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EXTERNAL MORPHOLOGY AND PALEOBIOLOGY OF *HELIOPHYLLUM HALLI* (ZOANTHARIA, RUGOSA), FROM THE MIDDLE DEVONIAN HAMILTON GROUP OF NEW YORK STATE

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ABSTRACT—*Heliophyllum halli* contains highly variable, mostly solitary rugose corals. Specimens reported here come from shaly beds of the Middle Devonian Hamilton Group in New York State. Early recognition of morphotype variation led James Hall to establish numerous species in the *H. halli* group that were later interpreted by John Wells in terms of varying life history. Life on unstable and/or soft substrates was facilitated for these corals by talons, root-like structures that allowed larval settling and post-larval development on hard particles such as echinoderm or shell debris. Variation in subsequent growth history is reflected in corallum shape and change in diameter. Straight growth axes reflect partial burial accompanied by vertical growth, while growth axis curvature resulted from unequal settling into substrate or alternatively, life at the surface of substrate, with sharp bends (geniculations) reflecting major changes in growth orientation. Decrease in diameter resulted from environmental stress, with greatest effects on the peripheral portion of the calice. Other major reactions to increased burial rate (through sinking or increased sedimentation) are epithecal secretion to form an outer wall for isolation of itself from surrounding sediment or decrease in polyp size as shown by terminal shrinking of the corallum diameter, at times nearly to zero. Yonge's (1940) summary of observations on living coral polyps suggests that the living *H. halli* was nonzooxanthellate, with an efficient system of feeding that utilized its multitude of tentacles without the help of cilia, which thus were able to generate currents to promote efficient sediment cleansing. Sediment shedding would also have been aided by polypal distension (swelling) above a reflexed calical margin.

H*ELIOPHYLLUM HALLI* contains corals with a remarkable variety of morphotypes. In the Middle Devonian Hamilton Group of New York State (Figs. 1, 2), solitary corals of *H. halli* occur in great abundance in slightly calcareous shales or argillaceous limestones. Variation in shape and associated features were adaptations to varying substrate and/or current conditions (Baird and Brett, 1983). Other ecological factors seem not to have been of critical importance. In contrast to many living corals, sunlight does not appear to have had much control on the corallum shape or distribution of *H. halli*, and the geologic occurrence of these corals apparently precludes their having had photosynthetic symbionts (zooxanthellae). The muddy sea floor that formed shaly strata was a soft substrate which would have smothered settling larvae, and could easily be put into suspension by wind- or storm-generated currents, resulting in very turbid sea water. These currents also would have caused scouring of mud layers that supported the solitary corals in their life position.

Variation within *H. halli* and allied forms has been recognized since early study of them in the nineteenth century. James Hall (1876) noted numerous forms in this complex, and regarded Hamilton Group *Heliophyllum* as containing seven species plus two subspecies. Since he did not include text in his *Illustrations of Devonian Corals* (1876), one must, to a certain degree, surmise his thinking with regard to their morphological variation. Hall's species and varieties, and their presumed basis for separation are as follows, with numbers one through six comprising solitary corals, with the two colonial forms following:

- 1) *Heliophyllum halli* E. & H., 1850,
- 2) *H. halli* var. *reflexum* (with reflexed dissepimentarium and comparatively small and shallow tabular depression),
- 3) *H. irregulare* n. sp. (apparently based on irregular corallum growth),
- 4) *H. arachne* n. sp. (containing strongly elevated carinae),
- 5) *H. degener* n. sp.? (coralla strongly contracted near top),
- 6) *H. halli* var. *obconicum* (based on its regular turbinate or trochoid form),
- 7) *H. proliferum* n. sp. (branching; the name was an objective homonym. The species is now recognized as *H. delicatum* Oliver and Sorauf, 1994), and
- 8) *H. confluens* n. sp. (massive, colonial).

This interpretation presumed a number of species and subspecies based on the varying shapes and other morphological features seen in *H. halli* individuals. These were later seen by Wells (1937) to result from changing substrate conditions, changing rates of sedimentation and the appearance of incipient and true coloniality within the group. Wells' study of variation in *Heliophyllum halli* was primarily based on specimens from the Hamilton coral beds in the Skaneateles Lake region of New York State. The title of his paper refers to individual variation within the species *H. halli*, although Wells retained many of the names of Hall as "formae" that occur in the Staghorn Point and Joshua coral beds. Most of the names used by Wells were informal, provided only for various categories of shapes and budding types, not as subspecific names. He utilized a series of latinized names for morphotypes, the "formae," here listed with the growth or developmental peculiarity that he used as the basis for naming the form, as follows (1937, p. 18):

- 1) *praecoquus*—reproductive precocity, resulting in multiple small buds in calice,
- 2) *obconicum*—physical stability during growth, with straight, conical corallum,
- 3) *typicum*—physical stability, with curved corallum,
- 4) *irregulare*—physical instability (and resultant irregular corallum),
- 5) *degener*—gerontism: senility (accompanied by terminal decrease in diameter),
- 6) *proliferum*—gerontic budding (today recognized as *H. delicatum*, a branching species),
- 7) *pravum*—irregular rejuvenation,
- 8) *arachne*—broadly conical corallum with growth rate of polyp faster than corallum,
- 9) *aplatum*—patellate corallum with growth rate of polyp faster than corallum,
- 10) *reflexum*—rate of growth in lumen (central part of calice) faster than in periphery, and,
- 11) *infundibulum*—rate of growth in periphery faster than in lumen (as above).

These morphotypes of *H. halli* are easily recognized within the species in the Hamilton population. The colonial forms have been discussed and illustrated by Oliver, who noted (1997, p. 56) that

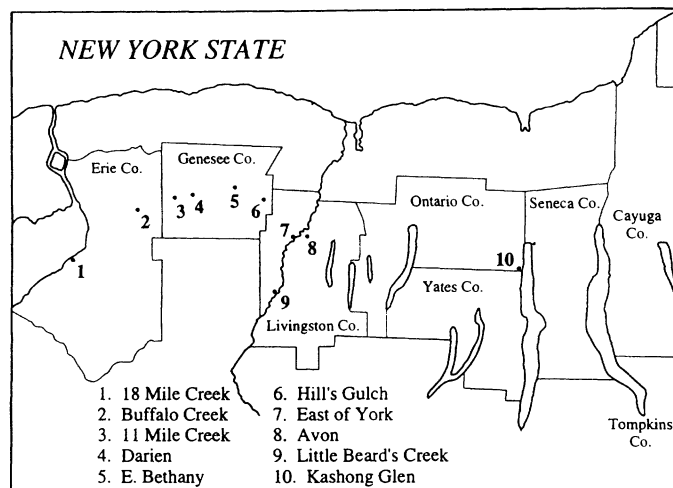


FIGURE 1—Locality map of part of New York State (adapted from Baird, 1979, and Baird and Brett, 1983), showing location of outcrops that provided specimens of *Heliophyllum halli* for this research. Detailed locations are to be found in appendices of these articles.

"Wells clearly considered his "formae" to be infrasubspecific." Wells did state that the massive colonial form, *H. halli confluens* was to be regarded as a true "variety" (1937, p. 18), taken by Oliver to mean that Wells considered it a valid subspecies.

