# COLONY GROWTH PATTERN AND ASTOGENETIC GRADIENTS IN THE CRETACEOUS CHEILOSTOME BRYOZOAN *HERPETOPORA*

by P. D. TAYLOR

ABSTRACT. The common Chalk anascan *Herpetopora* has runner-like encrusting colonies with uniserial branches. Following larval settlement, the ancestrula, described for the first time, budded two daughter zooids to initiate two first order colony branches which grew in opposite directions. Branches of higher orders were added by lateral zooidal budding from both sides of parent branches, usually at *c*. 80°. The 'mature' colony consisted of two conjugate sets of branches. Size/frequency distributions of zooidal length in *H. laxata* demonstrate the existence of two autozooidal polymorphs which differ in the length of their caudae. Independent astogenetic gradients of changing zooid size can be distinguished in each branch; in *H. laxata* these consist of an initial phase of progressively lengthening non-caudate polymorphs, followed by a threshold jump to a phase of caudate polymorphs, also of progressively increasing length. Each zooid in a colony could normally bud three potential daughters (one distal and two lateral). However, the frequency of buds actually formed declined with increasing branch order, and caudate autozooids generally budded more daughters than non-caudate autozooids in *H. laxata*. Intersections between branches had various possible outcomes; usually the growing branch terminated against the skeletal margin of the earlier branch, but sometimes growth deviated towards a pore window, probably by chemotropism, and occasionally branches were overgrown. Evidence of colony damage and repair includes 'intramural' budding, and normal and reverse polarity 'extramural' budding. Many colonies had complex histories involving mortality of zooids, fission, regrowth, and fusion. Functional interpretation of morphology suggests that growing colonies were proficient at exploring substratum space and seeking spatial refuges. They could withstand extensive damage and fragmentation, and had the capacity to repair damage and re-establish connections between the ramets formed by fragmentation.

AMONG colonial organisms, bryozoans provide a good opportunity to study developmental patterns in fossil taxa (e.g. Anstey *et al.* 1976; Taylor and Furness 1978; Podell and Anstey 1979; Lidgard 1985). Development of the colony, termed astogeny to distinguish it from the ontogeny of a solitary organism or an individual zooid in a colony, is manifested in the sequence of budded zooids, their changing morphology during colony development and the way in which they are arranged in the growing colony. It is easier to unravel astogeny in encrusting, two-dimensional colonies than in more complex erect colonies in which parts formed during early growth are often hidden. Especially suitable for astogenetic study are encrusting colonies with runner-like uniserial branches. Here the genealogy of the zooids and the temporal order of budding may be most obvious, as in the genus *Herpetopora* Lang, 1914.

Herpetopora is an anascan cheilostome classified currently within the paraphyletic Suborder Malacostegina and Family Electridae (see Taylor 1987). Species can be extremely abundant in the Upper Cretaceous chalks of north-west Europe. Thomas and Larwood (1960) last revised *Herpetopora* and placed it in synonymy with *Pyripora* d'Orbigny. This synonymy was rejected by Voigt (1982) and is also not accepted here because *Herpetopora* zooids lack a pustulose cryptocyst and lateral pore chambers with septulae, have considerably narrower and often much longer caudae than *Pyripora*, and colonies never develop oligoserial branches. Thomas and Larwood described two similar species which occur commonly in the English Chalk: *H. anglica* Lang ranges from the late Turonian to early Campanian, whereas *H. laxata* (d'Orbigny), distinguished by the slightly broader zooidal opesia, is found mainly in the late Campanian and early Maastrichtian. As
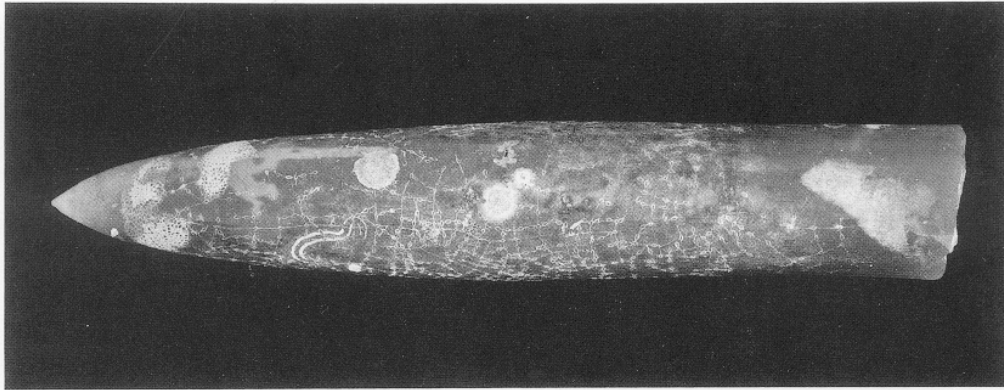
TEXT-FIG. 1. Colony of *Herpetopora laxata* (d'Orbigny) encrusting a guard of *Belemnitella*. BGS Yc 2708, Campanian, Compton, Hampshire. ×1·4.

Professor E. Voigt and Dr G. P. Larwood are together preparing a revision of *Herpetopora*, the systematics of the genus will not be further considered in this paper.

Colonies of *H. anglica* and *H. laxata* can be found encrusting a variety of skeletal substrata, including bivalves, echinoid tests, and belemnite guards. *H. anglica* is particularly common on shells of *Inoceramus* where other bryozoans tend to be relatively rare. However, it is very easy to overlook colonies because of their narrow branches and poor visual contrast with the substratum. Colonies frequently cover large areas of substratum, but are always incomplete, either because their substratum is fragmented, or because not all of their zooids are preserved. Typical specimens lack zooids formed during early colony growth but preserve numerous disconnected chains of zooids which may have been derived from one or more colonies. Consequently, it is impossible to study astogeny by assembling a 'growth series' of colonies of increasing size, as is often done in growth studies of solitary animals and in some bryozoan species (Håkansson 1975).

This paper aims to describe: the detailed growth pattern of *Herpetopora* colonies; their unusual astogenetic gradients; the hitherto unknown ancestrula and early astogeny of colonies; and morphological structures indicating extensive repair of damage in living colonies. These observations lead to a discussion of the factors controlling astogenetic gradients of zooid size, and aspects of colonial integration and functional morphology.

MATERIAL AND METHODS

The specimens used in this study are lodged in the collections of the British Museum (Natural History), abbreviated BM(NH), British Geological Survey, Keyworth (BGS), and Voigt Collection, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg (VH). A complete listing of the BM(NH) material is given by Thomas and Larwood (1960).

