

SOME ASPECTS OF COLONIALITY IN RUGOSE CORALS

by JERZY FEDOROWSKI

ABSTRACT. Early coloniality of *Heritschioides* sp. nov. from the Lower Permian (Upper Wolfcampian) of Texas has been studied in more than one thousand etched specimens. Ontogeny of the protocorallite differs from that of the only three known Devonian species. Septal insertion is initially of zaphrentoidal type. In early blastogeny the function of channels and *septal swellings* (new term) is of major importance. Division is thought to be an unimportant mode of reproduction and is associated with other modes, mainly lateral increase. The new term *lost structures* is introduced to describe offsets which are not capable of reaching maturity for some, probably genetic, reasons. They may appear in solitary as well as in colonial species, but are mainly associated with quasi-colonies. Capability to produce offsets should not be equated with maturity of an individual within the colony since this capability can be reached at different stages of individual development. Protopolyms and first asexually produced generations of polyps start to reproduce asexually earlier in ontogeny than polyps of astogenetically more advanced parts of colonies. The appearance of pseudo-offsets, pseudo-colonies, and composite colonies are regarded as being controlled at least in part by extrinsic factors.

PERMIAN rugose corals from south-western Texas have been studied most recently by Moore and Jeffords (1941), Ross and Ross (1962, 1963), and Fedorowski (1974). The large collection from this region belonging to the Department of Paleobiology, Smithsonian Institution is currently being studied by the present author, and this paper forms one part of that study dealing with some interesting aspects of coloniality.

The preservation of many silicified calices of corals in the collection is so perfect that certain characters of blastogeny, known previously only from serial sections, may be reinterpreted or made more precise. The interiors of other specimens are preserved partly in calcite, permitting the preparation of serial sections and acetate peels, and the results of this method were compared with the direct observations of calices. Excellent preservation of the material and the presence of specimens in different stages of astogeny (with protocorallites preserved) made a comparative palaeobiological study possible.

The precise systematic position of *Heritschioides* sp. nov. discussed here is not determined but will be described together with the remainder of the rugosans from south-western Texas in a separate paper. The stratigraphic position of the material is determined by Cooper and Grant (1972, locality USNM 728e) as being from the Bone Spring Formation of Upper Wolfcampian (Lower Permian) age.

ENVIRONMENTS

Environmental conditions discussed here are not based on field studies of sedimentology of the limestones, but observations on the corals themselves are introduced since they may add to previous environmental reconstructions (Stehli 1954) and, at the same time, aid in the understanding of some aspects of development and coloniality of the corals. I consider that all the specimens described belong to one species.

[*Palaeontology*, Vol. 21, Part 1, 1978, pp. 177-224, pls. 14-23.]

Dr. G. A. Cooper (*in litt.* 1974) writes that 'I think the corals probably belong to one population, but I would not say the same for the brachiopods'. All the specimens described here were etched from a few blocks of limestone coming from a single 60-cm thick bed (locality USNM 728e). However, according to both Dr. Cooper and Stehli (1954) the fauna of this limestone is redeposited. Stehli's (1954, p. 280) environmental reconstruction of the limestone is as follows:

The bottom seems to have consisted of lime mud in which were embedded worn and broken shells and patches of shell sand. The deposit was not a reef but an area of somewhat quieter water marginal to a reef or shoal area offering a solid bottom.

It is apparent that the deposit was formed in shallow water, but the exact depth cannot be determined. The worn shell debris and the position of the deposit, only 10 to 12 feet above an overlapped surface, all point to deposition in very shallow water.

It is difficult to place the shore exactly during formation of this deposit, for the sea was advancing across a surface of generally low relief and the situation is secondarily complicated by post-Permian warping along the Victorio flexure. The shore seems to have been within a few miles, and probably islands dotted the inundated surface.

An interesting feature of this and many other collecting localities is the complete imbalance of the organic assemblage. There are 10 times as many brachiopods as all others combined. Second in importance are the bryozoans which occur in large numbers, and include both stony forms and delicate fenestellids. Corals are present in moderate numbers.

The above reconstruction mainly concerns sedimentary conditions. It does not explain the primary living conditions of the fauna, although these conditions were most probably differentiated in spite of fact that all the skeletons were found in the same thanatocoenosis. The following short discussion on some characters of rugosans is introduced in order to show the importance of environmental influence in the development of colonies.

The microhabitats from which the corals came were differentiated as is indicated by the shape of corallites and colonies. Better-preserved samples may be grouped as follows:

1. Solitary corallites and protocorallites with strong talons (Pl. 15, figs. 10*b*, 13*a*; Pl. 16, figs. 6*b*, 8*b*; Pl. 17, fig. 1*a*; Pl. 21, fig. 6; Pl. 23, fig. 10*a*); colonies with attachment processes between corallites within the colonies and with large surfaces of attachment at the beginning of astogeny (Pl. 16, fig. 4*c*; Pl. 18, fig. 1; Pl. 20, fig. 5). All these corals were attached to a hard matrix, and may indicate a rocky bottom in a zone of wave activity or in an area affected by currents. One or two of the circumrotary colonies found in the collection (Pl. 21, fig. 1*a-d*) also belong to the group growing on a rocky or hard sandy bottom, as this was the only possibility for them to survive. They possess corallites growing in all directions and were probably overturned a few times without having been killed.

2. Quasi-colonies with no strong talons (Pl. 19, fig. 7*a*; Pl. 21, figs. 8, 9); weakly fasciculate colonies with no attachments between particular corallites (Pl. 17, fig. 7); small colonies in which only protocorallites were attached to the substrate (Pl. 16, figs. 2, 5, 7); and colonies consisting of long, parallel corallites (Pl. 21, fig. 11). Corals of this group form a majority in the collection, but most are preserved only as fragments. Lack of talons and other attachment processes indicates that they were inhabitants of rather quiet areas on a lime sandy bottom. Their habitats were not necessarily far from those of the first group, however.

3. The third group is an intermediate group. The following types of specimens can be included: corallites and small colonies attached to the internal parts of brachiopod shells, to fragments of corals or to other comparatively large fragments of debris (Pl. 15, fig. 6; Pl. 21, figs. 3-7; Pl. 23, figs. 1b, 2, 3); colonies of corallites packed closely to each other, but with no interconnecting processes (Pl. 17, figs. 6, 8; Pl. 21, fig. 4), and chain-like colonies (Pl. 18, fig. 3a, b). These specimens came from a bottom covered by larger fractions of calcareous sand and organic fragments offering many opportunities for larvae to settle.

Some other observed phenomena may also be connected with either the first or third group. Some colonies rapidly changed their direction of growth without being detached from the bottom (Pl. 17, figs. 1a-d, 4a-b), or grew only in one direction (Pl. 17, figs. 3, 5a-b). This must be related to currents and to rapid changes in their directions. Other corallites show many rejuvenescences and deep narrowings (Pl. 17, fig. 1c; Pl. 20, figs. 4a-b; Pl. 22, figs. 2, 10a-b) which are also related to environmental changes.

The three groups of corals listed above do not differ in internal morphology of corallites or in blastogeny. There are no strong boundaries between them and many corallites show intermediate characters indicating that there were no sharp boundaries between habitats. Their primary living area was probably a shoal, differentiated in morphology, with prevailing wide sandy areas colonized by the second group. There were also rocky, underwater dividing ridges with corals of the first group attached to them, and patches of coarse-grained lime sands inhabited by members of the third group. Local currents flowed at different velocities and in various directions. Waves might have swept the more elevated areas. These habitats may be compared with the coralgal lithofacies of Bathurst (1975).

There is little to add to Stehli's (1954) reconstruction as far as sedimentary conditions are concerned. Transportation of the material definitely took place, but not over a great distance and not along the sea-shore, as there is no evidence of rounding. The material was not segregated by current action. All three groups of corals in all astogenetic stages, as well as solitary corals, have been found together.

Such a mixture of ecologically and astogenetically different specimens was most probably caused by a common factor acting simultaneously in all areas where the corals lived. Storms with deep waves may have been important, as they might have affected all areas simultaneously. This is in agreement with observations by Ball *et al.* (1967) on recent sedimentary conditions on the Bahama Bank. The uprooted specimens and their broken fragments were mixed and partly crushed during transportation through the shallow water towards the sea-shore, but were deposited before reaching it. Dr. G. A. Cooper (*in litt.*) suggests that 'sedimentation was rapid', and this interpretation is certainly supported by the coral fauna. There is thus no reason not to consider the whole collection as belonging to a single population.

TERMINOLOGY

All terms are new unless noted to the contrary. My interpretation of some old terms may differ to some extent from previous meanings.

Channels (Fedorowski and Jull 1976)—openings between a parent and daughter corallite covered by a common parent/offset soft tissue.

bridged channels—openings as above, but bridged by a partition.

Colonies

composite colony (Oliver 1968)—a colony that was initiated by more than one protopolyp. Particular corallites may grow close to one another but their soft tissues are not united.

incipient colony (Fedorowski 1970)—a superindividual in which a parent corallite is the only mature corallite. Offsets produced in peripheral increase do not reach maturity for combined genetic and environmental reasons.

pseudo-colony (Fedorowski 1971, not in the sense of Spassky and Kravtsov 1974)—a cluster of individual corallites of the same species that grow close to one another, giving the impression of being produced by offsetting.

quasi-colony (Fagerstrom and Eisele 1966)—a superindividual in which a parent corallite is the only mature corallite. Offsets are *lost structures* (see below).

Division (widely used term)—characterized by the entire parent corallite being divided into two more or less equal descendent individuals.

offsetting-like division—a parent corallite is an easily recognizable specimen.

twins—a double-calice offset that looks like a corallite which is incompletely divided.

Lost structure—an offset produced in lateral increase that did not reach maturity for reasons other than environmental ones (probably genetic).

Pseudo-offset—a corallite that starts to grow in the calice of a dead specimen of the same species, giving the impression of being offset.

Rejuvenescence (widely used term)—an action of a polyp leading to reduction of dimensions by leaving part of some skeletal structures in a calice outside a new external wall.

axial rejuvenescence—a polyp retained in the middle part of its old calice, leaving peripheral parts outside its new external wall.

lateral rejuvenescence—a polyp leaves a large part of the periphery of its old calice outside its new external wall, but continues to develop all previous structures in the rest of its calice.

shallow rejuvenescence—closely comparable with deep narrowings of growth, but in contrast to them the new and old external walls are separated.

Septal pinnacles (Fedorowski and Jull 1976)—upper tips of internal parts of septa in a region of increase that continues to grow upwards. In cross-section they appear to be separated from *septal swellings* (see below) due to cessation of growth of the latter.

Septal swellings—upgrowths of upper margins of septa in a region of increase.

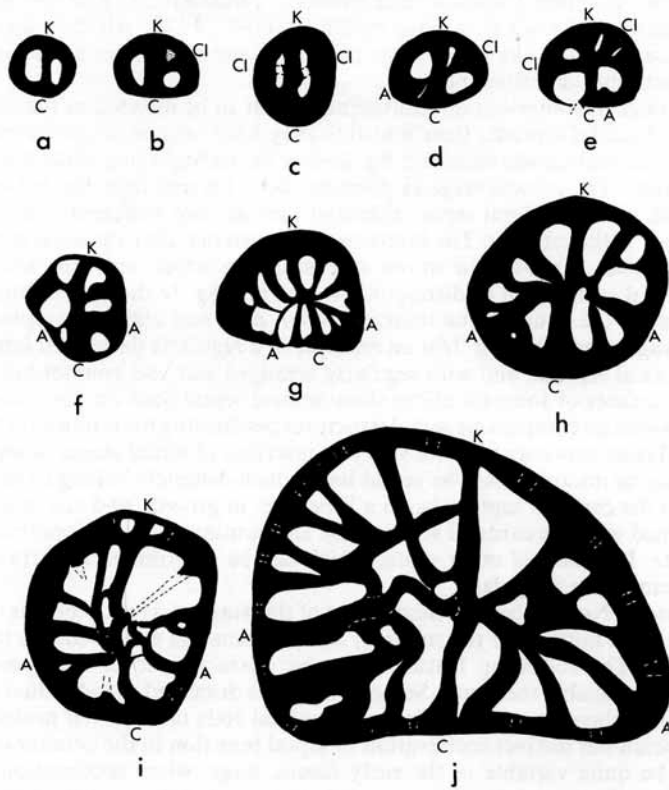
bounding septal swellings—structures that bound a region of increase and may be converted into new septa of a parent and a daughter corallite.

inside septal swellings—structures retained in a daughter corallite as main supporting elements of the base of its calice.

For other terms concerning blastogeny see Hill (1956) and Fedorowski and Jull (1976).

ONTOGENY OF THE PROTCORALLITE

All important stages of development and septal insertion, beginning with a very young brephic stage of approximately 0.75 mm diameter, possessing only one axial septum, were available for study (text-fig. 1). No aseptal, tube-like stage was observed directly, but well-preserved axial ends of some specimens suggest that the initial part of the protocorallite may have been a cup-like structure with no skeleton except for the external wall. That cup was later filled by sclerenchyme deposited by the basal ectoderm. Such solidly sclerenchymal tips were observed in quite a few corallites. It seems probable that the axial septum was inserted early, both on the basal disc and simultaneously on the wall in a common fold of the ectoderm. This type of development is a little different from that described by earlier workers in the only known protocorallites of three Devonian species. These are the Middle Devonian *Hexagonaria anna* (Whitfield) from Michigan studied by Stumm (1967) and Jull (1973),



TEXT-FIG. 1. Camera-lucida drawings of young ontogenetic stages of proto-coralites. C—cardinal septum; K—counter septum; A—alar septa; Cl—counter-lateral septa (indicated only when not obvious). All figs. $\times 15$.

a-f—brepheic stage. *a*, USNM 196565, early brepheic stage with an axial septum; *b*, USNM 196566, a counter-lateral septum is inserted next after axial septum; *c*, USNM 196567, probable existence of two counter-laterals prior to the alars; *d*, USNM 196568, one counter-lateral and one alar are the only recognizable lateral protosepta; *e*, USNM 196570, existence of only one alar septum is certain; a first metaseptum is inserted in counter quadrant; *f*, USNM 196569, six well developed protosepta.

g, h—neanic stage; arrangement of septa zaphrentoid; axial septum invariably present; an acceleration of septal insertion in counter quadrants; an irregular insertion of initials of minor septa; *g*, USNM 196571; *h*, USNM 196572.

i, j—late neanic stage; an axial septum is often divided into cardinal and counter septa; some septa, mainly protosepta, become elongated to form an axial structure; recognizable minor septa are definitely present; *i*, USNM 196573; *j*, USNM 196574.

and the Upper Givetian *Phillipsastraea hennahi* (Lonsdale) and *H. philomena* Glinski from Nakhichevanska S.S.R. studied by Ulitina (1973, 1974). All these species show a definite aseptal, tube-like initial stage of growth and the further insertion of septa different from that described below.

Brephic stage. Counter-lateral protosepta appear to be inserted as the next protosepta after the axial septum; their insertion may have been in sequence rather than together. The structure shown in text-fig. 1*b* may be the beginning of the first counter-lateral septum. The growth stage at diameter 0.9×1.6 mm (text-fig. 1*c*) appears to possess both counter-lateral septa, although they are not sufficiently distinct to be distinguished with certainty. The insertion of protosepta after the axial septum may be quite irregular. Text-fig. 1*d* shows an example in which only one alar and one counter-lateral septum can be distinguished, and text-fig. 1*e* shows insertion of a first metaseptum in the counter quadrant, although only one alar protoseptum can be barely distinguished. Text-fig. 1*f* is an example of a regularly developed later brephic stage with axial septum, and with regularly arranged alar and counter-lateral septa.

Wetted surfaces of some corallites show several septal lines on the outer surfaces of the walls with no comparable septal structures penetrating the interiors of the protocorallites. These lines may indicate very fast insertion of initial stages of septa. Some of them may be minor septa. The septal lines which definitely belong to minor septa adjacent to the cardinal septum begin a little later in growth, and can easily be seen as lines joined with the cardinal septum line and continued to the uppermost part of the corallite. Insertion of other septa, which can be determined as certainly as the minors, seems to be irregular.

