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Life strategies and function of dissepiments in rugose coral *Catactotoechus instabilis* from the Lower Devonian of Morocco

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This study focuses on the life strategies of small, dissepimented rugose coral *Catactotoechus instabilis* (representative of *Cyathaxonia* fauna) from the Emsian argillaceous deposits of mud mounds of Hamar Laghdad (Anti-Atlas, Morocco). Numerous constrictions and rejuvenescence phenomena as well as frequent deflections of growth directions among the studied specimens suggest unfavourable bottom conditions resulted from sliding down of the soft sediment on the mound slopes. Dissepimental structures observed on well-preserved calices and thin sections played an important role in the life of the coral, supporting their successful recovery after temporary burial within unstable soft sediment. The development of lonsdaleoid dissepiments, apart from being biologically controlled, was also strongly influenced by environmental factors. Such modifications in lonsdaleoid dissepiments growth were observed in phases of constrictions, rejuvenescence and deflections of growth, when their development was significantly increased in comparison to phases of their stable growth. Dissepiment morphology suggests that the process of formation of lonsdaleoid dissepiments in *Catactotoechus instabilis* is consistent with the hydraulic model.

Key words: Rugosa, corals, dissepiments, life strategies, Devonian, Hamar Laghdad, Morocco.

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Introduction

Small solitary Rugosa corals are often called the *Cyathaxonia* fauna sensu Hill (1938) or laccophyllid corals (Rózkowska 1969; Oliver 1992). Although, this group of Rugosa is commonly regarded as living in relatively deep water, they are also reported from shallower facies (Somerville and Rodriguez 2007) together with well-dissepimented and relatively large solitary and colonial corals (Oliver 1992; Somerville 1994; Fedorowski 1997; Scrutton 1998). The occurrence of this group in a wide range of facies representing various bathymetric and environmental conditions, proves their relatively wide tolerance. However, if not accompanied by shallow-water Rugosa, they may be used as indicators of relatively deep, cold, aphotic and quiet water (Kullmann 1997).

Corallites belonging to taxa of the *Cyathaxonia* fauna mostly lack dissepiments and possess a relatively simple septal structure. The lack of dissepiments (marginarium sensu Scrutton 1998) is the character that gives another name for the group i.e., “undissepimented” or “non-dissepimented” corals. There are, however, some exceptions where dissepiments (especially lonsdaleoid ones) sporadically occur in several taxa of the group. Here belongs *Catactotoechus* Hill, 1954, a genus known from the shaly and marly Devonian sediments. It was reported from four

relatively short time intervals of the following Devonian ages: Emsian of Morocco (Berkowski 2008), Givetian of Algeria (Birenheide and Schroeder 1999), Frasnian of Northern France (Rohart 1988, 2002), and Famennian of Australia (Hill 1954; Hill and Jell 1970) and China (Soto and Liao 2002). The development of dissepiments in so-called “non-dissepimented” corals must have given them some distinct advantages, which helped these animals to survive and grow in unusual biotopes.

The main purpose of this paper is to analyse the life strategy of the Emsian association of *Catactotoechus instabilis* Berkowski, 2008 and elucidate the morphogenesis and function of dissepimental structures in the growth and life of this exceptional example of “non-dissepimented” Rugosa corals.

Institutional abbreviation.—UAM TC, University of Adam Mickiewicz, Poznań, Poland.

Geological background and material

The *Catactotoechus instabilis* rugose coral association (assemblage C of Berkowski 2008) has been described from the

