The function of dissepiments and marginaria in the Rugosa (Cnidaria, Zoantharia)

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Abstract: Dissepiments of both Rugosa and Scleractinia formed in the same way, but in the former, are restricted (by definition) to the periphery, in a marginarium (dissepimentarium). The marginarium provided a buffer zone between the vital parts of the rugosan polyp and its physical environment, and may be regular or lonsdaleoid (with presepiments), or may lack dissepiments. Late Devonian and Carboniferous rugosans lacking dissepiments are small, restricted to deeper water and referred to as the "*Cyathaxonia* fauna". During several times of transition in the Palaeozoic (Ordovician to Silurian; Late Devonian to Carboniferous) non-dissepimented corals provided precursors for the evolution of populations characterized by presepiments, which in turn gave rise to populations with normal dissepiments. The most common function of dissepiments in the Rugosa was to provide support for the base of the polyp, as in the Scleractinia, but in rugosans the dissepimental area also was commonly molded to form a pedestal for the coral on hard substrate. Other functions apparently were to provide 1) anchoring of corallites in soft muddy sea floor, and 2) expansion of the flattened peripheral ciliated area of rugosan polyps. Marginaria thus can reflect major ecologic change, suggesting that this portion of the polyp body could be altered without mortal damage to Rugosa.

Key words: Dissepiments, Rugosa, marginarium, dissepimentarium, Paleozoic

Contents

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1. INTRODUCTION

The structure and configuration of dissepiments in the Anthozoa, and their locus of occurrence (in Rugosa, the dissepimentarium), are relatively well known (Pl. 1, Fig. 1). Dorothy Hill (1956) provided researchers with a rationale for study of the paleobiology and evolutionary development of the marginarium (dissepimentarium) in Rugosa when she noted that among the evolutionary trends in the Rugosa, the most important is, "the production of a marginarium between the epitheca and tabularium" (Hill, 1956, p. F256). The present paper focuses on development and function of the dissepiments and dissepimentarium (marginarium) within Middle and Late Paleozoic Rugosa.

Both Wells (1969) and Sorauf (1970, 1972) stated that dissepiments form identically in Rugosa and Scleractinia. Staining by Barnes (1970) showed that the first-formed layer of dissepiments is rapidly built, taking only several days. However, dissepiments occurring in a separate, specialized area of the corallite, the dissepimentarium, are a feature of many Rugosa, and this spatial restriction does not occur in Scleractinia, where they function as support structures for the polyp throughout (Fig. 1). Thus, the function of the dissepimentarium cannot be deduced by analogy with living corals. This difference is more than just semantic. By definition, in the Rugosa dissepiments are restricted to the peripheral zone within radially arranged corallites, whether solitary or colonial, except in some corals lacking tabulae and tabularium, the cystimorphs. There is also an
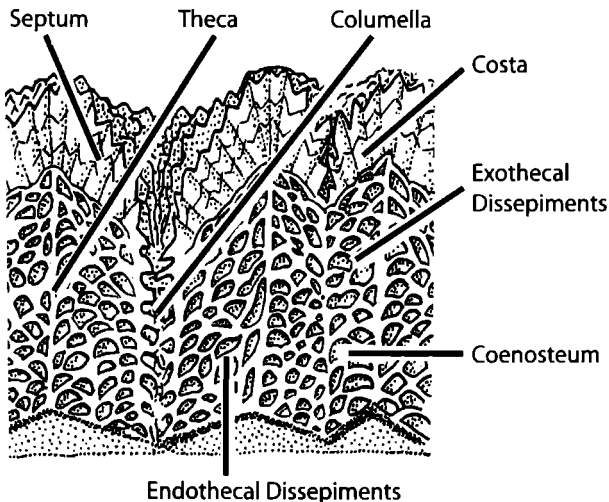

Fig. 1:
The occurrence of dissepiments and coenosteum in the colonial genus *Montastraea* (Scleractinia), from Wells (1956, Fig. 244).
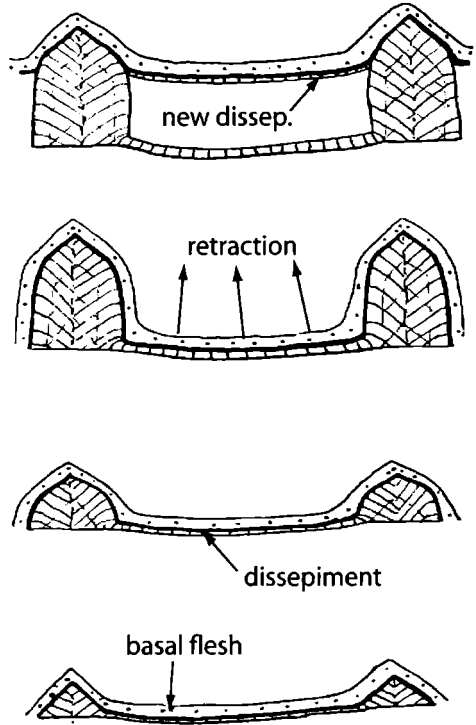
Fig. 2:
Hill's model (1936, Figs. 3–6) of the formation of idealized septa and tabulae (or dissepiments) through continuous growth on septal edges which displaced the polyp upwards, with subsequent positions forming series of tabulae.