Neanic stage. No step-by-step description of this stage of development is made here as it seems to be normal for the suborder Streptelasmatina and as such is reasonably well known. The following features may be characteristic of the species under discussion or, possibly the genus. Some of them are discussed as individual variation.

1. In most calices, and on the broken proximal ends of observed protocorallites, there is a small but distinct acceleration of septal insertion in the counter quadrants. This may be quite variable in the early neanic stage, when acceleration of septal insertion in only one of the counter quadrants can be observed (text-fig. 1*h*), but seems to be regular later. More or less equal numbers of septa in all quadrants in the early neanic stage is very uncommon.

2. The arrangement of septa is zaphrentoidal (text-fig. 1*g, h*), but they may be deformed because of flattening of the side of the corallite attached to the substrate. As a rule this is on the cardinal septum side. In the earlier part of this stage cardinal and counter septa are still joined, producing a regular axial septum to which the alar and counter-lateral protosepta are connected. In Plate 15, fig. 1*a, b* two phenomena are shown that may increase the understanding of calices as studied in transverse section: (a) the zaphrentoidal arrangement of the septa is more or less clear only on the bottom of the calice, while the arrangement of septa on the walls is almost radial, with the last pairs of metasepta slightly underdeveloped; (b) there is a distinct pseudocolumella in the centre of the calice, while in the comparable transverse section of the base of the calice only the connected cardinal and counter septa are visible. The cardinal septum is depressed before its junction with the axial lamella, which indicates the existence of a cardinal fossula.

3. During the early neanic stage the cardinal and counter protosepta of some corallites become separated. An important step in phylogeny takes place after separation, in that the cardinal septum remains elongate and the axial structure is built around its axial end. There is a general tendency for all the axial lamellae or axial ends of septa within the species to curve around the axial structure. The cardinal protoseptum and its axial lamella remain straight for a longer period than other septa or lamellae.

4. The construction of the axial structure may be variable and is heterochronic in most observed cases. Some small (approx. 3 mm diameter) specimens possess a kind of loose axial structure and separated cardinal and counter protosepta (text-fig. 1*i*) whereas other specimens which are almost twice as large (text-fig. 1*j*) retain the axial septum. Most commonly the axial structure is built with the axial lamellae joined to the axial ends of the septa just above the bottom of the calice, and with elevated axial tabellae. The axial structure of more advanced stages observed both in calices and in transverse sections just beneath the calices show a network of septal lamellae and axial tabellae. The cardinal protoseptum may be located in a narrow cardinal fossula, but it remains connected with its axial lamella along the bottom of the fossula.

BLASTOGENY

Lateral increase

Origin and function of more important structures. *Septal swellings* are the structural elements that originate directly from the upper peripheral margins of a few septa of the parent corallite (Pl. 14, figs. 2, 3*a*). These septa, located in a region of increase, stop to grow upwards and become grossly thickened by stereoplasmatic sheets to strengthen their mechanical resistance (Pl. 14, fig. 3*b*). Such a rearrangement of construction is conditioned by their new character, position, and function. Retaining fine septal structure they become converted into the main basal skeletal elements of an offset (Pl. 14, figs. 4*a*, 5*a*, 10). Their second important function is to border channels (Pl. 14, figs. 3*b*, 5*a*).

Situated more inwards towards a calice of the parent corallite, and directly united with septal swellings, are other skeletal elements that also originate from the upper margins of septa. These are *septal pinnacles*. In contrast to septal swellings they grow consistently upwards, preserving their character as vertical skeletal elements. Although they appear to be separated when observed in cross-sections made above septal swellings (Fedorowski and Jull 1976, text-fig. 3), they are in fact directly connected with the upper margins of septa (Fedorowski and Jull 1976, text-fig. 1; Pl. 14, figs. 4*a*, 5*b* herein). The etched septal pinnacles with new septa being formed on them are shown on Plate 14, fig. 5*a-b* to illustrate the relationship of parent septa, septal swellings, septal pinnacles, and new septa of an offset.

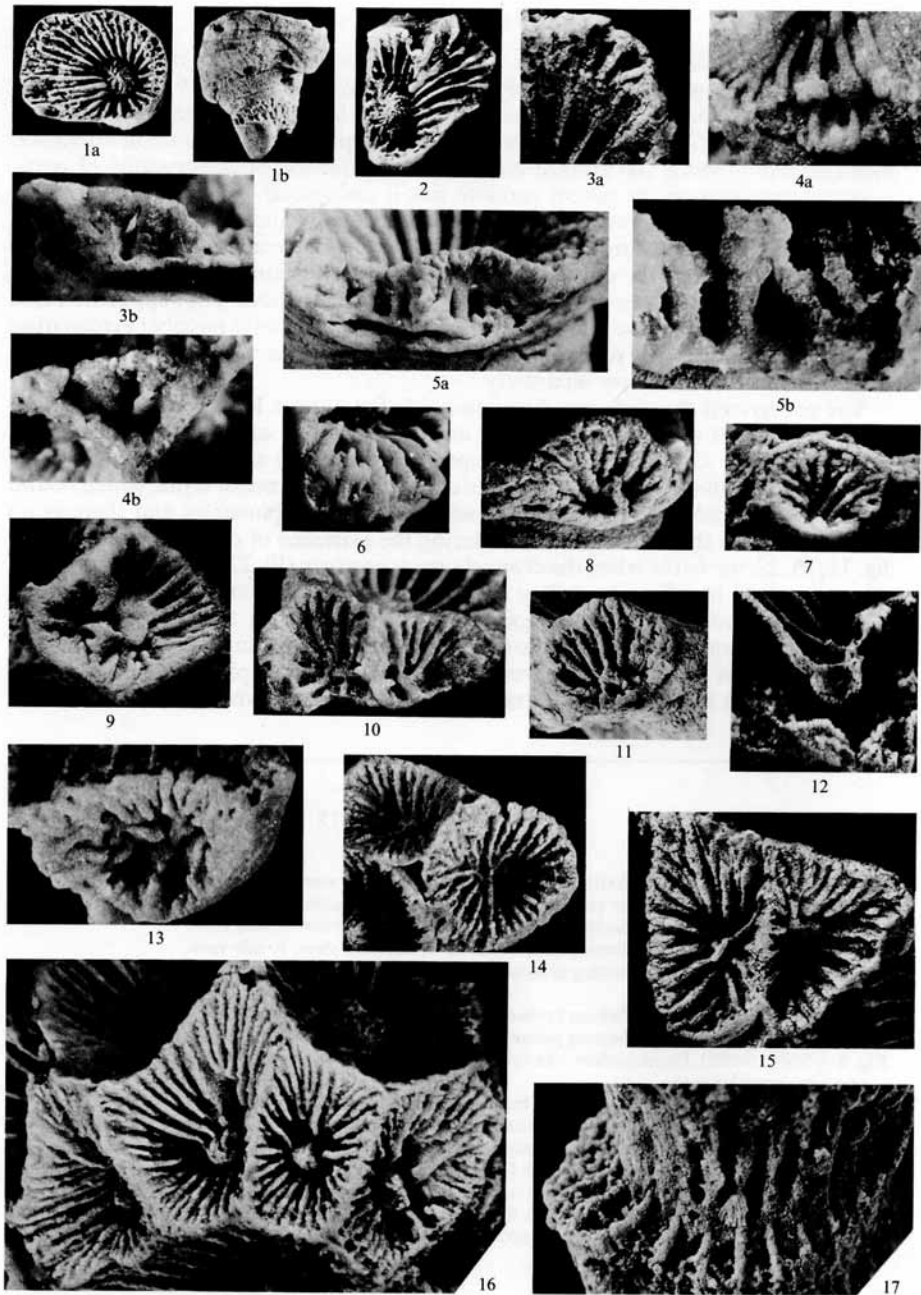
Interpretation of *channels* (Fedorowski and Jull 1976) based on serial sections can be supplemented by observations made on etched material. Channels were initiated simultaneously with septal swellings, are always located between them, and are ditch-like at their initial stage (Pl. 14, fig. 5*b*). Further development begins at the same time as the formation of new septa on the tips of septal pinnacles. These new septa are

quickly and distinctly thickened, tending to meet each other above the channels (Pl. 14, fig. 5*a*). Growing both vertically and laterally they soon form a solid partition which bridges the channels close to the parent polyp. These bridged channels are surrounded by skeletal structures extending continuously between parent and offset calices (Pl. 14, fig. 5*a*; Pl. 16, figs. 10*c*, 11). Such common structures must have been covered by a common soft tissue that connected the parent and the offset polyps.

The existence of tabellae, dissepiments, etc., between septal swellings in the common parent/offset area, and inside the youngest parts of offsets investigated in serial sections led to the earlier interpretation of channels and of the period of their activity. These structures are all secondary, i.e. were all built some time after the existence of open, bridged channels. An example of a young corallite completely separated from its parent corallite by a dividing wall, but connected to it by the channels is shown on Plate 22, fig. 6*a-c*. It seems clear that the soft tissues of these two polyps were united along the walls of the channels. On the other hand, however, there are examples of

EXPLANATION OF PLATE 14

- Fig. 1. USNM 196575, $\times 2$. False region of increase on widened shoulder of calyx; *a*, calicular view; *b*, side view.
- Fig. 2. USNM 196576, $\times 2$. A very beginning stage of blastogeny. Minor septa become contratingent to the majors.
- Fig. 3. USNM 196577, $\times 6$. *a*, hystero-brephic stage a little more advanced than illustrated in fig. 2. Septa only start to transform into septal swellings; *b*, another offset of the same colony showing well developed septal swellings, with septal pinnacles starting to bridge channels.
- Fig. 4. USNM 196578, $\times 6$. *a*, hystero-brephic stage with distinct, smooth septal pinnacles, common for major and minor septa of a parent corallite; *b*, another offset of the same colony with channels and with initials of septa on septal swellings in a calyx of offset.
- Fig. 5. USNM 196579. *a*, two neighbouring offsets in hystero-brephic (*left*) and hystero-neanic (*right*) stages. Differentiation in speed of development of inside and outside parts of an offset is well illustrated by the right offset. It also shows a secondary folding of septal swellings, converting them back into septa, $\times 6$; *b*, structure of a septal pinnacle, $\times 12$.
- Fig. 6. USNM 196580, $\times 6$. Early hystero-neanic stage with axial septum present.
- Fig. 7. USNM 196581, $\times 6$. Hystero-neanic stage with septa differentiated in length, but with no pseudocolumella. Traces of channels are still distinguishable.
- Fig. 8. USNM 196582, $\times 6$. Hystero-neanic stage with beginning of a pseudocolumella.
- Fig. 9. USNM 196583, $\times 6$. Two offsets belonging to different parents, as it is indicated by remainders of channels in the left offset.
- Fig. 10. USNM 196584, $\times 6$. Hystero-neanic stage. Beginning of development of axial structures, resulting from junction of axial ends of some septa.
- Fig. 11. USNM 196585, $\times 4$. Hystero-neanic stage.
- Fig. 12. USNM 196586, $\times 6$. Channel in lateral view.
- Fig. 13. USNM 196587, $\times 6$. Hystero-neanic stage. A thick, solid partition and insertion of septa close to an external wall. Pseudocolumella delayed in development.
- Fig. 14. USNM 196588, $\times 4$. Early ephebic stage with dividing wall developed, but with an axial septum, instead of pseudocolumella, still present.
- Fig. 15. USNM 196589, $\times 6$. Late neanic stage. Beginning of development of axial structures.
- Fig. 16. USNM 196590, $\times 4$. Late neanic stage. Four almost simultaneous offsets with well-developed axial structures.
- Fig. 17. USNM 196591, $\times 4$. A shallow rejuvenescence. Major septa are continued from the old to the new part of calice.



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quite young corallites that were cut off from the parent corallite, mainly or exclusively by the action of the parent polyp. These are lost structures (Pl. 23, figs. 7, 11).

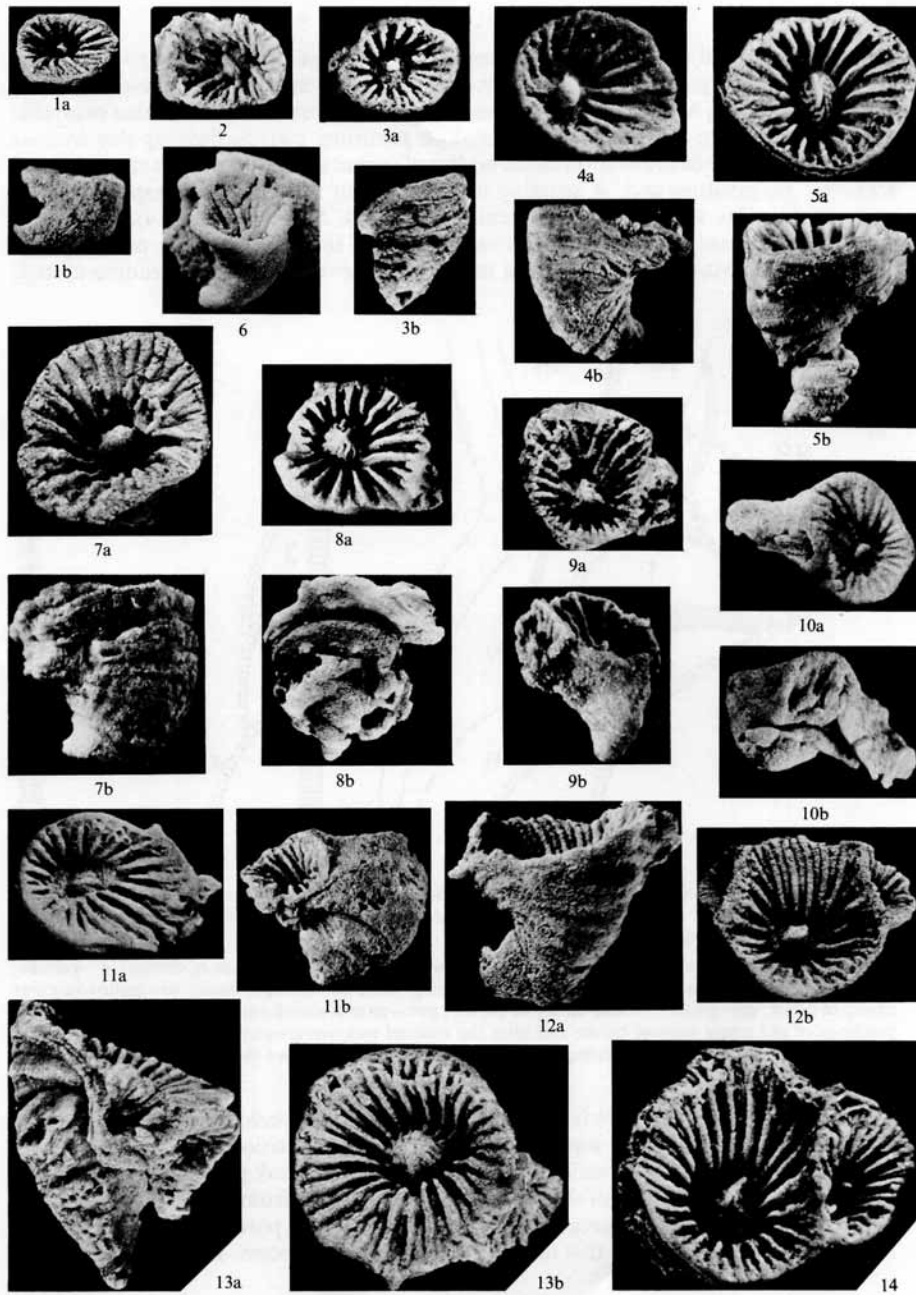
The process of disjunction of an offset and parent in channels is slow and develops step-by-step (Pl. 22, figs. 5, 6c; text-fig. 2A). Dissepiments are the main structural elements overgrowing the bridged channels. The direction of construction of particular dissepiments on the parent corallite side is centripetal. The newly constructed dissepiments in channels are convex towards the parent calice, when constructed on its side. The observed direction of appearance of dissepiments indicates that the uppermost row meets the upper margin of the bridged channel (Pl. 22, fig. 6c). The soft tissue must have covered both of these elements in contact. The supposition that it had atrophied along the line of contact seems to be the only possible explanation for the disjunction of the parent and offset polyps. The separated bodies were sealed over and continued to grow separately.