Detailed analysis of astogenetic gradients was undertaken in a single colony of *H. laxata* (d'Orbigny): BGS Yc 2708; Campanian, zone of *Gonioteuthis quadrata* (presumably the 'Hagenowia Horizon' at the base, C. J. Wood, pers. comm. 1986), 'Southampton Waterworks: new pit' (NGR SU 469236), Compton, Hampshire; collected by R. M. Brydone and presented by E. Brydone, 1943. This colony (text-fig. 1) encrusts a guard of the belemnite *Belemnitella* sp., and is exceptional in preserving the ancestrula and a large number of connected post-ancestrular zooids (though preservation of surface detail is poorer than in many other specimens). The principal growth axis of the colony is defined by the two first order branches which are orientated almost parallel to the length of the belemnite guard. The colony was drawn (text-fig. 2) using a drawing tube attached to a Wild M7 binocular microscope, rotating the belemnite guard about its long axis to enable inclusion of zooids around the full circumference; however, some peripheral zooids distant from the ancestrula and difficult to relate to the main mass of the colony were omitted. The resulting 'map' of the
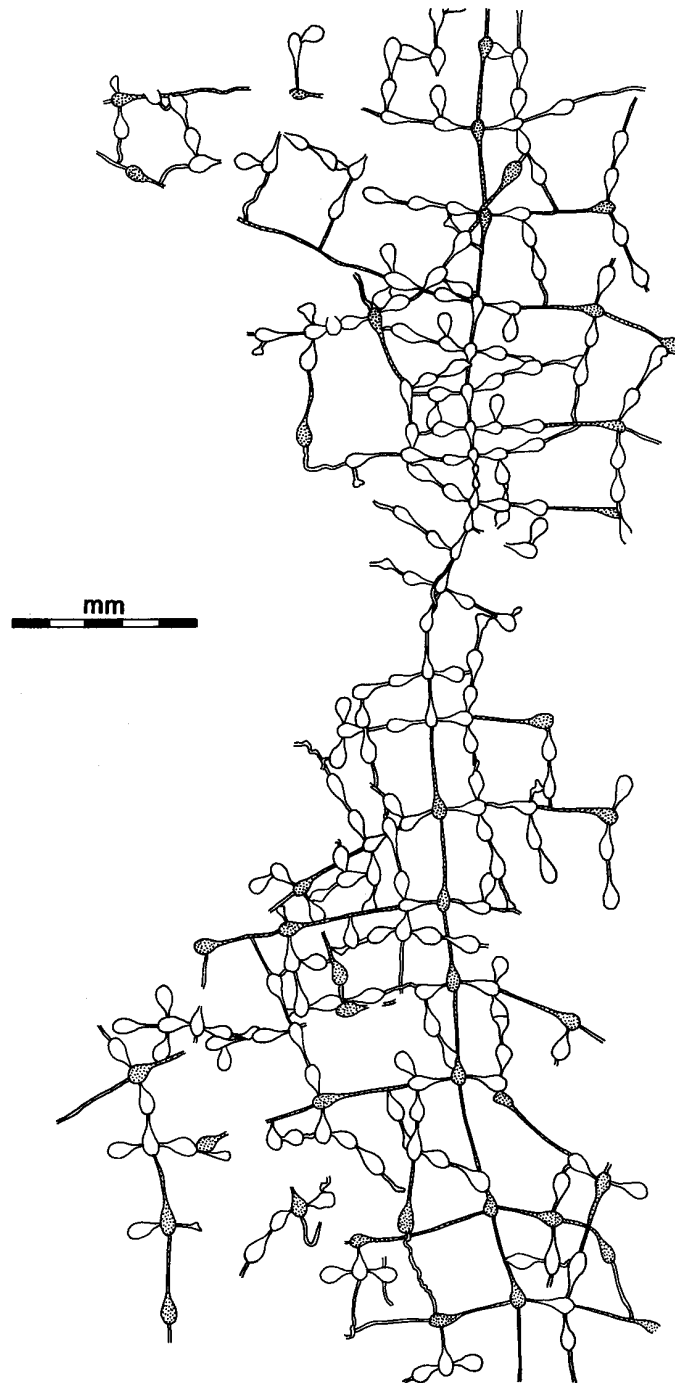
TEXT-FIG. 2. Drawing of part of *Herpetopora laxata* colony BGS Yc 2708. The first order branches of the colony are almost vertically orientated, and the caudate autozooids have been stippled.

colony included over 300 zooids, each of which was given a serial number. An eyepiece micrometer graticule was used to measure lengths and other dimensions of the numbered zooids. Angles between branches of the colony were measured to the nearest 5° using an eyepiece protractor graticule; slight curvature of zooids and the consequent problem in defining exactly their long axes precluded a more precise determination.

Observations of branch intersections and additional morphological features in BGS Yc 2708 and other specimens were initially made with the optical microscope but many specimens were then studied in more detail using an ISI 60A scanning electron microscope equipped to accommodate large, uncoated specimens (Taylor 1986c). It should be noted that all scanning electron micrographs in this paper are back-scattered electron images rather than the more conventional secondary electron images.

ZOOIDAL POLYMORPHISM

Autozooids

The feeding zooids of a bryozoan colony are termed autozooids. In fossil bryozoans, autozooids can often be recognized by comparison with closely related Recent species. Though not necessarily the commonest polymorph, autozooids are usually the polymorph to occupy the largest area of the living surface of the colony. The autozooids of *Herpetopora* are identifiable by analogy with Recent *Pyripora* and are the most numerous polymorph. They have a pyriform outline shape, dilated distally in the region of the opesia (Pl. 42, fig. 2). Unlike *Pyripora*, however, the opesia is not bordered by a pustulose cryptocyst. Closure plates occlude opesiae of some autozooids (text-fig. 3; Pl. 45, fig. 6), and the occurrence of impressions of the operculum on the closure plates substantiates the autozooidal nature of these zooids. So-called 'regenerations', indicating reparative budding (see p. 540), often occur as a concentric series of mural rims within the opesiae.

The proximal part of the autozooid is a slender cauda, sometimes slightly curved and of very variable length; the extreme range of autozooidal length within colonies of *Herpetopora* is due almost entirely to variability in the length of the caudae. As discussed below (p. 536), the length of successive autozooids increases distally along each branch of the colony. Histograms (text-fig. 4) of autozooidal length within colonies of *H. anglica* and *H. laxata* reveal a previously overlooked difference between the two species. In *H. anglica*, the size distribution is positively skewed but near normal, with modal and mean values of autozooidal length between 0·8 and 1·0 mm. Although autozooidal length appears to increase continuously along branches of this species (see p. 539), attaining a maximum recorded value of 6 mm in BM(NH) D.8213, branches with more than four zooidal generations are not often preserved and very long autozooids are comparatively rare.

