

# Computer-aided study of growth patterns in tabulate corals, exemplified by *Catenipora heintzi* from Ringerike, Oslo Region

ØYVIND HAMMER

Hammer, Ø. Computer-aided study of growth patterns in tabulate corals, exemplified by *Catenipora heintzi* from Ringerike, Oslo Region. *Norsk Geologisk Tidsskrift*, Vol. 79, pp. 219–226. Oslo 1999. ISSN 0029-196X.

A detailed study of a fragment of a colony of the halysitid tabulate coral *Catenipora heintzi* from the Norwegian Wenlock is presented. The specimen was collected from the Braksøya Formation near Nes, Ringerike. Closely spaced (0.1 mm) serial sections document astogenetical events and trends, including lateral and interstitial increase, branching, damage and regeneration, and lateral growth of individual corallites. Among these events, two previously undescribed phenomena are observed: connection to a neighbouring rank as a result of interstitial increase, and competition between polyps leading to atrophy. The studied specimen is discussed in the light of the theories for halysitid astogeny. This indicates the existence of rank branching, the preference for increase from the youngest corallite in a rank, an exclusive ability of new corallites to fuse with other ranks, regulation of lacuna size, occasional sediment smothering and possibly an annual periodicity in frequency of increase.

Øyvind Hammer, Paleontological Museum, University of Oslo, Sars gt. 1, 0562, Oslo, Norway

## Introduction

The Ordovician and Silurian halysitids belong to the tabulate corals. The alternative hypothesis of sponge affinity (Kazmierczak 1989) has not yet been substantiated (Wood et al. 1990). These beautiful chain ‘corals’ raise questions about how the growth and offsetting of individual corallites are co-ordinated to produce the observed morphology. Pattern formation in colonies of organisms is described as astogeny, analogous to the ontogeny of a single individual (Pachut et al. 1991).

There are still unsolved problems regarding the mechanisms of the halysitid astogeny. Different types of events occurring during astogeny have been identified, including settlement of larvae and several types of increase (offsetting of new corallites), but in most cases the causal triggers for these events are unclear. However, it should be possible to frame and test theories of halysitid pattern formation through detailed studies of fossil material from different environments. Computer simulation may also be useful in this respect (Hammer 1998).

Serial sections of a corallum fragment of *Catenipora heintzi* from Ringerike, Norway are presented here, with attempts to interpret its growth processes using the present state of knowledge on halysitid astogeny. It is hoped that this case study will demonstrate some of the key elements and enigmas of halysitid pattern formation.

## Halysitid astogeny

The basic processes of halysitid astogeny, best studied through serial sectioning, have been described by a number

of authors (Buehler 1955; Hamada 1959; Stasinska 1967, 1980; Lee & Noble 1990; Lee & Elias 1991; Hubmann 1996; Hammer 1998). A new colony is first initiated by the settlement of a planula larva on the substrate. This larva forms a protocorallite, which will start to increase and produce a rank (chain) of corallites. Increase at the end of a rank is termed *lateral increase*. Chains may also branch, either at their ends or internally, initiating new ranks (Stasinska (1980) disputed the existence of branching, claiming that apparent branching is no more than the settling of larvae close to an existing rank). When ranks meet through lateral increase, they make contact and fuse. In this way, a meshwork of ranks is produced, closing off open areas, which are termed *lacunae*. Through so-called interstitial increase, new corallites can also be initiated between corallites in an existing row, thus elongating it. Also, some fine-tuning of the geometry occurs by sideways growth of the corallites, sometimes leading to a polygonalization and regularization of the lacunae. While these processes are taking place, the colony is growing vertically.

The distinction between the *monoplanulate* and *polyplanulate* modes of halysitid astogeny was made by Lee & Noble (1990). In the monoplanulate mode, a single larva initiates the whole colony. In the polyplanulate mode, several larvae settled, generally at different points in time. These larvae initiated their own subcolonies, which later merged into a supercolony.

In addition to these basic mechanisms, it has become clear that influx of sediment often played an important role in the halysitid astogeny (Lee & Elias 1991). In these cases, it seems that the corallites barely protruded from the muddy sea floor. Despite the protection given by the