The overgrown channels are distinguishable for quite a long period of development in a parent corallite calice. They are marked by an apparent interruption of minor septa (Pl. 22, fig. 5). This 'interruption' is caused by a characteristic development of septal pinnacles and by the origin of partition. Two major septa, which bound particular channels, are continuously secreted on septal pinnacles and there is no major change in their structure either during the existence of open channels (Pl. 16, fig. 11; Pl. 22, fig. 6c) or when the channels are overgrown (Pl. 22, fig. 5). The situation of minor septa is different, as they are located in the loculi occupied by channels. They cease development at the point when channels begin to form (text-fig. 2A, position s_1 of septum) and their growth is not continued during the whole period of activity of open channels. However, when partition takes place septal structures appear between the major septa, exactly in the same loculi where the former minor

EXPLANATION OF PLATE 15

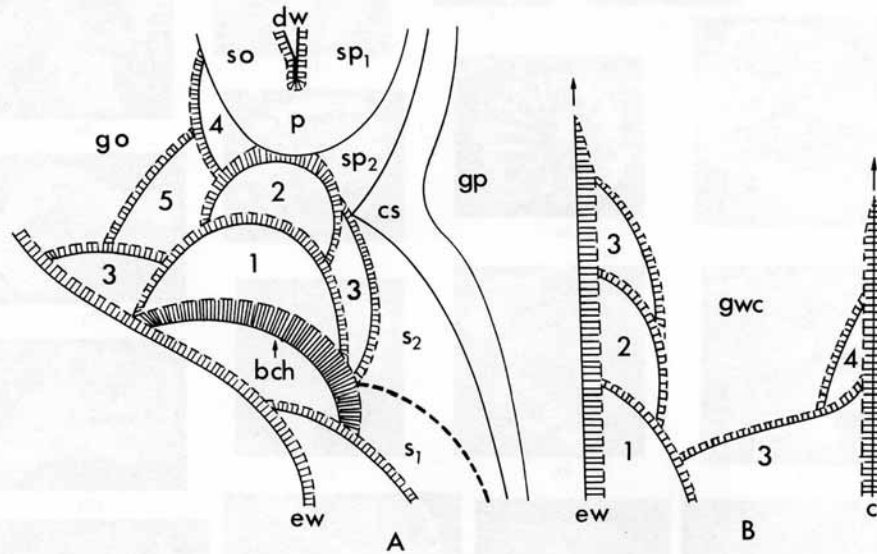
All figs. $\times 4$.

- Fig. 1. USNM 196592. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.
 Fig. 2. USNM 196593. Calicular view of non-offsetting protocorallite.
 Fig. 3. USNM 196594. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.
 Fig. 4. USNM 196595. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.
 Fig. 5. USNM 196596. Non-offsetting protocorallite. *a*, calicular view with well developed axial structure; *b*, side view.
 Fig. 6. USNM 196597. Non-offsetting protocorallite attached to inside of brachiopod shell.
 Fig. 7. USNM 196598. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.
 Fig. 8. USNM 196580. Protocorallite with first offset (see also Pl. 14, fig. 6). *a*, calicular view; *b*, side view of a very irregular shape.
 Fig. 9. USNM 196599. Protocorallite with first offset. *a*, calicular view; *b*, side view.
 Fig. 10. USNM 196600. Protocorallite with first two offsets produced early in ontogeny. Strong attachment to a bryozoan colony. *a*, calicular view with second offset; *b*, side view with first offset.
 Fig. 11. USNM 196601. Protocorallite with first offset. *a*, calicular view; *b*, side view.
 Fig. 12. USNM 196602. Protocorallite with two almost simultaneous offsets. *a*, side view; *b*, calicular view.
 Fig. 13. USNM 196603. Protocorallite with three first offsets. *a*, side view; *b*, calicular view.
 Fig. 14. USNM 196581. Calicular view of protocorallite with three first offsets (see also Pl. 14, fig. 7 and Pl. 23, fig. 7).



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septa were located (text-fig. 2A, position sp_1 ; Pl. 16, figs. 10c, 11). Shortly after the channels are overgrown by dissepiments the old minor septa start to grow upward, based on surfaces of these dissepiments (text-fig. 2A, position s_2). It is also probable that the new minor septa, which appeared on partition, start to develop downwards and inwards in the calice as soon as the bodies of parent and offset polyps are separated (text-fig. 2A, position sp_2). A seeming interruption of minor septa is especially well expressed in this stage of development (Pl. 22, figs. 5, 6c—loculum 4). In further growth of a parent corallite, septal invaginations of the ectoderm of a parent polyp in which the parts of the minor septa mentioned above are secreted become united.



TEXT-FIG. 2. A, reconstruction of overgrowth of channel, based in part on Plate 14, fig. 12 and Plate 22, figs. 5, 6c. Not to scale. B, appearance of particular structural elements in calice. Permanently upward-growing structures are indicated by arrows.

1-5—sequence of appearance of particular basal structural elements; bch—bottom of channel; c—pseudo-columella; cs—continuous minor septum; dw—dividing wall; ew—external wall; go—gastro-vascular cavity of offset; gp—gastro-vascular cavity of parent; gwc—gastro-vascular cavity; p—partition; s_1 , s_2 —positions of old minor septum before and after the channel was overgrown; so—new minor septum of offset; sp_1 , sp_2 —positions of new minor septum of parent before and after the channel was overgrown.

Starting from this point there is no trace of channels in the skeleton of a parent calice, and only continuous minor septa are seen (text-fig. 2A, position cs).

Because of technical difficulties all the processes which took place in channels were observed only from the side of the parent corallite. Judging from the depth of channels in the offsets they became overgrown here later than on the parent side. Observations in serial sections show that this too was a step-by-step process. Dissepiment-like or

tabula-like basal plates were built one after another between septal swellings as soon as the soft tissues of the parent and daughter polyps became separated.

The channels in most of the corallites studied are in pairs. This may have had some functional importance as the pair of channels would enable a flowing liquid to be divided into two currents—from the gastral cavity of a parent polyp through one channel and back through the other. This would make the currents more effective, as the food- and oxygen-bearing water would not be mixed with that from which the food and oxygen were already extracted. This is a rather speculative conception and it is also possible that water was pumped either by the parent polyp to the gastral cavity of the daughter or vice versa in one direction only. Of more importance than water supply seems to be the direct connection of soft tissues of these two polyps. This would enable the parent polyp to provide an offset directly with any required substances. These dual functions of the channels were especially important in the early stage of blastogeny when tentacles of the young polyp were either absent or underdeveloped, and the capability of the young polyp to grow independently was rather low. The lost structures, discussed below, may have resulted from premature separations of offsets.

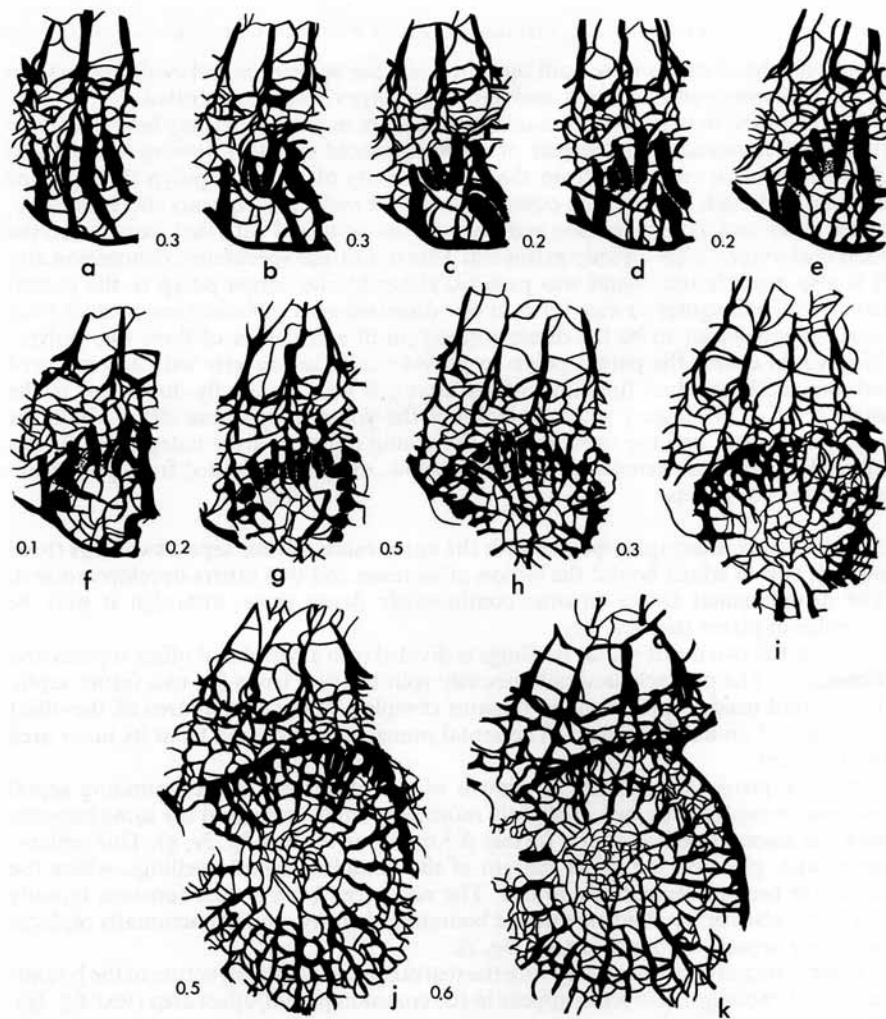
Serial sections. Blastogeny begins with the appearance of four septal swellings (text-fig. 3a), two of which bound the region of increase and two others develop inside it. The dissepimental tissue remains continuously dense there, although it may be irregular in places (text-fig. 3a).

One of the two inside septal swellings is divided into a peripheral offset septum and a pinnacle. The pinnacle is simultaneously split to form bases for two future septa. The second inside septal swelling remains complete in the central area of the offset and initiates an axial structure. The septal pinnacle is separated from its inner area (text-fig. 3b).

After approximately 1 mm of growth of the offset one of the bounding septal swellings is replaced by two or slightly more new, thick septa, and the same happens with the second swelling after a further 0.3 mm growth (text-fig. 3e, g). This replacement takes place on the upper margin of the bounding septal swellings, where the ectoderm became secondarily folded. The new septa have a dual function initially since they also form a solid partition, a bounding element, which functionally replaces bounding septal swellings (text-fig. 3g, i).

Approximately contemporary with the rearrangement of the structure of the bounding septal swellings, new septa appear in the common parent/offset area (text-fig. 3g). They are always closely connected with the septal pinnacles, being developed on the tips of them. Their function, as with those originating from bounding septal swellings, is twofold, both septal and bounding, since they form a solid partition connected directly with the partition built of the transformed bounding septal swellings (text-fig. 3i, k).

Septal insertion is irregular and differs from the regular zaphrentoidal insertion observed in protocorallites. This results from the very rapid transformation of the bounding septal swellings into septa, and the almost simultaneous appearance of new septa on the tips of pinnacles. Only on the peripheral wall of the offset are a few new septa inserted slowly (text-fig. 3d, e). Their sequence of appearance suggests that the



TEXT-FIG. 3. Lateral increase of USNM 196669 in serial sections. All figs. $\times 7$.

a, b, hystero-brephic stage with septal swellings (*a*) and long septal pinnacles (*b*). Cardinal septum is the only inherited septum. It becomes a base for an axial structure of the offset.

c-g, hystero-neanic stage with almost no insertion of septa during first 0.8 mm of growth (*c-f*) and with rapid insertion during next 0.2 mm (*g*). The bounding septal swellings are divided into two (*e*, left swelling) or many (*g*, right swelling) new septa. A partition is first built of septal pinnacles (*c-f*) and then of new septa (*g*).

h-j, neanic stage. Does not differ in structure from that of a protocorallite, except for a little more irregular arrangement of structural elements near the partition.

k, late neanic stage with partition still present, but with dividing wall simultaneously built from both sides of a common parent/offset area.

septum from which the pseudocolumella is built is the cardinal septum, and that this septum is inherited, located on the peripheral wall.

From its origin an axial structure (text-fig. 3c, d) is built around the axial end of one septum, but there is at least a short period of growth with a continuous medial plate (text-fig. 3b). Septal lamellae are irregular, curved, and may be distinguished from axial tabellae only by their fine structure.

Observations on calices and comparison with serial sections. The following discussion is based on a summary of observations made on many calices of offsets of different colonies. The beginning of blastogeny is marked by the rearrangement of structures of the shoulder of the calice, a part of which becomes wider and flatter (Pl. 14, figs. 2, 3a). This limited region is the only part of a corallite subject to changes due to increase. Most of the parent calice remains unchanged (Pl. 15, figs. 8a, 9a, 10a). The flattening itself is not indicative of the beginning of offsetting, as there are many deformations of calices related to attachment processes, etc. (Pl. 14, fig. 1a, b). A flattened calice caused by extrinsic factors may be distinguished from one at the beginning of offsetting in not having differentiated septa.

Growth of a new individual, in all observed cases, is initially directed inwards towards the calice of the parent corallite. Such a young offset is completely within and protected by that calice (Pl. 14, figs. 3b, 5a). This early hystero-brephic stage has a shelf-like shape and possesses two septal swellings as the only structural elements (Pl. 14, figs. 3a, 5a). During further growth of an offset, septal pinnacles are developed as supporting elements in the common parent/offset area (Pl. 14, figs. 3b, 4a, 5b). Their secondary folding to form the initial stages of new septa may be fairly clearly observed (Pl. 14, figs. 3b, 4b, 5a). These new septa develop quickly and expand laterally to form a solid partition and to bridge channels (Pl. 14, figs. 8, 10, 11, 13; Pl. 16, fig. 11).

The morphology described above differs from that of the hystero-brephic and hystero-neanic stages discussed earlier in the account of serial sections. There are no basal structural elements in the calices, while in sections many dissepiments and/or other basal plates are present between the septal swellings. The origin of these phenomena is discussed earlier in connection with channels.

A further aspect regarding development as seen in both calices and serial sections involves different rates of development of particular regions of offsets. In many examples (e.g. Pl. 14, figs. 7, 8, 10, 11) the inner regions of a young individual, close to the parent corallite, are generally higher, often significantly, than their outer regions. The inner regions are also more advanced in morphologic development, and in particular have many more septa. Only a few septa, mostly inherited, occur in the outer region of a young offset. The very rapid growth of the common parent/offset area is most probably caused by atrophism of a new polyp tending to deflect from the parent corallite. This may be explained by a need to occupy a water space which is not exploited by the parent polyp. These differences of speed of development of particular parts of the calice cause the internal structure of young corallites to be differentiated when observed in serial sections. Different parts of the same section (outer and inner) belong in fact to different stages of development since they were secreted at different times.