Interpretations applied to this group of rugosans, having no modern representatives, should utilize concepts that are generally accepted as applicable. Hubbard (1970), Elias (1984), Neuman (1988), Elias and Buttler (1986), Elias et al. (1988) and Scrutton (1998) have presented summaries of variation in shapes and support structures in solitary rugosans and their meanings as reflecting substrate conditions, rates of sedimentation and disturbance as factors in controlling shape. In evaluating their variability with substrate, Neuman (1988) illustrated hypothetical life histories for Silurian corals from Gotland (Sweden) and Elias (1984) and Elias et al. (1988) did much the same for Ordovician corals.

Material.—The corals that formed the basis for this study were selected from specimens of several museum collections, thus all of them have excellent preservation of external morphology and skeletal features. Such a basis for selection necessarily limits the amount of information available regarding sedimentary features and outcrop details. Specimens with PRI numbers reside at the Paleontological Research Institution in Ithaca, New York, and were almost all collected by Paul Krohn; from Little Beard's Creek, north of Leichesters, N.Y., the Erie Lake shore at Eighteen Mile Creek, Hamburg, N.Y., or from west of East Bethany, N.Y. (Fig. 1). Specimens with USNM catalog numbers, were borrowed from the biological collections at the U. S. National Museum of Natural History in Washington, D.C., and were collected by a variety of paleontologists over more than a century. Accurate placement of collecting localities is to be found in appendices of the papers by Baird (1979) and Baird and Brett (1983) listed at the end of this paper.

EXTERNAL MORPHOLOGY OF *HELIOPHYLLUM HALLI*

Heliophyllum halli coralla vary greatly in size and shape, apparently due to the ability of the polyps to adapt to different substrate characteristics, firmness (or softness), rapidity of sedimentation, size and stability of particles providing hard substrate for larval settling, and substrate scouring by bottom currents. Interpretation of the natural history of solitary *H. halli* here is based on shapes and change of shape, utilizing observations that have been made on habit and skeleton of fossil and living corals.

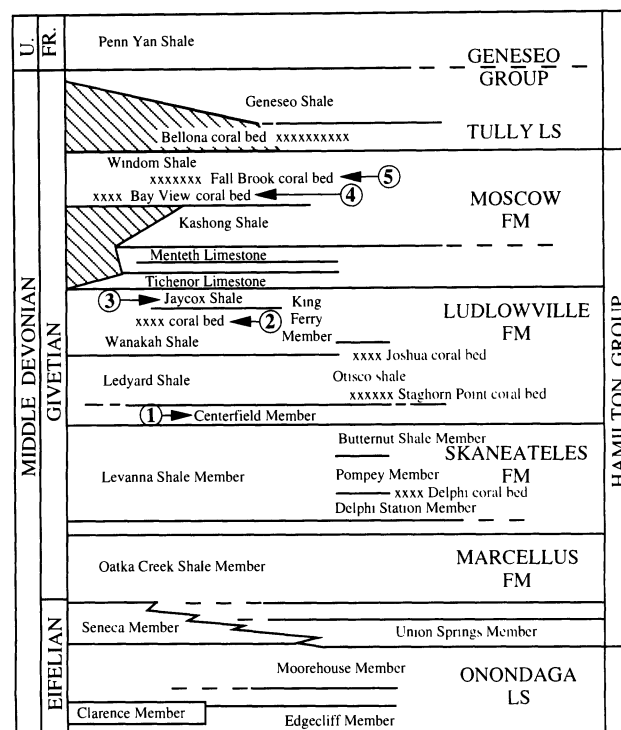


FIGURE 2—Stratigraphic sequence in western New York to illustrate position of the five horizons providing specimens of *Heliophyllum halli* for this study (stratigraphic section adapted from Oliver, 1993; Fr = Frasnian).

With minor exception, coloniality does not enter this discussion. However, it can be observed that many individual polyps (as reflected in their corallites) within poorly integrated, branching coral colonies reacted to substrate, rate of sediment accumulation or current strength in much the same way that solitary corals did. Coloniality does pertain to forms that Wells named *praeoquus*, *proliferum* and *confluens*. The Hall species *H. proliferum* (an objective homonym) is now referred to *H. delicatum* Oliver and Sorauf, 1994, a species that occurs as branching, dendroid colonies that are separate from *H. halli* and only have a limited stratigraphic occurrence. *Heliophyllum confluens* is a massive colonial subspecies of *H. halli* (Oliver, 1997, p. 58). *Heliophyllum halli* of the forma *praeoquus* of Wells occurs in numerous populations of *H. halli* from various horizons, expressed as abundant but short-lived budding late in the development of the corallum (Oliver, 1997, pl. 1, figs. 1–4, p. 57), suggesting that budding of this type was very possibly a response to life-threatening sedimentation rates or other environmental factors. The form still remains somewhat enigmatic as to its exact implications, but its distribution suggests that genes to trigger budding were widespread in this species (Oliver, 1997, p. 56). Nudds and Day (1997) have studied the effects of large amounts of fine clastic sediment on a Carboniferous branching coral and concluded that stunting, rejuvenation and the cessation of both sexual and asexual reproduction occurred in *Siphonodendron martini* under these conditions. Perhaps *H. halli*, when confronted by an overwhelming amount of fine clastic sediment, was similarly unable to reproduce sexually, but polyps budded repeatedly prior to their demise.

The paragraphs that follow deal exclusively with solitary forms of the species *H. halli*.

Symmetry and the cardinal fossula.—Development of bilateral symmetry varies within *Heliophyllum halli*. Such symmetry is

based on the morphology of a cardinal septum, generally an arrangement of thickened septa around the cardinal plane or development of a cardinal fossula where the septum is short. Elias (1984) and Elias et al. (1988) indicated that, in several Ordovician genera, the cardinal area is oriented in the downcurrent direction and occurs on the convex side of the corallum, so that the plane of corallum bilaterality is vertically oriented. No such preferred orientation of bilateral corals has been determined for *H. halli*; however, specimens here reported were not collected in situ.

Attachment (talons).—Scrutton (1998, p. 6), after summarizing attachment structures and scars in Paleozoic corals, made the observation that, "despite the small size, or apparent lack, of attachment scars in many of these corals, the availability of grains or shell fragments of a suitable size and orientation for the successful settlement and metamorphosis of the planula was presumably, in most cases, an important substrate requisite." He also suggested that, after an initial fixed stage, the great majority of Paleozoic corals lived free, on and/or in the sedimentary substrate during the rest of their lives. In *Heliophyllum*, coralla commonly show evidence of embryonic and post-embryonic attachment, with scars commonly accompanied by talons (root-like extensions of epitheca, Fig. 3.1). Talons have also been well illustrated by Scrutton (1998, fig. 3) and by Baird and Brett (1983, fig. 5d, 5g, 5i). Attachment scars often occur on the flank of the apex, but not at the tip. Those corals which do not have an apical attachment scar likely did not attach to a large particle, while those with talons always have a scar in the neighborhood of the apex, or on its flank (Fig. 3.2). As young coralla of *H. halli* developed, talons formed to maintain the area of attachment, which broadened as the diameter of the coral increased. Talons are an outgrowth of the dissepimentarium, formed during a rapid expansion of the coral at the same time that it developed the skeletal outgrowth. Talons are filled with small, irregular dissepiments, and form a base that conforms to irregularities in the hard object, thus helping to grip them and avoid sinking into soft substrate.