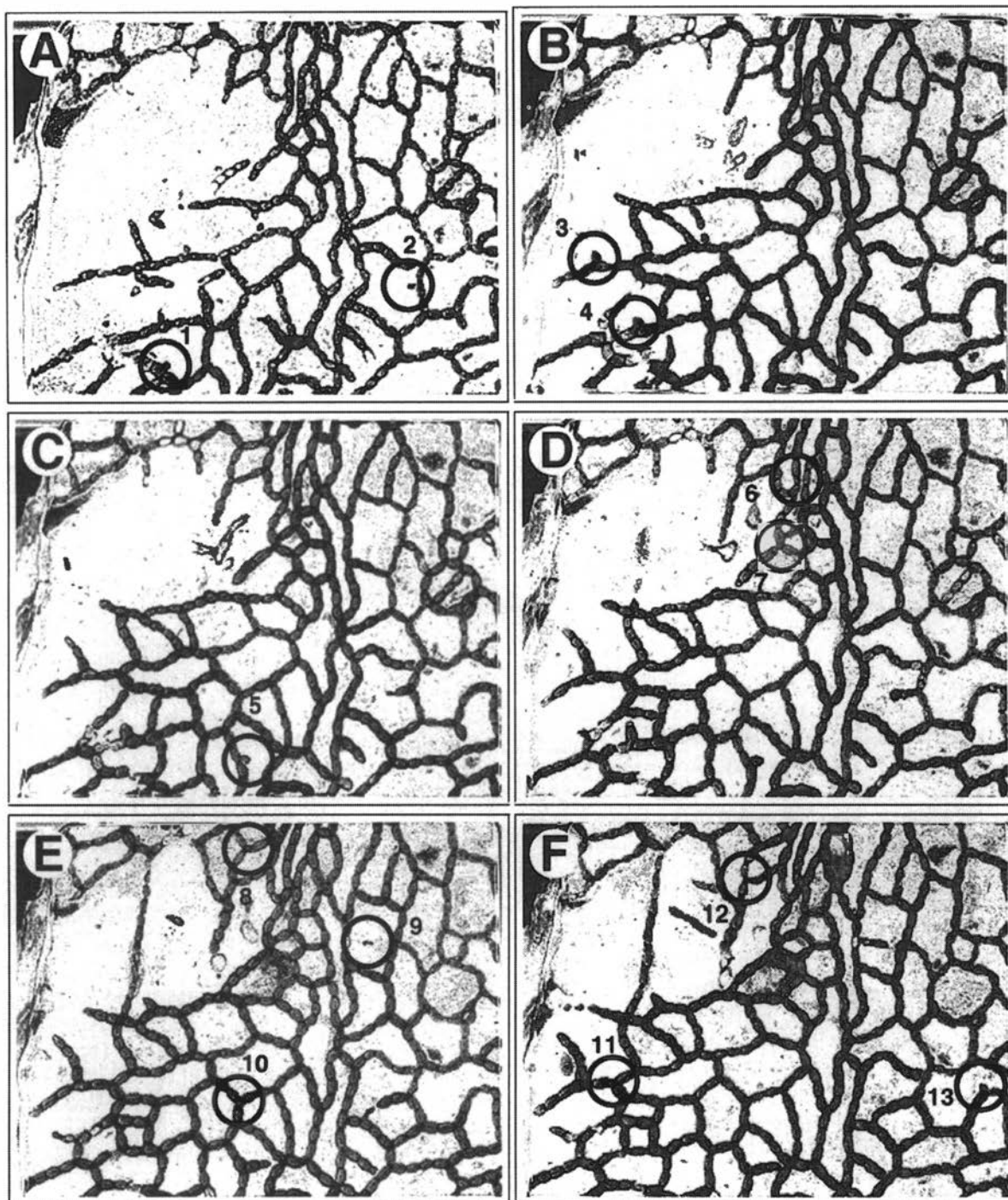


Fig. 1. A selection of serial sections of *Catenipora heintzi*. Some events are marked with circles. Numbers refer to Table 1. Figured sections are at levels 0.0, 0.8, 1.2, 1.7, 2.4, 2.9, 3.8, 4.5, 5.2, 5.7, 6.1 and 6.9 mm. The ordering is from left to right, then top to bottom. Scale  $\times 1.5$ .

lacunae, acting as small sediment traps, corallites were frequently smothered by mud and killed. Lee & Elias (1991) described how corallites were re-established by rejuvenation or through special modes of lateral increase from neighbouring corallites. The study of such colonies may give information about rate, direction and temporal distribution of sediment migration.

Finally, recent theoretical and observational work on living scleractinians and sponges (Kaandorp 1995) sug-

gests that increase is partly controlled by other environmental factors, in particular light and distribution of nutrients. Nutrient distribution is further affected by water currents. Such ecophenotypic effects are perhaps also applicable to halysitids, though this has not yet been clearly demonstrated.

Hammer (1998) proposed a set of hypothetical growth rules for halysitids. These rules are based on the ability of the individual polyp to sense the local density of corallites.