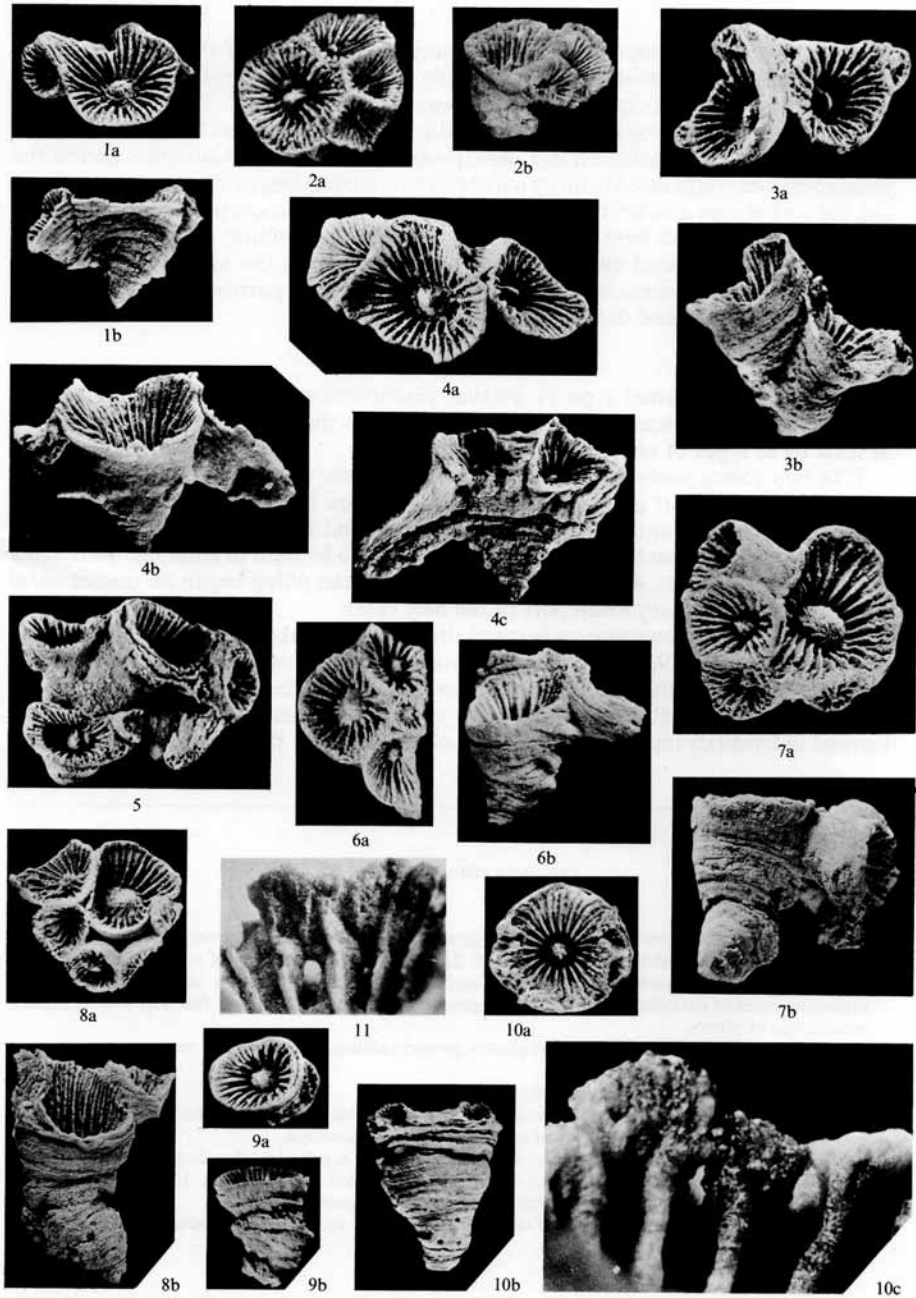
As in the ontogeny of protocorallites, but less clearly so, the arrangement of septa in young calices of offsets is zaphrentoidal. This can be established mainly by observation of the position of incompletely developed septa on the walls of calices (Pl. 14, figs. 7, 8, 10, 14). With further development this arrangement is modified by the appearance of basal elements and an axial structure, as seen in transverse serial sections.

The pseudocolumella is distinguished very early in most of the corallites examined. It is commonly connected to two septa orientated perpendicular to the partition between parent and daughter corallites. One of these two septa, commonly the peripheral (cardinal) septum dominates, while the counter septum, although connected directly to the pseudocolumella, is visibly not as prominent as the other. The fine structure of pseudocolumellae may be either monoseptal or biseptal. None of the axial ends of septa or septal lamellae are incorporated into it, although it may resemble a compound pseudocolumella (Pl. 14, fig. 16).

There is a rather distinct variability within young corallites in their shape and dimensions, speed of growth, appearance and differentiation of particular structures, etc. Most variations are not important as they are either small changes or appear within one colony and, as such, are somatic and may have been environmentally controlled. The positions of cardinal and counter septa appear to be of primary importance. In most observed corallites the cardinal septum is situated at the external wall of the offset and is inherited from the parent corallite. In four or five small colonies the situation is reversed, and in these cases the counter septum is the basic septum for the axial structure. Unfortunately all these colonies are at an initial stage

EXPLANATION OF PLATE 16

- Fig. 1. USNM 196604, $\times 2$. Protocorallite with two offsets arranged symmetrically due to attachment. *a*, calicular view; *b*, side view.
- Fig. 2. USNM 196605, $\times 2$. Protocorallite with four offsets arranged asymmetrically, all on one side. *a*, calicular view; *b*, side view.
- Fig. 3. USNM 196606, $\times 2$. A first asexually produced specimen starts reproduction and the protocorallite is offsetting for the second time. *a*, calicular view; *b*, side view.
- Fig. 4. USNM 196607, $\times 2$. Protocorallite with two generations of offsets. *a*, calicular view; *b*, side view; *c*, view of a very strong attachment and two offsets of a second generation.
- Fig. 5. USNM 196608, $\times 2$. Protocorallite producing two generations of offsets. One corallite of the first generation starts reproduction.
- Fig. 6. USNM 196571, $\times 2$. Protocorallite with four offsets belonging to two generations (see also text-fig. 1g). *a*, calicular view; *b*, side view.
- Fig. 7. USNM 196609, $\times 2$. Protocorallite with four asymmetrically arranged offsets of first generation. *a*, calicular view; *b*, side view.
- Fig. 8. USNM 196610, $\times 2$. Protocorallite starting to produce offsets very late in ontogeny. *a*, calicular view; *b*, side view.
- Fig. 9. USNM 196611, $\times 2$. Corallite with no offsets; only rejuvenescences are produced for a few times. *a*, calicular view; *b*, side view.
- Fig. 10. USNM 196579. Protocorallite starting to produce offsets late in ontogeny (see also Pl. 14, fig. 5*a, b*). *a*, calicular view, $\times 2$; *b*, side view, $\times 2$; *c*, channels, septal swellings, and new septa on septal pinnacles, $\times 12$.
- Fig. 11. USNM 196584, $\times 8$. Bridged channels and a solid partition above them (see also Pl. 14, fig. 10).



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of astogeny and it is impossible to determine the constancy of this character. It is classified here as an individual variant, mainly because of the morphologic similarities between these and other specimens of the species.

A dividing wall is built along the middle line of a partition by both corallites (Pl. 22, fig. 1). The separation is a slow process, and for a considerable period the young corallite is separated from its parent only by a partition, i.e. calices are separated but the soft tissues remain united above a partition. Heterochronic development of calices has to be noted here, since at the time when the dividing wall was built there were no other structural elements close to it, apart from the upper margin of the partition. All the elements seen in the sections close to the partition and the dividing wall were built later and deeper in the calice.

Division

Division is an abnormal type of asexual reproduction in colonies of the species discussed here. It appears in only a few specimens in the collection under study, and at least three types of origin may be distinguished.

1. In two young protocorallites (Pl. 19, figs. 3, 4) the division may be closely compared with, or is a part of rejuvenescence. In specimen USNM 196625 the polyp lost one-half of its calice and began organizing the second half for two individuals. The wall, based on septa and an axial structure, started to be built in a manner indicating division (Pl. 19, fig. 4). At an early stage, however, the polyp began an unsuccessful rejuvenescence in a very small part of the new calice.

USNM 196624 shows more advanced division which also may be compared with rejuvenescence (Pl. 19, fig. 3). The following characters can be noted: (a) approximately one-third of the calice of the protocorallite was lost at the beginning of the division; this is directly comparable with typical rejuvenescence: (b) the two newly formed individuals incorporated the rest of the calice of the protocorallite without

EXPLANATION OF PLATE 17

All figs. $\times 1.5$.

Fig. 1. USNM 196612. Asymmetrical young colony with two offsets of the first generation starting to grow perpendicular to the protocorallite (see also Pl. 23, fig. 11). *a*, bottom view of a strong attachment of protocorallite; *b*, side view of protocorallite and its first offset; *c*, top view showing many shallow rejuvenescences of corallites of a first asexual generation; *d*, calicular view of first and second asexual generations of offsets.

Fig. 2. USNM 196613. Two corallites (probably protocorallites) offsetting only once at early stage of ontogeny.

Fig. 3. USNM 196614. Directed growth of a young colony.

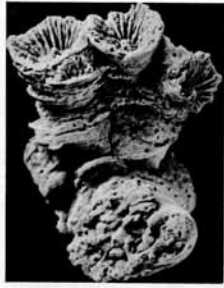
Fig. 4. USNM 196615. Umbrelliform colony with five almost simultaneous offsets. *a*, calicular view of parent corallite; *b*, side view showing an angle of growth of the offsets.

Fig. 5. USNM 196616. Asymmetrical growth of a young colony. *a*, side view; *b*, calicular view.

Fig. 6. USNM 196590. Young colony with crowded corallites (see also Pl. 14, fig. 16).

Fig. 7. USNM 196617. A weak colony with corallites widely spaced.

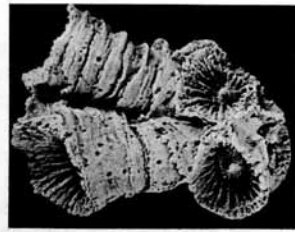
Fig. 8. USNM 196618. *a*, calicular view of crowded corallites; *b*, view of side opposite to a large, flattened attachment surface.



1a



1b



1c



1d



2



4a



3



6



4b



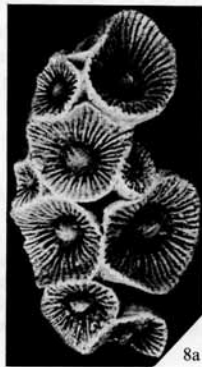
5a



5b



7



8a



8b

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any changes; this is typical of division: (c) the new structures formed in the middle of the old calice of the protocorallite have a mixed character. The new wall is similar to the regular wall of a rejuvenescent coral, but it is orientated in the manner characteristic for division. This influences the arrangement of septa inserted on these walls, which are directed towards the two centres.

2. USNM 196622 (Pl. 19, fig. 1) shows an offsetting-like division. The parent corallite is easily recognizable and the offset is produced on a wide, flat shoulder of the parent calice. The arrangement of septa in the common part of both corallites is different from that observed in regularly offsetting specimens. Two long, major septa bend from the margins of the common area towards the axial structure of the parent corallite. Three, most probably new, common parent/offset septa were formed in the space between them. Other septa in the offset side of the common area are established on dissepiments. There was obviously a continuous sheet of soft tissue covering the common skeleton between the two calices.

3. USNM 196623 (Pl. 19, fig. 2a, b) has a pair of 'twins' produced by the protocorallite of a small colony in which the first series of offsets was regular. At the base of the calice the twins are partly separated by two thickened, straight, major septa. Small, button-like structures on the surface of these two septa are probably new septa of twins. Similar twins have already been described by Jull (1974) in the Australian Lower Carboniferous species *Lithostrotion adjunctum*.

None of the discussed specimens developed by a regular division analogous to that described in Scleractinia, although the development in each example differs from typical offsetting. Division is a rare type of increase in Rugosa and in almost all records I know of it occurs together with other types of offsetting, as an exception. The reason for producing such new individuals is most probably somatic, and may be either pathological or may have resulted from environmental influence (e.g. rejuvenescence-like division). It seems to be insignificant as a taxonomic character. Dr. R. K. Jull (*in litt.*) kindly informs me that he possesses a few incomplete colonies of *L. adjunctum* in which the corallites increase exclusively by division.

Spassky and Kravtsov (1974) applied a new meaning to the term 'division' by including both axial increase and peripheral increase and calling them central division and peripherally calicular division. According to these authors both types of division involve the production of no more than six new individuals since they can be divided only by the protosepta. This seems to be correct as far as the central division (axial increase) is concerned. The septal character of new walls in this type of increase has been discussed many times (e.g. von Koch 1883; Smith and Ryder 1927; Ting 1940;

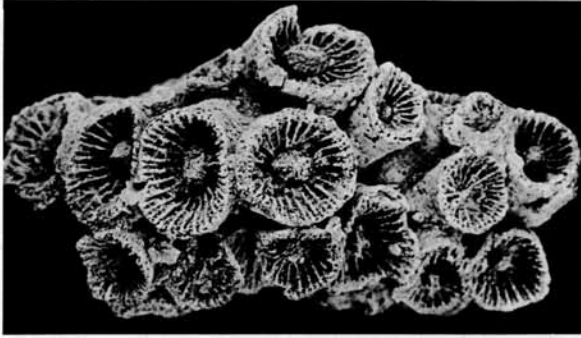
EXPLANATION OF PLATE 18

All figs. $\times 1.5$.

Fig. 1. USNM 196619. Composite colony. a, calicular view; b, side view.

Fig. 2. USNM 196620. Composite colony. Almost all corallites descend from one protocorallite; the other (lowermost on fig. 2b) produced only one lost structure. a, calicular view; b, side view.

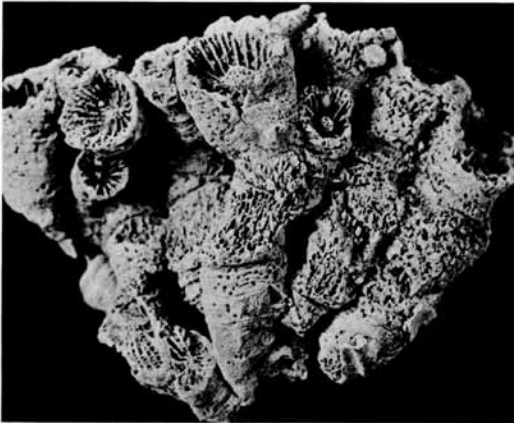
Fig. 3. USNM 196621. Chain-like colony. a, calicular view; b, bottom view showing two opposite directions of growth of corallites.



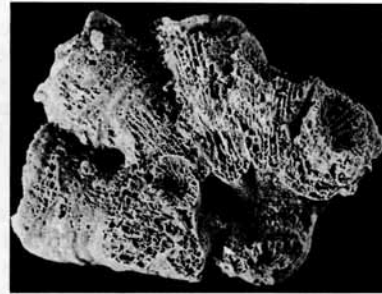
1a



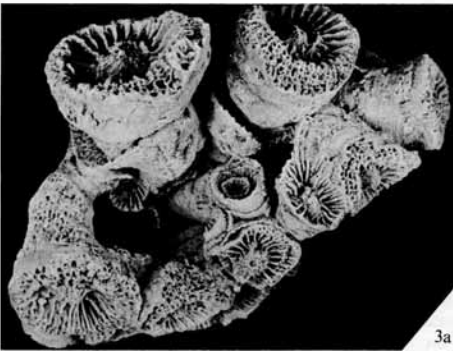
2a



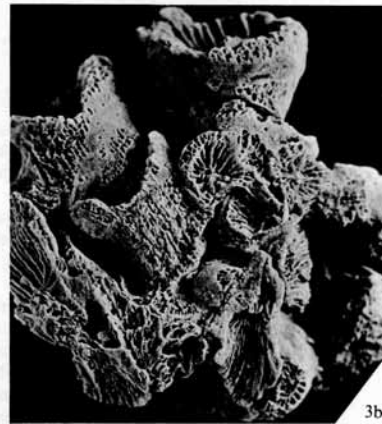
1b



2b



3a



3b

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Hill 1956; Oliver 1968; Fedorowski and Jull 1976). In *Polyadelphia polymera*, Spassky and Kravtsov (1974) showed that there may be either four, or as many as six and as few as two descendent corallites in this type of increase.

However, the other examples given by these authors are not convincing. There is no evidence for a protoseptal (and in general for septal) origin of the new walls. The lack of detailed study on any of the examples shown by Spassky and Kravtsov (1974) makes it impossible to reliably establish the origin and development of the types of increase mentioned by them. It seems probable, however, that the examples shown by them on their plate 2, figs. 2, 3 and possibly also fig. 4 represent division of a twin-type, while those on their plates 3 and 4 represent peripheral increase. Some examples of peripheral increase studied in detail by Jull (1965) and Fedorowski (1970) show that there may be more than six descendent corallites formed, and that they are clearly not connected with the protosepta as suggested by Spassky and Kravtsov (1974).

