-preserved networks in some intertabularial spaces have an outline along the internal shape of the space (Figs. 4E, 5B, D, G), possibly representing the edge of a sponge in life position. In some cases, sponge spicules or spicule networks are horizontally continuous from one intertabularial space to another via the mural pores in *Agetolites* (Fig. 5C–E). Occasionally, these sponge remains are also vertically connected from one intertabularial space to another space through incompletely formed or broken tabulae (Fig. 5F–G).

3.2.3. Other accessories

Mollusks (gastropods, cephalopods, and possibly bivalve shells) and bryozoans are common in the bed (Figs. 2H, 3A–B, H–J). Homogeneous dark micrite and peloids with sponge spicule networks partially filled the intraskeletal spaces of some mollusks, commonly forming geopetal structures (Fig. 3A). Bryozoans are also scattered within the micritic matrix with spicules (Fig. 3B, E). Other fossils including trilobites and unidentified small shells are mostly preserved intact in the bed (Fig. 3A).

3.2.4. Burrows

Burrows are common in micritic limestone of the studied bed (Figs. 2B, 3A, I–K). They are 0.4 to 4.9 mm in diameter and 1.6 to 20.1 mm in length, typically filled with light-gray micrite, and rarely filled with dolomitic micrite. Various shapes of the burrows in transverse sections include cylindrical, sac-like, oval and irregular forms (Fig. 3I–K). The outlines of burrow walls are usually indistinct, rather than sharp. Some burrows appear to be overprinted by other burrows (Fig. 3K). Preservation of sponge spicules tends to be poor near the burrows (Fig. 3J), as noted by Park et al. (2015). Bioturbation in the studied bed was interpreted by Park et al. (2015, Fig. 2) to represent ichnofabric index 3.

3.3. Substrate interpretations

The occurrences of nearly intact *Agetolites* and other organisms within micritic matrix of the bed suggest that they inhabited a calm, relatively low-energy environment. The termination of *Agetolites* coralla at different stages of growth banding indicates that they did not all die at the same time during a high-energy event. Burrow structures within micritic matrix indicate that the bed was originally unconsolidated sediment. Overprinted burrow structures in some places record common bioturbation activities. The common occurrence of gastropods, cephalopods, corals, and burrows indicates deposition in shallow and normal salinity conditions (Figs. 2B–H, 3A). Although the studied bed appears superficially to be coral-bearing micritic limestone, detailed petrographic observation reveals the presence of numerous sponge spicules within the muddy matrix. Some extensively preserved networks of sponge spicules within micritic matrix are suggestive of sponge-microbe alternating buildups (Luo and Reitner, 2016). The sponges must have flourished in the quiet depositional environment, possibly in the form of "sponge meadows" as suggested by Park et al. (2015, 2017).

4. Discussion

4.1. Disorientation and its causes

There are numerous literature reports of "disoriented" massive skeletons, such as those of colonial corals, stromatoporoids, and chaetetids, which are not preserved in their upright life orientation (e.g. Manten, 1971; Connolly et al., 1989; Kershaw, 1990). The two components of orientation are directional (i.e. azimuth) and attitudinal (i.e. inclination) (Toots, 1965b). Directional orientations of disoriented massive skeletons have seldom been measured and plotted. Such studies have usually been limited to elongate fragments of branching forms and to columnar forms (Kissling and Lineback, 1967; Baarli et al., 2016), although equidimensional forms were also included by Kissling and Lineback (1967). Attitudinal orientations of massive skeletons have rarely been measured and plotted (Hodges and Roth, 1986). It is recognized that some skeletons, disoriented during transport but deposited in life orientation, are no longer in life position (Philcox, 1971). In general, interpretations that massive skeletons are disoriented have been based on qualitative determinations that their attitudinal orientation differs from the presumed life orientation. Such an approach is followed in the present study, given the small size of the exposure, the massive nature and hardness of the bed that encloses the corals, and the limited number of specimens.