Thirty-six specimens of *H. halli* with talons were studied, as listed in Table 1; of these, most are only talon-bearing during a post-larval growth period up to a size where coral diameters are approximately 3.0 cm, with only three of them having talons persisting to a larger diameter (3.3, 3.8, 4.2 cm). The mean diameter for the 36 specimens is 2.0 cm, with a standard deviation of 0.82 cm. Table 1 shows the distribution of such "maximum talon-bearing" diameter in corals sorted from small to large for samples from each of five horizons, as listed in the table. The minimal diameter is rather similar (1.0, 1.3, 1.0, and 1.15 cm) for the Wanakah, Jaycox and two Windom horizons, respectively, but that for Centerfield Limestone specimens is somewhat smaller (0.6 and 0.7 cm) than for other horizons. In these individuals, talons developed to the following maximum coral diameters: 4.2 cm in the Jaycox Shale, 3.8 cm in the Fall Brook coral bed of the Windom Shale, and 3.3 cm in the Bay View coral bed of the Windom. It is supposed that this maximum diameter of talon-bearing corallum is dependent on 1) the size of particles forming solid substrate, 2) the firmness of substrate, and 3) the weight of the corallum and polyp. Presumably these larger diameters reflect the presence of large solid particles for support of the growing corals and their talons. Most such particles are echinoderm stem ossicles, brachiopods, bryozoans or other corals. The maximal diameter of talon-bearing coral varies for the five units sampled. The mean such diameter is 1.7 cm for eight corals from the Centerfield Limestone, 1.9 cm for six corals from the Darien coral bed of the Wanakah Shale, 2.2 cm for seven corals from the Jaycox Shale, 2.45 cm for four corals from the Bay View coral bed of the Windom Shale, and 1.95 cm for 11 corals from the Fall Brook coral bed of the Windom Shale. Mean values do not have any obvious significance here, due to the small number of

specimens, although minimal diameters may provide some indication of substrate firmness.

One must assume that successful solitary corals in areas of soft substrates are those whose larvae settled by chance on some hard material, as settling Devonian larvae would have been easily smothered, just as modern day larvae are. This apparently resulted in the development of talons in the few rugosan genera that could form them, as did *Heliophyllum* and *Cystiphyllodes* from the Middle Devonian, and *Tabulophyllum* from the Middle and Upper Devonian. Where the base of these talons is broad, commonly there is preserved the impression of a small brachiopod or crinoid columnal (Fig. 3.3). In quiet environments, where settling of substrate clays was limited and sediment soft, the post-larval apical development of the corallum lacked talons, so that the apex apparently became buried and the coral grew straight upwards into the water.

Overall shape; rate of expansion.—Individuals of *Heliophyllum halli* show a great variability in the rate of expansion of their skeletal diameter during ontogenetic development, and as a result, have shapes varying from patellate (Fig. 3.5, 3.6; forma *aplatus* of Wells, 1937) to trochoid to ceratoid (Fig. 3.4; forma *obconicum* of Wells, 1937). This reflects ecological conditions, and especially is reflective of varying firmness of support. In terms of weight distribution on soft substrate, rapid expansion of skeletal diameter would have been advantageous. Additionally, there is some evidence that large diameter was advantageous for coral survival of soft sediment deposition on polyps. Hubbard (1970, p. 203) referred to the 1931 work of Marshall and Orr, stating that their study of modern corals on the Great Barrier Reef indicates that "the larger the calice, the greater is the polyps' ability to withstand temporary muddy influxes." She noted that this is paralleled by caninioid rugosans in Visean (Lower Carboniferous) limestones of NW Ireland, where they are ubiquitous in lime mudstones while smaller diameter lithostrotionoid corals are more selectively distributed. Thus, calice size may have been a factor (as discussed below), along with having a larger area for distribution of weight, which may account for the abundance of trochoid and patellate shapes in *H. halli* living on and in soft mud.

A coral with a straight growth axis and growth lines perpendicular to it apparently lived partially or largely buried in substrate, with the rim of the calice situated at some viable distance above a soft substrate (Hubbard, 1970; Elias, 1984; Elias and Buttler, 1986; Elias et al., 1988; Neuman, 1988). Fedorowski (1997, p. 30) stated that it is proven that *Caninia* lived in a perpendicular position, based on examination of in situ specimens and on growth lines in this Carboniferous genus. Stability on sediment would have been one of the most critical needs of solitary rugosans, although, as Hubbard (1970, p. 203) has pointed out, for coralla growing vertically, the percentage of the corallum which may have been buried during the life of the polyp is conjectural. She suggested that it "seems unlikely that the . . . (coral) . . . would be stable if more than one-third of the corallum were exposed above the sediment-sea water interface, and this upstanding part might be considerably smaller." In *H. halli* this would suggest that straight ceratoid and/or trochoid coralla lived upright, with their apices partially (or considerably) buried in substrate. No in situ specimens of ceratoid *H. halli* were seen in this vertical position.

Curvature and geniculation.—Curved solitary corals have generally been interpreted as unattached, with their convex side underneath and their concave side up (Elias, 1984; Elias et al., 1988; Neuman, 1988). Such corallites of *Heliophyllum* apparently lived free on the sediment surface, or settled somewhat into soft substrate (Fig. 3.7, 3.8), with the curvature of their growth axis seemingly related to firmness of substrate. Curvature of the growth axis, as reflected by obliqueness of growth lines (Neuman, 1988)

shows differential growth of the corallum as the polyp continually strived for its optimal life position with its corallum rim horizontal, situated a comfortable distance above the sediment–water interface. Where substrate was firm, and sedimentation rates slow, the coral lay on the sediment surface and grew vertical to it, resulting in a curving axis as diameter increased upwards.

Curvature of coralla in *H. halli* is almost ubiquitous, with truly straight corals an extreme rarity in the Hamilton Group (Fig. 3.4). Numerous questions arise with respect to this curvature of the growth axis of solitary *H. halli*. Is the curvature an indication of the degree of softness and/or compactability of substrate, assuming that it is itself most often caused by non-uniform sinking of coralla into substrate? Does gradual and uniform curvature (Fig. 3.7) thus indicate a uniform rate of sinking into substrate? What are the implications of marked bending? Some individuals of *H. halli* show remarkable and strong bending (Fig. 3.8), resulting in a corallum shape that approaches scolecoïd. It is generally assumed (by analogy with modern corals) that this resulted from corals being toppled but surviving by rapidly renewed growth upwards (forma *irregulare* of Wells, 1937).

Study of *Heliophyllum* coralla indicates that the most common angle of curvature in *H. halli* is close to 90 degrees. This occurs in one of three ways, as follows:

- 1) Curvature totals close to 90 degrees, but much of the curving of the growth axis occurs during youthful stages of growth, followed by straightening of it, followed by (theoretically) vertical growth. An explanation of this is that the coral (Fig. 3.9, 3.10) fell or sank into substrate in such a way that the curvature developed rapidly, then the position of growth stabilized and the coral polyp grew straight upwards. It appears probable that the base of the coral was buried, thus providing support for the vertical portion of the corallum.