The terms axial increase and peripheral increase could be called 'division' as used by Spassky and Kravtsov in that the old polyp is divided into new ones. However, at first the origin of a central division (axial increase) differs from peripherally calicular division (peripheral increase; e.g. compare the schematic reconstructions of Fedorowski and Jull 1976), and there is no need to use new names for these reasonably well-known processes. This is especially so in this case when the proposed name 'division', is actually used for a rare, very variable, and taxonomically unimportant process in Rugosa, and also for an important process of different origin in Scleractinia.

Lost structures

This is a new term proposed here for any offset produced in the process of lateral increase and left underdeveloped far below an actual margin of the parent calice, with no evident external factors acting to stop its development. This definition expresses three main characters of these structures: (a) the progeny is never parricidal; (b) the progeny may reach varying stages of hystero-ontogeny ranging from the hystero-brephic to hystero-neanic stages. It dies underdeveloped, although the

EXPLANATION OF PLATE 19

Fig. 1. USNM 196622, $\times 3$. Offsetting-like division on shoulder of calice.

Fig. 2. USNM 196623. Colony with regular offsets and 'twins'. *a*, calicular view, $\times 1.5$; *b*, calicular view of the 'twin' type of division showing two major septa converted into walls which partly separate the 'twins', $\times 3$.

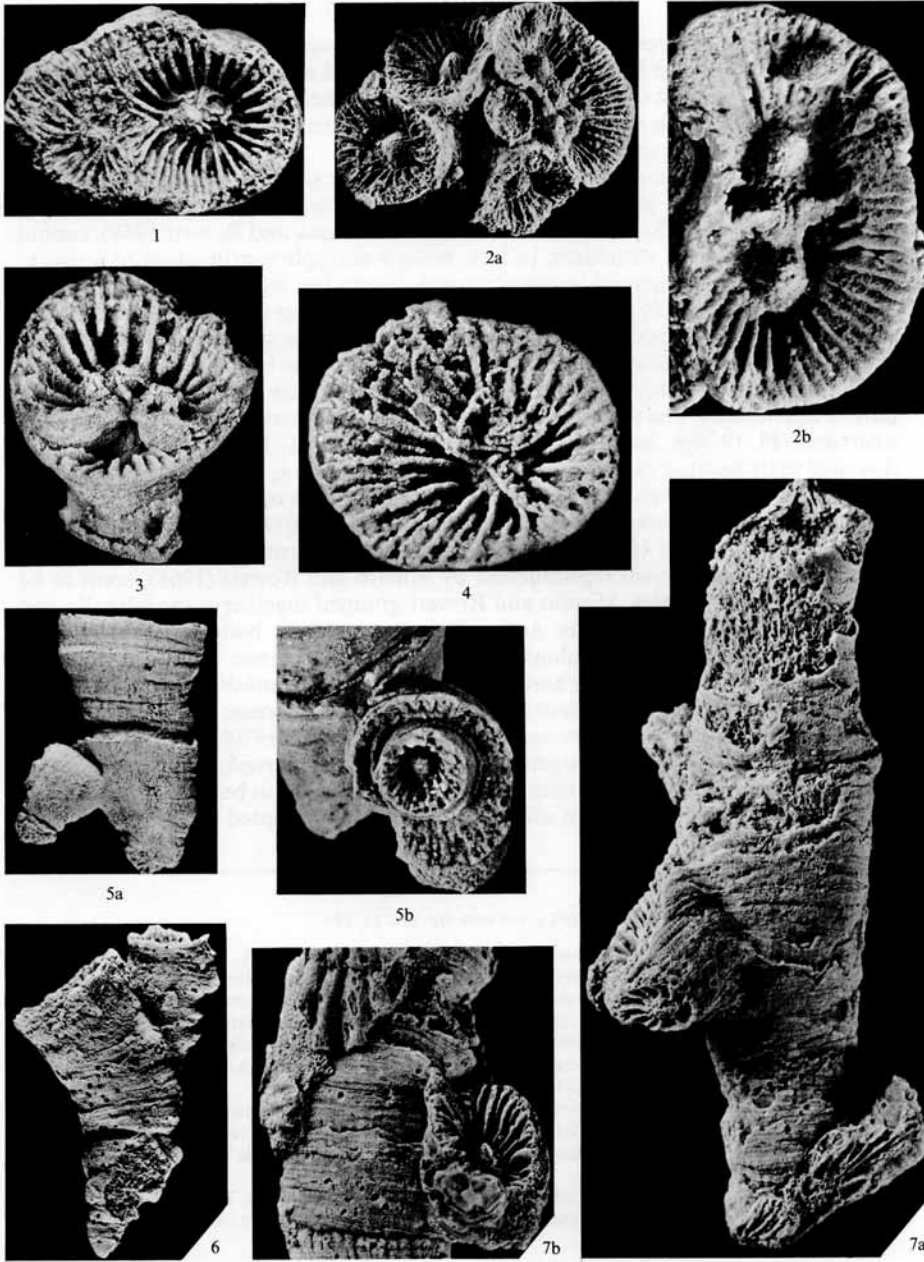
Fig. 3. USNM 196624, $\times 4.5$. Combination of rejuvenescence and division. New walls have no relation to parent septa and are supported by a skeleton of the old axial structure.

Fig. 4. USNM 196625, $\times 4.5$. Initial stage of division and rejuvenescence taking place in axial part of an old calice.

Fig. 5. USNM 196626. Probable protocorallite (proximal end not preserved) with a lost structure produced by division. *a*, side view, $\times 1.5$; *b*, calicular view of the lost structure showing its own rejuvenescence and a close relation to a shallow rejuvenescence of a parent corallite, $\times 3$.

Fig. 6. USNM 196572, $\times 1.5$. Protocorallite offsetting only once during its ontogeny (see also text-fig. 1*h*).

Fig. 7. USNM 196627, $\times 1.5$. A quasi-colony. *a*, protocorallite with two generations of offsets; *b*, fragment of protocorallite with an offset produced by division.



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parent continues to grow under the same external conditions; and (c) there is no fundamental difference between the lost structure and any normal, lateral offset in their increase, insertion of septa, and appearance of other structural elements, except that they did not reach morphological maturity. The reason for this underdevelopment is assumed to be genetic.

The above statements exclude all corals that produce peripheral offsets. Peripheral increase is parricidal, and the offsets, although underdeveloped in many known examples (e.g. Jull 1965; Fedorowski 1967*b*, 1970; Minato and Rowett 1968), cannot be compared with lost structures. In fact, being a multiple continuation of a parent corallite, offsets in peripheral increase are opposite to lost structures.

There are also laterally produced offsets which are not lost structures although they also died underdeveloped. Their underdevelopment is due to external factors, such as the rotation or fall of a colony to put the young corallite into sediment. Although similar to lost structures, these should be distinguished since they obviously have no genetic significance. The material described here includes many examples of both lost structures (Pl. 19, figs. 5*a*, *b*, 7*a*, *b*; Pl. 23, figs. 7, 9*a*, *b*, 11, 12) and young corallites that died early because of extrinsic factors (Pl. 15, figs. 8–14; Pl. 16, figs. 1–7; Pl. 18).

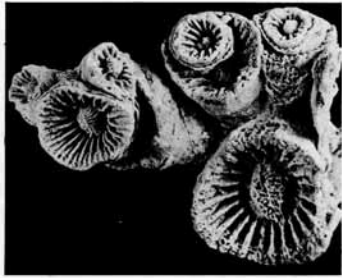
Offsets comparable with lost structures have rarely been reported in the literature. Offsetting in '*Craterophyllum verticillatum*' Barbour, 1911, studied in detail by Fagerstrom and Eisele (1966), and in *Timania rainbowensis* Rowett, 1969, studied from the aspect of asexual reproduction by Minato and Rowett (1968), seem to be the only known examples. Minato and Rowett grouped together some laterally and peripherally increased corallites and called them 'simple budding' forms. They equated this term with 'quasi-colonies' of Fagerstrom and Eisele. I take the view that '*Clisaxophyllum awa atetsuense*' and most probably also *Lonsdaleoides(?) nishikawai*, as described by Minato and Rowett, represent peripheral increase and as such should be called incipient colonies (term introduced by Fedorowski 1970), whereas 'colonies' of *T. rainbowensis*, which show significant similarity to '*Craterophyllum verticillatum*', belong to 'quasi-colonies'. The term 'simple budding' seems to be too general since it includes quite different modes of offsetting, and it is not adopted here.

EXPLANATION OF PLATE 20

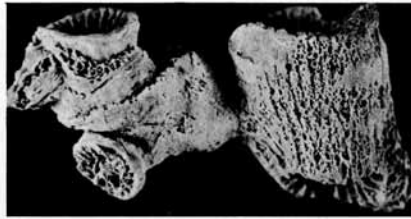
- Fig. 1. USNM 196628, $\times 1.5$. Axial rejuvenescence in quasi-colony (see also Pl. 23, fig. 12).
 Fig. 2. USNM 196629, $\times 1.5$. Directed growth of part of a colony. *a*, calicular view showing an axial (*right*) and lateral (*centre*) rejuvenescence, and a combination of lateral rejuvenescence with offsetting (*left*); *b*, side view of parent and offset corallites; *c*, bottom view of umbrelliform arrangement of offsets.
 Fig. 3. USNM 196630, $\times 1.5$. Axial rejuvenescence and a directed growth of offsets.
 Fig. 4. USNM 196631. Very deep narrowings of growth. *a*, side view, $\times 1.5$; *b*, continuation of external wall on the flat, horizontal surface of narrowed skeleton, $\times 3$.
 Fig. 5. USNM 196632, $\times 1.5$. Attachments of particular corallites inside a fasciculate colony.
 Fig. 6. USNM 196633, $\times 1.5$. Calicular view of colony showing axial and lateral rejuvenescences. The lower right calice shows three new individuals, which appeared in a way comparable with both rejuvenescence and peripheral increase.
 Fig. 7. USNM 196634, $\times 1.5$. A weak, simple colony showing directed growth. The protocorallite (*right*) is the only large corallite, but one of the offsets of the first asexual generation also attained the capacity to reproduce.



1



2a



2b



3



2c



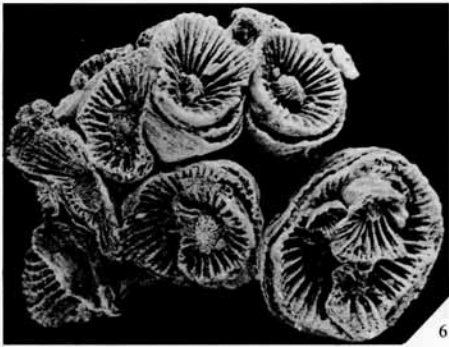
5



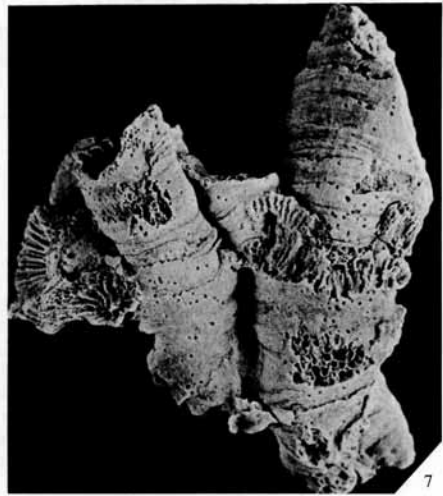
4a



4b



6



7

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Lost structures appear most commonly, but not exclusively, in connection with rejuvenescence. Similar observations were made by Fagerstrom and Eisele (1966, p. 595), who wrote: 'Rejuvenescence of protocorallites commonly occurs directly above each verticil. In addition to buds in verticils, many protocorallites bear buds randomly arranged between verticils or with random arrangements of buds throughout.' In some cases the polyp of a lost structure may be rejuvenated (Pl. 19, fig. 5*b*; Pl. 23, fig. 9*b*) or even produce its own offset (Pl. 19, fig. 7*a*). Nevertheless, it did not reach morphological maturity and died shortly after losing its direct soft-tissue connection with the body of the parent polyp. This direct dependence of a polyp of lost structure on that of a parent may be regarded as one of the main reasons for their early extinction. This is especially obvious in the case of rejuvenescence of a parent (Pl. 19, fig. 5*a, b*).

Observations of lost structures indicate that they are neither produced incidentally (since they show all characters of offsets), nor regular, healthy offsets, capable of reaching morphologic maturity. It seems likely that there are some species of solitary corals, or some populations, that possess the genetic potential to produce offsets. This is not a first-range character, however, and in regular circumstances it is suppressed by other characters. *T. rainbowensis* may be cited as an example. The genetic potential to produce offsets seems to be only initially developed in this species and its usage is probably stimulated by extrinsic factors. '*C. verticillatum*', although generally a solitary species, represents a more advanced stage of development of genetic potential to produce offsets. There are a number of corallites within this species offsetting many times during their ontogeny. However, none of them form a normal, healthy colony.

As far as I know no offsets comparable with lost structures have yet been reported from well-developed colonies. In the collection of *Heritschioides* sp. nov. discussed here, there is no well-developed colony in which any underdeveloped offset can definitely be called a lost structure. These structures are especially common in quasi-colonies (Pl. 19, figs. 5*a, b, 7a, b*; Pl. 21, figs. 8, 9; Pl. 23, figs. 9*a, b, 12*) and much less frequent in simple colonies, i.e. normal colonies resulting from a lateral increase, but developing very few branches during astogeny (Pl. 20, fig. 7; Pl. 23, fig. 11).

EXPLANATION OF PLATE 21

All figs. $\times 1.5$.

Fig. 1. USNM 196635. Circumrotary colony. *a-c*, different sides showing differentiated directions of growth of corallites.

Fig. 2. USNM 196636. Very late offsetting of a protocorallite showing a combination of deep axial rejuvenescence and lateral offsetting. *a*, calicular view; *b*, side view.

Fig. 3. USNM 196637. Non-offsetting protocorallite attached to inner surface of brachiopod shell.

Fig. 4. USNM 196638. Small hemispherical colony with crowded corallites.

Fig. 5. USNM 196639. Pseudo-colony with offsetting 'guest' corallite.

Fig. 6. USNM 196640. Protocorallite offsetting for first time at late ephebic stage.

Fig. 7. USNM 196641. Composite colony. A few corallites attached to the calice of a dead individual.

Figs. 8, 9. USNM 196642-196643. Quasi-colonies.

Fig. 10. USNM 196644. Probably a composite colony. Progeny of two protocorallites tend to grow together.

Fig. 11. USNM 196645. Chain-like colony.



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Heritschioides sp. nov. belongs to the type of colonial species in which a group of individuals may possess only a weak ability to produce offsets. This capability may be developed to a different degree in different specimens and in some of them it is also suppressed by other characters, as discussed above for the solitary corals. Similar results may thus be achieved in the development of a colony, although from opposite origins. In the one case a 'colony' (mainly quasi-colony or incipient colony) originates from a solitary coral, while in the other it originates from a protocorallite of a generally colonial species, in which the character of coloniality, weakly fixed in its genetic code, is suddenly stimulated. Such a protocorallite or solitary corallite polyp, although capable of creating a daughter polyp, is not able to provide it with the complete genetic potential for regular development. As a result the daughter polyp cannot mature.

In all three species discussed above (*Heritschioides* sp. nov., '*C.*' *verticillatum*, and *T. rainbowensis*), solitary corallites with no offsets produced at any stage of ontogeny are also known to occur. The frequency of such corallites is greatest in *T. rainbowensis*, which is primarily solitary and belonging to a solitary genus, and least in *Heritschioides* sp. nov., which is generally colonial, and belongs to a colonial genus. This indicates that the types of structures discussed and an initial coloniality may appear either as an incipient character or as rudimentary feature. In both cases it is marked by similar types of offsets—i.e. lost structures.