Various possible causes have been proposed for the disorientation of colonial corals, stromatoporoids, and chaetetids (Kissling and Lineback, 1967; Manten, 1971; Abbott, 1974; Kobluk et al., 1977; Kershaw, 1984; Hodges and Roth, 1986; Harrington, 1987; Miller and West, 1997; Young and Elias, 1995). Disorientation is most commonly attributed to water energy, such as the action of waves, unidirectional currents, bidirectional currents (e.g. tides), and especially high-energy events (e.g. storms). This may involve the removal of supporting sediment by the scouring action of bottom currents, or the direct impact of flowing water under sufficiently high-energy conditions. Other causes of disorientation include changes in the organism during growth, which may lead to imbalance resulting in detachment from hard substrates or foundering in soft substrates. The activity of other organisms, including bioturbation of soft substrates and boring of attachment sites on hard substrates, may cause instability and disorientation. Disturbance by predators or grazers has also been suggested. Following burial, disorientation may result from differential pressure related to soft-sediment deformation or reef growth.

A number of factors are considered to affect the probability of disorientation in the case of colonial corals, stromatoporoids, and chaetetids (Kissling and Lineback, 1967; Manten, 1971; Abbott, 1974; Kobluk et al., 1977; Kershaw, 1984, 1990; Hodges and Roth, 1986; Harrington, 1987; Kershaw and West, 1991; Young and Elias, 1995; Miller and West, 1997). These factors can be grouped into four categories. The first category involves the skeleton itself. Disorientation is more likely if size is small, weight and density are low, and centre of gravity is high. In terms of growth forms, bulbous and columnar types are less stable than domical and laminar types. Round shapes are unstable compared to flat shapes. The second category involves the object's relation to the substrate. A small basal surface reduces stability. If the base is not attached to a hard substrate or embedded in sediment, the probability of disorientation increases. The third category involves the nature of the substrate. Low sediment cohesion promotes grain movement, so disorientation is more probable on sandy than muddy substrates. The presence of aligned clasts within the sediment may increase stability. Close spacing of objects on the substrate surface may