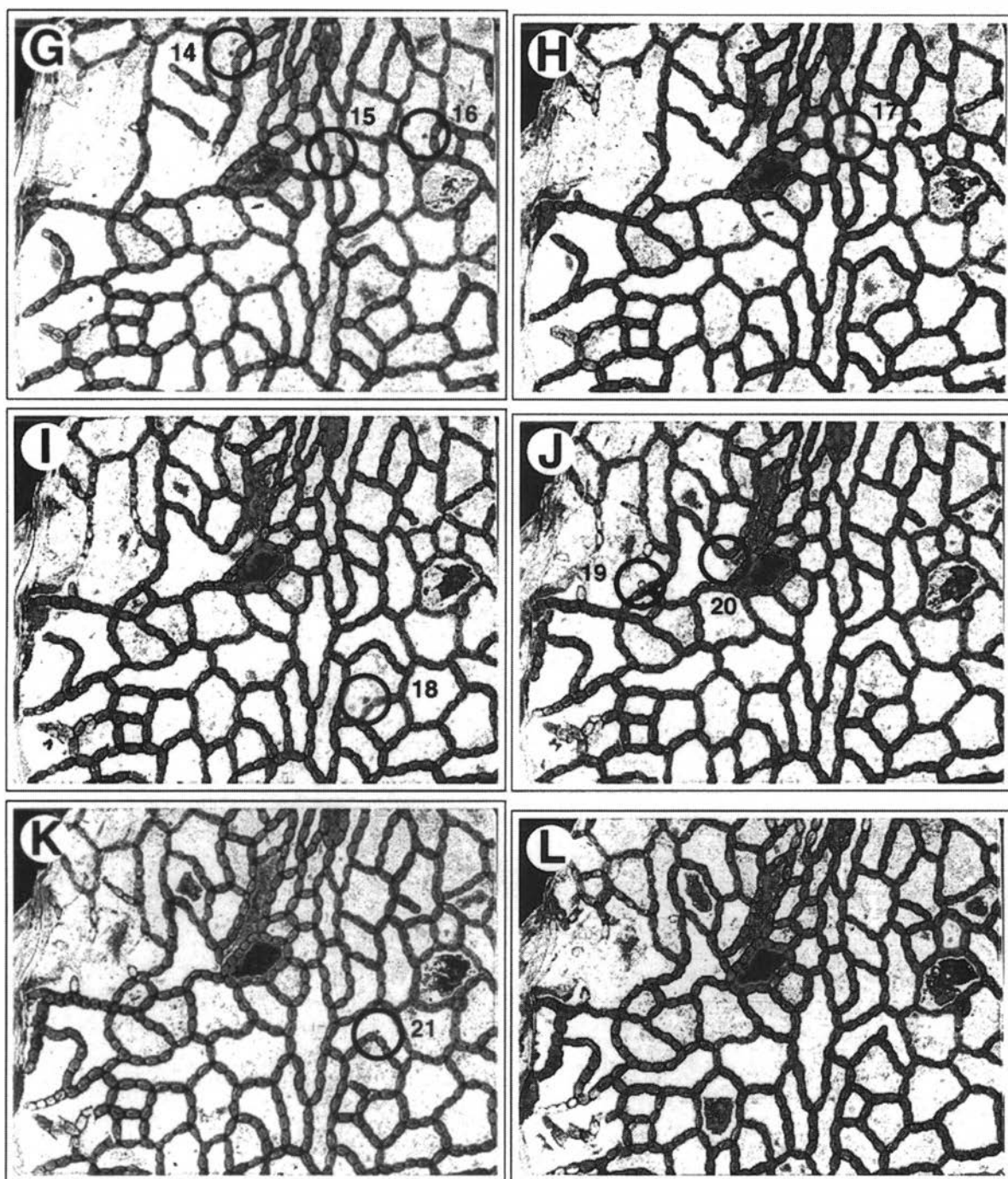


Fig. 1 (continued)

This would be done by measuring the concentration of nutrients (which are depleted by the polyps) or waste products, or perhaps by using especially secreted pheromones. The existence of such 'knowledge' of proximity to other corallites was thoroughly treated by Kaandorp (1995) for Recent scleractinians. The halysitid growth rules, which were implemented in a computer program, include the following (for details, and references to similar work on other colonial organisms, see Hammer (1998)):

1. Free ends of ranks of corallites will continually be

elongated through lateral increase. This increase occurs in the direction of the negative gradient of the density field, thus giving a tendency for growing ranks to avoid existing ranks.

2. Branching occurs when the density drops below a certain threshold value, that is, in favourable positions away from other corallites.
3. Existing corallites grow laterally down the density gradient, away from other corallites.
4. Neighbouring corallites in a rank cannot be pushed too close together. A 'spring' effect keeps a characteristic distance between neighbours.

Table 1. Comments to events marked in Fig. 1.

No.	Event
1.	Branching
2.	Branching, possible settlement
3.	Branching
4.	Branching
5.	Branching
6.	Interstitial increase. Fuses with neighbouring rank.
7.	Interstitial increase
8.	Interstitial increase
9.	Settlement?
10.	Interstitial increase
11.	Interstitial increase
12.	Interstitial increase
13.	Branching
14.	Branching
15.	Branching towards dead corallite, splitting lacuna
16.	Branching or settlement
17.	Axial increase/rejuvenation
18.	Branching or settlement
19.	Branching
20.	Branching or settlement
21.	Branching

5. If the distance between neighbouring corallites increases above a certain value due to lateral growth, interstitial increase is initiated.