REJUVENESCENCE

This is a common process permitting a prolongation of existence of particular corallites within colonies. As there is only a quantitative difference, any example in which a polyp loses a part of its old calice and starts to build a narrower one without either dividing its soft body or opening a new mouth, should be called rejuvenescence. It may happen only once, or it may take place with irregular frequency during the hystero-ontogeny of particular corallites. It may be weak or intensive, i.e. smaller or greater parts of the old calices may be lost and replaced by new structures.

There are many examples of 'shallow' and *irregular rejuvenescence* within the collection, such as some parts of the corallites shown on Plate 14, fig. 17; Plate 17, fig. 1; Plate 20, figs. 1, 7; Plate 21, fig. 8; and Plate 22, fig. 8. Such rejuvenescence may involve the whole circumference of the calice, or only a part of it. The external wall, outer parts of the dissepimentarium, and peripheral parts of septa, are the morphological structures which are lost during the process. The new wall bounds remaining parts of the calice. The whole rejuvenescence of this initial type resembles a regular but deep growth line of the external wall. The only difference is that in rejuvenescence the external wall loses its continuity. This may happen when the polyp is diminished rapidly, but not deeply, instead of contracting gradually. In some cases the margin of the old calice is slightly deflected inwards (Pl. 23, figs. 1*a*, *b*), indicating that the regular process of reduction in size had started and was replaced by rejuvenescence. All more axially located skeletal elements remain unchanged in any of the above examples. There are also quite remarkable decreases in observed diameter that did not cause a break of the external wall, but the wall continued to grow almost horizontally into the calice (Pl. 20, fig. 4*a*, *b*).

The next stages of change in skeletal morphology during rejuvenescence are seen in the collection but only the final steps are described here since the intermediate stages can easily be deduced. Two types of rejuvenescence are observed in which a large part of the calice is involved. They may be given names parallel to those referring to types of offsetting, i.e. *axial rejuvenescence* and *lateral rejuvenescence*. These types are not as constant as in blastogeny and intermediate examples are known.

In *axial rejuvenescence* the central part of the corallite, the axial structure, and the axial parts of the major septa, and most probably also the central part of the polyp, remain in place and are almost unchanged. The number of lamellae in the axial structure may be reduced, or the thickness of septa may be changed, but these changes are not fundamental. The whole external ring of the calice, i.e. the dissepimentarium, the minor septa, and the external parts of major septa were lost. The diminuted polyp started its new stage of development with a mixed skeletal morphology—an advanced internal part and a juvenile, often thickened, peripheral part. This type of rejuvenescence may take place many times during the development of particular corallites (Pl. 19, fig. 5*b*; Pl. 20, figs. 1, 3, 6; Pl. 22, figs. 10*a-c*, 12).

Lateral rejuvenescence (Pl. 20, figs. 2*a*, 6; Pl. 21, fig. 7; Pl. 22, fig. 7) takes place where a given part of the periphery of the old calice remains unchanged. This is common in the collection under study. The polyp retained approximately one-half of its skeleton and built a new external wall within the old calice. The axial structure, which is not included in the new calice, seems to be a mechanical support for the new external wall (Pl. 22, fig. 4). Also in this type of rejuvenescence the new corallite possesses a mixed skeleton. The polyp retained a part of the old external region of the calice and built a new axial structure and new structural elements on the inner part of the calice.

All these types of rejuvenescence seem to be similar in one important feature, viz. a new mouth is not opened and the oral disc, as well as the remainder of the soft tissue, is not divided since the number of septa present before, during, and after rejuvenescence remains more or less the same.

There are a few significant irregularities in rejuvenescence within the collection. In some specimens (Pl. 22, fig. 3) it is impossible to determine how much of the calice was lost as there is no wall separating the presumed surviving part from the rest of the calice. On the other hand, there is only a very limited part of the corallite which obviously continued to grow, and in this part a new axial structure was built.

An initial stage of simultaneous offsetting and rejuvenescence is shown in Plate 22, fig. 8 and a more advanced one in Plate 21, fig. 2*a, b*, and Plate 22, fig. 7. In the last example, the offsets are lost structures that ceased to develop as soon as the polyp lost the near-by part of the calice which was starting its rejuvenescence.

There is also another example of renovation, closely resembling rejuvenescence, but which should not be equated with it. This occurs when more than one individual develops from the old one, indicating that new mouths had been opened. This is very similar to peripheral increase in regular offsetting, and in fact should be compared closely with that process. However, it is sometimes obviously connected with rejuvenescence, as shown in Plate 20, fig. 6 (lower-right corner). This may be additional support for the Fedorowski and Jull (1976) thesis that peripheral increase

should be treated in most cases as multiple rejuvenescence. The process in this case is so deep that it leads to the fragmentation of the soft tissue and to the loss of part of it.

ASTOGENY

Offsetting and the problem of maturity

Maturity in previously described types of colonies. The problem of determining maturity in *Rugosa* is very important since only comparison of mature corallites can establish intraspecific variability, boundaries of species or subspecies, etc. At the same time the problem is difficult to solve since there are no common criteria to use for all groups of corals. The problem of maturity is especially important in colonial species, in which variability within the colony is superimposed on intraspecific variability.

It is generally accepted that the capacity to produce offsets is one of the best criteria of maturity. In most colonies previously studied in detail (e.g. Smith 1915; Smith and Ryder 1926, 1927; Rózkowska 1960; Jull 1965, 1967, 1974*a, b*; Fedorowski 1965, 1967*a*) one can observe many examples. Offsetting corallites within the colony may differ a little from each other in their morphology and measurements, but almost all are presumed to be secreted by mature polyps. Probably the only youthful offsetting individual yet reported is that illustrated by Jull (1974*a*, fig. 7₂). There are also other corallites in normally developed colonies, the polyps of which did not reproduce asexually although their structure and measurements are similar to those of offsetting specimens (Fedorowski 1965; Ulitina 1974). In some colonies there is only one, or just a few corallites producing offsets (Beklemishev 1958). This phenomenon is not yet adequately investigated and requires more careful study, especially the comparison between otherwise similar offsetting and non-offsetting

EXPLANATION OF PLATE 22

- Fig. 1. USNM 196646, $\times 3$. Partition separating two corallites is replaced by a dividing wall.
 Fig. 2. USNM 196647, $\times 1.5$. Rapid narrowing of a calice.
 Fig. 3. USNM 196648, $\times 1.5$. Lateral rejuvenescence in very limited area of an old calice.
 Fig. 4. USNM 196649, $\times 3$. Deep rejuvenescence. Bottom of a new calice hangs on an old axial structure.
 Fig. 5. USNM 196650, $\times 9$. Partly overgrown channel (indicated by arrow) with 'interrupted' minor septum.
 Fig. 6. USNM 196651. *a*, probable quasi-colony, $\times 1.5$; *b*, offsets separated from parent by dividing walls. The left offset is united with the parent by bottom channels, $\times 3$; *c*, part of calice showing open (1, 2) and partly overgrown (3, 4) channels, $\times 7.5$.
 Fig. 7. USNM 196652, $\times 3$. Contemporaneous deep, lateral rejuvenescence and offsetting.
 Fig. 8. USNM 196653, $\times 1.5$. Contemporaneous shallow rejuvenescence and offsetting.
 Fig. 9. USNM 196654, $\times 3$. Marginal rejuvenescence on wide shoulder of calice.
 Fig. 10. USNM 196655. Cyclic rejuvenescence. *a*, calicular view, $\times 1.5$; *b*, side view, $\times 1.5$; *c*, axial view showing relation between external and internal parts of major septa and new wall, $\times 4.5$.
 Fig. 11. USNM 196656, $\times 7.5$. Relationship between septa in old and rejuvenated calices, and position of a new wall, convex outwards.
 Fig. 12. USNM 196657, $\times 1.5$. Composite colony showing axial rejuvenescence of corallites.



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corallites. Both types of corallites seem to be morphologically mature, but as yet the factors that stop offsetting in one group are unknown.

In addition to normally developed colonies there are at least two types of 'coloniality' known, which can only be classified formally as colonies. They are the quasi-colonies and incipient colonies discussed above. Colonies of '*Craterophyllum*' *verticillatum* Barbour, studied in detail by Fagerstrom and Eisele (1966), provide almost all the known information on quasi-colonies. In these colonies the protocorallite is the only morphologically (and most probably also sexually) mature individual, and the offsets never reach the degree of development of the protocorallite, although they may be quite numerous and may be produced many times during the development of the protocorallite. These offsets are the lost structures described earlier.

Incipient colonies studied by Jull (1965) and Fedorowski (1967*b*, 1970) appear in some solitary corals (e.g. *Ceratophyllum*, *Spirophyllum*) and show another aspect of the problem of maturity in Rugosa. There is no second generation of offsets produced in such 'colonies', and the corallites of the asexually produced generation are, almost without exception, morphologically underdeveloped compared with the protocorallites. In this sense incipient colonies may be compared with quasi-colonies, as the protocorallites are the only completely developed individuals in both of them. This is the only similarity, however, since modes of offsetting and the reason for extinction of progenies are entirely different.

Maturity of solitary corallites and protocorallites in Heritschioides sp. nov. The collection contains hundreds of specimens in different stages and types of astogeny, as well as solitary corals. All of these specimens are here considered to belong to one species and one population. Some of the solitary corals are immature since they possess either obviously juvenile characters, or their mature characters are underdeveloped. Some of them are not immature since they are morphologically advanced in ontogeny and have structures and dimensions (text-fig. 5*B*) typical for colonial corallites that are most advanced in hystero-ontogeny. Since this species is generally colonial, solitary corals in the population should be regarded as potential protocorallites with protopolyps in which the capacity to produce offsets has not been realized.

In most of the well-preserved young colonies, a first offset appears on the protocorallite after 4–6 mm of growth, but it may appear as early as after approximately 2 mm (USNM 196692). The protocorallite is very juvenile in character when its protopolyp offsets so early. It does not possess a dissepimentarium, and the arrangement of its septa is zaphrentoidal with the axial structure at an early stage of development (Pl. 15, figs. 9*a*, 10*a*). The protopolyp is the only individual within the colony having the capacity to produce offsets at such a young stage of ontogeny. In Tables 1–3 the basic measurements of representative specimens are given to show similarities and differences among offsetting specimens in particular stages of astogeny.

Protopolyps that begin to produce offsets during the middle or late neanic stage of morphological development possess protocorallites with a dissepimentarium built of one or a few verticils of dissepiments, a quite well-developed axial structure, and radially arranged septa (Pl. 15, figs. 12*b*, 13*b*, 14). Protocorallites, the protopolyps of which started to produce offsets while in an advanced stage of ontogeny, are rare in the material studied (Pl. 16, figs. 8*a*, *b*, 10*a*, *b*; Pl. 19, fig. 6; Pl. 21, fig. 6). In some cases

TABLE 1. *a*, Solitary corallites.

Specimen number	Length	Diameter of calice	Number of septa	Remarks
196671	6.1	4.6 × 4.0	12–14?	
196670	8.1	6.2 × 5.3	18 × 2	
196673	12.1	10.1 × 8.4	19 × 2	
196666	23.2	8.8 × 8.5	21 × 2	
196674	26.1	9.9	22 × 2	Calice broken in p-t
196660	12.1	11.0 × 8.3	22 × 2	
196637	19.0	11.4 × 10.0	22 × 2	
196672	33.0	11.8	24 × 2	Calice broken in p-t

b, Protocorallites with hystero-brephic stages of first offsets.

Specimen number	Length	Diameter of calice	Number of septa	Remarks
196600	3.7	5.2 × 4.1	15–16 × 2	
196568	4.3	5.2 × 4.4	16 × 2	
196675	5.6	5.1 × 3.4	15 × 2	
196602	7.2	6.9 × 5.5	17 × 2	
196580	7.4	6.9 × 5.5	17 × 2	
196595	7.5	7.0 × 5.7	15–16 × 2	
196596	8.8	7.4 × 6.2	19 × 2	
196579	13.5	11.8 × 10.6	21 × 2	

c, Colonies in which first asexual generations of corallites start to produce offsets.

Specimen number	Length	Genera-tion	Diameter of		Number of septa	Remarks	
			Firstly offset. pc	Calice			
196606	13.2	pc	3.7 × 3.4	8.0 × 8.0	22 × 2		
	11.4	a		10.8 × 6.7			20 × 2
196668	11.3	pc	4.8 × 4.0	12.8 × 9.2	22–23 × 2		
	10.5	a		11.4 × 8.2			20 × 2
	7.5	b		10.5 × 6.5			19 × 2
	6.0	c		9.1 × 6.7			19 × 2
	21.0	pc		12.3 × 10.7			24 × 2
196618	18.2	a	4.0 × 3.0	12.0 × 9.5	22 × 2		
	15.5	b		10.0 × 9.4			22 × 2
	15.0	c		8.9 × 8.7			21 × 2
	?	d		7.2 × 6.6			19 × 2
	10.7	e		8.0			?18
	196608	8.5		pc			5.8 × 6.0
196608	8.8	a	5.8 × 6.0	7.3 × 4.5	18 × 2	Not offsetting	
	10.5	b		9.5 × 9.0			21 × 2
196616	11.5	pc	6.5 × 6.0	11.8 × 10.5	26 × 2		
	8.0	a		10.3 × 8.8			20 × 2
	6.0	b		8.3 × 7.1			19 × 2
	6.0	c		8.0 × 5.0			16 × 2
	9.0	d		9.8 × 7.6	20 × 2	Not offsetting	

See Table 4 for explanation of abbreviations.

they produced many offsets almost simultaneously around the shoulder of the calice (Pl. 16, fig. 10a, b), but they may have produced only one offset (Pl. 19, fig. 6).

Judging from these observations, there is no simple relationship between capacity to produce offsets and the stage of morphological development of the protopolyp and its protocorallite. Protopolyps of all the protocorallites discussed attained the capacity to produce offsets at quite different stages. This being so, is it reasonable to regard this character as diagnostic of maturity?

No general answer is currently available. It is possible to assume, however, that such a wide variability of so important a character as asexual reproduction must have been fixed in the genetic code of polyps, and that not only was an opportunity to produce offsets coded, but also its potential or degree of necessity. These factors, together with environmental influences which suppressed or emphasized them, resulted in the situation discussed above. Therefore it seems necessary to distinguish two kinds of maturity of protocorallites: 1, morphological maturity, i.e. the stage at which the protocorallite reaches the highest degree of individual development, but does not start to degenerate gerontically; and 2, the capacity to produce offsets. This may be reached at different stages of ontogeny and is individual. This character may not develop at all when not strongly fixed in the genetic code, and the polyp then produces only a solitary corallite. In this case the potential to produce offsets may be suppressed by an environmental influence.

Maturity of asexually produced corallites in Heritschioides sp. nov. As noted earlier, most of the protopolyps were in an early stage of ontogeny when they first produced offsets. Supposing this to be a rule, one can observe that the first asexually produced generation reached its capacity to produce offsets at a more advanced stage of morphological development than the protopolyps. Corallites of this generation possess a dissepimentarium and well-developed axial structure. They do not show any clearly juvenile characters but their polyps almost always begin their asexual reproduction before reaching complete morphological maturity (Pl. 16, figs. 3, 5).

TABLE 2. Separate, subcylindrical corallites.*

Specimen number	Actual length	Diameter of calice	Number of septa	Remarks
196681	33.5	19.0 × 16.6	25 × 2	
196682	33.0	19.5 × 17.7	23 × 2	
196683	52 × 5	15.8 × 15.0	24 × 2	
196684	32.4	18.0 × 16.4	24 × 2	
196685	32.5	16.6 × 15.7	23 × 2	
196686	33.5	14.4 × 14.2	23 × 2	
196687	47.5	15.9 × 15.3	24 × 2	
196688	55.5	13.4 × 11.4	22 × 2	Margin of calice broken
196689	38.5	15.0 × 14.4	25 × 2	
196690	40.5	15.0 × 12.6	23 × 2	
196691	50.5	16.8	25 × 2	Margin broken in p-t
196613	33.8	14.5 × 14.1	25 × 2	
	30.8	13.8 × 13.6	26 × 2	Composite colony?
196665	33.2	17.2 × 16.0	22 × 2	Quasi-colony?