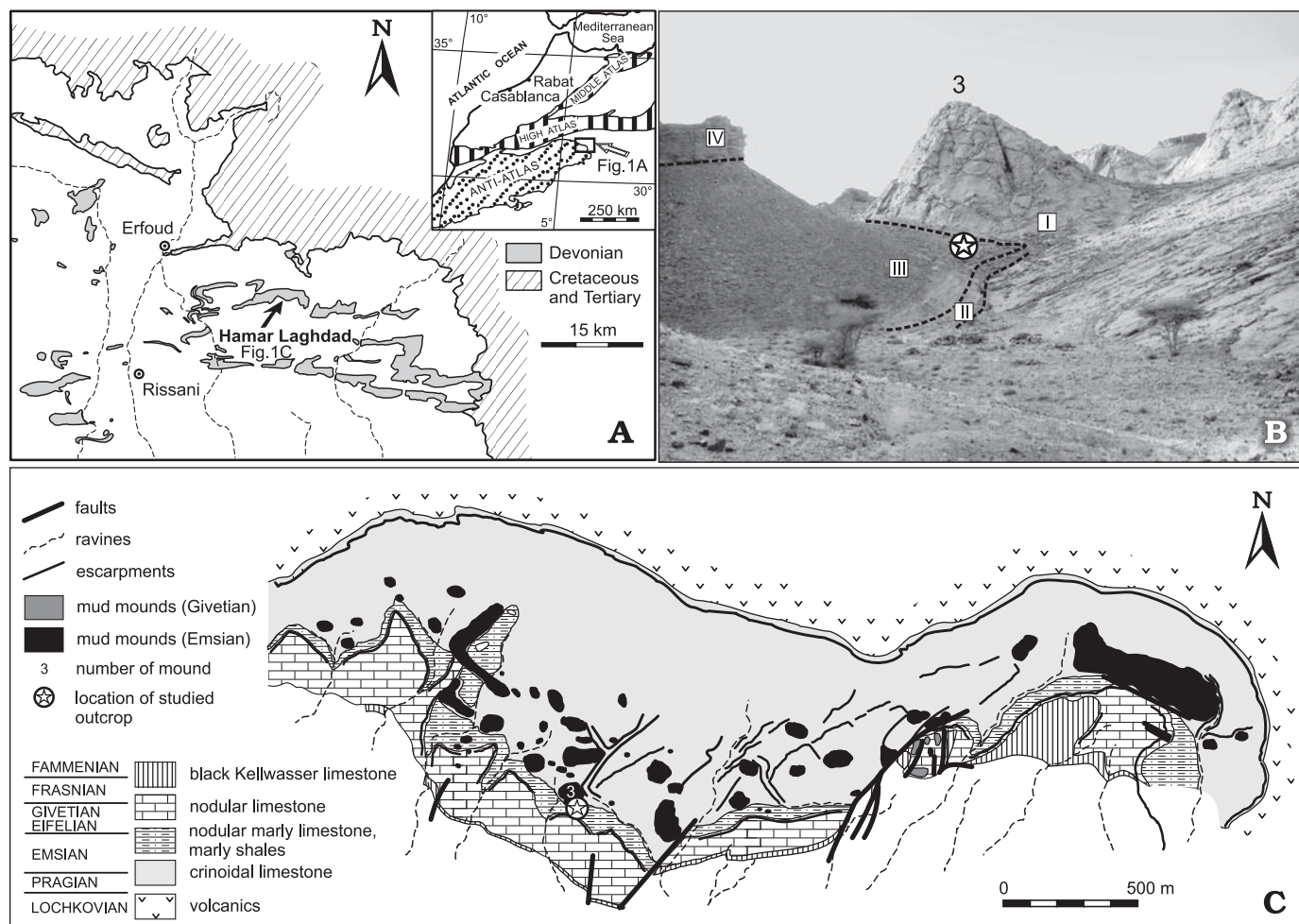


Fig. 1. **A.** Simplified geologic map of northeastern Anti-Atlas, Devonian rocks and Hamar Laghdad are indicated. **B.** Outcrop marked by star in circle on southeastern slope of the mound 3 (view from the east). Separated lithologic units marked as roman numbers in squares: I, Saheb el Rhassel Group (Kess-Kess Formation); II, Amerboh Group (marly nodular limestone); III, Amerboh Group (marly shale with marly limestone intercalations); IV, Bou Tchrafine Group. **C.** Detailed geological map of Hamar Laghdad with distribution of particular types of Devonian rocks. Star in circle indicates outcrop, where studied corals were collected. Drawings A and C courtesy of Belka (1998 and unpublished)—updated here.

marly shale covering mud mounds of Hamar Laghdad, located approximately 16 km southeast from Erfoud in the eastern Anti Atlas in Morocco (Fig. 1A, C). This area is famous for the perfectly exhumed conical-shape mud mounds (e.g., Roch 1934; Massa et al. 1965; Hollard 1974; Alberti 1982; Brachert et al. 1992; Wendt 1993; Belka 1998; Aitken et al. 2002; Berkowski 2004, 2006, 2008; Belka and Berkowski 2005; Cavalazzi et al. 2007). Mud mounds were formed in the Late Emsian, along syndimentary faults that served as conduits for migration of hydrothermal fluids (Belka 1998, Mounji et al. 1998). In the central and western parts of Hamar Laghdad hydrothermal activity was terminated by the end of *Polygnathus inversus* Conodont Zone, when the process of burial of these mounds started and continued into the *Polygnathus serotinus* and *Polygnathus costatus patulus* conodont zones. At that time more than 50 mud mounds existed as isolated submarine hills, up to 50 metres high, in close proximity to each other, which were subsequently buried by soft argillaceous sediments (Berkowski 2008). During the time of burial, the

covering sediments were mostly clayey and soft with only relatively small hard particles of biogenic origin. Due to their position on the steeply sloping flanks of the mounds these sediments often became unstable. As a result, losing their cohesion, they temporarily flowed down the slopes of the mounds together with their dead or alive inhabitants (Berkowski 2008). Only those sessile organisms survived, which developed some characters preventing them against being buried in soft sediment. Benthic organisms of these argillaceous deposits are mostly small Rugosa corals accompanied by tabulates, crinoids, bivalves, articulated brachiopods, and small phacopid trilobites. Rugosans are represented here by an almost monospecific association composed of numerous specimens of *Catactotoechus instabilis*, which have been found partly in life positions, restricted to the south-eastern flanks of the mound number 3 of Brachert et al. (1992) (N 31°22'28" W 4°03'12"), within the covering sediments (Fig. 1B, C). They are the subject of palaeoecological and palaeobiological investigations presented in this paper.

Analysis of *Catactotoechus instabilis* life strategy

The studied association of *Catactotoechus instabilis* displays a strong diversity of size and shape (Fig. 2). The average size of the most studied mature corallites are 0.5–4 cm. Typically, their shapes are ceratoid to trochoid, but in many cases they are irregular due to frequent changes of growth direction and may become strongly cornute or scoleoid (i.e., worm-shaped). Their calices are relatively shallow, in most studied specimens with typically developed calices, their depth, i.e., height/diameter ratio varies between 0.4–0.8. On the other hand, they reveal strong diversity in diameter dimension due to frequent process of constriction resulting mostly from various type of rejuvenescence phenomena and extensions of corallites in times of favourable conditions. Measured diameters vary from 0.4 to 2.2 cm, but typically are 0.8–1.5 cm. The strong variation in the shape of the specimens belonging to the association seems to result from four biologically and ecologically controlled factors: the strength of the attachment structures of the corallite, the stability of the host hard particles (mostly of biogenic origin), stability of the sediment and the rate of sediment influx.

Settlement strategy and initial growth.—The process of settlement of the larvae (planulae) is one of the most important stages of the coral life determining its future success or failure in growth and development. For the successful settlement of planulae a stable and relatively hard substrate is needed. Neuman (1988) suggests that the rugose coral larvae were not able to survive if settling strictly on soft unstable

substrates devoid of at least small hard grains for their attachment.

The settling larvae in majority of the individuals in the studied association seems to adapt a fixosessile, apically cementing life strategy (sensu Neuman 1988). Typically the initial parts of the corallites are firmly attached by talon structures to detrital hard particles i.e., tabulate coenostea (Fig. 2A), fragments of crinoids stems (Fig. 2B), molluscan shells or trilobite carapaces. In many cases they used the external walls of the corallites of dead or alive individuals (Fig. 2C, F), forming gregaria (pseudocolonies) composed of corallites of this same population. Some of them settled on the remaining part of the calicular rim of the alive specimen, after the rejuvenation process and inflicting further competition between the host specimen and newly settled juvenile corals (Fig. 2G). Others, less common in the studied assemblage, in which the larvae settled on small grains embedded in soft sediment did not develop talons (Fig. 2D, E). They either grew upward rooted in the soft sediment or floated on it, rapidly extending their width. Both types of settlement and growth are typical for soft, argillaceous sediments with embedded, here and there, hard particles of mostly biogenic origin, which had been fully exploited by sessile organisms as the base of their attachment.