1.5 cm
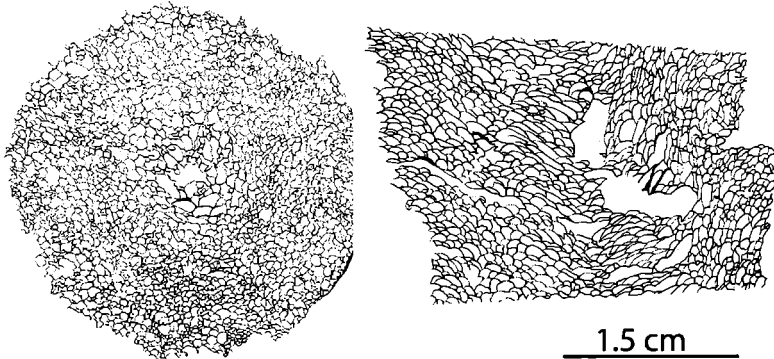
Fig. 3: *Plasmophyllum (Plasmophyllum) secundum schlueteri* (WEDEKIND, 1921), illustrating morphology of this cystimorph rugosan. Here, dissepiment formation was not dependent on growth of septa, which are lacking. Illustrations from BIRENHEIDE (1964); transverse, thin section #16453$_1$ (Pl. 3, Fig. 2), longitudinal, thin section #16453$_2$ (Pl. 14, Fig. 67). Scale bar equals 15 mm.

important difference in skeletal topography, as scleractinians have septa projecting above the dissepimental surface (OGILVIE, 1896), while this is demonstrably not the case in some rugosans (Fig. 3).

OGILVIE (1896, p. 157) was one of the first to discuss the configuration and manner of formation of dissepiments in living corals, presenting her ideas rather compactly, in terms of how dissepiments are formed in the "typical Astraeids". She made the assumption that other corals do things the same way, which is largely but not totally correct. OGILVIE noted that, "At the close of each growth-period in typical Astraeids, the basal portion of the aboral body-wall situated between the radial invaginations deposits a layer or floor of calcareous dissepiments". She hypothesized that the aboral wall is drawn upwards gradually and continuously during the period of active growth of the septal edge, thus forming arched dissepiments through withdrawal of flesh. Finally, she noted, a period of 'pause' sets in, and, "the body wall between the septa remains supported on its many-arched floor which is then completed and thickened" (op. cit., p. 157). One of OGILVIE's remarkable statements regards the topography of the uppermost surface of the calice. She stated that, "The last-formed floor of dissepiments is *always some distance below the septal edges.*" (Italics are hers.) "Usually some five or six septal growth-segments are present between the dissepiments and the growing edges of the primary septa. This fact allows lateral thickening of the septal growth-segments to go on during the interval which elapses between their first laying down at the septal edge and the ultimate withdrawal of the body-wall of the polyp. Complete withdrawal of the body-wall from any particular tier of trabecular parts in a septum is of course marked by the formation of a dissepimental floor at the horizon just above it." (op. cit., p.157). She also suggested that primary septa in Scleractinia are generally thickest because they extend to the greatest height above the dissepimental floor, and have undergone lateral thickening during a larger number of growth periods. BARNES & LOUGH (1993) presented a model for biocrystallization of coral skeleton in *Porites* with similarities to this older scheme.

HILL's hypothesis (1936, p. 191) was that, during formation of dissepiments, the crystals forming them are continuously formed at right angles to the surface of the secreting ectoderm. She suggested that septal trabeculae are formed in point-like invaginations of the basal disc, with secretion of crystals "more copious at the apex of the trabecular invagination". The resultant stretching upwards of the polyp's basal flesh caused the polyp to eventually pull away from the previous dissepiment. Thus, the discontinuous formation of dissepiments reflects a "periodic relief of stress", (HILL, 1936, p.192). WELLS (1969) noted the hypothesis of WEDEKIND (1937) that coral polyps secreted liquid or gas into space formed between a pre-existing dissepiment and the basal disc, and WELLS also remarked (1969, p. 25) that it is more probable that this fluid-filled space developed by hydraulic lifting of the polyp.

1.1. Formation and function of dissepiments

Although the foregoing details several opinions regarding the formation of dissepiments, this paper focuses primarily on the biological and ecological significance of the dissepimentarium. Here is first presented a brief summary of the mode of emplacement of

series of dissepiments. In discussing their origin, one needs to keep in mind that, in non-septate corals such as some cystimorph rugosans (Cystiphyllidae, Plasmophyllidae, etc.), they formed as a series of blister-like structures (Fig. 3) under up-pocketed basal ectoderm, with little development of septa. WELLS (1969) suggested that the basal disc lifted to form a space filled with liquid or gas, and referred to this as "Wedekind's Theory"; to date it has not been accurately determined whether there is or is not additional fluid involved. WELLS noted (1969, p. 18) that this theory was supported by the need for liquid or other some substance to occupy the subpolyp space because, "Nature abhors a vacuum."

The general purpose of basal (or horizontal) skeletal elements, such as dissepiments or tabulae, is the support of the base of the polyp. However, this is only a generality, and does not precisely state specific functions and adaptations of the dissepiments and dissepimentarium. In the following, lonsdaleoid dissepimentaria are discussed, ones having presepiments peripherally disrupting septa, their appearance as skeleton having in part predated later-formed septa. There may be sound palaeobiological reasons for development of this peripheral zone in rugosans; it is postulated that in Silurian and Devonian corals, the weak peripheral development of septa and greater development of lonsdaleoid marginaria are related to life in turbid water and on or in a mud substrate. There are several ways in which this development could have been useful to rugosans living on soft substrate.

2. OBSERVATIONS

The dissepimentarium can be composed of small, numerous dissepiments (Pl. 1, Figs. 1, 2), or fewer and larger ones, perhaps reflecting rapidity of growth and skeletal development by the coral polyps, and cyclic change in size is common in the Rugosa. This can vary greatly within single populations of a species. The marginarium is somewhat irregular, but often is a surprisingly plastic portion of the corallite. Dissepiments and/or presepiments can be bulbous or very elongate and thin, interleaved with surrounding fine sediment (Pl. 1, Figs. 2, 6), or forming a wall of closely spaced, steeply inclined dissepiments at the inner margin of the dissepimentarium, thus separating it from the tabularium. There also may be a stout outer wall separating the marginarium (dissepimentarium) from surrounding sediment.