These hypothetical growth rules will be referred to later in connection with the specimen studied here.

## Material and methods

A fragment of a halysitid colony (PMO 162.614) from the Wenlock of Ringerike, Norway, embedded in a hard limestone matrix, was serial sectioned. Owing to its stratigraphical position in the Braksøya Formation (Worsley et al. 1983), the dimensions of corallites, the dimensions and shape of lacunae and the lack of intercorallite tubules or preserved septal spines, the specimen is assigned to *Catenipora heintzi* (Stasinska 1967).

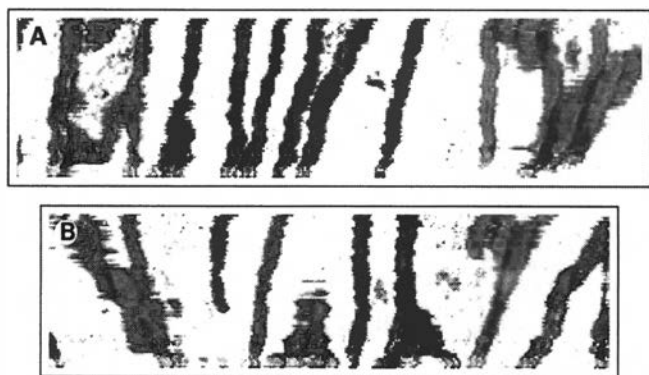


Fig. 2. From the volume data given by the horizontal sections, a computer can show any slice through the volume. Above is shown a vertical slice in the left-right direction of Fig. 1. Below is a vertical slice taken in the up-down direction of Fig. 1. Note the subparallel orientation of corallites. Scale  $\times 2$ .

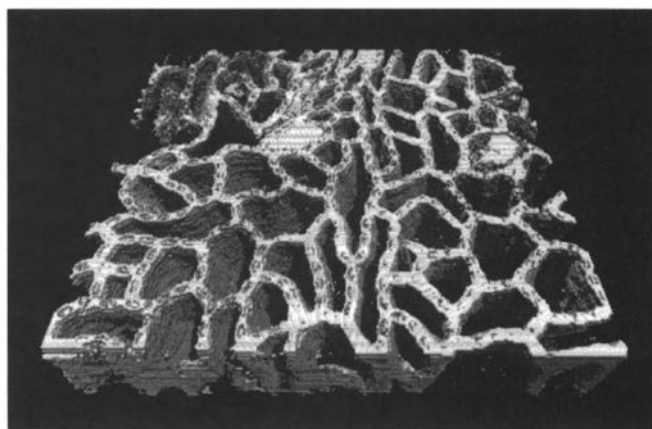


Fig. 3. Computer model (volume rendering) of serial sections from the 0.0 to the 6.0 mm levels, viewed from above.

A rectangular fragment, with horizontal dimensions of 4.3 by 3.4 cm, was serially ground on a Struers Accutom 50 machine. The surfaces were treated with alcohol to increase contrast, and directly scanned on a flatbed scanner at a resolution of 0.125 mm/pixel; 78 sections were made at 0.1-mm intervals, giving fine vertical resolution through a 7.7-mm thick slab. The images were manually aligned using the corners of the right-angled specimen block, then slightly image processed (sharpened), and finally inverted. A selection of the images is presented in Fig. 1. The close spacing between the sections is necessary to capture events of increase and settlement right at their initiation, so that the relationships between events and the geometry at the particular instance can be studied.

From this set of images, a computer can present any slice through the sectioned volume, whether horizontal, vertical (Fig. 2) or oblique.

As shown in Figs. 3 and 4, the stack of images can also be used to produce a three-dimensional computer model of the coral (e.g. Herbert et al. 1995). Apart from giving a general overview of the specimen, this is not very useful however, and gives no more information than reasonably

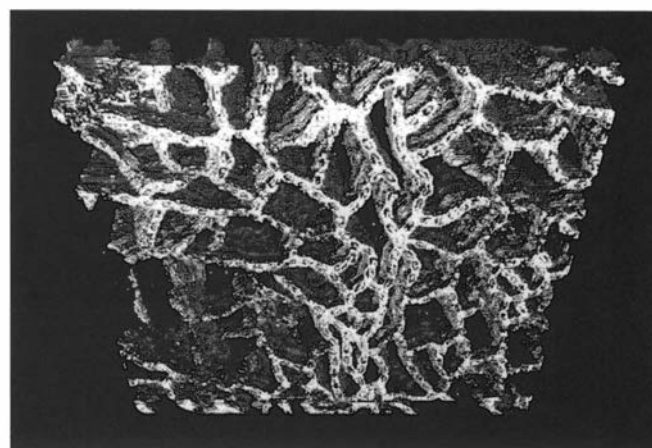


Fig. 4. Computer model of serial sections from the 0.0 to the 5.5-mm levels, viewed from below.