Growth strategies.—Many of these specimens reveal a marked diversity of corallite shape after an initial growth period. This is the result of varied ecological factors that caused important skeletal modifications during corallite growth. Among these, the most prominent are: expansions and constrictions of the corallite diameter, rejuvenescence, and deflection of growth direction. Although the differences between these

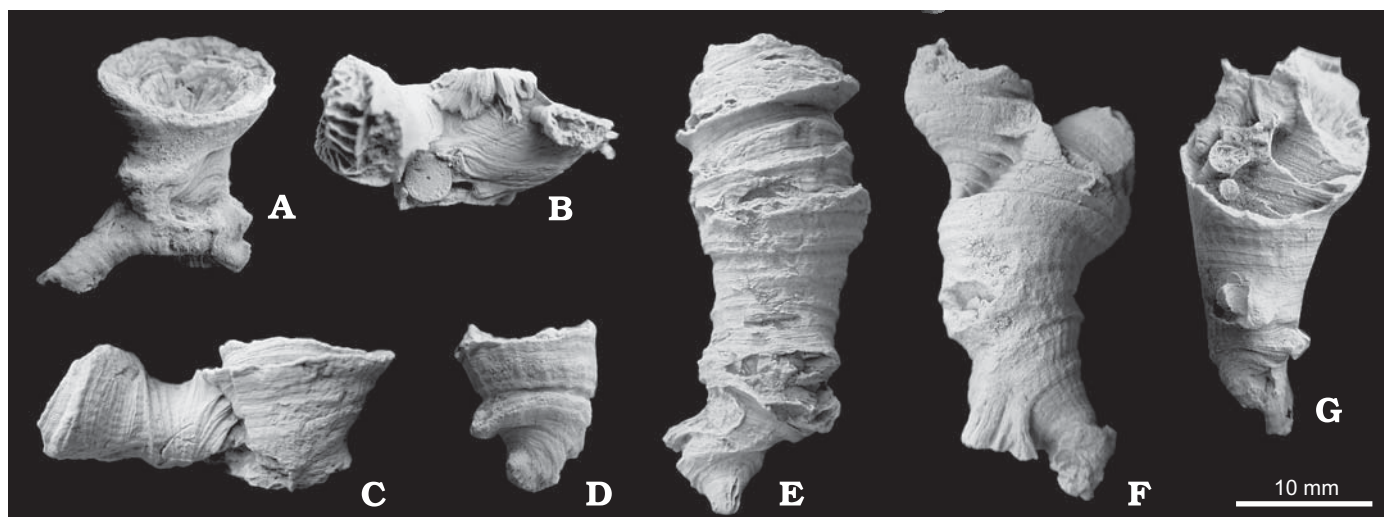


Fig. 2. External characters of the corallites of rugose coral *Catactotoechus instabilis* Berkowski, 2008, Hamar Laghdad (Morocco), Emsian. **A.** Specimen UAM Tc/B HD3/232 showing attachment to auloporidae tabulate coral (below). **B.** Specimen UAM Tc/B HD3/242 showing attachment to fragment of the crinoid stem. **C.** Specimen UAM Tc/B HD3/217 showing two corallites attached to each other, note expansion phase of growth after rejuvenescence in calicular part (above). **D.** Specimen UAM Tc/B HD3/238 showing weak constriction phase, note lack of attachment structures. **E.** Specimen UAM Tc/B HD3/237 showing successive constrictions and expansions during growth as well as deflection of growth direction in the juvenile stage; note lack of attachment structures. **F.** Specimen UAM Tc/B HD3/233 showing attached juvenile specimen on external wall near calice causing deflection of growth of calicular part of the corallite, note well developed attachment structure (talon). **G.** Specimen UAM Tc/B HD3/214 showing rejuvenescence and deflection of growth caused by settlement and growth of 3 juvenile specimens on the left part of calicular rim (competition).

modifications are easily distinguished, the boundaries between them are not sharp and it is possible to find intermediates. These have been observed both in well attached, fixo sessile forms and others, which lay directly on or were rooted within the soft sediment and therefore lack any attachment structures.

Expansion, constriction, and rejuvenescence.—Constriction and expansion of the corallite diameter reflect contraction and expansion of the polyp, which in turn apparently reflect changes (sometimes cyclic) in the ecological conditions influencing polyp health. The external wall of the corallite is marked by growth wrinkles that reflect expansion of coral diameter. Thus, the calice became broader or reduced, more or less rapidly. Extensional growth phases are characterized by relatively slow, mostly gradual and undisturbed growth. In this case the expansion of the polyp was restricted by the width of the calicular rim used by the polyp as the base for the newly-formed skeletal structures. This phenomenon is closely connected with initial growth of the polyp in its brepic and juvenile stages of growth, but may also proceed after constriction phases (Fig. 2C, D). On the other hand constrictive phases probably happened rapidly, thus the contracted polyp used various parts of previously formed calice. There are two main types of contraction phenomena (Fig. 3). (i) Weak and slow, marked only by narrowing of the corallite diameter. In this case, the polyp gradually reduced its diameter without leaving any part of the calice, and as a result, the external wall remained continuous. (ii) Marked and relatively abrupt, where a portion of the calice is left outside of a newly-formed external wall. In the latter case, the polyp

withdrew completely or partly from the calicular rim and began to form a new wall interiorly to the previously formed calice. As a result it abandoned the calicular rim and some of the inner calicular skeletal elements, which were no longer used to form new skeletal structures. This process is often called rejuvenescence.

Rejuvenescence is a common phenomenon observed in all groups of fossil (for a review see Scrutton 1998) and living (e.g., Chevalier and Beauvais 1987) corals. Fedorowski (1978: 180) redefined the term as “an action of a polyp leading to reduction of dimensions by leaving part of some skeletal structures in a calice outside its new external wall”. Both types, weak and strong contraction (rejuvenescence), may proceed axially or laterally (Fig. 3). Axial contraction (or rejuvenescence) occurs when the central part of the calice and also the central part of the polyp remain in place almost unchanged, whereas their marginal parts are narrowed. In contrast to this, lateral rejuvenescence takes place when a polyp leaves only a part of the calicular periphery on a given side of the calice, whereas the other side remains unchanged.