2.1. Width of dissepimentarium (marginarium)

Study of the paleobiology of caninioid corals from the Early Carboniferous of Ireland led HUBBARD (1970) to observe that there is a close connection between the width and variation in width of dissepimentarium in rugosans and fluctuating environmental conditions. HUBBARD (1970, p. 202) listed what she called "original skeletal peculiarities". These are with regard to, 1) distance between tabulae, 2) "suppression of the dissepimentarium", and 3) skeletal thinning. The distance between tabulae is variable in these corals, commonly they are grouped into areas with more and fewer tabulae. She also noted that tabulae are sometimes unusually thin and more widely spaced than usual,
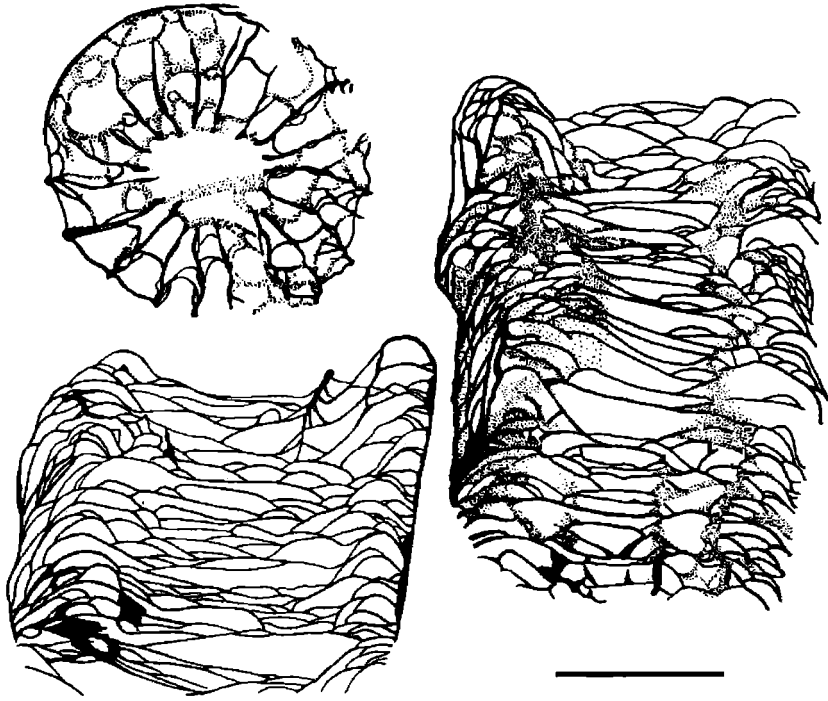
Fig. 4: *Kielcephyllum cupulum* Rozkowska, 1969. Late Devonian (Famennian), Kadzielnia, Poland, to show development of "lonsdaleoid vesicles" (tabellae) forming calicinal prominence around the more central part of the tabularium. These figures are from Rozkowska (1969, p. 108, Fig. 40). Scale bar equals 15 mm.

coinciding with narrowing of the dissepimentarium (Pl. 1, Fig. 6). As narrowing develops, the tabularium maintains a nearly constant diameter while the dissepimentarium shows a marked reduction in area. In the extreme, it is difficult to discern a dissepimentarium. The skeletal thinning was taken by Hubbard to reflect adverse conditions in which the coral could not sustain its usual rate of secretion of skeleton, as it coincides with widely spaced tabulae and restricted dissepimentarium. This would appear to be the opposite to growth banding in modern corals, where more rapid growth of skeleton results in lighter skeleton.

The width of the lonsdaleoid dissepimentarium has been shown to be highly variable in *Tabulophyllum traversensis* from the Middle Devonian of Michigan (Sorauf, 1996). Population studies here clearly showed that for a relatively large number of specimens examined (168), there was normal distribution of total diameters and length of septa in the population, and plotting area of lonsdaleoid dissepimentarium showed a geometric curve with a steep initial slope, indicating that most individuals have a small dissepimentarium, although some few individuals have as much as 24 times the minimum area.

2.2. Shape of calice

Since the dissepiments in Rugosa are deposited at or near the upper surface of the corallite calice, on the calicinal platform, rows of dissepiments reflect the shape of the base of the polyp. In some genera and families the development of specialized dissepiments seems to reflect modification of this upper surface. Such is seen in Late Devonian corals, with the formation of circumoral ridges of the Famennian Friedbergiidae and the horseshoe dissepiments of the Givetian and Frasnian Phillipsastreidae (Fig. 4). In the Famennian genus *Friedbergia* described by Rozkowska (1969), topography is commonly developed at the periphery of the calice even though not formed by dissepiments *per se*, but by tabellae (or fragmented tabulae). This development of calicinal topography is also obvious in the phillipsastreids where horseshoe dissepiments formed circular ridges at the surface (Pl. 2, Fig. 3).

The development of marginaria filled with dissepiments or presepiments was perhaps an adaptation providing a functional advantage, such as allowing ease of distension of polyps for the shedding of sediment. Thus, it is important to study the surface of the calice and longitudinal sections, focusing on the presence, width, steepness or bulbosity of individual dissepiments, reflexing of the calice and arching of the dissepimentarium, or formation of a steep marginarial wall; all are ways to modify the calicinal surface. All provide clues to the paleoecology of rugosans.

Studies of modern corals have provided information regarding sediment rejection by modern scleractinian polyps. Hubbard & Pocock (1972) listed connections between calice shape and sediment rejection. Noting that the direct means for sediment rejection are cilia, tentacles, distension and mobility, they listed a number of their findings, among which are some that deal with the shape of the calice. These are pertinent to considerations of the role played by dissepiments and presepiments in modifying this shape. They found that polyps reject sediment by distension through stomodeal up-take of water to an approximately constant 300–400% of normal volume. They also noted that the "distension potential is directly related to the surface area of the calice". Particles that are larger than silt-size are generally removed (Hubbard & Pocock, 1972, p. 617) by "controlled distension and in some species, tentacular action." Efficiency of distension and mobility was shown to be closely related to calice geometry; thus, they suggested that active polyps have higher calicinal relief among other characters (op.cit., p. 617). In rugosan corallites this suggests that the size and shape of dissepiments are important, especially in forming arching or cupping of the calice.