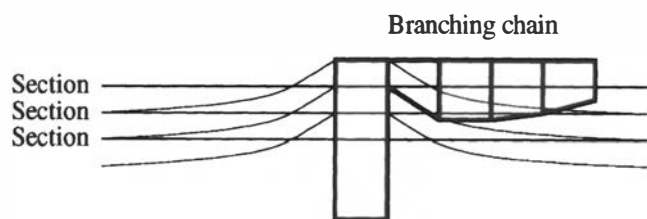


Fig. 5. Onlap of sediment onto a rank could cause a true rank branching to be misidentified as planula settlement in horizontal serial sections.

well-preserved silicified specimens prepared with acid. The real use of serial sectioning in this case is that it gives a series of images that approximately represent isochronous planes through the specimen. With these data, astogeny can be closely followed as a function of time, admittedly using the probably inaccurate assumption of constant growth rate (Elias & Lee 1993). A computer animation has also been produced from these images, showing a 'time-lapse' movie of pattern formation over a period of perhaps one year (the QuickTime file can be downloaded at <http://www.toyen.uio.no/~ohammer>).

The assumption that the sections approximate to isochronous surfaces is based upon the observation that halysitid corallites are usually oriented at right angles to the external surface of the colony (presumably in order to maximize distance from other corallites). Since the corallites are reasonably parallel in the studied area of the colony (Fig. 2), this area of the colony must therefore have grown with only slight curvature. It is still possible that the surface of the colony was more curved in other areas, or that the colony was hemispherical but very large, giving low curvature, but this would not make the assumption of approximately isochronous sections in the studied area invalid. For small, hemispherical colonies, this correspondence between time and vertical distance might not exist, as isochronous surfaces would rather consist of concentric, spherical shells. These time surfaces can still be reconstructed, being oriented at right-angles to the corallites.

The uncertainty about the degrees of taphonomic and diagenetic effects is a recurrent problem in the study of halysitids. There are certainly indications in the studied specimen that the corallum may have been damaged prior to final burial. Corallites emerging without the characteristic cup shape must have been damaged from below. In some cases it is obvious that sediment has infilled the corallite from below until stopped by a tabula, indicating damage to the underside of the colony before final burial. A number of well-preserved, unequivocal astogenetical events are clearly preserved in the specimen, but caution is necessary.

### Rank branching and planula settlement

It has now been established that true rank-branching does

occur in at least some species of halysitids (Lee & Noble 1990; Hubmann 1996). Still, it can be difficult to ascertain whether apparent branching events are rather just special cases of larval settlement close to existing ranks (Stasinska 1980). In the present specimen, some branching offsets do seem to be initiated at a small distance from the existing rank (event nos. 2, 16 and 18, Fig. 1), raising the possibility that true branching does not occur in *Catenipora heintzi*. If these pseudobranchings really are planula settling events, one would have to explain why they almost always occur so close to existing ranks. Possibly, the larvae preferred to attach to existing corallites. The mechanism might have been passive drift or 'Brownian' motion until a rank was encountered, or a more active chemotactical homing behaviour as in barnacles (Clare et al. 1995). It is also well documented that halysitid larvae showed a preference for attachment to hard substrates like shelly fragments and other corals (e.g. Buehler 1955).

There is one simple effect that could disguise true branching as planula settlement close to a rank. If new offsets prefer to start growth on the substrate instead of suspended at a distance above it, newly branching ranks would tend to follow undulations in the surface profile. A slight banking of sediment against the flank of the original rank would then give the illusion of non-contact between the rank and the new branching offset (Fig. 5). Similarly, a mound of negligible height (on the order of 0.2 mm) inside a lacuna might give the impression that the new rank developed from both sides of the lacuna simultaneously, meeting in the middle, which would be a highly unlikely event. The rank that is initiated at event 2 in Fig. 1A shows this type of behaviour. A depression inside a lacuna might give the impression that a planula settled in the middle, with a bidirectional increase towards both sides, as in event 9 (Fig. 1E).

The uncertainty about the nature of these apparent branchings may make this specimen irrelevant for testing growth rule 2 mentioned above. Still, it may indicate that branchings tend to occur in less crowded areas. The only clear exception among 14 observed branching events is event 15 (Fig. 1E), but this may be a special case because of the proximity to a dead corallite to the upper right (see below).