Autozooidal size distribution in *H. laxata* is distinctly bimodal. The modal value of the first peak (0·8–1·0 mm) corresponds with that of *H. anglica*. The second, smaller peak has a modal value of 2·0–2·4 mm and is positively skewed. Very few autozooids occur in the length range of 1·4–1·6 mm between the two peaks. Bimodality implies autozooidal polymorphism in *H. laxata* and permits the distinction of two types of autozooids:

a, 'non-caudate autozooids' less than 1·6 mm in length (Pl. 42, fig. 2);

b, 'caudate autozooids' more than 1·6 mm in length and with relatively long caudae (Pl. 42, fig. 3).


EXPLANATION OF PLATE 42

Figs. 1–4. *Herpetopora laxata* (d'Orbigny); except for 1, all are back-scattered SEM images. 1 and 3, BGS Yc 2708, Campanian (*quadrata* Zone), Compton, Hampshire. 1, proximal part of colony with narrow, runner-like branches encrusting a belemnite guard (circular white patches are abraded sheet-like bryozoans), ×2·8. 3, caudate autozooid, ×42. 2, BM(NH) D.42375, branch (originating just beneath centre of right margin and growing WNW) consisting of two non-caudate autozooids followed by a caudate autozooid, Campanian (*mucronata* Zone), Webster's Pit, Norwich, Norfolk, ×22. 4, BM(NH) D. 42361, damaged zooid (with two lateral buds) followed by a caudate kenozooid (with incomplete lateral buds), Campanian (*mucronata* Zone), Thorpe St Andrew, Norfolk, ×32.
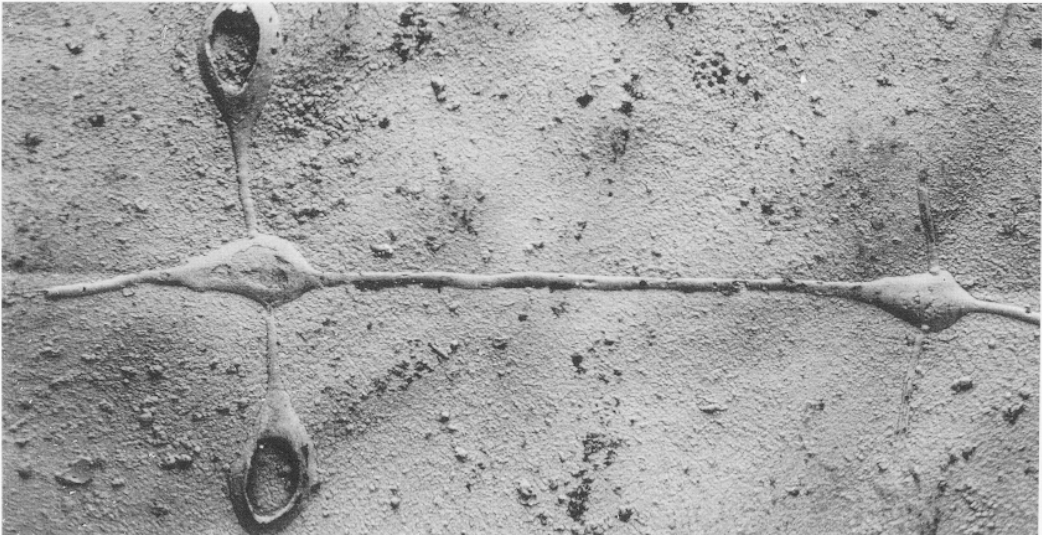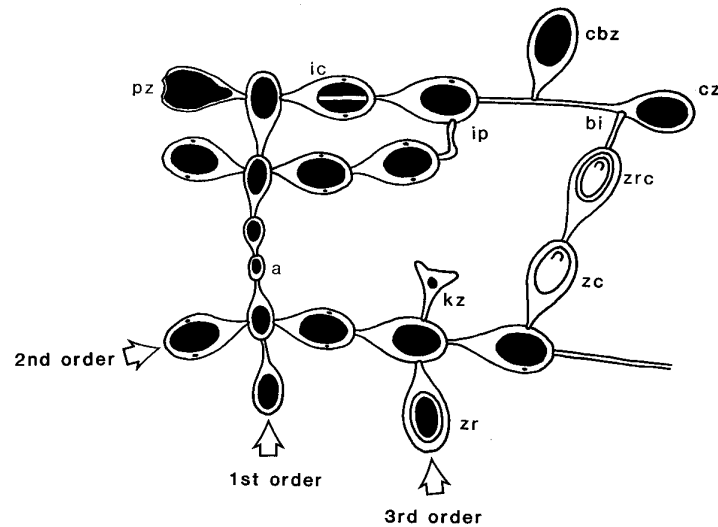
PLATE 42
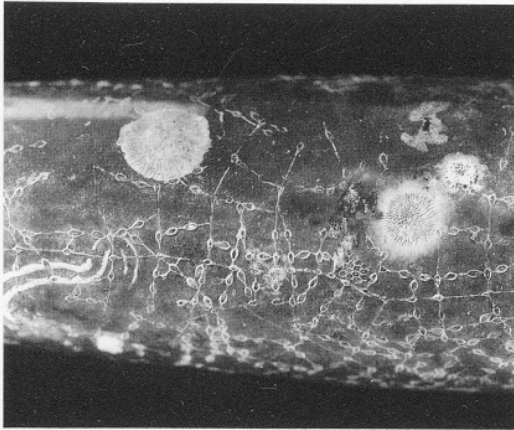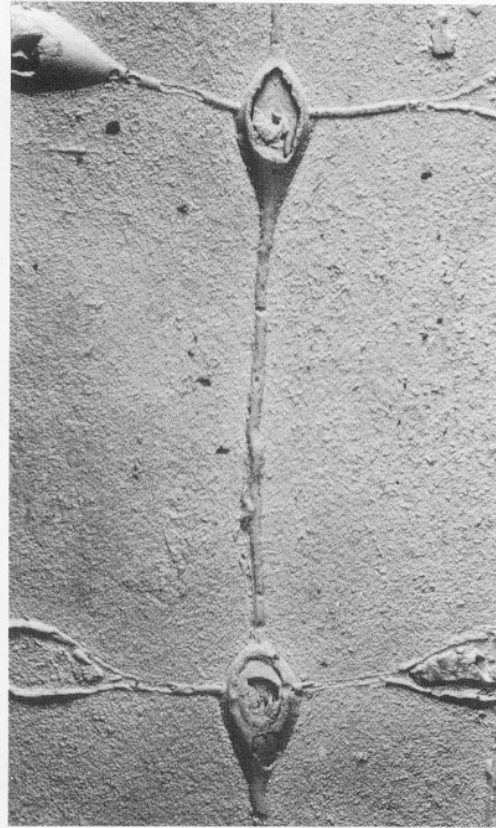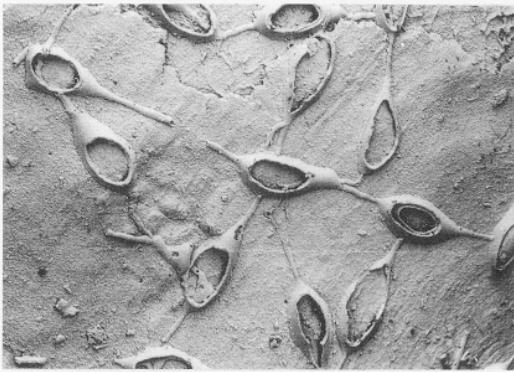
TAYLOR, *Herpetopora*