2.3. Symmetry of dissepimentarium

It is important to analysis of coral life position to examine the symmetry of development of the marginarium, whether it is regular or lonsdaleoid, as both seem to be about equally prone to modification with growth orientation. Within symmetrically developed marginaria, there are also variations in the regularity of individual dissepiments as some are very thin and leaf-like in *Tabulophyllum rotundum* (Pl. 1, Fig. 1), where these are interleaved with muddy sediments.

Species of *Siphonophyllia* from Famennian strata show the same feature (Pl. 1, Fig. 3). *Tabulophyllum magnum* from the Frasnian of Iowa is a very large solitary coral showing interleaving of surrounding mud and its lonsdaleoid dissepimentarium (Pl. 1, Fig. 6). *Tabulophyllum rotundum* from the same strata also has very thin, symmetical outgrowths (Pl. 2, Fig. 2), here the overall diameter of the coral decreases upward without much change in the tabularium.

Asymmetrical development of the dissepimentarium is generally seen to accompany curvature (especially extreme curvature or geniculation) in solitary corals. In such circumstances, the dissepimentarium is invariably broader on the convex side of the coral, and the diameter of the tabularium remains more or less the same, except for gradual increase through growth. This is shown in geniculate individuals of *Heliophyllum halli* (SORAUF, 2001, p. 27), where most differential growth of the corallum is due to differential growth of the dissepimentarium, with more and larger dissepiments characterizing the convex side of the corallite.

2.4. Cyclomorphic variation

Variation in the rugosan dissepimentarium is generally cyclic, termed cyclomorphic by SCRUTTON (1998, p. 13). Variation in area is reflected as expanding and contracting of the marginarium in solitary corals, at times expressed as rather mushroon-like lateral growth of dissepiments. This is not just seen in solitary corals (Pl. 1, Fig. 6; Pl. 2, Fig. 1), but also is well developed in amural colonies of some genera, where there is remarkable cyclomorphic variation in size and density of skeletal elements in Devonian *Iowaphyllum* (SORAUF, 1998) and in Silurian *Arachnophyllum* and *Prodarwinia* (SCRUTTON, 1988, 1998). The two groups of corals are characterized by the occurrence of septal crusts which occur cyclically (SCRUTTON, 1988, Pl. 6; SORAUF, 1998, Pl. 7). Both have the development of wall ridges delineating corallites on the septal crests. In both there is also cyclomorphic occurrence of very large, irregular, blister-like dissepiments occurring in layers between crusts (see SCRUTTON, 1988, Pl. 7; SORAUF, 1998, pl .6). In these homologous colonies, variation in skeleton density is expressed by alternating septal crusts (dense skeleton) and zones of large, bulbous dissepiments (light). Additionally, spacing between corallites and the resulting area of corallites varies somewhat within colonies depending on rates of budding.

2.5. Development of marginaria through geological time

The Rugosa twice went through sequential development of faunas comprising only rugosans lacking dissepimentaria with the subsequent appearance of faunas with lonsdaleoid dissepiments which then gave rise to faunas with regular dissepiments. This is seen in solitary rugosans of Middle and Late Ordovician age passing upwards into the Early Silurian (NEUMAN, 1984; ELIAS, 1984), and in Late Devonian (Frasnian and Famennian) to Early Carboniferous (Tournaisian and Visean) corals (SANDO, 1980; HILL, 1981; SANDO & BAMBER, 1985; SORAUF & PEDDER, 1986; WRZOŁEK, 2002). Why was this development advantageous for Paleozoic corals?

NEUMAN (1968, p. 232) illustrated an Ordovician rugosan, *Paliphyllum suecicum*, with a dissepimentarium remarkably like that of Devonian *Tabulophyllum*, with similar fine sediment infilling the periphery as in species of *Tabulophyllum*. He later (1984, p. 121) stated that, "Dissepiments of lonsdaleoid type seem to be the oldest kind, represented in *Neotryplasma* and *Paliphyllum* from Baltoscandia (of late Middle Ordovician and Late Ordovician age, respectively). Several genera with lonsdaleoid dissepiments developed during the Llandovery (e.g. *Arachnophyllum* and *Microplasma*). The first genus with small, globose dissepiments seems to be *Protocyathactis* from the Late Ordovician, and during the Llandovery a number of genera with globose dissepiments developed." Thus, the sequence here is clear.

Similarly, one sees a sequential development of post-Frasnian rugosans, with small, non-dissepimented corals dominating early Famennian faunas, leading to late Famennian (Strunian) platform faunas dominated by larger corals, many of which have lonsdaleoid dissepimentaria (SORAUF & PEDDER, 1986; SORAUF, 1992; POTY, 1999; WRZOŁEK, 2002). The sequence is repeated in the Early Carboniferous coral faunas of North America, as reported by SANDO & BAMBER (1985).

Analysis of the *Cyathaxonia* fauna indicates that the great majority of the deep water Famennian taxa were non-dissepimented and small (see SORAUF & PEDDER, 1986, Fig. 5). WRZOŁEK's work (2002) indicates that:
1. Cystiphyllida are represented in this fauna by four genera of the Palaeocyclidae, all of which lack dissepiments.
2. Stauriida are represented by three suborders, the first of which, the Metriophyllina, has 43 genera occuring in the fauna, of which ten genera in six subfamilies (23% of the fauna) have some sort of development of dissepiments, one genus of which has lonsdaleoid dissepiments (*Guerichiphyllum*). A second suborder, the Stereolasmatina, contains 38 genera which occur in the *Cyathaxonia* fauna, but of these, only one genus with dissepiments occurs. A third suborder occurs, the Plerophyllina, represented by 48 genera in the fauna, but with only four genera having a dissepimentarium.

The Famennian fauna contains 40 genera, of which eight have a dissepimentarium (two are lonsdaleoid, and an additional one has dissepiments in late growth stages only). Two of the 40 genera (*Laccophyllum* and *Barrandeophyllum*) have tabellae that are shaped like dissepiments and may have had a similar function.