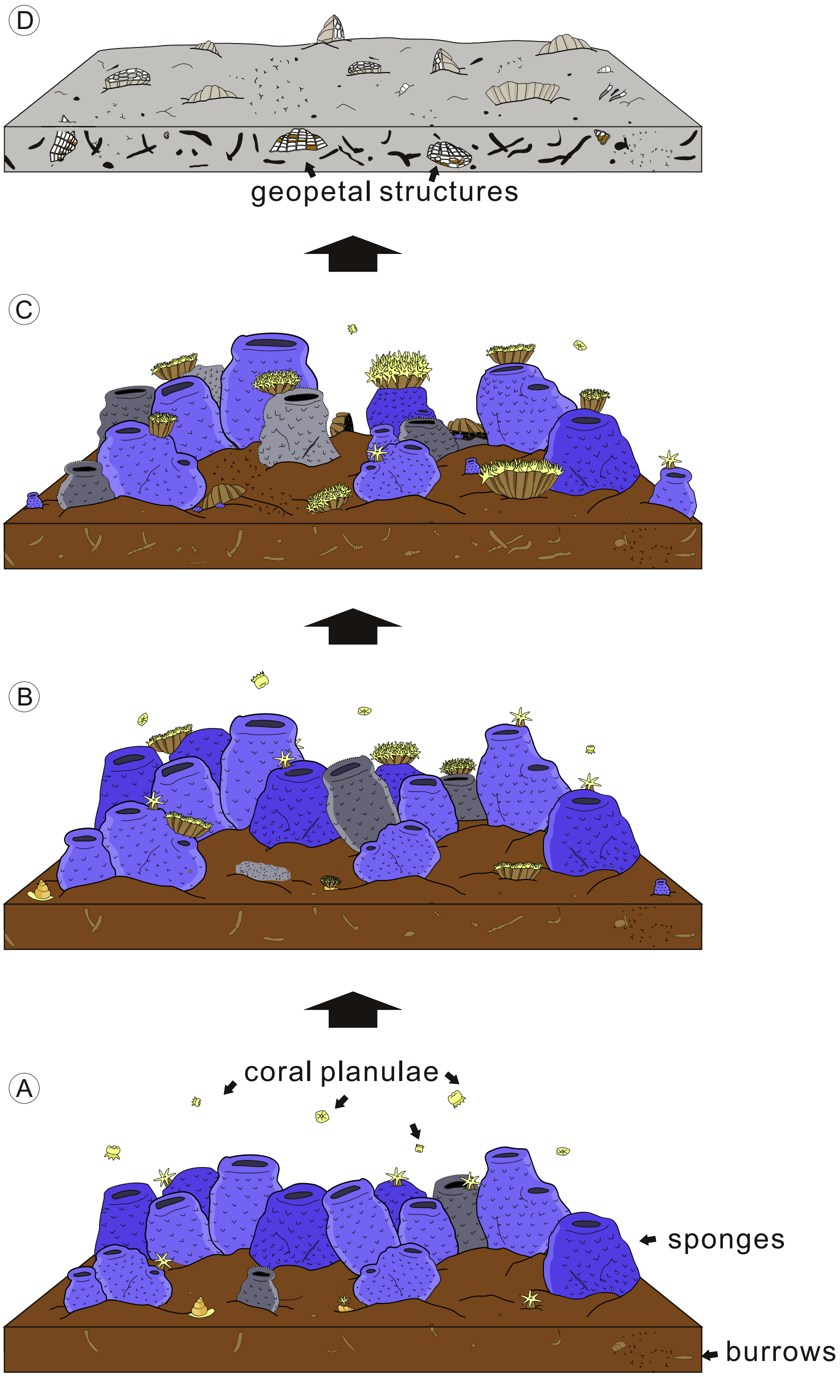

Fig. 6. A speculative palaeoecologic reconstruction depicting development of the studied bed. (A) The "sponge meadow" provided an ephemeral substrate on burrowed, micritic sediment; many *Agetolites* larvae settled on sponges, some settled on soft mud, and a few attached to shells. (B–C) Disorientation of corals that grew on sponges may have occurred when a host sponge could no longer support the weight of a coral and collapsed, or increasing weight or imbalance of a coral caused it to fall off the sponge, or a coral became detached when the sponge died and decomposed. (D) Burial of variously oriented coralla and formation of geopetal structures within them, as observed in the outcrop today.

inhibit their movement. A moving object, which might otherwise tend to be deposited upright, may be preserved in a disoriented position if it comes to rest against a stationary object. The morphology of the substrate surface may affect the probability of disorientation. For example, steeper slopes promote instability. The fourth category involves water motion. An increase in current velocity or turbulence may lead to disorientation.

In the case of the studied bed, the fine-grained lithology and absence of high-energy features, such as erosional surfaces and graded bedding, suggest that rapid water flow or storm events were not responsible for disorientation of *Agetolites* coralla. In a study involving Devonian stromatoporoids comparable in size to *Agetolites*, Harrington (1987) reported many disoriented stromatoporoids in very fine-grained lithologies. Therefore, he considered a high-energy cause to be unlikely, suggesting instead that occasional mild increases in current strength resulted in scouring, undermining, and disorientation. In the present study, although shelly fossils generally seem to be randomly oriented, some small, cylindrical coralla of *Tryplasma* recumbent on the surface of the bed have parallel alignment (Fig. 2G). This is consistent with the possibility of at least intermittent low-energy currents. Some unattached *Agetolites* coralla have concave basal surfaces, which may indicate that sediment cohesion was sufficiently low to permit scouring or winnowing at the corallum margin during growth (Scrutton, 1998, Fig. 17c).

The low domical to hemispherical growth form and broad base of *Agetolites* would have promoted stability. The growth axes of coralla show little evidence of redirection (Fig. 4A–F), indicating that the corals remained upright while they were alive. Therefore, it seems unlikely that sediment removal due to scouring or winnowing was sufficient to cause tilting during life. Similarly, changes in shape or weight distribution during growth of the corals were insufficient to cause attitudinal shifting. Continued upward growth following partial mortality (Fig. 5A) indicates that the event causing death of some polyps, possibly involving sediment deposition, did not result in disorientation of the colony. Imbalance due to infiltration of sediment into the corallum, either pre- or post-burial, seems unlikely because only a very small proportion of intracorallum space became occupied by foreign material. Although bioturbation in the studied bed was moderately intensive (Figs. 2B, 3A, I–K), it did not result in disorientation that corals could recover from during life. There is no evidence of damage to coralla that can be attributed to the activity of borers or predators. Intrastratal deformation prior to or after lithification is ruled out as a cause of coral disorientation. There are no sedimentary features indicating soft-sediment deformation, and geopetal structures within the coralla conform to the stratigraphic “up” direction (Fig. 4A–G).