The material is much too small to allow testing of temporal distribution of events with any significance. If (pseudo) branchings appear randomly in a Poisson process (Brown & Rothery 1993), we would expect a negative exponential distribution of intervals between consecutive events. Such a distribution can not be rejected with the available data (exponential Shapiro-Wilk test,  $p = 0.10$ ). The concentration of apparent branchings around the 0 mm level and the 4 mm levels is, however, intriguing (Fig. 6). If the halysitids occasionally spawned in synchrony, perhaps annually, like modern corals, the resulting peaks of larval settlement might possibly be detected in more extensive serial-sectioning studies (see Scrutton (1998) for a review of the evidence for episodic peaks of offsetting in tabulates). Elias & Lee (1993) suggested a halysitid growth



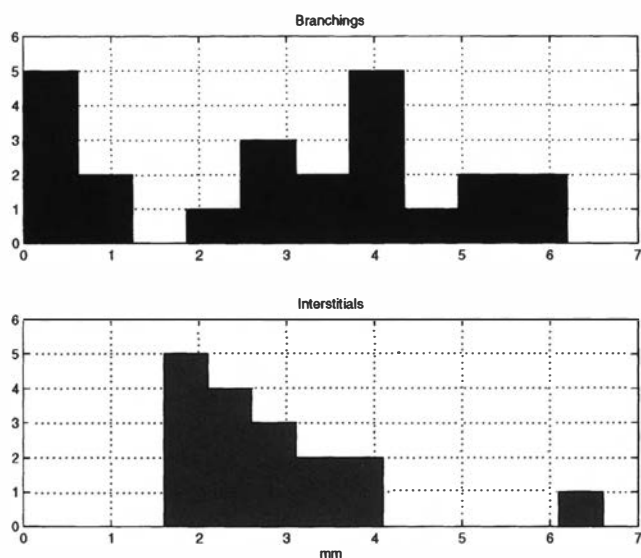


Fig. 6. Number of branchings (top) and interstitial increases (below) as a function of sectioning level or time.

rate in the range of 4.9–10 mm per year, on the basis of cyclical variations in microborings and distances between tabulae (see also Scrutton 1998). The present serial sectioning of 7.2 mm would then represent about one year of growth. Unfortunately, tabulae are not sufficiently well preserved in this specimen to allow such measurements.

### Interstitial increase

Interstitial increase is common in the studied specimen (Fig. 1, events 7, 8, 10, 11, 12), but it is noteworthy that most of these events take place at intersections between three or four ranks, rarely within a single rank. Following the views of Stasinska (1980), interstitial increase only occurs from the youngest corallite in a rank, an interstitial increase event at a position of intersection would indicate a previous collision event at that position. However, interstitial increase within a rank is common in other halysitid species (Hubmann 1996).

Event no. 6 represents an odd case where an apparent interstitial offset within a rank comes in close contact with a neighbouring rank and fuses with it, thus dividing an elongated lacuna. A close-up of this event (Fig. 7) shows that the coenenchyme at each side of the new corallite expands significantly, and perhaps more than usual during interstitial increase, fusing with the neighbouring rank. This mode of increase, intermediate between interstitial increase and branching, has not been previously described. It is of great value in understanding a particular aspect of halysitid astogeny, because it demonstrates the ability of a new offset to fuse with other corallites instead of avoiding them, as older corallites do (rule 3 above). This must be the same mechanism as the one responsible for fusion when

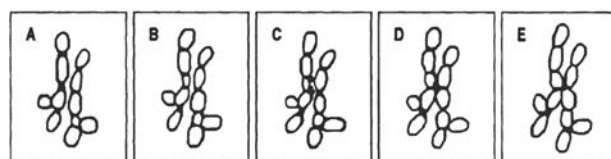


Fig. 7. Close-up of event no. 6, showing an interstitial offset that fuses with neighbouring rank. Levels 1.4, 1.8, 2.0, 2.2 and 2.6 mm.

lateral offsets collide with another rank. If new corallites avoided existing ranks, such fusion would be difficult.

### Death and regeneration

Dead corallites are recognized by their open-ellipse appearance in the sections, caused by sediment infilling (Lee & Elias 1991). The infilling will have penetrated a small distance down the corallite, until stopped by a tabula, and actual death may therefore have occurred at a slightly later point in time than the first appearance of infilling. The cause of death may have been starvation, disease or predation, but death over a larger area is likely to be a result of smothering. The corallites in the studied area of the colony seem to have been struggling against sediment influx particularly visible in the left side of the figures, where new offsets were frequently killed and later disappeared in the succession, followed by more successful colonization. Some of the features in this area, however, seem to be due to damaging taphonomical effects, and the development is somewhat confusing. More limited mortality events can be seen in the right half of the illustrated sections.

There are several examples of regeneration (*sensu* Lee & Elias 1991) in this specimen. One case is marked as event 17, where two small corallites appear in the position of a previous, dead corallite (Fig. 8). Interestingly, the smaller of these corallites later disappears again, evidently as a result of competition with its 'brother'. Such atrophy has not been previously described in halysitids.