Polyp contraction, which is manifested by constriction of skeleton growth, may be connected to various reasons: extrinsic, related to surrounding physical, chemical and biological environmental conditions or intrinsic, related to the overall condition of the polyp. It is possible to speculate that the axial contraction is an effect of decreasing diameter of the pedal disc due to its resorption, caused by e.g., lack of food sources. On the other hand, lateral contraction is in most cases relatively rapid and seems to be an effect of extrinsic factors. Among them the most prominent are: partial burial of the calicular part of the skeleton, falling and a resulting recumbent posture of the corallite, injury caused by other organisms, competition between coral and other incrusting fauna etc.

Most examples of constriction and rejuvenescence in the studied association display the lateral types. They were observed on the external wall and in longitudinal sections (Fig. 4) but also on well preserved calices (Fig. 5).

Weak constriction is manifested by delicate narrowing of the corallite diameter on the external wall (Fig. 4B, D). In this case the wall is continuous on each side of the corallite but in the lateral type it can be narrowed only on one side. In longitudinal section it is clearly distinguishable by increasing size and/or number of dissepiments, which in first stage caused narrowing of the tabularium (Fig. 4B₂, D₂), and reflects gradual contraction of the polyp. This type was also observed on well preserved calices (Fig. 5B), where it is manifested by narrowing of the tabularium by lonsdaleoid dissepiments.

Strong constriction i.e., rejuvenescence is clearly distinguishable on external wall (Fig. 4A, C, E) in places where the part of the wall is destroyed on a given side of the corallite. It is often easy to identify an abandoned portion of septa and dissepiments inside well preserved calices (Fig. 5C). In longitudinal section it is well distinguishable by the remaining part of the calicular floor on a given side (Fig. 4E: on the left

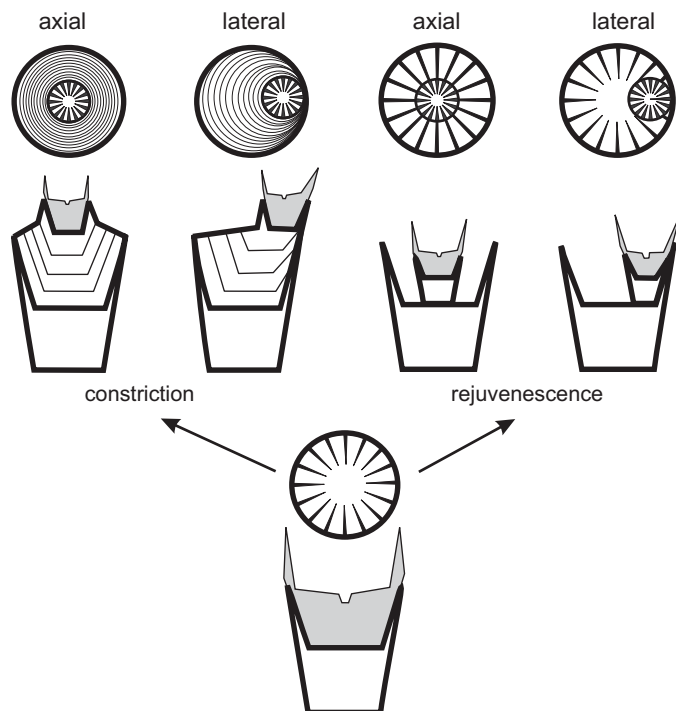


Fig. 3. Schematic drawing of constriction and rejuvenescence phenomena showing their axial and lateral types.