TEXT-FIG. 3. Diagram of a hypothetical colony of *Herpetopora laxata* showing arrangement of branches and other morphological features. Abbreviations: a, ancestrula; bi, branch intersection (type 1) entailing termination of the growing branch; cbz, caudally budded zooid; cz, caudate autozooid; ic, intramural cauda; ip, cauda growing into pore window (branch intersection type 3); kz, kenozooid (opesiate); pz, partially formed zooid; zc, autozooid with closure; zr, autozooid with intramural reparative bud; zrc, autozooid with intramural reparative bud which has a closure. Branches of orders 1-3 are indicated.

As both types of polymorph may be found with closure plates bearing opercular impressions of similar size, both are thought to have been autozooids. Other aspects of their skeletal morphology appear identical, although the distally dilated parts of caudate autozooids are often narrower. In addition, the frequency of closure plates is greater in caudate autozooids; in colony BGS Yc 2708, 24 of 54 (44 %) caudate autozooids have closure plates whereas only 43 of 276 (9 %) of non-caudate autozooids have them. The possibility that caudate autozooids are in reality cormidia formed of a proximal kenozooid and a distal autozooid is difficult to dismiss. However, there are no indications in abraded examples of the pore plate that would be expected between the two

TABLE 1. Lengths (in mm) of non-caudate and caudate autozooids in *Herpetopora laxata* colony BGS Yc 2708. S.D. = standard deviation; C.V. = coefficient of variation.

|	Non-caudate	Caudate
Mean	0·97	2·61
S.D.	0·198	0·989
C.V.	20·4	38·0
Range	0·27-1·47	1·83-8·28
Determinations	236	63
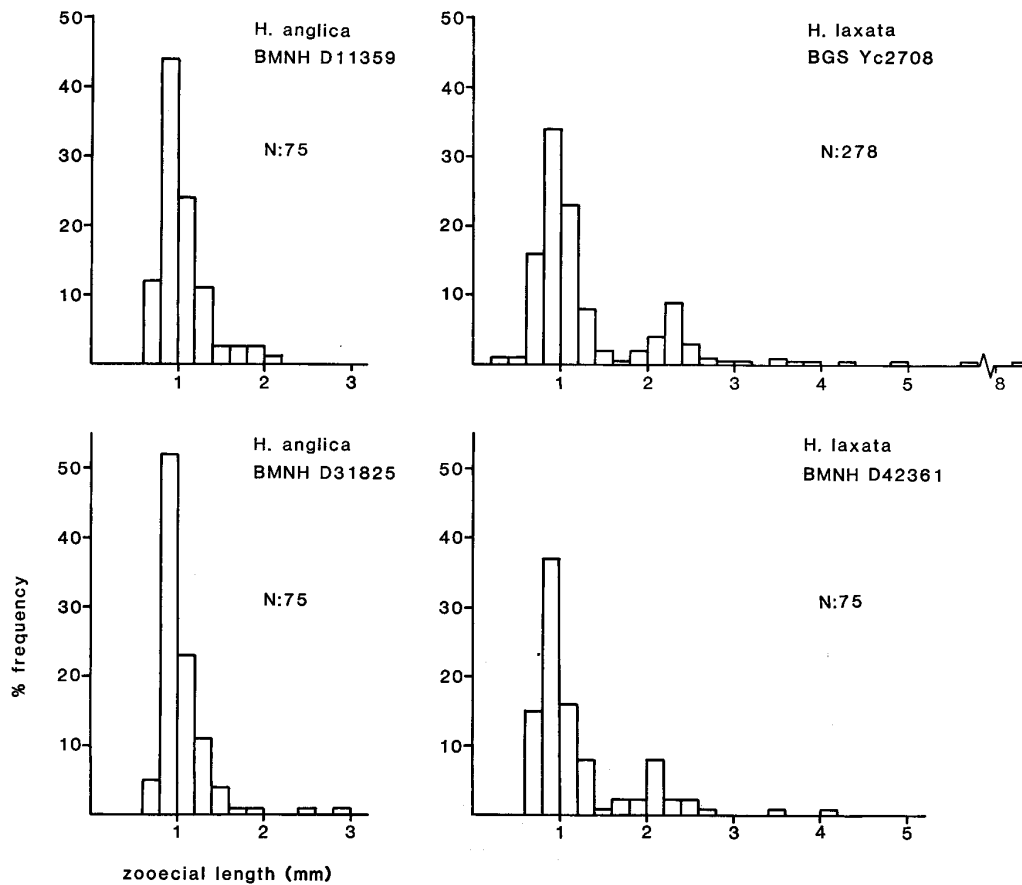
TEXT-FIG. 4. Frequency distributions of autozooidal length in two colonies of *Herpetopora anglica* and two of *H. laxata*.

zooids, and no junction is visible in external morphology. Table 1 gives mean values and ranges for non-caudate and caudate autozooids in BGS Yc 2708.

The frequency distribution of autozooidal lengths (text-fig. 5) in the same colony of *H. laxata* has been broken down according to branch order number (see p. 529). First and second order branches growing across free substratum space are typically long and therefore contain a large number of caudate autozooids. It should be noted that the atypically small autozooids in the first order branches are those budded during early colony growth (see p. 529).