Influx of sediment, causing smothering, may be connected with storm events or turbiditic flows. The Braksøya Formation is interpreted as representing a relatively shallow-water, marginal marine carbonate environment, possibly even with occasional emergence (Worsley et al.

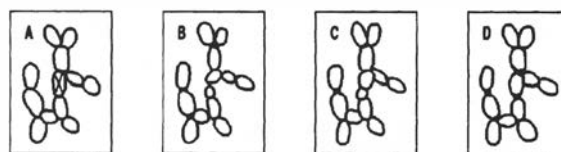


Fig. 8. Rejuvenation in the position of a dead corallite (marked with a cross). One of the emerging offsets disappears again, presumably through competition. Levels 4.1, 4.6, 4.7 and 5.0 mm.

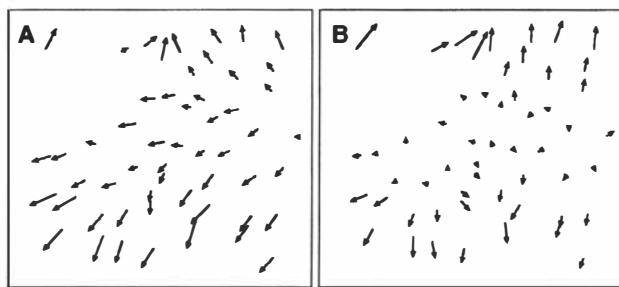


Fig. 9. Growth displacement vectors for  $N = 54$  corallites, from the 0.0-mm to the 5.0-mm sectioning levels. The vector field to the right is corrected for mean displacement.

1983), and therefore probably located above the storm weather base. Tidal currents and fair weather wave action may also have been responsible.

### Lateral growth

The small vertical increment in these serial sections makes it possible to trace the lateral growth of individual corallites, without connecting the wrong pairs. Figure 9 shows the displacement vectors for  $N = 54$  corallites, starting at the 0.0-mm sectioning level and ending at the 5.0-mm level. Pairs were carefully connected by tracing the positions at intermediate levels. The vector field shows an obvious bias of displacement to the left, which may partly be due to oblique sectioning with respect to the original time horizons. In order to clarify the differential

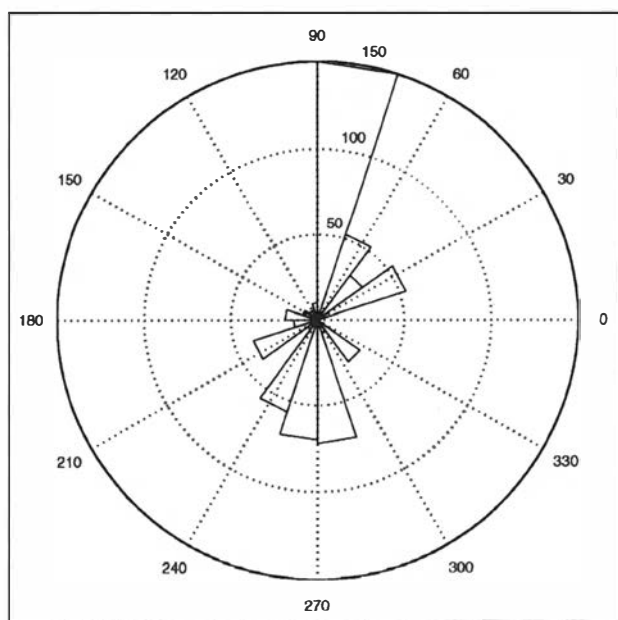


Fig. 10. Rose diagram of corrected displacement vector field from Fig. 9, weighted by vector lengths.

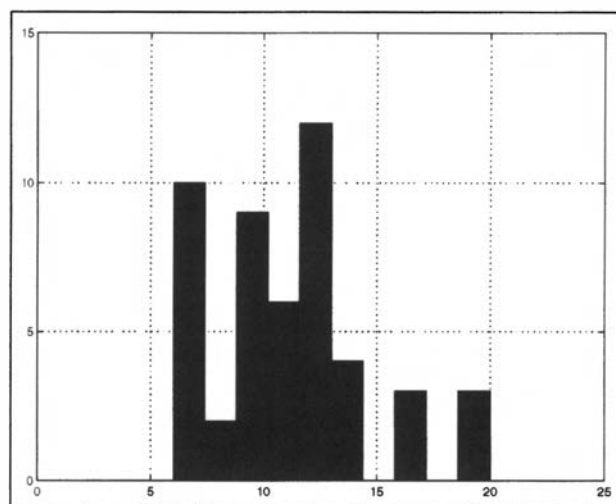


Fig. 11. Distribution of sizes of lacunae at the 6.3-mm level, measured in number of corallites.  $N = 49$ , mean = 11.2, var. = 12.2.

growth trends, this bias, corresponding only to a common translation of all corallites, can be removed by subtracting the mean displacement vector from all vectors, as shown in Fig. 9.