- 2) Curvature totals close to 90 degrees, with curving of the growth axis continuing quite uniformly during the coral's life. Some of the corallum (at the least, perhaps most) would have been lying on substrate or on slight indentations in the substrate surface, with the convex side forming a keel-like base to the corallum (Fig. 3.11, 3.12).

- 3) Curvature totals close to 90 degrees, but the change in the direction of growth occurred quickly enough that an "elbow bend" occurs within the coral, a geniculation. This is generally regarded as the result of submarine erosion of sediments that would have been supporting the coral, causing toppling as a result. Corals then appear to have lain on substrate, with the geniculated corallum resulting in a near vertical orientation of the later part of the corallum with an accompanying horizontal position of the coral calice. Possible variations on this theme are shown in Figure 3.11 and 3.12. One corallum (Fig. 3.12) shows a restriction of its coral diameter, very sudden geniculation, and the secretion of a solid epithecal wall covering the tabularium and inner dissepimentarium of the larger and bulkier portion of the corallum, which had formed prior to toppling. *Heliophyllum halli* commonly secreted this sort of external epithecal wall to keep out sediment, whether as a result of tumbling, or as a result of rapid accumulation of sediment.

Where curvature of coralla is much less than the above, in the range of 35 to 45 degrees, one apparently can make the assumption that the coral was at least partially buried in order to support the growth axis in the attitude that is intermediate between lying horizontal or growing vertically. It also seems in these cases that differential sinking into substrate (as suggested by Elias, 1984; Neuman, 1988) was another major cause of curvature.

Geniculation is regarded as always or most often due to toppling (Fig. 3.9, 3.10). For corals lying on the sea floor, geniculation was probably common and frequent, occurring as a result of rolling by current action. Thus, sharp angle bends in coralla of

rugosans reflect the ability to react quickly to being toppled by current (or other) activity. Such is rare in Ordovician and Silurian rugosans (Elias, 1984; Neuman, 1988), but is common in the Devonian genera *Heliophyllum*, *Tabulophyllum* and *Cystiphyllodes*, as well as in Carboniferous genera discussed by Hubbard (1970). Geniculations are shown in Figure 3.13. In this corallum, the effect of toppling is also seen in a marked diminution of the coral diameter just above the "pre-toppling" surface. New epitheca also commonly forms just above the newly geniculate part of the coral, as in Figure 3.12. This suggests that the vital area of the polyp was in contact with surrounding sediment and walling off of this sediment was necessary for survival.

Study of geniculation in thin section.—Thin sections of complete geniculate *Heliophyllum halli* coralla were made from corals of the Centerfield Limestone at Brown's Creek, east of York, New York and from the Hungry Hollow Formation at Thedford, Ontario. These show characteristics which pertain to all geniculate *H. halli*, as follows:

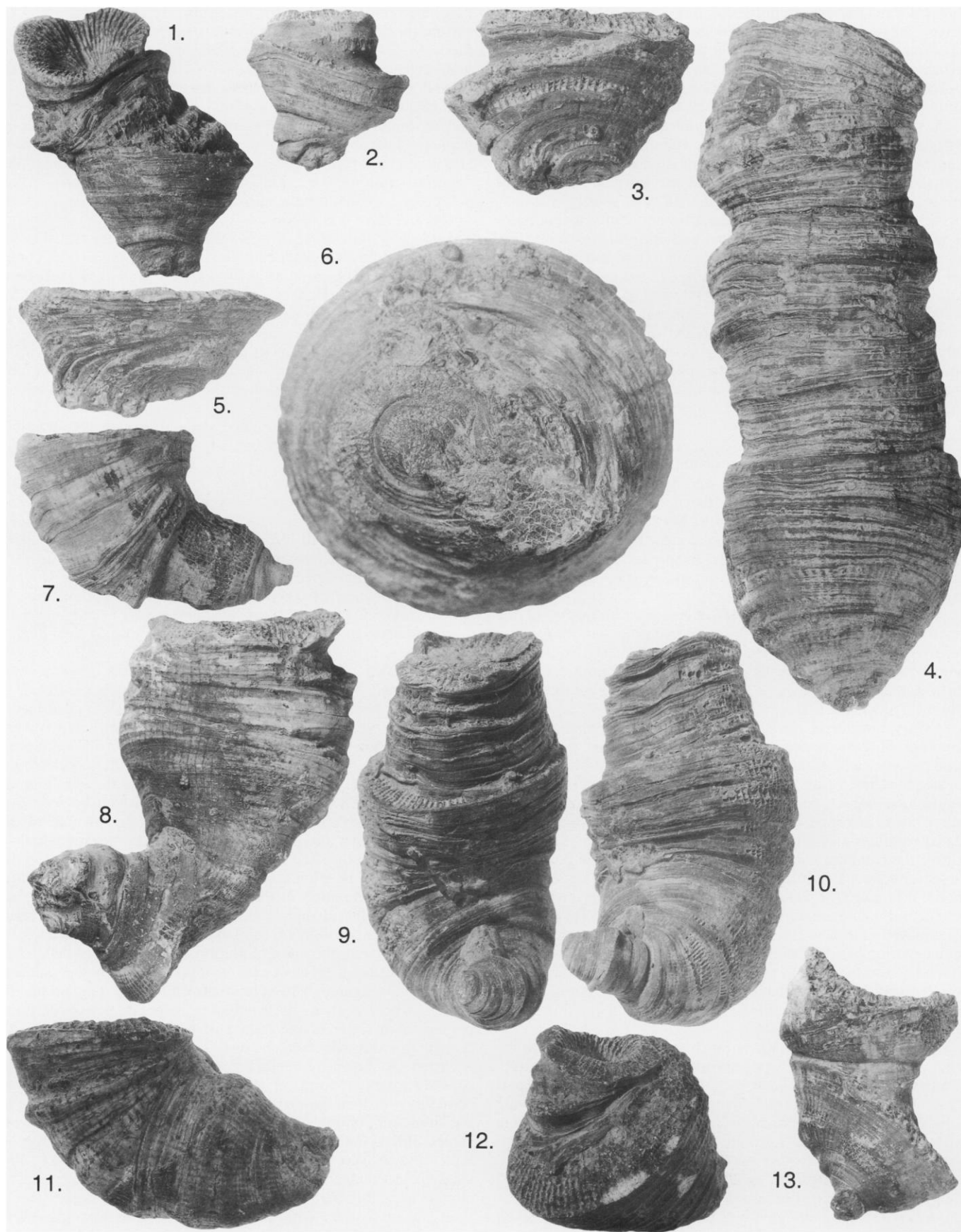
- 1) Re-orientation of growth direction occurred rapidly,
- 2) Most skeletal modification occurred in the dissepimentarium,
- 3) Very little change is seen in the diameter of the tabularium, and,
- 4) In extreme cases, continued skeletal growth was possible only by the polyp wholly or partially abandoning the preexisting calice.

Geniculate individuals of *H. halli* apparently record a life crisis that resulted from toppling of the corallum into soft substrate. The corals studied in thin section underwent reorientation and changed growth direction by 90, 72, 69, 69, 30 and 16 degrees in these six specimens. Other individuals of the species varied up to a maximum of 120 degrees, seen in an individual from the Hungry Hollow Formation of Thedford, Ontario. This reorientation of growth direction occurred during a short period of skeletogenesis, so that specimens (Fig. 4.1–4.3) underwent close to a 90 degree geniculation in a short distance, in one specimen within 3.8 cm of axial growth (Fig. 4.3).