All of the corals in the *Cyathaxonia* fauna are small, and most dwelt in deep water. Many were survivors (19 genera) of the ecological disruption that occurred during the latter part of the Frasnian. Other genera, many with lonsdaleoid dissepiments (POTY, 1984; SORAUF, 1992; POTY, 1999), appeared in late Famennian carbonate shelf deposits to form the Strunian fauna.

The data of SANDO & BAMBER (1985) supports the statement by SANDO (1980, p. 625) that the number of shallow water coral genera increases upwards in the sequence from Famennian into Tournaisian strata. Non-dissepimented coral genera are most abundant at the base of the Tournaisian, with the subsequent increase first of genera with lonsdaleoid dissepiments, including *Vesiculopyllum* and *Guerichophyllum*, then in later Tournaisian, *Caninia*, *Stelechophyllum*, *Zaphriphyllum* and several others. Genera with regular dissepiments appear in younger strata. In North America this accompanied shallowing that took place in the Cordilleran region and development of widespread carbonate shelves.

3. DISCUSSION

The foregoing indicates that dissepiments of soft-bottom-dwelling corals with lonsdale-oid dissepimentaria and presepiments functioned either for support, as most did, or for anchoring of the polyp in the upper part of underlying or surrounding sediment, as well as for improved living on shallow carbonate shelf areas. It is assumed that normal (regular) dissepiments almost always function primarily for polyp support and attachment within the calice.

3.1. Support function

The support function of the dissepimentarium is operative in several similar situations, both apparently connected to soft bottom environments. In one case, the development of talons or a flat-bottomed pedestal appears where a larval rugosan polyp has settled on a hard object, such as brachiopod (Pl. 1, Fig. 5); and in the other case, where the rugosan corallum is supported on soft substrate, and the dissepimentarium apparently functions to spread weight out onto substrate (Pl. 1, Fig. 4). Both are well shown in *Tabulophyllum traversensis* from Middle Devonian strata of Michigan and New Mexico. This species had the ability to develop a broad, flat base which formed a mold of the tesselated surface of the receptaculitid *Sphaerospongia* (SORAUF, 1987). Apparently larval settlement was on the receptulitids (whether dead or alive), and formed the flat base by modification of the dissepimentarium. More common in this and several other species of *Tabulophyllum* that occur within the Middle and Late Devonian is support on soft bottom sediments. This is well shown by *Tabulophyllum rotundum* (SORAUF, 1998, Pl. 8, Fig. 8), which has asymmetric dissepimental outgrowths on the convex side of the corallum. In the Late Devonian of Iowa, *Tabulophyllum magnum* shows marked expansions and contractions, with considerable asymmetry of the dissepimentarium (Pl. 1, Fig. 2) and the species also contains large individuals that have great deal of interleaving of dissepiments and surrounding sediment, while at the same time maintaining constant diameter of the tabularium (Pl. 1, Fig. 6). Expansion of the dissepimentarium here correlates with levels of wider than normal spacing of tabulae, and contraction correlates with complete tabulae that are heavier than normal. The observation by HUBBARD (1970) and by SORAUF (2001) of this phenomenon associated with geniculations in corals from shaly habitats reinforces this interpretation of the support function.

The shape of dissepiments, generally somewhat hemispherical, commonly rounded, bending upwards, or blistering, is suggestive of a fluid nature for the supporting medium. As pointed out by D'ARCY THOMPSON (1914), surface tension causes small bodies of liquid to be rounded; thus the shape of dissepiments which approach the hemispherical may reflect either the fluidity of underlying fluid or sediment, or the surface tension of the flesh itself. This is not at the same scale (cellular level) as suggested by THOMPSON, but rather at the scale of "blisters" in the rugosan dissepimentarium. The suggestion by WEDEKIND (1937, p. 28) was, "The lifting of the polyp however, can only succeed through its forming an enduring space beneath the basal disc by excretion of gas or liquid which will then be covered by carbonate" (JES translation). This point was also made by WELLS (1969, p. 19).

3.2. Anchoring function

The anchoring function appears to be best illustrated in several species in which the dissepiments are very thin, less than 0.5 mm, and/or, elongate and irregular, forming a network in surrounding sediment. These are often removed by weathering, especially in specimens collected from the outcrop.

Tabulophyllum rotundum (in SORAUF, 1998), as shown above has very well-developed leaf-like extensions of the dissepimentarium into surrounding shaly matrix (Pl. 2, Fig. 2). These are very thin, symmetical outgrowths, but can have asymmetrical development, greater on the convex side of the corallum. Here, the outgrowths are symmetrical but, while corallite diameter decreased upward, the tabularium did not change much, as the dissepimentarium is the locus of almost all reduction in corallum diameter. Another specimen of this species exhibits very delicate dissepiments forming an irregular network in fine sediments surrounding the coral (Pl. 2, Figs. 7, 8). This very delicate structure is thought to have been an effective anchor for the coral.

PEDDER & MURPHY (2003), describing Early Devonian corals from Nevada, have illustrated (2003, Figs. 5.9, 7.15, 8.14) spectacular specimens of *Papiliophyllum* and *Eurekaphyllum* that have a dissepimentarium formed of extremely thin and irregular dissepiments, which apparently were buried in mud, thus escaping subsequent destruction during weathering out of the fossils, if not previously by currents or bioerosion.

SORAUF (1992) illustrated several Famennian species with well-developed and abundant lonsdaleoid dissepiments, characteristic of late Famennian Strunian faunas. *Siphonophyllia folia* has a particularly extensive "mud-platform" built of presepiments (Pl. 1, Fig. 3), with a clear inner wall between the lonsdaleoid part of the coral and the inner part of the corallite. Most of the corals from this unit (the Percha Shale) have extensive "interleaving" of the dissepimentarium and surrounding mud. Skeletal elements are very thin where they are isolated in the mud.