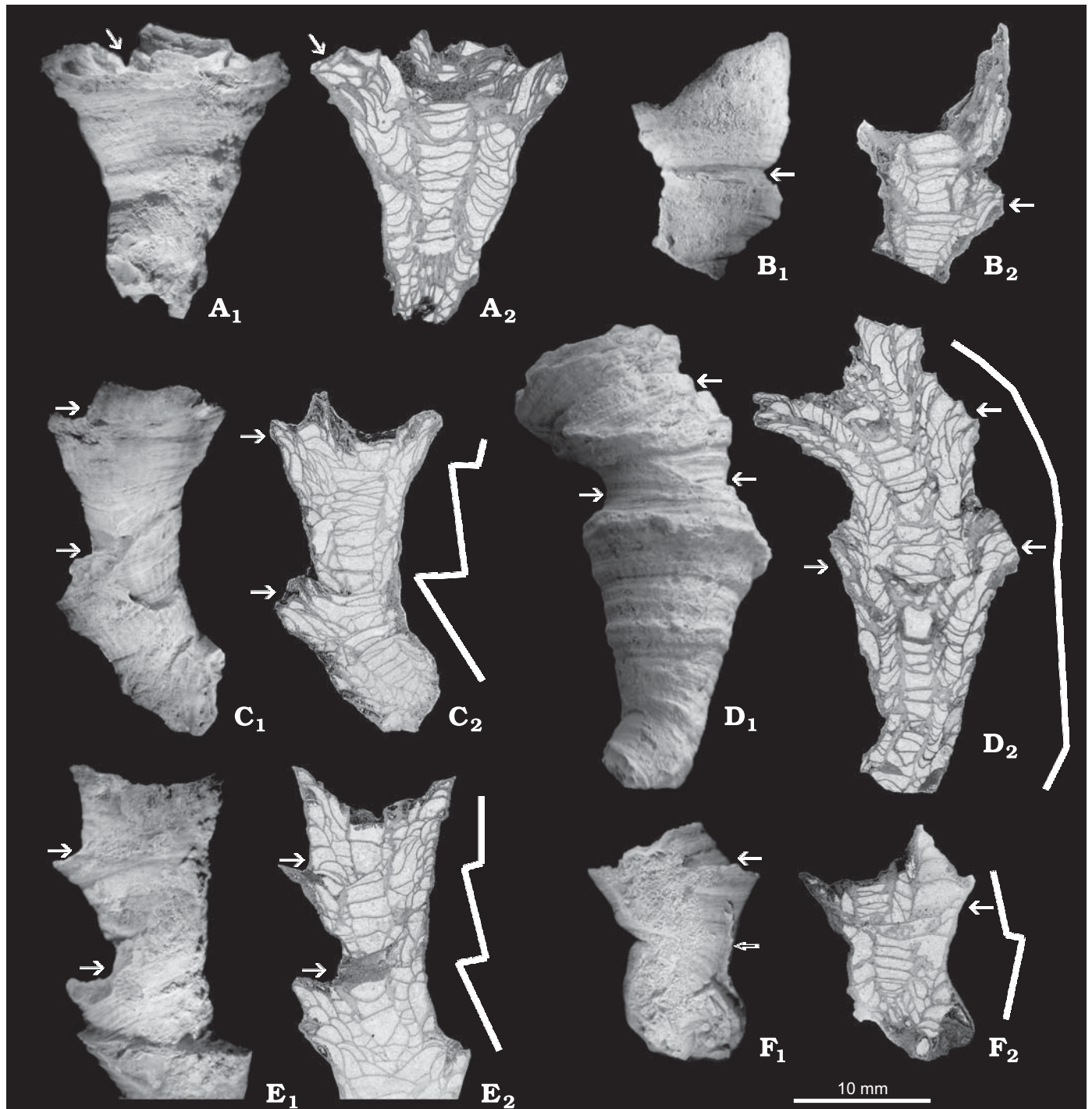


Fig. 4. External view (A₁–F₁) and equivalent longitudinal sections (A₂–F₂) of the studied specimens of rugose coral *Catactotoechus instabilis* Berkowski, 2008, Hamar Laghdad (Morocco), Emsian (Devonian). Arrows show constriction and rejuvenescence phases of growth, note on external walls they are higher than in inner part on longitudinal sections following morphology of the calice. White lines (C–F) show deflections in growth direction. **A.** Specimen UAM Tc/B HD3/243 showing widely expanding corallite and strong rejuvenescence in the calicular part of the corallite, note lack of dissepiments in expanding phase on the left side. **B.** Specimen UAM Tc/B HD 3/240 showing temporal weak constriction followed by extension phase, note markedly reduced diameter of the central lumen (aulos) caused by development of dissepiments in constriction phase. **C.** Specimen UAM Tc/B HD3/244 showing two weak rejuvenescences accompanying unidirectional deflections of growth. **D.** Specimen UAM Tc/B HD3/246 showing expansion phase followed by three weak constriction phases; note relatively gradual unidirectional deflection of growth. **E.** Specimen UAM Tc/B HD3/206 showing two strong rejuvenescences causing rapid unidirectional deflections of growth. **F.** Specimen UAM Tc/B HD3/204 showing deflection of growth direction caused by interaction with auloporoid tabulate coral (marked by black arrow) incrusting external wall of the corallite.

side), which was often invaded by sediment. The process of rejuvenescence thus is characterized by narrowing and/or

shifting of the tabularium and formation of a new wall with dissepiments (Fig. 4 A₂, C₂, E₂).

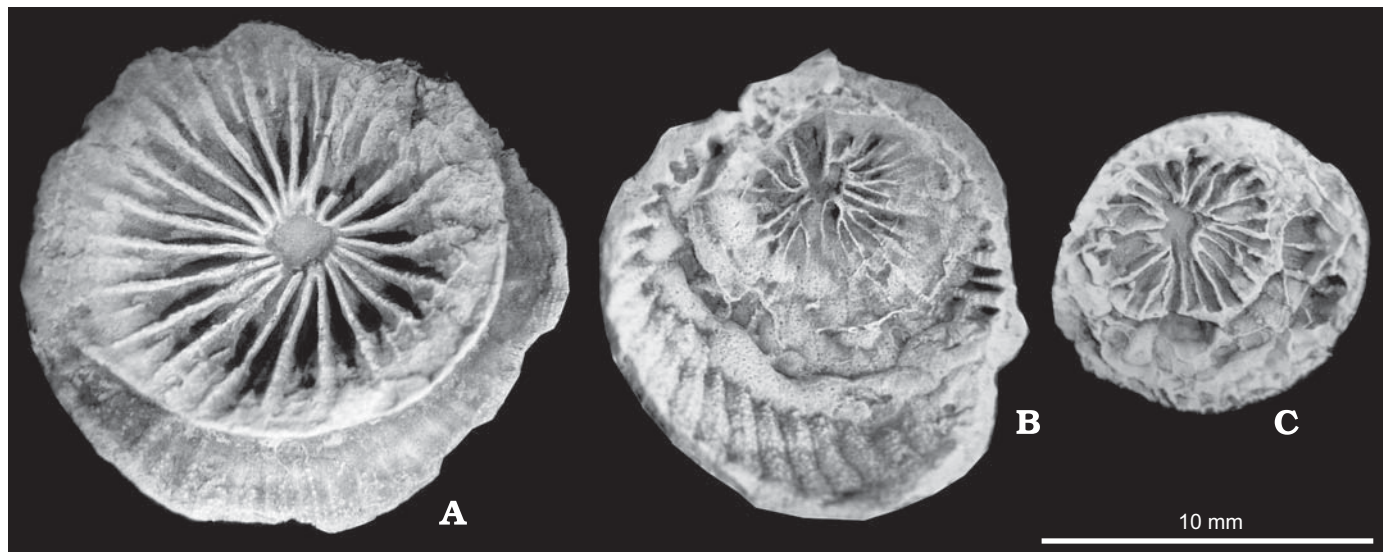


Fig. 5. Well preserved calices of the rugose coral *Catactoechochus instabilis* Berkowski, 2008, Hamar Laghdad (Morocco), Emsian. **A.** Specimen UAM Tc/B HD3/217 showing inner calicular structures of extending calice after rejuvenescence; note well developed septa of both orders. **B.** Specimen UAM Tc/B HD3/212 showing increase of large lonsdaleoid dissepiments formation and simultaneous constriction and shifting of the septal apparatus; note large dissepiment covering previously formed septa. **C.** Specimen UAM Tc/B HD3/211 showing strong and abrupt constriction of the corallite; note that the wall of rejuvenated part of the corallite is surrounded by a new wall and dissepiments outside it are not fully developed.