The second point above is seen in all specimens sectioned, to a greater or lesser degree, and is at least partially related to the change in angle of growth undergone by the coral polyp. Where the geniculation angle is large, so too is the size differential in dissepiments between the dissepimentarium on the concave (inner) side and that on the convex (outer) side of the corallum, as in the individuals shown in Figure 4.2–4.4. It can be seen that not only are dissepiments very large on the convex side of the corallum, but that those on the concave side are smaller than usual, providing the skeletal growth differential that supported the coral polyp in a position approaching verticality. Figure 4.3 illustrates a slight variation in the mode of readjustment of the corallum, in that the dissepimentarium on the convex side is characterized by expansions of coral skeleton that extended laterally out into sediment, providing a platform for upward growth.

The diameter of the tabularium is little affected by geniculation in the corals figured here. The diminishment of tabularium diameter, where present, occurred over a longer period of time, perhaps as a result of the failure of the *Heliophyllum* polyp to remain vigorous, which can be due to smothering. Where toppling occurred, as shown by geniculations in the corallum, polyps apparently were able to maintain their vigor and secrete skeleton to coincide with their new growth axis. Change that does occur in the tabularium of geniculate corals is limited to the tabulae themselves; at the bends tabulae are more complete and widely spaced than those above or below (Fig. 4.2, 4.4). These two figures also show the coincidence between levels of complete, widely spaced tabulae and large peripheral dissepiments.

In extreme cases, with aberrant growth after toppling, coral polyps apparently were tenacious enough to secrete skeleton out



of a very small corner of the dissepimentarium, to thus rejuvenate, as if a smaller corallum had formed due to budding (Fig. 4.4). In this figure, the corallum extends over a sediment-filled calicinal pit, with epitheca forming its basal and lateral wall. This individual grew out of the corner of the preexisting dissepimentarium, and is not a later, adventitious epibiont. The *Heliophyllum* polyp had remarkable plasticity and viability. Perhaps an even finer example of tenacity is shown in Figure 4.5 and 4.6. The first visual impression here is that the upper corallum grew on a toppled individual. Close examination of the boundary between the two coralla, however, indicates that septal trabeculae are continuous across the boundary between them, and there is no wall present. I conclude that the lower skeleton formed prior to toppling into sediment and the polyp exited it, but continued upward growth, as shown in the upper part of the skeleton (Fig. 4.6).

Constriction (with rejuvenation).—Constriction and rejuvenation are common within individuals of *Heliophyllum halli* from the Hamilton Group (Fig. 4.7, 4.8). All authors who have studied this feature agree that it resulted from the stressing of coral polyps (Hubbard, 1970; Elias, 1984; Neuman, 1988; Scrutton, 1998). This is supported by the following observations:

1) Commonly an epithecal wall is formed at a new, smaller diameter above a constriction,

2) Most often the tabularium is little affected by the contraction, which is largely taken up in the dissepimentarium of the corallum, and

3) One generally sees regular constrictions in coralla, suggesting that stress conditions were periodic or episodic and frequent. What is regarded as "constriction and rejuvenation" in rugose corals results from short term stress, shown by rapid and marked decrease in diameter (constriction). This is followed by continued growth with a gradually increasing diameter (rejuvenation), as in Figure 5.1, in the forma *pravum* of Wells (1937, p. 18).

Most decrease in diameter is caused by the loss of a portion of the outer dissepimentarium without much change in the diameter of the tabularium. This helps in understanding the biology of the coral, as reflected in its skeletal morphology, where the dissepimentarium apparently was a buffer zone for the coral polyp, serving to separate it from its surroundings. Fedorowski (1997, p. 32) also noted that the tabularium width remains constant (or nearly so), whereas the dissepimentarium varies to reflect small changes in the width of the oral disc due to external factors. The dissepimentarium also is the part of the corallum modified during the formation of structures to deal with substrate (e.g., talons near the base, plate-like expansion of the calicinal rim over soft sediment). The return to "normal" rates of expansion implies that the coral benefited from the return to conditions for vigorous growth. This also indicates that the function of the polyp margin could be temporarily impaired by contact with sediment.

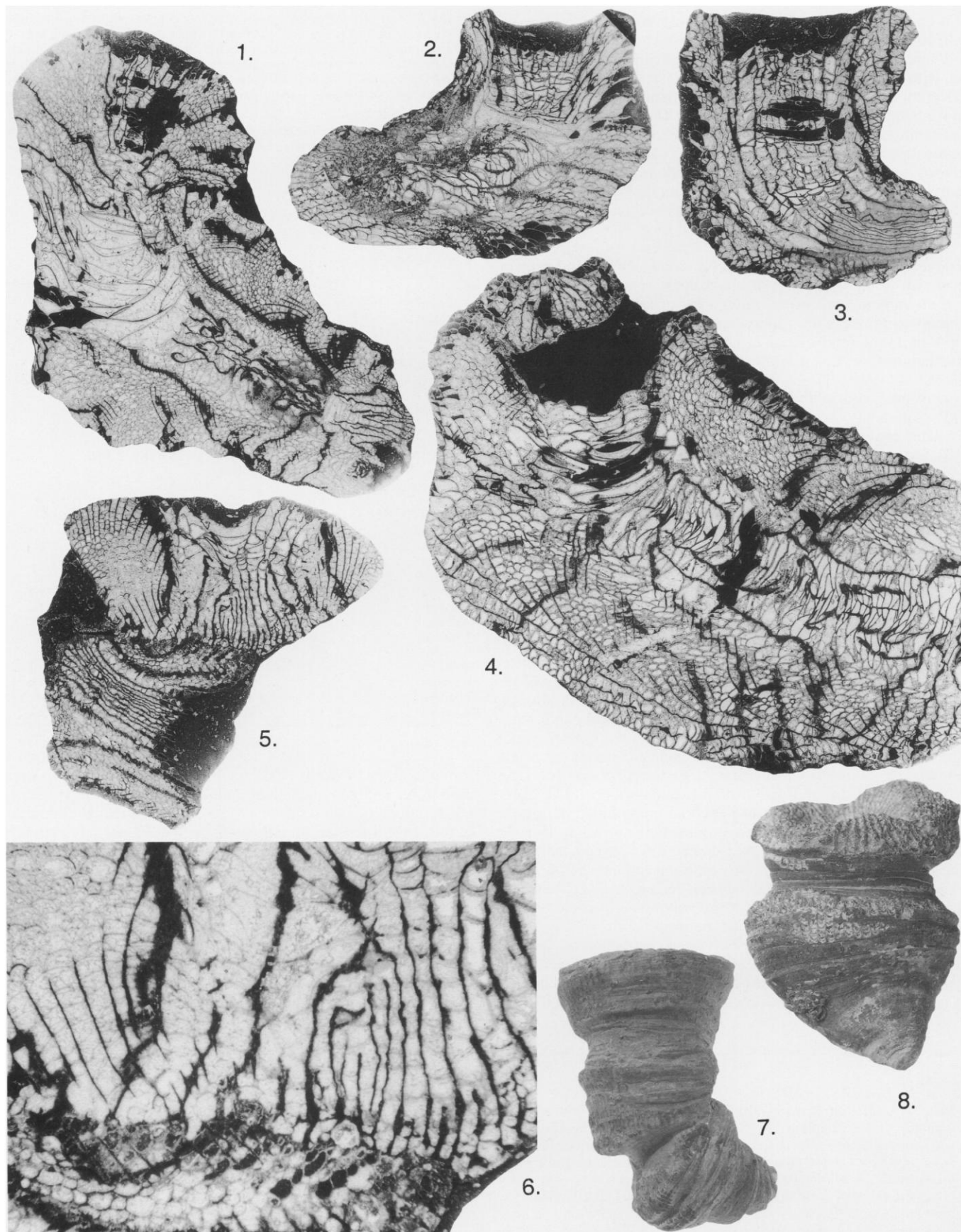
Diameter diminution (degeneration).—Contraction of corallum diameter in *Heliophyllum halli* indicates that soft sediment is in contact with the margin of the polyp, causing shrinkage of polyps. In *H. halli*, individuals showing this character were placed in the