3.3. Dissepimented and non-dissepimented rugosans

SORAUF & PEDDER (1986) illustrated shallow water rugosans with large diameter and well-developed dissepimentarium from late Frasnian strata. These were preferentially eliminated by the late Frasnian Hangenberg event (or events). *Hankaxis mutabilis*, illustrated from the late Frasnian of Belgium (SORAUF & PEDDER, 1986, Pl. 1, Fig. 1) shows a great amount of lateral expansion of the dissepimentarium, up to a maximum diameter of more than 6 cm. It displays interweaving of trabeculate crust layers alternating with dissepiment layers, with the calice having a low, "volcano-like" profile. The function of this broad dissepimentarium is enigmatic. If seen in living scleractinian corals it would be assumed that it had a sunlight-gathering function, but such seems unlikely in the Rugosa, where there is little or no supporting evidence of photosynthesizing symbionts, much of the cause of phototropism in scleractinians.

Illustrations of Late Devonian (Frasnian and Famennian) non-dissepimented corals were published at the same scale as dissepimented ones by SORAUF & PEDDER (1986, p. 1271), making it clear that the former were very small, with diameters only 1/4 to 1/5 that of average solitary Devonian rugosans. Does a broad dissepimentarium reflect

phototrophism? Perhaps, but it more likely reflects a way to achieve maximal size without developing an extremely large gut, oral disc and/or numerous tentacles. In this case, the formation of a broad dissepimentarium would have provided some of the benefits of coloniality connected to large size and lateral spreading without the necessity of the budding process.

WRZOŁEK (2002) noted that the greatest decrease in diversity for the *Cyathaxonia* fauna (of small, oceanic? deeper water corals) occurred in the Early and Middle Devonian, rather earlier than for large, carbonate shelf dwelling rugosans, near the end of the Frasnian. This suggests that there was a loss of habitat in the oceanic realm, perhaps due to plate movement causing closing of the "East Laurasian Sea" (WRZOŁEK, 2002). This group of (mostly) non-dissepimented rugosans occupied considerably different habitats than did the larger, dissepimented forms. It is noteworthy that rugosans in the "recovery faunas" of late Famennian (Strunian) age are characterized by numerous species with lonsdaleoid dissepimentaria. Presumably, the *Cyathaxonia* fauna provided surviving rugosans to populate a post-Frasnian/Famennian Extinction revival of coral faunas. These faunas, when moving into shallower water from deeper water, into more dynamic shelf environments, may have required a buffer between the tabularium and surrounding physical environment. This reaction to sediment and water in motion perhaps caused of the re-development of dissepiments in the latest Devonian and Carboniferous.

The evolution of rugosans from the late Famennian (Strunian) into the Carboniferous involved a complex history of homeomorphy and intense intraspecific variation, unraveled in large part by POTY (1999). He noted that extremely variable Strunian species underwent partial extinction at the Devonian–Carboniferous boundary, with survivors evolving into Carboniferous types with morphologies characterized by various and complex columella, differing dissepiment types and complex marginaria. POTY (1999, p. 16) noted that the parent species had, "a large potential for adaptation in many new, free niches." Much of this adaptation was focused in the development of a complex marginarium. The early expression of this evolutionary development is the lonsdaleoid form. *Guerichophyllum*, which occurrs in the *Cyathaxonia* fauna, may be one of the earliest to show this adaptation of non-dissepimented corals for life on a soft substrate. The faunas of the Mississippian, as reported by SANDO & BAMBER (1985), clearly indicate that, as faunas moved from deep water onto shallow shelves at this time, first presepiments and a lonsdaleoid dissepimentarium appeared and were most prominently developed. Afterwards, the regular dissepimentarium developed and became abundant in faunas of the later Early Carboniferous shelves. SANDO (1980, p. 625) suggested that a reservoir of predominantly deep-water corals existed somewhere during the latest Devonian (Famennian) time and that these corals provided the gene pool from which the Early Mississippian corals evolved. POTY (1999) has been specific as to how this happened.

3.4. Colonial rugosans

The function of dissepiment-filled coenosteum, as it occurs in such amural colonial corals as *Arachnophyllum*, *Prodarwinia* and *Iowaphyllum*, perhaps resulted from one of several causes. The area of individual corallites varies among colonies and also within

colonies and species of these genera. However, there is in each a minumum area for adult corallites. This suggests several possibilities, such as:

1) Corals used this large area for collecting food that was settling out of sea water along with sediment. The colonies do not show epibionts. Cilia and mucus on ciliated colonial ectoderm might have aided in the feeding process, moving food to the mouths of individual polyps, as in some scleractinians.

2) Large areas of ciliated tissue would have helped in the removal of fine sediment. It is perhaps better to interpret the success of large polyps in this function (HUBBARD, 1970) as having to do more with the abundance of tentacles and non-specialization of cilia on the oral disc rather than large polyp size *per se*. Cilia along with mucus, function to remove fine sediment.

3) The rugose corals had photosymbionts (zooxanthellae), thus the larger area would have been beneficial for collection of sunlight (as seen in flat, platy modern colonial scleractinians). I regard this as improbable because of the common occurrence of these rugosans in fine-grained strata.

The area of coenosteum (Fig. 1) varies among colonies and within colonies. If the dissepimentarium functions as a "buffer zone" for solitary corals, then a similar function can be assumed for dissepimental coenosteum, especially in amural colonies. Then, spacing between corallites would be maintained to provide tentacles with "sweeping distance" for feeding. The development of wall-like ridges extending upwards from septal crusts (Pl. 2, Fig. 4) apparently indicates where the junction between individuals occurred.

More generally speaking, in colonial corals, spacing and presence or absence of a wall between individuals within the colony may effectively dictate the size and shape of the dissepimentarium. Then, much of the internal morphology of individual corallites is dictated by the genetic composition of predecessors of these colonial forms, implying that the evolution of colonial corals was from solitary corals, with major skeletal characters at least partially inherited.