* Some corallites may be solitary. Most have proximal parts largely broken. See Table 4 for explanation of abbreviations.

TABLE 3. Colonies more advanced in astogeny.

Specimen number	Length	Genera- tion	Diameter of		Number of septa	Remarks
			Firstly offset pc	Calice		
196680	29.5	pc	4.0 × 3.0	12.0 × 11.0*	25 × 2	Without calice
	10.0	a		8.2	20 × 2	Partly broken
	24.5	a ¹		11.6 × 11.2*	25 × 2	Without calice
	8.5	a ²		8.4 × 7.2*	21 × 2	Without calice
	5.0	a ^{2a}		5.0 × 5.0*	17 × 2	Without calice
196590	21.0	pc	4.5 × 3.5	12.8 × 12.6	25 × 2	
	26.0	a		14.6 × 12.4	26 × 2	
	12.5	a ₁		11.6 × 10.0	19 × 2	Not offsetting
	12.5	a ₂		11.4 × 10.2	20 × 2	Not offsetting
	11.5	a ₃		11.8 × 7.6	19 × 2	Not offsetting
	25.0	b		15.3 × 11.7	23 × 2	
	11.5	b ₁		12.0 × 8.0	22 × 2	Not offsetting
196634	48.7	pc	?6.5	19.4 × 18.2	26 × 2	Beneath calice
	32.5	a		16.4 × 10.0	23 × 2	
	10.0	a ₁		11.6 × 10.8	21 × 2	Not offsetting
	16.5	a ₂		10.2 × 10.0	21 × 2	Not offsetting
	14.0	a ¹		12.0 × 9.2	21-22 × 2	Not offsetting
196645	35.5	pc	?	16.0 × 16.0	26 × 2	
	45.5	a		16.8 × 16.2	?	Max. diameter
				13.8 × 12.7	24 × 2	Rejuvenescence
	23.0	a ₁		12.6 × 11.4	22 × 2	Not offsetting
	23.5	a ¹		13.1 × 10.3	21 × 2	
	21.5	a ^{1a}		14.2 × 12.6	21 × 2	Not offsetting
	16.0	a ²		11.7 × 11.1	21 × 2	Not offsetting
	29.0	pc		16.2	27 × 2	Broken in p-t
	25.0	a		14.4	26 × 2	Broken in p-t
	23.5	a ₁		8.8 × 8.0*	21 × 2	?Not offsetting
196676	21.5	a ₂	12.3	21 × 2	Broken in p-t	
	17.0	a ₂	11.2 × 8.0	20 × 2	Not offsetting	
	13.5	a ¹	12.4 × 11.2*	22 × 2		
	16.0	b ¹	12.8 × 11.0	22 × 2		
	19.0	c ¹	9.7*	21-22 × 2		
	17.5	pc	≈12.5	?		
	30.0	a ₁	16.0 × 15.0	26 × 2		
	20.0	a ₁	13.0 × 12.0*	24 × 2		
	14.5	a ₁ ^a	9.8 × 9.0*	21-22 × 2	Not offsetting	
196621	14.0	a ₁ ^b	8.2 × 7.0*	20 × 2	Not offsetting	
	?	a ₁	12.6 × 11.8*	27 × 2		
	14.0	a ₂	10.4 × 9.0*	22 × 2	Not offsetting	
	10.0	a ₂	10.0 × 9.0*	22 × 2	Not offsetting	
	10.0	a ¹	8.0*	22 × 2	Broken in p-t	
	8.0	a ^{1a}	7.6 × 5.6	21 × 2	Not offsetting	
	28.0	pc	?	13.2 × 12.0	22 × 2	
	16.5	a	6.6*	19-20 × 2		
196678	15.0	b	12.0 × 11.0*	19 × 2		
	23.0	?c	12.0*	22 × 2		
	9.0	?c ₁	9.8 × 9.0*	18 × 2		
	10.0	?c ₂	10.2 × 9.0*	22 × 2		
	12.0	a ¹	10.2 × 10.0*	19 × 2		
	16.0	b ¹	11.2 × 9.0*	19 × 2		

* Uppermost margin of a calice is broken. See Table 4 for explanation of abbreviations.

Probably only later generations and, as observed here, only randomly a second asexual generation, started to produce offsets when in a fully mature morphological stage. Unfortunately there are no large colonies in the collection and no further observations of advanced astogeny are possible.

The morphological maturity of asexually produced polyps, similarly to that of protopolyps and their protocorallites, is not automatically correlated with capacity to produce offsets. In general it seems to be dependent on the generation of offsets to which the particular individual belongs, or at least to the stage of astogeny (early or late). In the same way as for protocorallites, the morphological maturity of other corallites should be distinguished from the capacity of their polyps to produce offsets. This is especially important in early stages of astogeny.

Ulitina (1974) reached a different conclusion regarding measurements of corallites produced at different stages of astogeny. According to her studies of *Hexagonaria philomena* Glinski, there is no difference between corallites within the colony as far as astogenetic stage is concerned. She did not state, however, whether the specimens were measured exactly at the level of offsetting. This would make a fundamental difference, since all corallites observed in the present study continue to increase their dimensions after producing offsets.

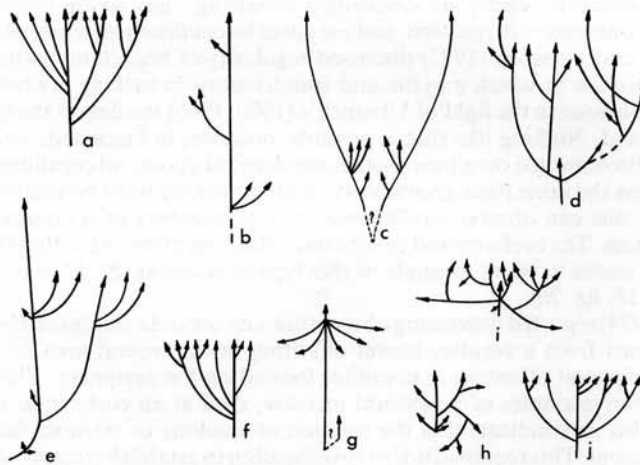
Growth and pattern of fasciculate colonies

Fasciculate colonies of rugose and tabulate corals, in a broad sense of the term, have a dual character. All mature polyps in such a colony are generally completely separated from one another. Coates and Oliver (1973, p. 11) stated that particular polyps in such colonies '... are in every way similar to solitary corals except that they occupy the numerous extremities on one skeleton (corallum)'. This statement may lead to misinterpretation as corallites of no colony are 'in every way' similar to solitary corals, since the latter have a differentiated genetic code. However, the same authors (1973, p. 4) clarified their point in defining a colony as '... a group of individuals, structurally bound together in varying degrees of skeletal and physiological integration, all genetically linked by descent from a single founding individual' (my italics). If the stressed phrase in this definition is restated as '*all the asexually produced corallites are diploid and all possess the same fixed genetic code*', then the fundamental difference between separate corallites of fasciculate colony and solitary corals becomes more obvious. Any fasciculate colony should be regarded as a genetic unit which, as a whole, and only as a whole, may be compared with a solitary coral.

Astogenetic studies on graptolites (e.g. Urbanek 1960, 1966, 1973) and hydrozoans (e.g. Schenk 1965) show the very important, leading role of the sexually produced, founding individual of the colony. The morphogenetically active substances (Urbanek's 1966 term) produced by this individual stimulated growth and shape of the colony and of particular asexually produced individuals. In all these colonies, however, the first sexually produced individual is permanently connected with the rest of the colony. This is not so in the material discussed here or in any other fasciculate colonies of rugosans in which all individuals are completely separated. Neither stimulative activity of the first individual, nor any common and directly controlled colony activity can be considered, and all the common actions of a colony must be explained in a different way. The members of the colonies are genetically identical,

however, and as such should possess the same tendency for growth of offsetting, and as a result, of pattern. In fact there are obvious regularities in tiny details of offsetting, but one can hardly find any in patterns, apart from the synchronic offsetting discussed below. In my opinion it is almost impossible to indicate any genus or species of rugose corals which produce fasciculate colonies according to a constant scheme, although there are such colonies among Tabulata (e.g. *Halysites* or Auloporidae). However, the question of a direct connection of polyps, especially in Auloporidae, appears to be an open one. In the case when polyps are united, the regularity of such colonies may be discussed using the categories employed for graptolites and hydrozoans.

Oliver (1968) illustrated some patterns in fasciculate colonies and discussed the importance of this character. He stated (p. 21) that 'In most colonies, however, the general pattern is consistent, at least after the initial few generations of offsets', but he also considered (p. 22) that the similarities of patterns of initial growth of some massive colonies '... probably represent a generalized pattern characteristic of corals forming massive coralla through lateral increase'. Not even such a weak regularity has been observed in the material described here, and particular colonies start to grow in many ways (text-fig. 4). It can only be stated that no symmetrical and/or exactly simultaneous production of two or more offsets is observed in the



TEXT-FIG. 4. Examples of patterns in colonies of *Heritschioides* sp. nov.; a, USNM 196618 and f, USNM 196668—asymmetrical colonies; b, USNM 196627—quasi-colony; c, USNM 196613—most probably composite colony composed of two quasi-colonies; d, USNM 196667—dendroid colony tending to chain-like arrangement; e, USNM 196634—asymmetrical, simple colony, intermediate between normal and quasi-colony; g, USNM 196615—umbrelliform arrangement of offsets; the lowermost, separated corallite may be an attached specimen; h, USNM 196635—circumrotary colony; i, USNM 196621—chain-like colony overturned in early astogeny; j, USNM 196616—symmetrical colony.

protocorallites, although the influence of the substrate may lead to such an impression (Pl. 15, fig. 12*b*; Pl. 16, figs. 4*c*, 6*a*).

The patterns observed in *Heritschioides* sp. nov. may easily be compared with Oliver's (1968) text-fig. 2, C-E, G, and there are also more types present (text-fig. 4 herein). This diversity of pattern of young colonies of one species, and their connection in some cases with extrinsic factors, makes it probable that this is not a genetically fixed taxonomic character, apart from a very general predisposition to produce a given type of colony (e.g. dendroid, phaceloid, etc.). In more variable species, as in the example described here, this predisposition is absent. The enormous variability of pattern and growth form makes it obvious that there was no gene determining a common colony pattern for the species.

Some of the diagrams in text-fig. 4 illustrate an obvious and strong influence of extrinsic factors on colony pattern. Rotary offsetting (text-fig. 4*h*) or asymmetrically umbelliform offsetting (text-fig. 4*g*) resulted from current action which either rolled the colony on the substrate or was directed from only one side. In the latter case a protocorallite may have survived, but it stopped growing (Pl. 17, fig. 4*a*, *b*). Some cases of symmetry or asymmetry (text-fig. 4*a*, *f*, *j*) are related to the substrate on which the young colony developed. A large attachment surface indicates that the colony encrusted the bottom during a young stage of development (Pl. 16, fig. 4*c*).

One phenomenon—cyclic or synchronic offsetting—has to be emphasized, as it is directly connected with pattern, and may also be conditioned genetically. Bulman (1955, 1958) and Urbanek (1973) discussed regularity of branching pattern of some graptolite colonies in which a cyclic and simultaneous branching is observed. This seems to be obvious in the light of Urbanek's (1960, 1966) studies on the leading role of a siculozoid. Nothing like that is possible, however, in fasciculate colonies with completely disconnected corallites. But, as emphasized above, all corallites within the colony possess the same fixed genetic code, and the colony must be treated as a unit. If this is so, one can observe similar reactions of members of a colony to similar extrinsic factors. The cyclic or/and synchronic offsetting observed within the colonies studied here seems to be an example of this type of reaction (Pl. 17, figs. 3, 5*a*, *b*, 6, 7, 8*a*, *b*; Pl. 18, fig. 2*a*).

Ulitina (1974) reported interesting observations on cerioid colonies of *Hexagonaria*, in which, apart from a regular, lateral offsetting in the central area of the colony there is a peripheral offsetting in corallites located on the periphery. The parent, as in most known examples of peripheral increase, died at an early stage of hystero-ontogeny. This may indicate that the reaction of a colony to extrinsic factors is not equal throughout. This requires further investigation to establish whether the environment affects the peripheral corallites more strongly, or whether they are supported to a lesser degree by the colony community. These, and some other factors, may act together.

Spassky and Kravtsov (1974) emphasized growth and patterns of colonies as highly important features in systematics. They followed Spassky's (1965) theory that all rugosans had been divided in their early evolution into two main branches: Solitaria (= solitary corals) and Associata (= colonial corals). These two branches are supposed to have developed independently and parallel to one another throughout the history of rugosans. Many examples (e.g. the families Phillipsastraeaidea,

Aulophyllidae, Waagenophyllidae, as well as all the known orders) show that this division is artificial, and that higher taxonomic units (starting from families) contain closely related solitary and colonial corals. The species discussed here is a good demonstration of this artificiality. It includes not only different forms of colonies, but also different forms of growth, both solitary and colonial.

According to the further subdivision proposed by Spassky and Kravtsov (1974, Table 2) the types of colonies and reproduction within rugosan genera and families should be very constant. This is correct in quite a few genera, but it cannot be generalized. As stated above, types of colonies and their patterns appear to be as variable as any other character in Rugosa and particular genera have to be treated individually. These features seem to be of no use for most families and for almost all higher taxonomic units, and neither are the type of reproduction (sexual-asexual), type of coloniality (real colonies-'pseudo-colonies' in Spassky and Kravtsov's sense) and form of growth (solitary-colonial). The history of rugose coral evolution is full of examples of closely related solitary and colonial genera, or fasciculate and massive colonies in the same family.

Intercolony variation

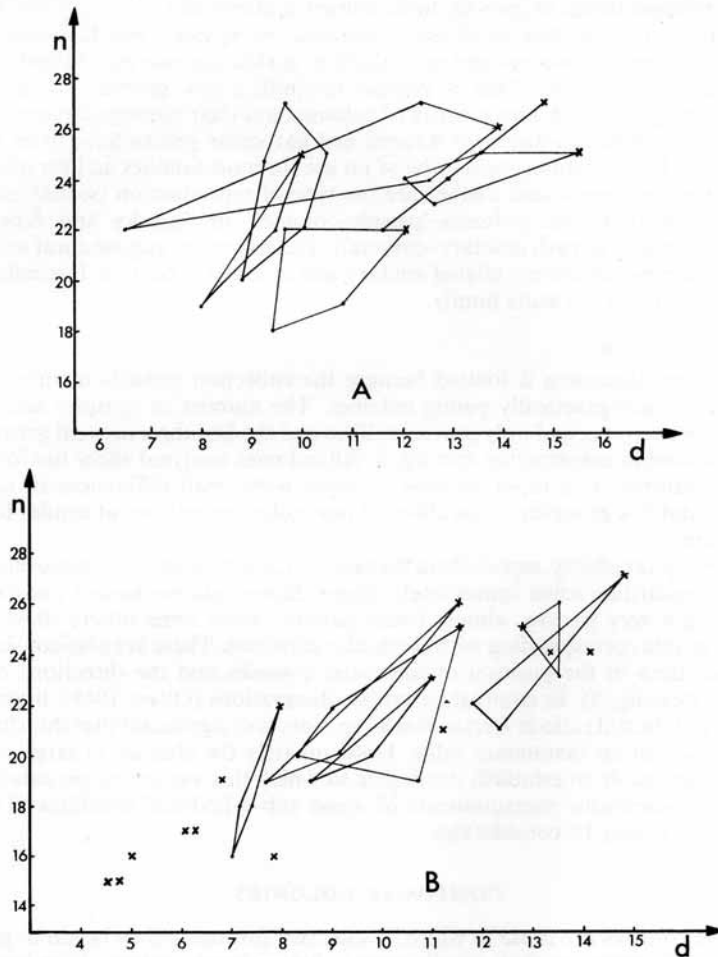
The following discussion is limited because the collection consists mainly of well-preserved but astogenetically young colonies. The number of samples analysed is limited to twenty-one, and only protocorallites and the first three asexual generations have been used in constructing text-fig. 5. All colonies analysed show the following common features: 1, a rapid increase of septa with small differences of corallite diameter; and 2, a grouping of corallites of particular generations at similar levels in the diagram.