Deflection of growth direction.—As upward growth is typical for corals, any deflections of the corallite reflect changes of growth direction during the polyp's life. Such deviations in most cases are caused by extrinsic factors such as bottom currents, soft and unstable sediment, or interactions with other organisms. The phenomenon of deflection of growth direction may occur very early in the ontogeny, especially in specimens not attached firmly to stable objects and also in later ontogenetic stages. Juvenile specimens previously attached only to small grains often became recumbent on soft sediment, and again formed skeletons trying to recover an up-facing position. A similar recovery process is represented in mature specimens by the scolecoïd shape of corallites, where several deflections can be traced during the complete growth of the corallite. Growth deflections can also co-occur with phenomenon of lateral rejuvenescence. In fact, most specimens revealing lateral rejuvenescence caused by partial burial of the calicular part of the corallite commonly changed growth direction soon thereafter.

The majority of specimens of the investigated *Catactoechochus instabilis* association show frequent changes of corallite growth direction. These changes are clearly marked by growth wrinkles (rugae) on the corallite external wall and reflect past positions of the calicular rim, i.e., the edge of the calice (Fig. 4C–F). Hence, it is easy to trace periods of stable upward growth of the corallite, as well as the events of their reaction to extrinsic factors causing deflections of their growth direction. This is evident in longer, ceratoid and scolecoïd forms. Here several successive deflections of the corallite appear during their growth history. External surfaces and longitudinal sections of most specimens studied show that repeated deflections proceed in this same direction (Fig. 4C–E), mak-

ing corallites cornute rather than scolecoïd. This suggests they were subject to one repeated, unidirectional process. Taking into account bottom topography of the sea floor, and the character of its sediment, it would seem that these corals lived on the slopes of mud mounds, within and upon the soft and unstable sediment had simply gradually moved downslope, causing this recumbence. This process, when relatively strong and abrupt, may have caused the partial burial of their calices and polyps and resultant lateral rejuvenescence (Fig. 4E).

Deflections of growth direction have been also observed in specimens, that interacted with other organisms exploiting their skeletons for attachment. Among these organisms, rugose corals of the same species and tabulate corals predominate as incrusting fauna (Figs. 2F, G, 4E).

Note on dissepiments

To understand the process of the formation of dissepiments a careful study of the relationship between the polyp's basal disc and the skeleton is needed. Wells (1969) summarized three models, which have been postulated for the process of dissepiments formation. First, mechanical, tension-induced proposed first by Ogilvie (1896) and further summarized by Hill (1936). Ogilvie (1896) suggested that the ectoderm is detached and lifted as the effect of periodic growth of the septal edges, and consequently during the period of pause a new dissepiment is secreted and thickened. Hill (1936) stated that crystals forming dissepiments are secreted continuously at right angles to the surface of the basal ectoderm of the polyp. She further suggested that the space between the existing dissepiments sur-

rounded by septa, trabecular in nature, and the basal ectoderm of the polyp have been created by stretching upward of this part of the polyp. As a result the polyp pulls away from the previously secreted dissepiments to give space for the formation of new blisters. Kato (1963) analyzed this model in a slightly different way. He suggested spasmodic detachment and upward shift of an unfolded part of the ectoderm. Contrary to these opinions Matthai (1914) proposed the second model followed later by Weyer (1972). These authors claim that dissepiments are formed as a result of horizontal infolding of the column wall, where the dissepiment is secreted between layers of ectoderm. In such a model the polyp finally is divided horizontally, and the lower part is cut off and is going to decay. Matthai's (1914) concept was rejected by Wells (1969) and most later coral workers who noted that the nature of the microstructure of dissepiments is not the same as of septa, hence it could not be secreted within the folded pocket of ectoderm. The third model has been proposed by Wells (1969) who followed Wedekind's (1937) observations that the polyp's basal ectoderm secreted liquid or gas between existing dissepiments and the basal disc. As a result basal disc lifted to form a space filled by liquid or gas, and subsequently starts to secrete a dissepiment centripetally. This process called "blistering" was studied in detail by Sorauf (1970) on several taxa of scleractinian corals. He distinguished three types of dissepiments: tabular, interseptal and thecal, suggesting that among them tabular dissepiments, found in deep-water *Lophelia*, might be analogous to those occurring in the Rugosa. Additionally, Sorauf (1970) suggested the presence of a mucopolysaccharide-like template filling the space between the skeleton and the basal calicoblast ectoderm of the polyp, which help to keep the ectoderm in a position of newly formed dissepiment.

The geometry of horizontal structures of the corallite may be convex, flat or concave with reference to corallite direction of growth. Most types of dissepiments are convex whereas tabulae and tabellae in most cases are flat or even concave. The diversity in geometry seems to reflect a different kind of "blistering" process responsible for the formation of a given structure. Assuming both, mechanic and hydraulic models as valid, it seems most probable that flat and concave structures might be formed following both ways, but those which are convex must follow the hydraulic model of Wells (1969). In this model the process of lifting is triggered by the ectodermal secretion of liquid between existing structure and basal ectoderm. Hence, it may be assumed that this process may produce hydrostatic pressure of the liquid, which seems to play an important role in three successive steps during formation of dissepiments: (i) it helps to detach the ectoderm from the skeleton in the place where the new structure is going to be formed; (ii) it lifts the ectoderm to the final position of the new structure; (iii) it shapes a detached basal ectoderm within the void, which finally gives shape to the secreted structure. In the first two steps, forming the space for the new structure, the hydrostatic pressure of the liquid secreted between the basal ectoderm of the polyp and the already exist-

ing skeletal elements has to be higher than the pressure occurring within the soft body of the polyp. During the third stage the hydrostatic pressure may stay high or become even higher to produce a convex structure or lower to form flat or concave ones. Hence, the degree of protuberance of the newly-formed structure is a function of the diverse hydrostatic pressure in enclosed spaces between the already existing skeletal elements and the basal ectoderm of the polyp. Following this model, the convex geometry of most dissepimental structures seems to be a result of relatively high hydrostatic pressure of the fluid secreted by the basal ectoderm to the space between the skeleton and the polyp. Such convex structures cannot be formed following only the mechanic model proposed by Ogilvie (1896) or Hill (1936), as it does not explain the presence of high hydrostatic pressure. On the other hand, we can easily apply it to structures, which are flat or concave, since as in this case the pressure in the cavity may be as high as within the polyp or even lower.