TABLE 1—List of talonate *Heliophyllum halli* specimens showing distribution of maximum "talon-bearing" diameter by horizon. Diameter (cm) refers to maximum growth size (as measured by diameter) that the coral attained while still forming talons for support on a hard object. Horizons are shown on Figure 2, and localities on Figure 1. Note that there are several horizons represented within the Windom Shale, each listed with locality name (c.b. = coral bed).

Horizon	Diameter (cm)	Locality
Centerfield Ls.	0.6	East Bethany
Centerfield Ls.	0.7	East Bethany
Centerfield Ls.	1.7	East Bethany
Centerfield Ls.	1.6	East Bethany
Centerfield Ls.	1.7	East Bethany
Centerfield Ls.	2.2	East Bethany
Centerfield Ls.	2.4	East Bethany
Centerfield Ls.	2.7	East Bethany
Wanakah Sh.	1.0	Darien
Wanakah Sh.	1.6	Darien
Wanakah Sh.	2.5	Darien
Wanakah Sh.	2.0	Darien
Wanakah Sh.	2.4	Darien
Wanakah Sh.	2.0	Darien
Jaycox	1.3	Hill's Gulch
Jaycox	1.5	Hill's Gulch
Jaycox	1.5	Hill's Gulch
Jaycox	2.0	Kashong Glen
Jaycox	2.2	Buffalo Creek, Bullis Bridge
Jaycox	2.8	Bethany
Jaycox	4.2	11 Mile Creek
Jaycox	4.2	11 Mile Creek
Windom	3.3	Bay View c.b. - 18 Mile Creek
Windom	2.7	Bay View c.b. - 18 Mile Creek
Windom	1.0	Erie Cliffs at 18 Mile Creek
Windom	2.8	Erie Cliffs at 18 Mile Creek
Windom	2.8	Fall Brook c.b. - Little Beard's Creek
Windom	1.9	Fall Brook c.b. - Little Beard's Creek
Windom	1.8	Fall Brook c.b. - Little Beard's Creek
Windom	1.2	Fall Brook c.b. - Little Beard's Creek
Windom	1.9	Fall Brook c.b. - Little Beard's Creek
Windom	1.2	Fall Brook c.b. - Little Beard's Creek
Windom	2.5	Fall Brook c.b. - Little Beard's Creek
Windom	1.2	Fall Brook c.b. - Little Beard's Creek
Windom	1.4	Fall Brook c.b. - Little Beard's Creek
Windom	3.8	Fall Brook c.b. - Little Beard's Creek

forma *degener* by Wells (1937, p. 18). As noted above, it is common to see rapid contraction of diameter in these corals (Fig. 5.1), but additionally, one occasionally sees a more gradual diminution of this same diameter. An extreme is seen in Figure 5.2, a straight, ceratoid corallum which expanded slowly and uniformly during its first 4.5 cm of growth, then contracted slowly and uniformly during its last 2.3 cm of growth (as measured on the axis). The apex of this coral is not well preserved, but talons were present until the coral had a diameter of 1.5 cm. The coral then realigned itself slightly and grew straight upward until it terminated. The contraction at the proximal end of the corallum resulted in a much reduced size in the final, elliptical corallum (1.2 × 1.6 cm). The maximum diameter of the round corallum is 3.3 cm, occurring

FIGURE 3—*Heliophyllum halli*, external photographs to illustrate variation in sizes and shapes of coralla. 1–3, corals from the Centerfield Ls., Francis Road, west of East Bethany, N.Y.; 1, PRI 49396, coral with talons accompanying an attachment scar (×1); 2, PRI 49397, attachment scar near corallum apex or its flank (×1); 3, PRI 49398, having impression of small brachiopods or crinoid columnals (×1); 4, PRI 49399, Windom Sh., lakeshore at Eighteen Mile Creek, Hamburg, N.Y., with a ceratoid corallum (×1); 5, 6, PRI 49400, Jaycox Sh., Darien, N.Y., a patellate corallum from the side (×1) and bottom (×1.5); 7, 8, Windom Sh., Little Beard's Creek, Leichester, N.Y.; 7, PRI 49401, with a curving growth axis as size increases (×1); 8, PRI 49402, forma *irregulare* with one major geniculation (×1); 9, 10, USNM 509789, Centerfield Ls., west of East Bethany, N.Y., a coral with decreased diameter and epithecal sheath, side view (×1) and frontal view (×1); 11, USNM 509790, Jaycox Sh., Hill's Gulch, near Pavilion, N.Y., coral with optimal shape for resting directly on substrate (×1); 12, USNM 509791, Jaycox Sh., Hill's Gulch, Pavilion, N.Y., with marked geniculation and epitheca (×1); 13, PRI 49403, Windom Sh., Little Beard's Creek, Leichester, N.Y., illustrating the stable shape after a toppling event (×1).



approximately 3 cm below the calicinal rim. Since the corallum is almost uncurved, this individual apparently was partly buried during much of its growth, and was slowly overwhelmed by sedimentation that was too rapid to allow the polyp to remain its minimal distance above surrounding sediment for health. The coral was exhumed shortly after death, and lay on the sea floor while epibionts (bryozoa and tabulates) settled and grew on the coral epitheca.

Generation of epitheca.—A major reason for the success of *Heliophyllum halli* was its ability to wall off sediment when the coral was toppled into surrounding soft substrate; it apparently could construct epithecal wall rapidly. When the coral was growing normally as an adult, well-adapted to favorable environmental conditions and the rate of sedimentation increased, the coral commonly contracted and secreted an epithecal wall. Deposition of epitheca resulted in isolation from surrounding sediment. This development of epitheca associated with toppling and constriction of diameter is shown in Figure 3.12 and 3.13. During reorientation after toppling there was a constriction of about one-third the total previous diameter, with all decrease in size concentrated on the convex side, which would have been in contact with substrate. Epitheca was deposited to wall off this side of the corallum. Once the bend had been made (successfully) there was a sudden increase in corallite diameter, forming a flat-bottomed overhang over the constricted area (Fig. 3.13). Secretion of epitheca was irregular, and only incompletely plastered over the tops of septa, perhaps due to part of the calice being buried by sediment.