Autozooidal polymorphism, excepting the distinction between brooding and non-brooding autozooids, has been recognized in relatively few cheilostome bryozoans (see Silén 1977 for a review of polymorphism in bryozoans). The most similar example to *H. laxata* occurs in the Albian 'malacostegan' *Spinicharixa dimorpha* Taylor. Colonies of this species have uniserial chains of caudate autozooids which budded non-caudate autozooids distolaterally to infill the areas of substratum between the caudate autozooids (Taylor 1986b). As in *Herpetopora*, the caudate autozooids of *S. dimorpha* very often have closure plates.
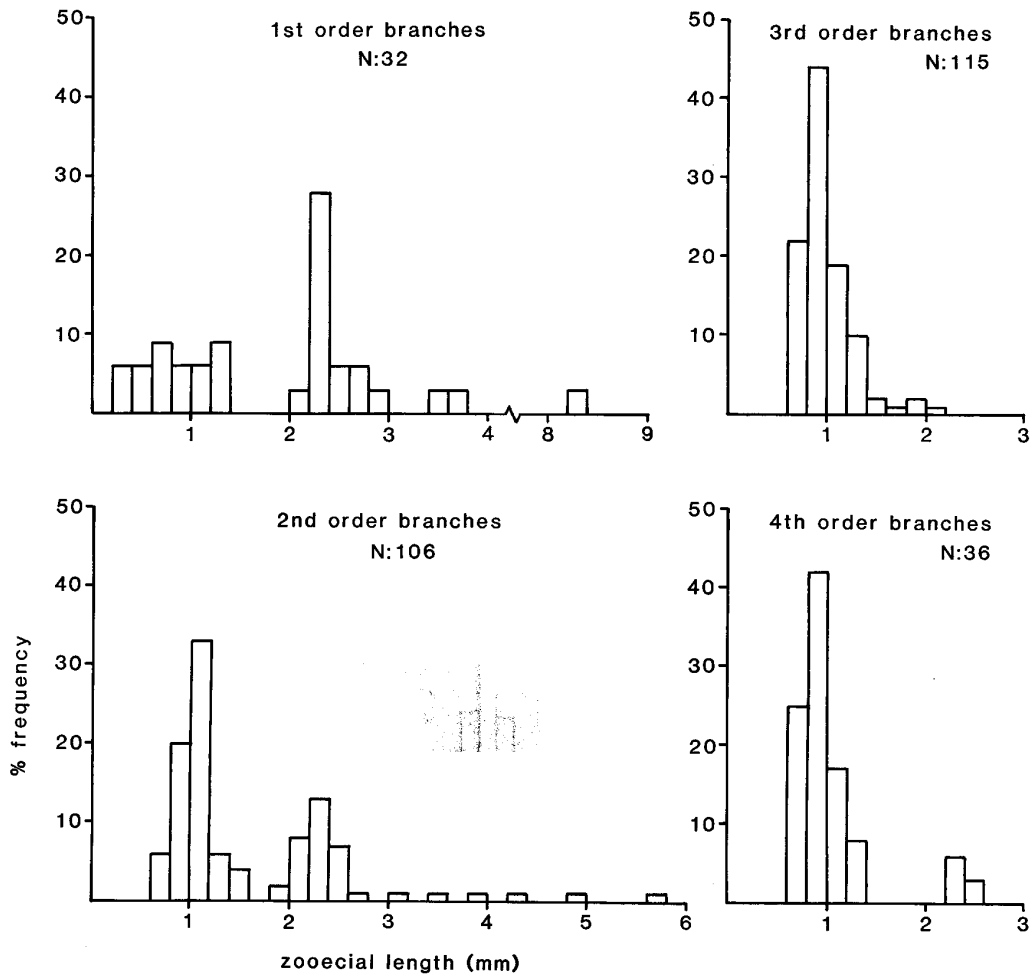
TEXT-FIG. 5. Frequency distributions of autozooidal length in branches of different orders in *Herpetopora laxata* colony BGS Yc 2708.

EXPLANATION OF PLATE 43

Figs. 1-6. *Herpetopora laxata* (d'Orbigny), back-scattered SEM images. 1, BGS Yc 2708, colony origin showing the ancestrula (just right of centre) and early generations of budded autozooids, Campanian (*quadrata* Zone), Compton, Hampshire, × 36. 2 and 3, VH 10300, Lower Maastrichtian, Hemmoor, W. Germany. 2, ancestrula and the two periancestrular zooids, × 55. 3, ancestrula showing closure plate bearing an opercular scar, × 220. 4–6, BM(NH) D.42361, Campanian (*mucronata* Zone), Thorpe St Andrew, Norfolk. 4, caudate autozooid (with occluded intramural bud) which in addition to the usual distal and two lateral buds, has produced a proximolateral bud (origin arrowed) and two closely spaced caudal buds, × 32. 5, type 3 branch intersection in which a cauda has curved in growing towards the lateral pore window of a neighbouring zooid, × 93. 6, type 2 branch intersection (overgrowth) followed by type 3 intersection in which the overgrowing cauda has deviated towards the left lateral pore window of the overgrown zooid, × 37.
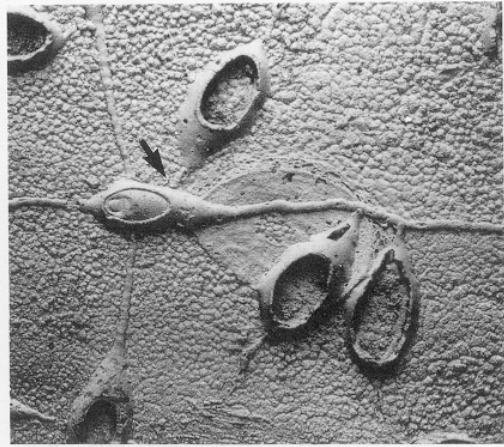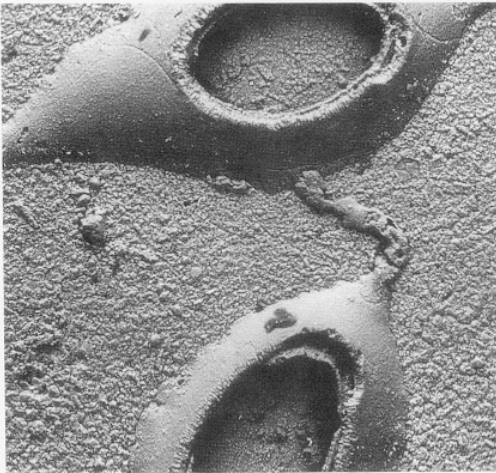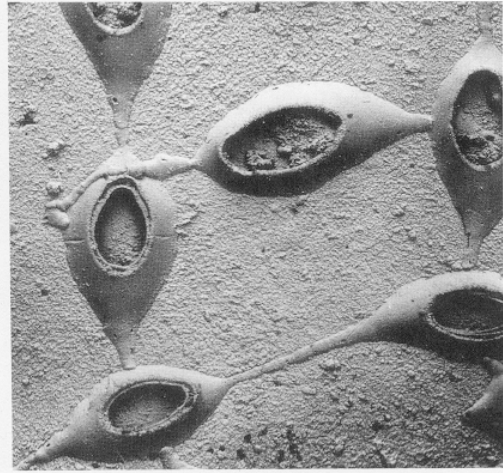
PLATE 43