3.5. Paleobiology

The tabularium, as opposed to the dissepimentarium, appears to remain quite uniform in its diameter, regardless of expansion and contraction of the dissepimentarium (Pl. 1, Fig. 6; Pl. 2, Figs. 1, 2). Presumably expansion and contraction can be correlated to variation in the rapidity of sedimentation, more rarely reflecting events (storms, fungal or bacterial infestations). Apparent functions of the dissepiments and marginarium are several; 1) support for the coral, 2) anchoring for the coral, and/or 3) maintenance of area for protective purposes or for feeding. FEDOROWSKI (1997, p. 32) also noted the constancy of the tabularial diameter while the width of the dissepimentarium "varied, reflecting small changes in the width of the oral disc resulting from extrinsic factors […]." Calicinal prominences such as in the phillipsastreids (Pl. 2, Fig. 3) then may mark the former position of the innermost ring of tentacles on the oral disc of rugosans. FEDOROWSKI's insightful reconstructions of rugosan polyps (e.g. FEDOROWSKI, 1997, Fig. 6) show the inner ring of tentacles approximately at the boundary between the tabularium and the marginarium. We can easily imagine at least two rings of tentacles located on

the rugosan oral disc, with one ring surrounding the tabularium and one or more on the surface covering the marginarium, with tentacles remaining in a relatively fixed position. Then tentacles would have tended towards being concentrated at the periphery of the tabularium and over the marginarium in many rugosans, with the following results:

1. If the coral polyps had photosynthesizing symbionts, spreading would be advantageous to expose larger amounts of flesh to sunlight. In the Rugosa this was probably not the case, but larger area would have aided in feeding, especially by the tentacles, located in flesh above the marginarium, and also by cilia, collecting settling materials, both food and sediment, and in the latter case, functioning for its elimination. This assumes that the Rugosa, like all other Anthozoa, had cilia on all exterior ectoderm, as well as the ability to secrete mucus.
2. Distribution of weight on soft substrate was apparently of great importance, a great advantage to rugosans living on and in shaly substrate. This is the common lithology rugosans are found in. Numerous authors, such as ELIAS (1984, p. 533) and NEUMAN (1988, p. 98), have suggested that a frequent life style for solitary Rugosa was lying on the substrate, only slightly indenting the surface.
3. Anchoring of corals was apparently important for some rugosans, and here I have focused on those living partially buried within sediment. YONGE (1940) observed that few corals die as a result of sediment raining on them, but instead emphasized the dangers of sediment encroaching on the margin of the polypal basal disc.

These corals were well adapted for life on soft substrates. We should expect that they had effective cleansing by cilia, ciliary currents and secretion of mucus. Those corals that have an interleaving of the dissepimentarium and sediment show a lack of mobility and were probably fixed, upper surface epifauna. The non-dissepimented corals of the Paleozoic are generally seen in shaly and/or deep water environments, reflecting an effective adaptation for living in areas with slow rates of sediment accumulation. They probably lived on the sediment surface, with their small size making it possible to remain at the top of water saturated fine-grained sediment at the sediment-water interface. Corals with well-developed dissepimentaria were better suited to shallower, more dynamic environments with higher rates of sedimentation and turbid waters.

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Plate 1

Magnifications as stated.

Figs. 1, 2: *Tabulophyllum magnum* WEBSTER & FENTON, 1924. Fig. 1: x 1. Fig. 2: x 0.9. Late Devonian of Iowa, transverse and longitudinal sections illustrating the central tabularium and marginal dissepimentarium of this large Upper Devonian genus. *Tabulophyllum magnum* has both normal dissepiments (between septa) and presepiments, peripheral dissepiments predating formation of septa.

Fig. 3: *Siphonophyllia folia* SORAUF, 1992; x 1.6. Late Devonian (Famennian) of New Mexico. Transverse thin section showing well developed presepiments, with septa here restricted to the inner part of the corallum.

Fig. 4: *Tabulophyllum magnum* FENTON & FENTON, 1924; x 1.7. Late Devonian (Frasnian) of Iowa. These small dissepiments were primarily for support on soft substrate.

Fig. 5: *Tabulophyllum ehlersi* FENTON & FENTON, 1924; x 3.6. Late Devonian (Frasnian) of Iowa. Support on hard substrate (brachiopod shell) developed out of the dissepimentarium.