It is obvious that the expanding trend is not isotropic (equal in all directions), but largely constrained to the upwards and downwards directions in the figure, above and below the horizontal midline, respectively. In Fig. 10 a rose diagram shows the angles of the vectors with their mean removed. The angles are also weighted by vector lengths. If this anisotropic trend continues, it will lead to further N-S stretching of the lacunae, making them even more elongated in this direction. At the 0.0-mm level section, this process may already have been proceeding for a while, and be responsible for the elongation seen already in the first section.

This anisotropic expansion may be due to crowding, in the sense that the observed area is in conflict with other regions of the corallum, or opposing unfavourable substrate conditions, to the right and left. The 'spring' effect (rule 4), combined with lateral growth towards lower density (rule 3), would then produce the bilateral expansion. This possibility cannot be tested without studying a much larger area. Alternatively, offsetting towards water currents oriented vertically in the figures (Hamada 1959; Hammer 1998) may have caused the elongation in these directions, but the currents would have to be bidirectional in order to produce the bimodal vector distribution. Tidal currents would be one possibility, compatible with the supposed intratidal setting of the Braksøya Formation (Worsley et al. 1983).

### Sizes of lacunae

Size and shape of lacunae are commonly used characters in halysitid taxonomy. The distribution of sizes of lacunae in

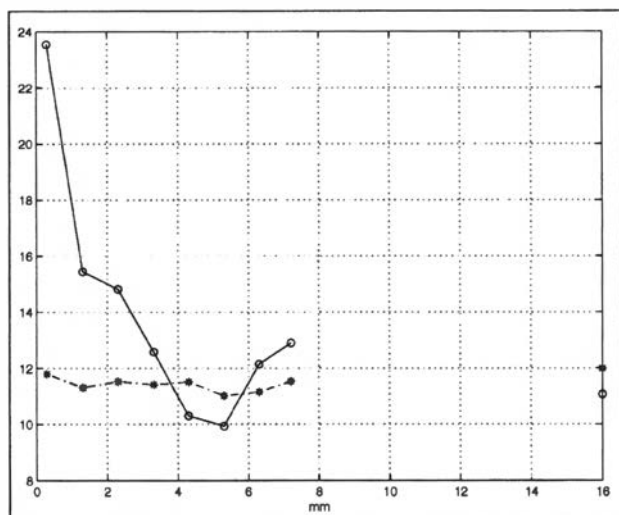


Fig. 12. Mean (asterisks) and variance (circles) of sizes of lacunae as a function of sectioning level. The rightmost data points were found from a cut made 9 mm above the last of the serial sections.

the present specimen is shown in Fig. 11. Similar values for mean and variance were found for different specimens of the same species at the same locality, indicating some specific stability at least in similar environments. The distribution is decidedly non-Normal (Shapiro–Wilk test,  $p < 0.01$ ), showing a sharp cut-off for small lacunae. As discussed by Hammer (1998), this is not in accordance with simple models for random subdivision of lacunae by new ranks during astogeny.

Also, sizes of all lacunae were determined for each millimetre through the specimen, and the changes in mean and variance plotted (Fig. 12). The mean size stays almost constant, while the variance decreases over time. This may be compared with the somewhat diverging, non-quantitative earlier reports on other halysitids (e.g. Lee & Noble 1990). The constancy of mean size and decreasing variance may indicate some ability to regulate the sizes of lacunae according to the local density, as predicted by the growth rules given above (Hammer 1998).

## Conclusion

The study of halysitid astogeny is complicated by several factors, including taphonomic and diagenetic effects, difficulty of extraction from hard matrices, and rapid growth. Partly as a result of this, but mainly because of the limited amount of work on the astogeny of this group, the intriguing questions regarding self-organization and regulation in halysitid colonial structures are still mainly unanswered. More statistical and morphological studies of complete colonies from different environments, studies of

regeneration after damage and how growth is influenced by competition with other organisms are necessary.

As shown by the specimen studied here, there is a large diversity of events and processes taking place during the halysitid astogeny. These processes can be of use when reconstructing palaeoenvironments. Furthermore, taxonomic confusions could be avoided if one is able to discriminate between genetically and ecophenotypically determined morphological features.

**Acknowledgments.** – The specimen described here was collected by the 'Friends of the Paleontological Museum, Oslo' (PalVenn). Thanks are extended to B. E. E. Neuman and D. A. T. Harper for useful comments on the manuscript. This paper was produced as part of the project 'Lateral inhibition models in developmental palaeobiology', supported by the Norwegian Research Council.

Manuscript received August 1998

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