Intercolony variability, especially in the ratio n/d , seems to be much more important than the similarities noted immediately above. Some colonies have a constant n/d ratio giving a very narrow, almost linear pattern, while some others show widely scattered points corresponding with particular corallites. There are also considerable differences both in the position of particular colonies and the directions of their resultants (text-fig. 5). In contrast to earlier observations (Oliver 1968), intercolony variability of the n/d ratio in *Heritschioides* sp. nov. is so significant that this character possesses almost no taxonomic value. Unfortunately the absence of large colonies makes it impossible to establish the degree to which this variability persists in later astogeny. Comparable measurements of some sub-cylindrical corallites (Table 2) indicate that it may be considerable.

COMPOSITE COLONIES

Composite colonies are those in which at least two protocorallites began to grow so closely to each other that their coralla seem to belong to one colony. They have been described previously only in fasciculate forms (Oliver 1968). According to Oliver composite colonies show distinct differences in measurements between corallites descended from different protocorallites. The n/d ratio was even selected as the best criterion on which to distinguish the composite colony from the regular one. In the collection studied here the differences between corallites descended from different

protocorallites are not much greater than those among the products of the same protocorallites (Table 4). There may be two reasons for this disagreement: 1, Oliver (1968) selected for his study astogenetically advanced colonies with cylindrical corallites, while my study involves a sampling of small, astogenetically young



TEXT-FIG. 5. Ratios of 'n' (number of septa) to 'd' (diameter of corallite in mm). Points corresponding with individual corallites of the same colonies are separately contoured to show the ratios within colonies and their interrelations in species. Protocorallites of individual colonies and those which only started to produce first offsets (diagram B) are marked by crosses. A— n/d ratio measured beneath calices. B— n/d ratio measured close to margins of calices.

TABLE 4. Composite colonies

Specimen number	Length	Genera-tion	Diameter of		Number of septa	Remarks		
			Firstly offset pc	Calice				
196619	10.5	pc-1	3.2 × 4.2	?	18 × 2*	Incomplete		
	23.5	a		10.4 × 8.6	20 × 2			
	37.0	b		11.2 × 10.2	25 × 2			
	33.0	b ₁		11.0 × 7.5	21 × 2			
	16.5	b ₁ ⁱ		11.5 × 8.7	25 × 2			
	16.5	b ₁ ⁱ		11.4 × 10.4	27 × 2			
	32.5	c		11.5 × 8.2	22 × 2			
	19.0	c ₁		10.4 × 8.2	21 × 2		Not offsetting	
	12.0	c ₂		8.2 × 7.3	19 × 2		Not offsetting	
	9.5	c ₃		8.0 × 5.6	19 × 2		Not offsetting	
	35.0	pc-2		11.2 × 11.0	20 × 2*			
	33.5	pc-3		12.0 × 10.0	22 × 2*			
	196620	20.6	pc-1		15.6 × 13.0		23 × 2	Not offsetting
		26.0	a		14.2 × 13.6		21 × 2	
22.5		b		10.4 × 10.2	20 × 2			
15.0		c		8.7 × 8.3	18-19 × 2			
11.0		d		9.2 × 7.0	18-19 × 2			
12.0		e		8.4	19 × 2			
26.0		pc-2		14.4 × 12.0	21 × 2			
14.5		pc-1	≈ 6.5	10.5 × 7.0	22 × 2	One lost structure		
196662	16.0	pc-2	≈ 6.5	9.0 × 6.8	20 × 2	Not offsetting		
	6.3	a		8.0 × 7.2	20 × 2			
	3.0	b		7.8 × 7.0	18 × 2			
196658	20.5	pc-1		12.8 × 8.6	28 × 2	Juvenile		
	?	a		10.0 × 7.0	22 × 2			
	?	b		9.4 × 8.6	20 × 2			
	?	c		9.4 × 9.4	20 × 2			
	?	c ₁		5.5 × 4.5	14 × 2			
	?	c ₂		5.3 × 4.9	17 × 2			
	?	a ¹		9.0 × 9.0	21 × 2			
	?	b ¹		8.0 × 6.6	17 × 2			
	?	c ¹		8.6 × 7.0	20 × 2			
	16.5	pc-2		10.5 × 9.1	28 × 2			

Explanation of symbols

pc—protocorallite.

a, b, c . . . A first ring of offsets produced by a protocorallite.

a¹, b¹, c¹ . . . }
 a², b², c² . . . } Next rings of offsets produced by a protocorallite.
 etc. }

a_{1, 2, 3 . . .} b_{1, 2, 3 . . .} }
 a_{1¹, 2, 3 . . .} b_{1¹, 2, 3 . . .} } Second, third, fourth, etc., asexually produced generations of offsets coming
 a_{1^{1a}, b, c . . .} b_{1^{1a}, b, c . . .} } from a first ring of offsets of a protocorallite.
 etc. }

a^{1a}, b . . . b^{1a}, b . . . }
 a^{2a}, b . . . b^{2a}, b . . . } A first asexually produced generation of offsets coming from second and next
 etc. } rings of offsets of a protocorallite.

colonies. This may overemphasize the differences. However, no other observations are available for comparison. 2, species studied by Oliver are constant in their dimensions, while my material is variable.

As with the dimensions, the morphology of corallites in composite colonies does not vary more than in regular, single colonies (Pl. 17, fig. 2; Pl. 18, figs. 1*a*, *b*, 2*a*, *b*; Pl. 23, figs. 1*a*, *b*, 4*b*, 5*b*). In all my observed composite colonies, only one of the protocorallites produces most of the offsets and, as a result, only one colony is well developed, while the other (or others) is weaker. There are also no offsetting corallites of the same species accompanying the colonies (Pl. 18, figs. 1*b*, 2*b*). In some composite colonies a synchronic offsetting of different components is observed (P. 23, figs. 1, 5). This may emphasize the importance of extrinsic factors in forcing polyps to produce offsets.

PSEUDO-OFFSETS AND PSEUDO-COLONIES

The material under study provides additional examples of phenomena connected with coloniality. A larva might have settled and produced a new polyp between the septa of a dead corallum of the same species that remained in its life position. The skeleton of the new coral grew quite rapidly, filling the interseptal space of the dead corallite and overgrowing some of its septa. It may happen that the cardinal and counter septa of the young corallite form a line directed towards the centre of the 'host' corallite, exactly as during blastogeny (Pl. 23, fig. 6). Two other corallites with the same type of pseudo-offsets, but more advanced in ontogeny are shown on Plate 23, fig. 8. There are also some corallites that show more obviously their pseudo-offsetting relationship (Pl. 23, fig. 3). In this case the larva settled on the calice margin of a 'host' corallite and produced a corallum which overgrew the dead corallite margin from both sides.

The phenomenon of pseudocoloniality may appear in a situation where either a few or many larvae (especially when short-lived), settled together and produced a cluster of solitary corallites growing so closely to one another that the circular shape

EXPLANATION OF PLATE 23

- Fig. 1. USNM 196658, $\times 1.5$. Young composite colony. Both protocorallites produce offsets. *a*, calicular view; *b*, side view.
 Fig. 2. USNM 196659, $\times 3$. Young composite colony. Only one protocorallite produces offsets.
 Fig. 3. USNM 196660, $\times 1.5$. Pseudo-offset.
 Fig. 4. USNM 196661, $\times 1.5$; *a*, *b*, three young corallites attached to each other, growing in different directions to form pseudo-colony.
 Fig. 5. USNM 196662, $\times 1.5$. Composite colony. *a*, side view; *b*, calicular view.
 Fig. 6. USNM 196663, $\times 3$. Pseudo-offset. A young corallite started to grow between septa of the dead one.
 Fig. 7. USNM 196581, $\times 4.5$. Lost structure (see also Pl. 14, fig. 7 and Pl. 15, fig. 14).
 Fig. 8. USNM 196664, $\times 1.5$. Well-developed pseudo-offset.
 Fig. 9. USNM 196665, $\times 1.5$. Probable quasi-colony.
 Fig. 10. USNM 196666, $\times 1.5$. *a*, *b*, pseudo-colony with very strong talon in upper part of one of corallites.
 Fig. 11. USNM 196612, $\times 3$. Lost structure (see also Pl. 17, fig. 1*a-d*).
 Fig. 12. USNM 196628, $\times 3$. Lower part of quasi-colony showing lost structures (see also Pl. 20, fig. 1).



FEDOROWSKI, coloniality in rugose corals

of calices became distorted by crowding. Such a cluster, or a weaker one, may be produced on the external wall of a living or dead specimen of the same species and close to the margin of its calice. This gives the impression of a colony with the large corallite being the parent. Such pseudocolonies have been described previously by Fedorowski (1971) from serial sections. Similar examples in *Heritschioides* sp. nov. are observed mainly on young corallites of this generally colonial species, and as such may be regarded as potential composite colonies (Pl. 23, fig. 4a, b). Sometimes a cluster of larvae settled on a dead corallite calyx (Pl. 21, fig. 7). Corallites produced by these larvae either remained solitary or created weak colonies similar to quasi-colonies.

GROWTH OF RUGOSE CORALS

Discussion of the growth of polyps and their skeletons has been renewed recently by Weyer (1972), who did not agree with Wedekind's (1937) views as recently emended by Wells (1969). Instead, Weyer returned to the conception of von Koch (1896) and Matthai (1914) that the margin of a calice is the only permanently upward growing part of a body and skeleton, while the bottom elements are cut off, together with the soft tissues, each time that a new basal skeletal element is built. This is the so-called 'lack of space' hypothesis of Matthai (1914), according to which a calice is adequate only for those soft parts and organs that are actually in it. There would be no room for the body if the bottom of the polyp were pushed upwards to build new basal skeletal elements. To justify this theory Weyer (1972) discussed a number of examples, e.g. synapticulae in Scleractinia and the axial synapticulae in Calostylidae, the structure of some tabulate corals, the existence of an ostracode shell between dissepiments, and the structure and growth of marginal dissepiments in *Manicina areolata* studied by Sorauf (1970), etc. Since the manner of growth of polyps and their skeletons is integrally connected with blastogeny, the subject is discussed further here.

All speculations on growth in recent synapticulate or other scleractinians are avoided here, as the only satisfactory way to solve the problem is to study the relationship between soft and hard parts in recent examples. There must remain a recognizable part of the soft body just beneath the last basal skeletal element if the body is really cut off, and all stages of living corals are easily available.

The fine structure of marginal dissepiments in *M. areolata* and their manner of growth as reconstructed and discussed by Sorauf (1970, text-fig. 6), in no way supports a supposition that they cut off the underlying soft body. On the contrary, Sorauf (1970, p. 16) agreed with Wells's (1969) interpretation of coral growth. In correspondence (March 1976) Dr. Sorauf wrote:

I have never seen downward growth of dissepiments. In every specimen I have noted or studied to this date all of them have thickened toward the calyx. Only a primary sheet forms by lateral growth, and then thickening occurs by crystal growth towards the base of the polyp. Even in *Manicina* where I felt I could distinguish a third layer (lower spherulitic), it was not developed at or near the junction line where the primary layer joined to complete the first blister.

The presence of an ostracode shell between two dissepiments may be added to by a few other reported observations of foreign bodies embedded in corallite skeletons (see Oliver 1975). These very restricted records argue spectacularly against the theory

of cutting off the bottom body in polyps. If this manner of growth had existed there would be many more examples of incorporation of foreign bodies, such as shells of eaten creatures, grains of sand, etc., all of which would have been covered over and incorporated in the skeleton.

The 'lack of space' in the calice would be an argument in a case where a simultaneous and rapid separation of a complete body from a skeleton were proved. However, no evidence for that is retained in the skeleton of rugosans. On the contrary, any longitudinal section clearly shows that particular basal elements of a corallite are connected to the underlying and neighbouring elements in a manner indicating their gradual and individual appearance. The particular elements appear axially from the margin of the calice (text-fig. 2B). Only a very limited extra space is needed in a calice when particular basal skeletal elements appear individually. Additional space is provided continuously by the upward-growing peripheral wall of the calice. This excess of space in calices was one of the bases for Hill's (1936) 'mechanical' theory of growth in corals.

The structure of the Calostylidae and of some Tabulata (e.g. *Cleistopora*, *Donetzites*, *Yavorskia*) does not prove the 'cut-off' theory. Preparation of longitudinal serial sections through such corals for detailed study of the fine structure, would be the only basis to study this. Such a study has not been made, and was not possible here because of lack of material. A body could have been drawn out from any apparently closed skeletal trap as seen in only one section, through an opening not seen in that section. To prove that the medial line of a skeletal trap (if septal in structure) is connected throughout its circumference would be the only possible way to be sure that the soft body was really cut off. The existence of tabulae does not prove this, as they may easily close exits of skeletal traps after evacuation of a body.

Some additional observations are also opposed to the 'cut-off' theory. Most basal elements in Rugosa are convex. This situation may exist only when the soft body, which secretes the skeleton, is supported by something before the skeleton is available. A compressed gas may be this supporting force. It may be replaced later by water, which is in agreement with observations that the spaces between skeletal elements are often filled with water. The presence of a convex and unsupported soft body would be mechanically possible only if it were much lighter than water, but this has never been proved. The 'cut-off' theory also does not explain what happens to mesenteries when the basal part of a polyp is cut off, or how the new basal skeletal elements are attached to the underlying structures which are still covered by soft parts.

Rejuvenescence appears to be important in proving that there is no soft body left beneath basal structural elements. Detailed study of serial sections (Fedorowski 1965*b*) and observations here on etched material show that the process of separation of the soft body from the skeleton begins close to the bottom of the calice. Deep rejuvenescence may repeat a considerable part of ontogeny (Fedorowski 1965*b*, text-fig. 2). The separation is translocated up to the margin of the calice and it includes contemporary basal elements and septa, as is easily seen on etched specimens (Pl. 22, figs. 10*c*, 11). The newly built wall is convex outward and downward. It hangs on septa or attaches to them as a regular wall (Pl. 22, figs. 10*c*, 11). It would be impossible to explain such a construction and interconnections of a new wall, septa, and basal elements if any of these structures were not covered by a soft body. This example

shows that the soft body is not differentiated according to the structural element that it builds, and that it goes through the same processes on septa and on basal skeletal elements. It also shows that the polyp may be compressed very considerably if necessary, so that the lack of space in a calice is not a factor. There is no need to look for separate explanations of regular growth and rejuvenescence. The difference is not a matter of quality but of degree of the same factors acting in both cases.

The overgrowth of channels (Pl. 22, figs. 5, 6c; text-fig. 2A) as described here also shows that this is a step-by-step process leading to a meeting of an uppermost dissepiment with an upper part of a bridged channel. This is so even in the case of lost structures retained by a parent corallite. The plates overgrowing pores in *Tabulata* (von Schouppé and Oekentorp 1974) belong in the same category. To construct a new tabula above a pore or above a bridged channel, and to cut off the underlying body seems to be the simplest way of separating two polyps, but this is not the observed case and a special plate is secreted to close the pores or there is special construction of dissepiment-like structures to close the channels. Both these structures are connected to the underlying elements in the same manner as observed in the development of regular basal structures.

Acknowledgements. I am particularly grateful to Dr. G. Arthur Cooper and Dr. Richard E. Grant for providing the Texas specimens for study. My warmest thanks are also due to Professor Maria Rózkowska for important discussions on coral development, and to Dr. William A. Oliver, Jun. and Dr. Robert K. Jull for very fruitful discussion, for many interesting suggestions, and for reading and correcting the manuscript. Finally, I thank Mr. Antoni Pietura for photographing the specimens.

This study was supported by Smithsonian Institution Grant FR4-60100. Type and figured specimens are housed in the United States National Museum of Natural History (USNM).

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Typescript received 10 July 1976

Revised typescript received 15 March 1977