TAYLOR, *Herpetopora*
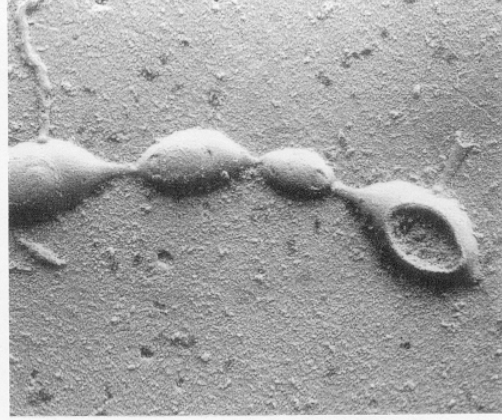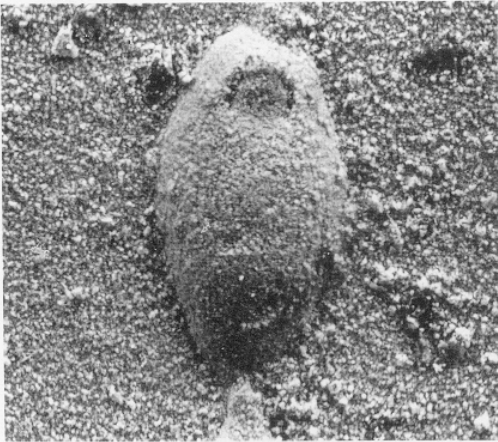
Kenozooids

The term kenozooid is generally applied to a range of cheilostome heterozooids (i.e. non-feeding zooids) lacking tentacles, functional guts, and opercula (cf. avicularia). Kenozooids typically have a comparatively simple skeletal morphology, are usually smaller than autozooids, and are often present in fewer numbers.

Many kenozooids (text-fig. 3; Pl. 44, figs. 3 and 5) in *Herpetopora* resemble similar polymorphs in closely related genera such as *Pyripora*, *Pyriporopsis*, and *Conopeum*. Like the autozooids, these kenozooids have a narrow cauda of variable length, but instead of having an ovoidal distal part, the kenozooid has a subtriangular distal outline, narrower than an autozooid and with a small circular to longitudinally elliptical opesia. Some of these 'opesiate kenozooids' have closure plates which differ from those of the autozooids in the absence of an opercular scar. Prolongations of variable length may extend from the two distolateral corners of the kenozooid. These are usually blind but on occasions connect with other zooids in the colony (Pl. 44, fig. 3). The overall shape of the kenozooid can be highly irregular and asymmetrical, sometimes (but not always) in relationship to growth within a restricted space, e.g. where branches intersect. Opesiate kenozooids arise as lateral or distal buds from an autozooid (or possibly as fused buds from two autozooids), and do not normally produce buds of their own (i.e. they usually occur as terminal zooids within branches). Voigt (pers. comm. 1987) notes that kenozooids occur in abundance on substrata with numerous obstacles, e.g. echinoid tests with tubercles.

In addition to opesiate kenozooids, two other types of kenozooids are present in *Herpetopora*. The outer parts of very long branches may comprise a continuous, stolon-like cauda which is difficult to subdivide into individual zooids. However, occasional dilations, smaller in width than an autozooid, signify the distal ends of a second type of kenozooid (Pl. 42, fig. 4). These 'caudate kenozooids' lack an opesia and show no indications of having had one which was subsequently occluded by a closure plate. Their identification as kenozooids (rather than sections of autozooidal caudae) is supported by their similar length to contiguous autozooids, and the occurrence of paired lateral buds originating from their dilated distal ends.

When a growing branch intersected and abutted the side of an existing branch (see p. 533), a third type of 'kenozooid' was formed. This is simply a length of cauda of a presumptive autozooid which was unable to develop into either an autozooid or an opesiate kenozooid because of the spatial restrictions imposed by branch abutment.

ANCESTRULA AND EARLY GROWTH

Ancestrula

The ancestrula has not been previously described in *Herpetopora* and an initial search among the numerous colonies in the BM(NH) collections was unsuccessful. This may seem surprising in view of the abundance of *Herpetopora* in the Chalk. However, pre-mortem loss of the ancestrula and early parts of the colony may occur very commonly in runner-like bryozoan colonies which experience considerable partial mortality (i.e. death of individual zooids though not necessarily the entire colony). The high incidence of reparative structures in *Herpetopora* (see p. 540) confirms the widespead occurrence of pre-mortem colony damage. It is notable that the ancestrula was also undescribed until recently (Taylor 1986a) in the closely related living species *Pyripora catenularia* (Fleming).

Two colonies of *H. laxata* are now known with their ancestrulae intact: BGS Yc 2708 (Pl. 43, fig. 1) and VH 10300 (Pl. 43, figs. 2 and 3). The ancestrulae are very small (Table 2), ovoidal in outline shape, and attain their maximum width about mid-length. Opesiae of both ancestrulae are occluded by closure plates, convex in VH 10300, but apparently flat (?compressed) in BGS Yc 2708. The junctions between the closure plates and the surrounding gymnocyst, and the ultrastructural details of the closure plates are poorly preserved. Both closure plates bear distal, crescent-shaped impressions of the operculum (Pl. 43, fig. 3). No spines or open lateral pore windows are visible in either ancestrula.

TABLE 2. Dimensions (in mm) of the ancestrula in two colonies of *Herpetopora laxata*. Height and width of the operculum are estimated from impressions on the closure plates.

	VH 10300	BGS Yc 2708
Length	0·22	0·20
Width	0·12	0·11
Opesia length	0·17	0·14
Opesia width	0·09	0·06
Operculum height	0·02	0·02
Operculum width	0·03	0·04

The simple ancestrular morphology of *H. laxata* is similar to that of *P. catenularia*. The principal differences are that the ancestrula of the living species is about twice the size and has a more extensive proximal gymnocyst with the opesia occupying only the distal half of the frontal surface (Taylor 1986a).

Early growth

The ancestrula produces two buds, one distal and one proximal (Pl. 43, figs. 1 and 2). These periancestrular zooids initiated the two first order branches of the colony which grew in opposite directions parallel to the long axis of the ancestrula (text-fig. 2). In BGS Yc 2708, in which the two first order colony branches are orientated parallel to the encrusted belemnite guard (text-fig. 1; Pl. 42, fig. 1), the distal branch grew towards the apex of the guard and the proximal branch towards the alveolus. The distal periancestrular zooid is larger than the proximal periancestrular zooid in both colonies, and whereas the distal buds have open opesiae, the proximal buds have closure plates. If the relative size of the periancestrular zooids corresponds to their order of budding, then the proximal bud would have formed before the distal periancestrular bud.