Summarizing the present state of knowledge, the two models i.e., mechanic and hydraulic, seem to be the most plausible for the explanation of the formation of dissepiments. Whether one of these concepts or both are responsible for the formation of different types of basal elements seems to remain an unsolved question up to date, although some new remarks on it can be made considering lonsdaleoid dissepiments of the corals studied herein.

Dissepiments in *Catactotoechus instabilis*.—Two main types of dissepimentaria (marginaria) may be distinguished in Palaeozoic Rugosa corals: 1, interseptal, mostly regular in nature, with various kind of relatively small dissepiments formed between existing septa, and 2, transeptal or pre-septal (lonsdaleoid and cystiphylloid), mostly irregular, where dissepiments are relatively large and in most cases disrupting septal growth, and which often become the base for the repeated septal development. The *Catactotoechus instabilis* association analyzed in this paper possess transeptal (i.e., lonsdaleoid) dissepiments, which developed on the relatively large areas of the calice. Contrary to interseptal dissepiments they formed more or less bulbous, and mostly irregular in outline vesicles, which were not limited by the septal walls. Therefore, it appears that their shape and size was limited only by the ability of the polyp to create and maintain the free space between the already existing skeleton and the basal ectoderm. It seems that in such an instance, hydrostatic pressure was fully responsible for pushing up and shaping the ectoderm prior to formation of transeptal dissepiments (Fig. 6). In most cases transeptal vesicles covered previously formed septa or septal crests disrupting their growth and subsequently became the base for their repeated formation. This recurrence is well visible on transversal sections of the corallite, where dissepiments, mostly convex toward the axis, display septal crests on their topmost part (Fig. 7A, B). Formation of these types of dissepiments seems to proceed in a somewhat different mode (Fig. 6E–H). We can imagine that during the process of lifting the basal ectoderm

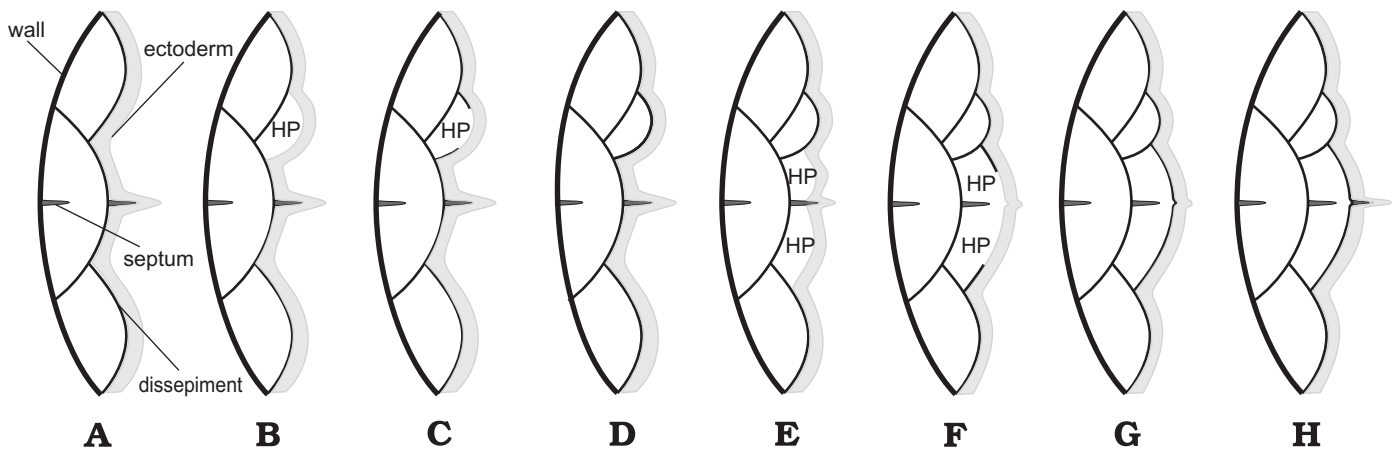


Fig. 6. Schematic drawing showing successive stages of formation of lonsdaleoid dissepiments. **A–D.** Smaller dissepiment created between septal pockets. **E–H.** Larger dissepiment created in place with septal pocket, disrupting septal growth. Note hydrostatic pressure (HP) between basal ectoderm and skeletal structures is here responsible for the pushing up the ectoderm and shaping the dissepiment. Morphological nomenclature refers to all figures (A–H).

must have left the skeleton together with the fold of the septal pocket. Hence, the already existing septal crest in the place where the dissepiment was formed must have been finally stripped off of the septal pocket. The pocket was either partly or fully straightened during this process. Both possibilities have been observed in the fossil record as the occurrences or lack of invaginations of “dark line” on the underside of dissepiments (Fig. 7). Longitudinal sections of the studied corallites show that in undisturbed growth dissepimentarium formed one or two rows of relatively regular, flat lonsdaleoid dissepiments. In the extending phases following contractions they could even disappear (Fig. 4A). But when growth was more or less disturbed their development increased rapidly. In the phases of weak contraction they became more numerous and/or relatively large and bulbous, making the diameter of the central lumen and finally the whole diameter of the calice decreased (Fig. 4B, D). In case of strong contraction caused by e.g., partial burial of the calicular part they developed a floor for the rejuvenescence process on the undisturbed part of the calice (Fig. 4E). Similarly, when the corallites changed growth direction, their development increased on the convex side of the specimen to fill the space between the newly-formed wall and the central lumen and, finally, deflecting growth direction. Detailed investigation of longitudinal section of the specimen displaying deflection of growth caused by interaction with the tabulate coral, indicates that this process started by formation of several, large tabulae-like dissepiments sealing off previously formed calicular structures on the affected side of the calice (Fig. 4F). Here they formed a new floor inclined at an angle of 10–30° to the previous one. Next, large steeply sloping lonsdaleoid dissepiments were secreted by the polyp on the disturbed side of the calice. This process consequently caused shifting of an axial part of the corallite to the opposite side of the calice (Fig. 4F). During this process the polyp shifted only the central part of its pedal disc, being fully attached to calicular rim, as documented by continuous formation of the wall (Fig. 4F).