Evidently, the coralla of *Agetolites* in the studied bed were dead when disorientation occurred, or died as a result of disorientation. The termination of coralla in different cyclomorphic stages indicates that the corals did not die simultaneously, and that death could presumably occur at any time of year. A specimen with overgrowth relationships among several undamaged coralla in different orientations (Fig. 4G) supports the interpretation that coralla became disoriented at different times. The specimen also indicates that events causing disorientation did not necessarily result in the burial of coralla, and that neither exposure prior to burial nor the burial process resulted in significant breakage or abrasion. In the studied bed, relatively large coralla tend to be preserved in life orientation (possibly life position; Fig. 2B, C), whereas disoriented specimens are typically smaller (Fig. 2D–F). If episodes of scouring or winnowing resulted in disorientation and death of some corals, those that survived in a tilted position would be expected to have redirected their growth axes. However, none of the coralla record significant changes in growth direction.

Previous proposals accounting for the disorientation of massive skeletons do not seem to satisfactorily explain the occurrence of *Agetolites* in the studied bed. Although there is evidence for low-energy water movement and moderately intensive bioturbation, those processes apparently had minimal effect on the corals, at least while they were alive. Therefore, we present a new hypothesis (Fig. 6A–D). The abundance of sponge remains in micrite of the bed (Fig. 3E–G, J–K) suggests that extensive “sponge meadows” colonized the soft, muddy substrate in a calm environment (Park et al., 2015). The presence of spicule networks in calices and intracorallum spaces of *Agetolites* (Fig. 5B–I) indicates a close association between corals and sponges.

When coral larvae descended from the water column above the studied bed, a few attached to shells or coralla scattered on the substrate and developed into encrusters (Figs. 3H, 4G). Some larvae may have attached to small grains (Scrutton, 1998), yielding corals that grew on exposed areas of sediment. Such corals may have been able to expand to a relatively large size, which conferred stability that possibly enabled them to remain in life position (Fig. 2B, C). The majority of coralla, however, are smaller and disoriented (Fig. 2D–F). We suggest they developed from larvae that settled on sponges, which would have provided a firmer but smaller surface than the muddy sediment (Fig. 6A). The unique example of a small *Tryplasma*, with its base still attached to a spiculate sponge (Fig. 3C–D), demonstrates that corals could grow on such a surface. It is possible that the typically concave or irregularly curved bases of *Agetolites* coralla conformed to the shapes of host sponges. In one example, the base of an *Agetolites* corallum is in contact with sponge remains (Fig. 4A). However, it is unclear whether the coral was attached to a sponge during life, or a sponge encrusted the corallum after disorientation exposed its basal surface, or isolated sponge spicules were deposited on the overturned corallum. Three scenarios are proposed for the disorientation of *Agetolites* (Fig. 6A–D): (1) a living sponge could no longer support the weight of a coral and collapsed; (2) increasing weight or imbalance of the coral caused it to fall off the sponge; or (3) the coral became detached when the sponge died and decomposed. If the coral was alive, sudden deposition in a disoriented position within muddy sediment presumably killed it. This would account for the preservation of coralla with minimal evidence of redirected growth, abrasion, or breakage (Fig. 4A–G). Bioturbation of the sediment disrupted delicate sponge remains (Fig. 3J–K; Park et al., 2015), but may have been insufficient to cause further disorientation of *Agetolites* coralla.