Early budding patterns are known in three other pyriporids (Voigt 1982; Taylor 1986a): *P. catenularia* (Fleming), *P. huckei* Buge, and *Pyriporopsis portlandensis* Pohowsky. In the two latter species there is a distal and a proximal (or almost proximal) periancestrular bud, as in *H. laxata*. However, *Pyripora catenularia* differs in having two additional, lateral periancestrular buds. Colonies therefore possess four branches of the first order orientated at about 90° to one another. Like *Herpetopora*, the smaller size of the proximal periancestrular zooid in *Pyriporopsis portlandensis* may imply that it too was budded before the distal zooid.

LATER COLONY GROWTH

Budding loci and branching angles

Most postancestrular zooids in *Herpetopora* have, in common with many cheilostomes (see Silén 1987), three potential sites of budding which can be termed budding loci. These are situated one distally, and two laterally to distolaterally on either side of the zooid (Pl. 42, fig. 4; Pl. 45, fig. 6). From the distal locus was budded a zooid orientated parallel to and extending the branch of the parent zooid. Zooids budded from each of the lateral loci were orientated at 70–110° to the parent zooid (see p. 530) and initiated new branches of an order one higher than that of the parent zooid. For example, whereas distally budded zooids in a first order branch contributed to that first order branch, each laterally budded zooid formed a new branch of the second order (text-fig. 3).

The exact position of the lateral budding loci varies from opposite the mid-point of the opesia to between the mid-point and the distal end of the opesia. Often the two lateral loci are not

TABLE 3. Branching angles (measured to the nearest 5°) between different
branch orders in *Herpetopora laxata* colony BGS Yc 2708.

	Branch orders				
	1-2	2-3	3-4	4-5	5-6
Mean	83·7	79·7	79·6	81·4	81·3
S.D.	7·94	8·91	7·35	—	—
C.V.	9·5	11·2	9·2	—	—
Range	70–105	50–100	60–90	75–90	75–90
Determinations	50	78	25	7	4

precisely opposite one another. Lateral budding loci that have not given rise to a bud may be visible as pore windows in the gymnocyst close to the level of the substratum. In some specimens the gymnocyst (here used for all inferred exterior walls, both frontal and vertical) is sufficiently transparent to show that the pore window leads to a parallel-sided canal which passes through the thick vertical wall and opens into the interior of the zooid. The canal is not dilated, as in *P. portlandensis* (Banta 1975), nor is there a pore plate of the kind present in the pore chambers of many other cheilostomes (see Banta 1969). Distal budding loci are similar to lateral loci except that at least some appear to possess an apparent pore plate which may be visible in abraded specimens as a transverse wall between the zooid and its distal bud (Pl. 44, fig. 1).

Daughter zooids are not usually formed from all three potential budding loci. One or both of the lateral loci very commonly fails to produce a daughter zooid, and occasional failure of the distal locus may also occur resulting in branch termination. The frequency of bud formation at lateral loci decreases markedly in branches of higher orders. For example, in BGS Yc 2708, lateral buds are about seven times more common in zooids belonging to first than third order branches (see p. 535).

Angles between parent branches and laterally budded daughter branches are variable. The observed range in BGS Yc 2708 is 50–105°, with a mean value of about 80°. Differences in branching angle according to the orders of parental and daughter branches are slight and probably insignificant (Table 3). However, an early astogenetic decrease in branching angle is evident if angles between the first order branches and their second order daughters are plotted outwards from the ancestrula (text-fig. 6). Branching angle declines gradually from about 100° until the typical value of about 80° is reached after approximately nine zooidal generations. Attainment of this astogenetic repetition of branching angle is roughly coincidental with the major threshold in zooid length discussed below (p. 536).

Zooids were occasionally budded from sites other than the distal and two lateral loci. A very


EXPLANATION OF PLATE 44

Figs. 1 and 4. *Herpetopora anglica* Lang, back-scattered SEM images. 1, BM(NH) D.4189, right lateral bud and its reparative bud, both heavily abraded (the remains of a possible pore plate are visible at the distal end of the original bud), Coniacian or Santonian, Chatham, Kent, ×49. 4, BM(NH) D.45920, original (left) and reparative (right) buds partially superimposed, Santonian (*Uintacrinus* Band), Margate, Kent, ×65.

Figs. 2, 3, 5. *H. laxata* (d'Orbigny), back-scattered SEM images, BM(NH) D.42361, Campanian (*mucronata* Zone), Thorpe St Andrew, Norfolk. 2, reverse polarity intramural opesiate kenozooid within a badly damaged non-caudate autozooid, ×53. 3, intramural opesiate kenozooid within non-caudate autozooid, and small opesiate kenozooid (bottom left) linked to an autozooid (centre right) by a cauda which overgrows the autozooid with the intramural bud, ×78. 5, complex arrangement of branches comprising kenozooids and autozooids, including examples with long caudae, closure plates and intramural buds, ×21.
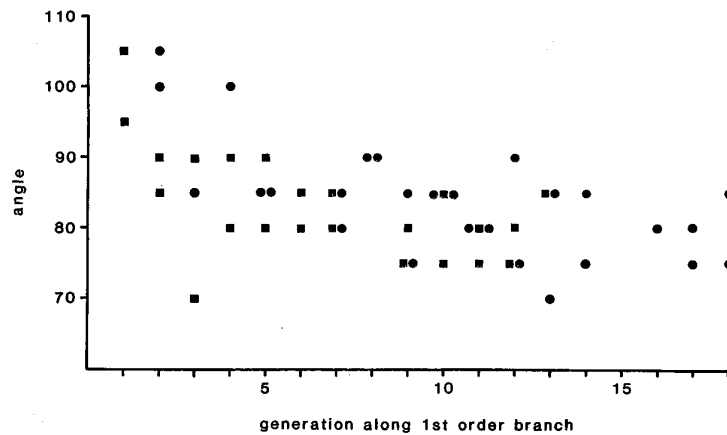
PLATE 44
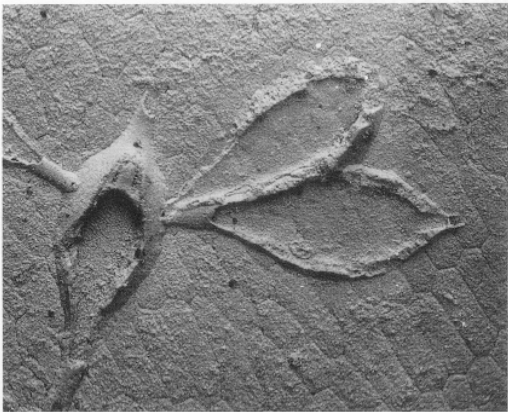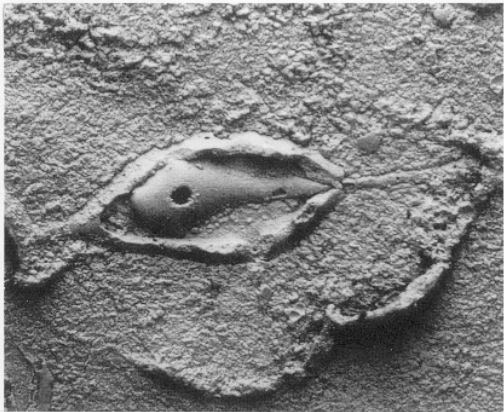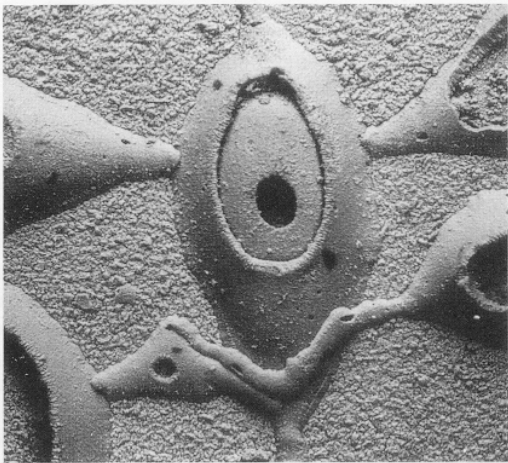
TAYLOR, *Herpetopora*