Fig. 6: *Tabulophyllum magnum* FENTON & FENTON, 1924; x 1. Upper Devonian (Frasnian) of Iowa, longitudinal section shows dramatic expansion and contraction of the dissepimentarium of this coral, which lived on soft substrate. Note that the tabularium does not contract and expand, but that tabulae are more widely spaced at irregular intervals.
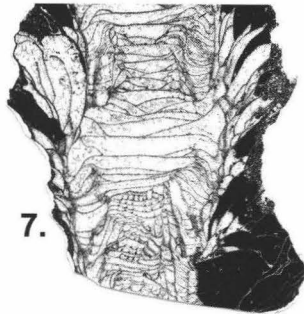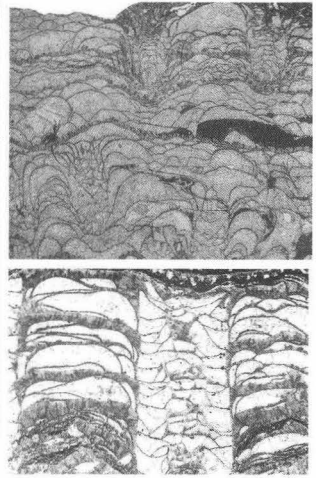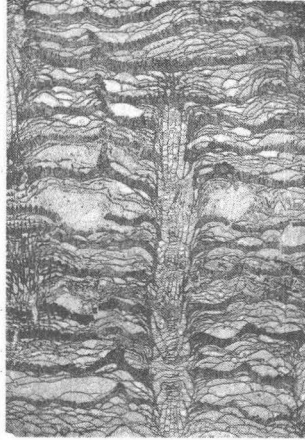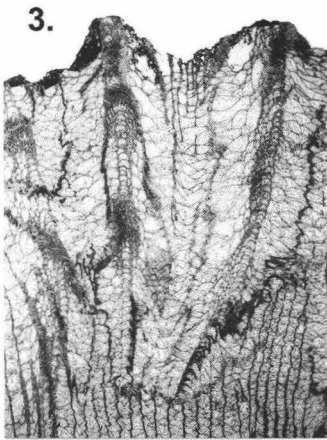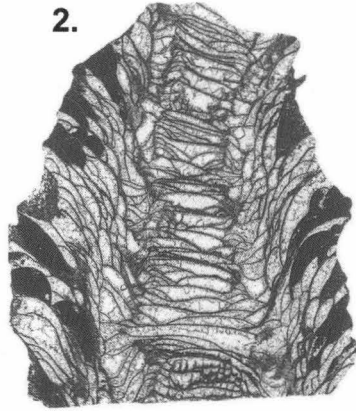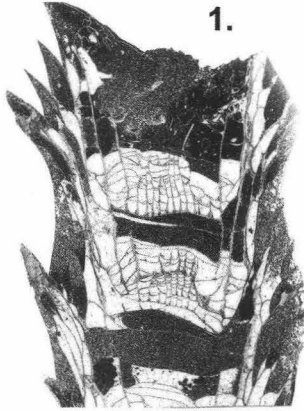
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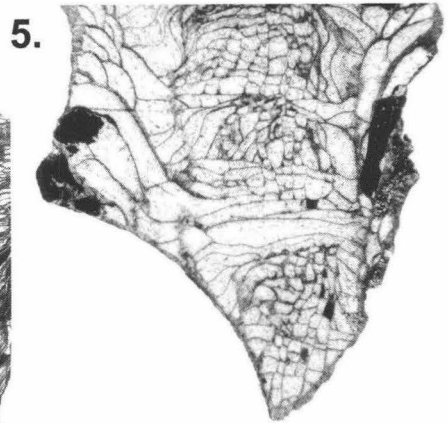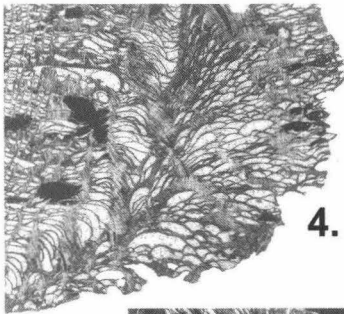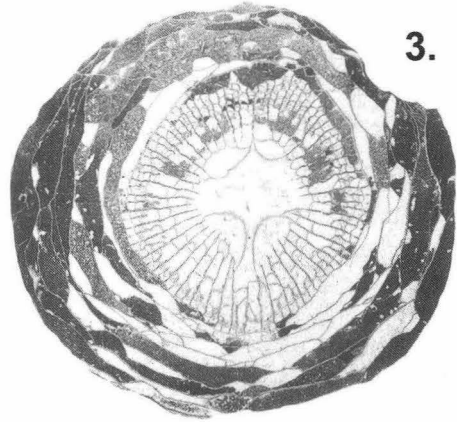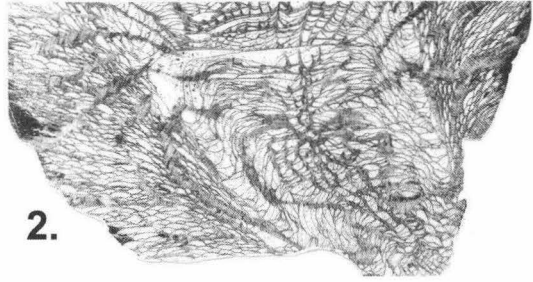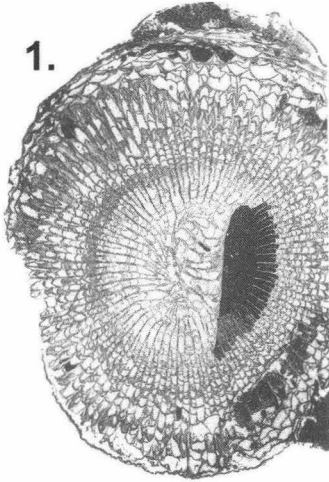
Plate 2

Magnifications as stated.

Fig. 1:   *Tabulophyllum mutabile* SORAUF, 1998; x 1.75. Fine dissepiments are here inter-leaved with fine-grained sediment surrounding the coral. Late Devonian (Frasnian) of Iowa, longitudinal section.

Fig. 2:   *Tabulophyllum rotundum* FENTON & FENTON, 1924, Late Devonian (Frasnian) of Iowa; x 2.2. This coral shows that a dissepimentarium is becoming smaller, probably due to excess sedimentation. However, the tabularial diameter does not show much decrease in size.

Fig. 3:   Horseshoe dissepiments in *Pachyphyllum crassicostatum* WEBSTER, 1908. Late Dev-onian (Frasnian) of Iowa; x 2.1. The longitudinal section of *P. crassicostatum* illus-trates not only the uniform row of horseshoe dissepiments, but also the calicinal prominence formed over the horseshoes and fans of septal trabeculae centered over the row of horseshoe dissepiments.

Figs. 4, 5, 6:   *Iowaphyllum johanni*, (HALL & WHITFIELD, 1873), Frasnian (Late Devonian), Iowa, characterized by "wall ridges" formed of septal crusts and great variation in the size and shape of dissepiments in colonial tissue separating corallites. Fig. 4: x 1.5. Longitudinal view of individual colony with heavy, trabeculate crust occurring at regular intervals, wall ridges and irregularity of dissepiments. Fig. 5: x 1.4. Colony with extreme irregularity of layers and dissepiments, both in size and shape. Crusts are thin, dissepiments are extremely irregular. Fig. 6: x 3. Colony with regular crusts and regular but very large dissepiments forming coenosteum between corallites.

Figs. 7, 8:   *Tabulophyllum rotundum* FENTON & FENTON, 1924, from the Late Devonian (Fras-nian) of Iowa. Fig. 7: x 1.5. Fig. 8: x 8. Illustrations from SORAUF (1998, Pls. 8, 9), illustrating the presence of extremely thin extensions of dissepiments extending into fine-grained sediments. These dissepiments were utilized for anchoring purposes. These thin dissepimental extensions are only rarely seen in rugosans as they are easily destroyed during weathering.

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