4.2. Ephemeral substrates

In general, larvae of Palaeozoic corals are known or suspected to have attached to hard objects, ranging in size from a tiny grain of sediment or shell fragment to a large skeletal object or lithified surface (Scrutton, 1998). In rare cases, however, corals attached to soft organic material that was not preserved in the fossil record. The coiled protocorallum of the Mississippian solitary rugosan *Cyathaxonia tantilla* is considered to have grown around a planktic algal filament (Sando, 1977; Ausich and Smith, 1982). At one locality, coralla of the Devonian solitary rugosan *Metriophyllum gracile* have an attachment groove, interpreted to indicate growth on the vertical stem of a benthic alga (Holwill, 1963). Some coralla of four Silurian rugosan genera also have scars suggesting that each was attached to a stem, possibly algal (Vinn and Toom, 2016). Similarly, the Devonian tabulate coral *Kerforneidictyum kerfornei* is thought to have attached to algal stems (Lafuste and Plusquellec, 1976). Modern scleractinian coral larvae can settle on living crustose and branching coralline red algae (Heyward and Negri, 1999; Harrington et al., 2004; Ritson-Williams et al., 2010) and articulated calcareous green algae (Nugues and Szmant, 2006). They are also known to settle on crustose non-coralline red algae (Heyward and Negri, 1999).

There have been a few reports of solitary rugose corals and auloporid tabulates attached to Late Palaeozoic demosponges having rigid skeletal frameworks (Finks, 1960; Gundrum, 1979). The living sponge may have been quite firm, with its soft parts forming only a thin layer above the skeleton (Finks, 1960, p. 42). When the corals became attached, some sponges may have been in upright life orientation, whereas others were overturned (Gundrum, 1979). In some cases, the corals evidently grew on live host sponges (Finks, 1960, p. 67), but in other cases the sponge was probably dead (Finks, 1960, p. 93). Ziegler (1964, pl. 10, Fig. 1) illustrated the holdfast of an octocoral on a Cretaceous sponge. Several modern groups of colonial and solitary anthozoans that lack calcareous skeletons are able to colonize the outer surfaces of living demosponges (Swain, 2012; Kazanidis et al., 2016, Table 2). Modern epizoic calcareous bryozoans that colonize the surfaces of ephemeral substrates, such as living sponges, are released when the hosts decay (Hageman et al., 2000). In the case of the studied Ordovician bed, a unique specimen indicates that the solitary rugosan *Tryplasma* was able to attach to a spiculate sponge (Fig. 3C–D). The possibility that the co-occurring tabulate coral *Agetolites* could also attach to such a surface, and subsequently become free, cannot be ruled out.

5. Conclusions

The studied bed in the Late Ordovician Xiazhen Formation of southeastern China contains two species of the tabulate coral *Agetolites*, *A. maxima* and *A. oculiporoides*, the solitary rugose coral *Tryplasma*, mollusks, trilobites, and bryozoans. An abundance of spiculate sponge remains suggests that extensive “sponge meadows” were present, and the occurrence of spicule networks in calices and intracorallum spaces of *Agetolites* indicates a close association between sponges and corals. The fine-grained, burrowed lime mudstone lithology with many intact, unabraded fossils, in a bed that lacks high-energy sedimentary structures, suggests deposition in a calm to low-energy environment.

However, more than half of the agetolitid coralla occur in toppled or overturned orientations. Within disoriented coralla of *Agetolites*, the stratigraphic "up" direction recorded by geopetal infillings does not correspond with the original growth direction. The agetolitids did not undergo significant changes in growth direction during life and died at different times, rather than during a single event. They were either dead when disorientation occurred or died as a result of disorientation. Such features suggest that the coral heads fell to the seafloor without the influence of high-energy currents.

To explain such disorientation of massive corals, it is hypothesized that some *Agetolites* larvae settled on biodegradable substrates, consisting of sponges that formed "sponge meadows". The resulting corals subsequently tumbled down to the surrounding muddy sediment as they gained weight during ontogeny and/or after the death and decomposition of host sponges. If the coral was alive at the time, sudden deposition in a disoriented position within muddy sediment killed it. A small *Tryplasma* corallum still attached to a spicule network provides evidence that corals were able to attach to such sponges.

Disorientation of massive skeletons in the geological record, such as those of colonial corals, has most commonly been attributed to water energy, particularly high-energy events such as storms. The present investigation of Ordovician tabulate corals in a micritic limestone bed provides a new hypothesis involving ephemeral substrates, in this case consisting of spiculate sponges.

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