Generation of a tube-like wall of epitheca around a straight corallum of contracted diameter is shown in Figure 3.9 and 3.10, where the straight portion of the corallum grew upwards, perched on its curved juvenile skeleton, with several minor constrictions, to a maximum diameter of 4.3 cm, then constricted, leaving the outer half of the dissepimentarium uncovered. Epitheca was secreted around the final 2.5 cm of growth, with diameters of 3.2 to 2.8 cm, diminishing to the final calicinal rim. This indicates that sedimentation encroached on the "viability" space of the polyp, which constricted to occupy the tabularium and the inner part of the dissepimentarium only, and survived in this somewhat lessened condition.

Other epithecal construction is apparently tied to toppling, with a subsequent walling out of sediment in contact with the polyp. This is seen in Figure 3.12. The corallum had talons until reaching the approximate diameter of one and a half centimeters, at which time there began a rather short period of curvature. Following this, the corallum is straight and expands rapidly, attaining a maximum of 4.3 cm in the distance of about three to three and a half centimeters above the talon-bearing portion. This resulted in an expanded turbinate shape. The coral was then toppled, and in a brief episode, rotated more than 55 degrees to once more put the calice in a near horizontal position. On the upper side, the latest calicinal rim is only three to four millimeters from the rim at the maximum (pre-toppling) diameter, although the new rim is greatly displaced from the preexisting one on the convex side, now facing

downwards. Here, secretion of epitheca walled off the tabularial pit of the preexisting calice, although virtually all of the dissepimentarium was left open to soft sediment of the substrate (seen in Fig. 3.12).

Several remarkable specimens of *H. halli* from the Centerfield Limestone at East Bethany show very rapid secretion of epitheca during constriction, forming a flattened cover to the calice, with only a very small corallum opening at the center (Fig. 5.3–5.5). The first is small, measuring 4.4 cm in length on the convex side. The coral began as a patellate-turbinate form, with well-developed talons that remained fixed to a flat, hard substrate during first growth to 1.3 cm diameter. Then the coral was no longer talonate, and there was a well-developed constriction (to 1.1 cm), then followed by a sharp expansion (to 1.6 cm), with development of a curving form which swung through a 20 degree arc. During the last 1.4 cm, the growth axis remained straight (and upright?). Then, suddenly and surprisingly, there was contraction of the corallum diameter that resulted in a flat epithecal capping of the calice (Fig. 5.3), with a central area (diameter = 3 mm) remaining open. Apparently the coral then died. This truly remarkable record suggests a polyp's struggle against "suffocation." The advantage (if any) of forming such an operculum-like cap to the corallum is not known. Such an epithecal cap might have served to keep sediment out of the calice. However, it is not apparent whether this could have been advantageous to the polyp or if it is only a by-product of a shrinking diameter in a slowly smothered polyp.

The second corallum is a much larger, rounded trochoid form that approaches 11 cm in length and reached a maximum diameter of 4.7 cm. It then was constricted to 1.6 cm, with epitheca deposited over the former calicinal platform. The constricted coral did not die immediately, but instead lived long enough to secrete a 3 mm long corallum at this restricted diameter (Fig. 5.5).

PALEOBIOLOGY OF *HELIOPHYLLUM HALLI*

The foregoing section concentrated on the interaction between *Heliophyllum halli* and underlying or surrounding sediment. Additionally, the species has skeletal characters that are related to its ability to live in proximity to soft substrate and cleanse itself of settling sediment: 1) coral diameter; 2) number of septa, related to number of polypal tentacles; 3) exsert outline in outer part of calice; and 4) ornamentation of septa.

Living coral polyps generally cleanse their surface (especially their oral surface) through a combination of ciliary currents and mucus streams. Yonge (1930, 1940) and Marshall and Orr (1931) found that large diameter solitary corals in modern shallow water environments of the Great Barrier Reef (Australia) effectively utilize ciliary currents to cleanse their oral surfaces. Cilia are present on all ectoderm, and with the exception of those in close proximity to the mouth or within the gut, have the removal of sediment and digestive leftovers as their primary role (Yonge, 1930, p. 55). This role is modified in some of the smaller reef-dwelling species (such as species of *Porites*) where ciliary currents are important in moving food to the mouth. In these, use of cilia in feeding

FIGURE 4—1–6, Longitudinal thin sections of *Heliophyllum halli*, to show growth characteristics during geniculation, as shown internally by skeletal features; 1, PRI 49404, Hungry Hollow Fm., Thedford, Ontario, Canada, a coral with a stable base after toppling, and a growth differential between the dissepiments shown at the left and right sides of the section ($\times 1.5$); 2–6, corals from Centerfield Ls., Brown's Creek, east of York, New York; 2, PRI 49405 ($\times 1.5$) and 3, PRI 49406 ($\times 1.5$), two specimens illustrating growth differential in dissepimentarium and uniform diameter of tabularium during geniculation; 4, PRI 49407, a large specimen showing the growth differential in opposite sides and development of complete, widely spaced tabulae during geniculation, and final growth over sediment-filled calice by youngest part of the individual ($\times 1.5$); 5, 6, PRI 49408, overview of toppled coral with later upward growth ($\times 1.5$); 6, enlarged portion of 5 showing continuity of septal trabeculae from toppled form below to vertically growing coral at top ($\times 5$). 7, 8, External views of *Heliophyllum halli* showing "rejuvenation" and geniculation; 7, USNM 509792, Wanakah Sh., Darien, N.Y., simple constriction and recovery ($\times 1$); 8, PRI 49409, Windom Sh., Little Beard's Creek, Leichester, N.Y., geniculation with subsequent expansion ($\times 1$).