Functions of dissepiments.—In a general sense, dissepiments, like other horizontal elements of the corallite are structures supporting the base of the polyp. Sorauf (2007)

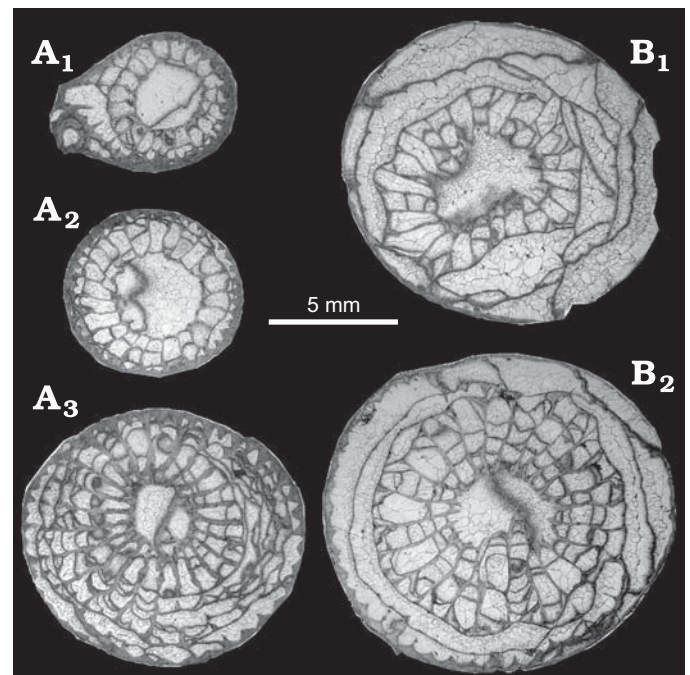


Fig. 7. Successive transversal sections showing development of lonsdaleoid dissepiments in two corallites of rugose coral *Catactotoechus instabilis* Berkowski, 2008, Hamar Laghdad (Morocco), Emsian. **A.** Specimen UAM Tc/B HD3/200; **A₁**, juvenile stage of growth showing interaction with aloporeid coral; note dissepiment on this side; **A₂**, next stage showing one row of lonsdaleoid dissepiment-extension phase of growth; **A₃**, mature stage of growth showing increase in development of dissepiments in constriction phase of growth; note that diameter of central lumen (aulos) is narrowed. **B.** Specimen UAM Tc/B HD3/201; **B₁**, constriction phase of growth showing irregular lonsdaleoid dissepiments narrowing septal area; note invaginations of dissepiment in places where septal crests are formed; **B₂**, extension phase of growth showing decrease of lonsdaleoid dissepimentarium and expansion of septal area.

distinguished also two other functions of dissepiments i.e., anchoring for the coral and maintenance area for feeding and/or protective purposes. He further claimed that the dissepimentarium provided to the living parts increased area for tentacles and cilia, and hence, improved chances for food collection and sediment elimination. The dissepimentaria of Rugosa may be composed of small, mostly interseptal dissepiments or larger lonsdaleoid ones. The latter disrupt septal growth and often become the base for the repeated septal development. It is commonly accepted that interseptal dissepimentaria occurring both in solitary and colonial corals are the characters typical for the relatively shallow-water taxa. This type of dissepiments makes the coral skeletons denser, stronger and finally heavier. Thus, it seems that the main function of this kind of dissepiments is to reinforce the coral skeleton against vigorous hydrodynamics caused by waves and bottom currents. On the other hand, lonsdaleoid dissepimentaria or presepiments are typical of taxa living in/on soft muddy substrate (Somerville and Rodriguez 2010) and/or in relatively turbid water (Sorauf 2007). Moreover, formation of such dissepiments requires less energy than in the case of septal formation and consequently they develop much faster than other skeletal elements. Their development decreases the amount of skeletal fabric within the corallite making the density of coral skeleton low, thin and relatively light. Hence, their occurrence played a completely different function. Analysis of lonsdaleoid dissepiments in specimens of studied association of *Catactotoechus instabilis* presented above allowed to add one more function to these structures. Increase of their development in phases of constrictions, rejuvenescence and deflections of growth versus their limited increase in phases of extension of the calice and stable upward growth show that lonsdaleoid dissepiments played an important function in the recovery phenomena by providing support for the shifting base of the polyp and making these processes relatively fast and successful.

Conclusions

Study of dissepimentaria and growth interruptions of *Catactotoechus instabilis* association from the Emsian argillaceous sediments covering Hamar Laghdad mud mounds allows the following conclusions to be drawn:

- All examined specimens *Catactotoechus instabilis* lived on a soft bottom, which temporarily lost cohesion and stability due to high inclination of the seabed. This is clearly proved by frequent successive rejuvenescences and constrictions of the studied corallites and numerous, mostly unidirectional changes of their growth directions as well. These phenomena were caused mostly by corals sliding down the slope within soft sediment during their life.
- The corals were successful in recovering from unfavourable conditions. This is manifested by numerous successful rejuvenescences and frequent deflections of growth directions and most likely linked with the presence of lonsdaleoid dissepiments. Development of this type of dissepiments is here regarded as one of the most important factors increasing the speed and effectiveness of reorientation of corallites of *Catactotoechus instabilis*.
- Variability of lonsdaleoid dissepimentaria in corallites of *Catactotoechus instabilis* seems to be linked strongly with extrinsic ecological factors. This variability is often manifested in one corallite by increased development of lonsdaleoid dissepimentarium in constriction and rejuvenescence phenomena or in phases of change of growth direction of the corallite, as well as decrease or even lack of their formation in expansion phases. Hence, quantitative determinations of dissepiments cannot be regarded as an important taxonomic value of this species. On the other hand, their strong diversity and character might be useful for determination of variation in ecological conditions, especially these controlled by the stability of sediment and interactions with other organisms.
- Formation of lonsdaleoid dissepiments in *Catactotoechus instabilis* is consistent with hydraulic model of Wedekind (1937) and Wells (1969).

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