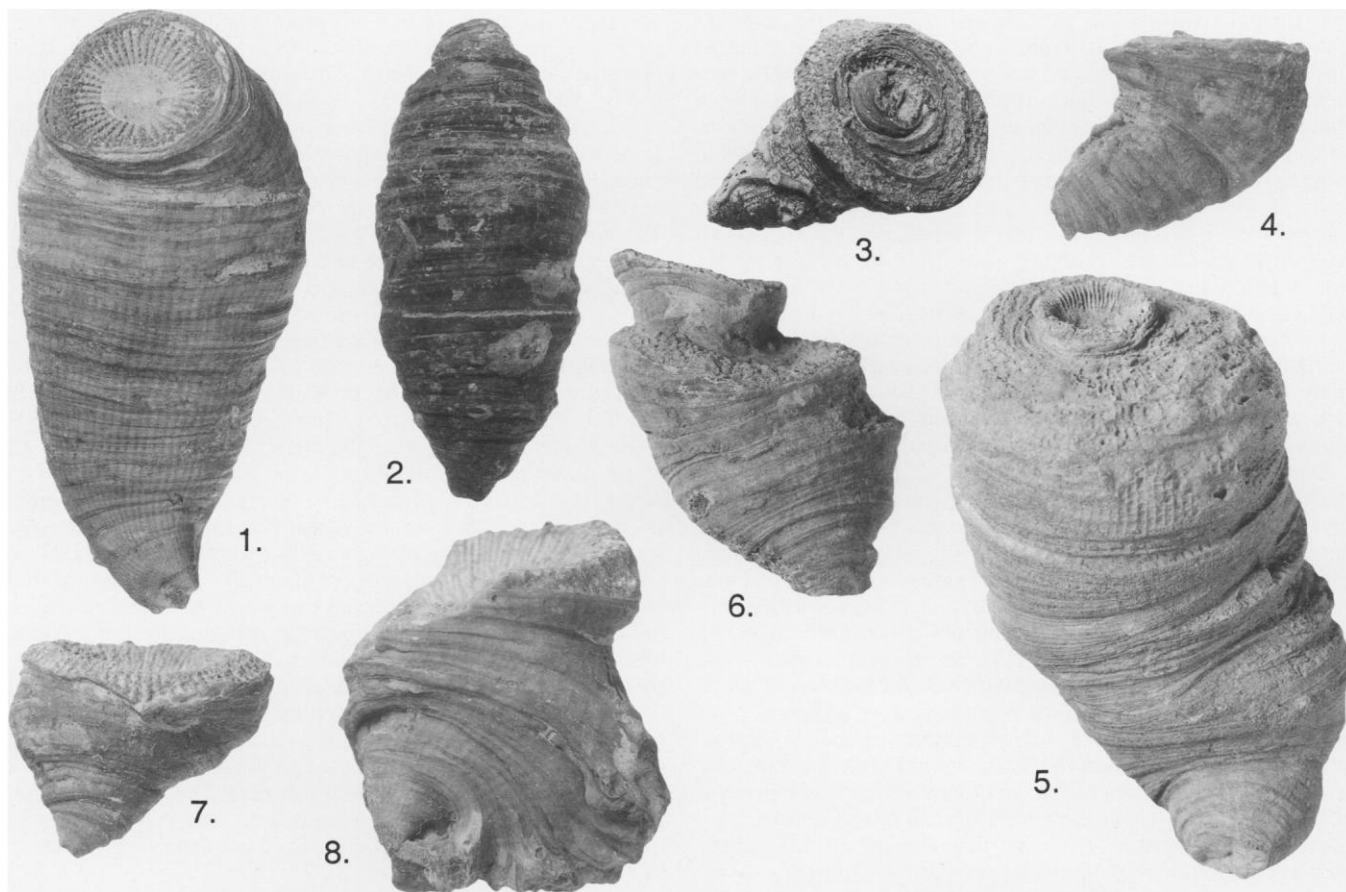


FIGURE 5—External views of *Heliophyllum halli* to illustrate variation in coralla. 1, PRI 49410, Jaycox Sh., Kashong Glen, N.Y., forma *degener*, with decreased diameter in youngest calice ($\times 1$); 2, USNM 509793, Jaycox Sh., Hill's Gulch, Pavilion, N.Y., straight coral with diameter increasing and then slowly decreasing to termination ($\times 1$); 3–7, Centerfield Ls., Francis Road, west of East Bethany, N.Y.; 3, PRI 49411, small corallum with a flat “theca-top,” oblique ($\times 1$); 4, PRI 49411, side view ($\times 1$); 5, PRI 49412, coral with terminal period of growth at a greatly restricted diameter ($\times 1$); 6, PRI 49413, coral with renewed growth at a restricted diameter ($\times 1$); 7, PRI 49414, corallum with reflexed septa, as seen from side ($\times 1$); 8, PRI 44649, Jaycox Mbr., Bethany, N.Y., this specimen, a true “survivor,” with numerous talons, bends, and reflexed septa as aid in gripping during polypal distension ($\times 1$).

decreases the efficiency of their sediment cleansing (Yonge, 1940, p. 362). As a generality, healthy corals can rid themselves of considerable amounts of mud each day, but “individual specimens vary greatly” (Marshall and Orr, 1931, p. 129). Experiments in the ocean and in the laboratory showed that two species of *Fungia* were especially successful at cleansing, using secreted mucus and ciliary currents to sweep mud off the oral surface. Smaller corals (such as *Porites*) depend to a greater extent on current action for sediment cleansing. However, “When a form with a large-polyp, such as *Favia* or *Symphyllia*, expands at night, the polyp rises to some distance off the skeleton and this must help to throw off the sediment” (Marshall and Orr, 1931, p. 130). They further noted that, “Corals can and do live in slightly turbid waters, and for a limited period can withstand large quantities of sediment falling from above.”

Heliophyllum halli is characterized by 1) a large to very large calicular diameter; 2) large numbers of septa, upwards of 100 in adults (it thus had numerous tentacles); 3) septa ornamented with numerous cross-bar carinae; and 4) an upper septal outline that commonly arches, forming an exsert calice (Fig. 5.7). This species generally occurs in fine grained rocks, so it can be concluded, both from skeletal form and occurrence, that in fact, it was very good at shedding fine sediment. *H. halli* would have had an efficient way to feed, utilizing its numerous tentacles, so that cilia

could have all been devoted to the task of removal of sediment and metabolic waste from the polyp's oral surface. The additional characteristic of a reflexed calice, seen extending tens of millimeters above the calicinal rim, with carinate septa, suggests that polypal distension would likewise have been an efficient way for *H. halli* to expel sediment. Carinae on the upper and lateral surfaces of septa further strengthened the attachment of flesh during extension. For modern corals, there also is the important observation by Marshall and Orr (1931), further emphasized by Yonge (1940), that the most critical aspect of the relation between the coral and sediment is not how much sediment is “raining” down on the coral, but rather, how much sediment is building up and encroaching on the basal tissues of the coral from the underside. Thus, it is supposed that the position of the basal tissues of the *Heliophyllum* polyp at the rim of the calice, with respect to surrounding fine sediment, is what determined bending, twisting, and generation of epitheca.

Discussion.—The remarkable success of *Heliophyllum halli* in eastern North America during the Devonian may have resulted in large part from two characters, one, the ability to react effectively to toppling and other causes of “burial,” and the other the probable ability of polyps to cleanse themselves of sediment efficiently, using cilia-generated currents and polyp distension. Attachment of coralla by talons is characteristic of this genus (and

several other genera of Devonian rugosans), and clearly reflects a larval preference for hard substrate (Fig. 5.8). The rate of expansion of corallum diameter, straightness of the growth axis, geniculation, "rejuvenation," and formation of epithecal tubes are all related to rates of sedimentation, the nature of substrate (especially its softness or firmness), and to current strength and scouring of sedimentary bottom, with accompanying toppling of corals.

The observations by Yonge and others of the Great Barrier Reef of Australia in the late 1920s are especially appropriate here. By analogy, these indicate that *H. halli* was a nonzooxanthellate coral, with all its cilia on the oral surface of the polyp devoted to the removal of particulate material. Feeding would have utilized the abundant tentacles accompanying numerous septa. The reflexed margin of the calice and carinate ornamentation of septa suggest that this coral also cleansed its oral surface by polypal distension, with the distended polyp able to lift some centimeters above the calicinal rim of the corallum.

The effect of sediment on *H. halli* was necessarily large in order to have such a remarkable effect on the shapes of individual coralla. This is striking, especially with respect to the observations on modern corals by Marshall and Orr and by Yonge that strongly suggest that it is the sediment building up under the edge tissue of the coral polyp that is difficult for the coral to deal with. *Heliophyllum halli* shows a number of possible reactions, as reflected by its skeletal morphology.

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