TEXT-FIG. 6. Scatter diagram showing astogenetic gradient in angle of branching between first and second order branches according to zooidal generation along the first order branches. Dots are angles from the proximal first order branch, squares from the distal first order branch. Measurements made to the nearest 5° from *Herpetopora laxata* colony BGS Yc 2708.

few zooids produced proximolateral daughters which originated from a budding locus opposite the proximal end of the opesia (Pl. 43, fig. 4). These proximolaterally budded zooids are orientated at about 120° to the parent zooid and initiated branches which grew proximolaterally relative to the parent branch. More frequently buds arose from the caudal regions of parent zooids with long caudae (Pl. 43, fig. 4). These caudally budded zooids are orientated at approximately 90° to their parent, two or more may originate from the same parent, and there is no apparent pattern in their distribution. The formation of caudal buds is unclear; open pore windows signifying possible additional budding loci have not been observed in the caudae of caudate zooids. It seems possible, therefore, that the formation of caudal buds may necessitate either skeletal resorption or damage in order to breach the cauda and form a site for zooidal budding.

Unless reparative growth has occurred (see p. 540), the sequence of budding within a single branch is unequivocal and follows a proximal to distal direction. However, the relative timing of bud formation between branches is not easily inferred in view of possible between-branch variations in budding rates. One possible source of between-branch variation is retardation of lateral bud formation, suggested by the common occurrence of open lateral pore windows from which a bud has not yet formed in zooids with a fully formed distal bud. This would be conceivable in *Herpetopora* because the rarity of semi-formed zooids suggests that bud formation was probably episodic (similar to the intrazooidal budding defined by Lidgard 1985, but not necessarily involving a pore chamber).

Observation of branch intersections can be used to estimate the extent of between-branch variations in budding rate. Because later zooids must abut or overgrow earlier-formed zooids (see p. 533), major differences in budding rate between branches will result in the common occurrence of intersections in which the abutting or overgrowing zooid has a lower generation number than the abutted or overgrown zooid. This is not the case in colony BGS Yc 2708; in only 7 of 59 (12 %) intersections does the abutting or overgrowing zooid have a lower generation number than the abutted or overgrown zooid. Therefore, appreciable differences in budding rates between branches seem to have been uncommon in *Herpetopora*, and any retardation of lateral bud growth relative to distal bud growth was probably minor.

TEXT-FIG. 7. Diagram of types of branch intersection observed in *Herpetopora* colonies. In type 1 intersections, the growing branch terminates against the existing branch, immediately in the case of type 1*a* but after partial overgrowth in the case of type 1*b*. Complete overgrowth occurs in type 2 intersections. Type 3 intersections involve growth of a cauda towards an open pore window. Head-on collisions between growing branches result in type 4 intersections.
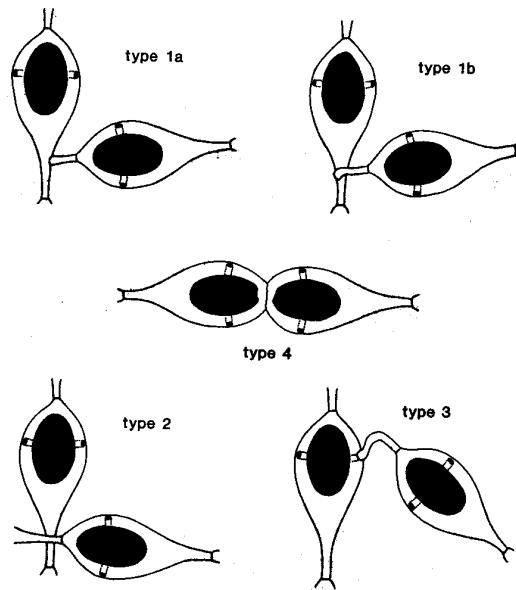
Basic colony growth pattern

Positions of budding loci and orientations of daughter zooids, and consequently colony branches, resulted in the following basic pattern of colony growth in *Herpetopora*. The two first order branches grew distally and proximally from the ancestrula, forming a 'backbone' to the colony. From both sides of the first order branches there diverged numerous second order branches in a rib-like arrangement at angles of about 80° to the first order branches (as in text-fig. 2). Third and higher order branches continued the pattern, branches of odd number orders orientated subparallel to the first order branches, and branches of even number orders subparallel to the second order branches (text-fig. 3). This conjugate pattern of branches, resembling the trichotomous branching pattern illustrated by Harper (1985) for a hypothetical modular organism, is disrupted in real colonies by variability in branching angles, slight curvature of branches, failure of buds, the presence of obstacles to branch growth, and irregularities in the shape of the substratum.

Branch intersections

Numerous examples of branches intersecting one another can be observed in colonies of *Herpetopora*. Branch intersections occurred routinely as growing branches collided with existing branches, or more rarely as two growing branches met. The availability of colony BGS Yc 2708 with a large number of connected zooids provides an opportunity to study the varying types and frequencies of branch intersections which occurred demonstrably within a single colony (and therefore a genetic entity). A total of fifty-nine branch intersections were observed in BGS Yc 2708, and qualitative observations were also made on several other colonies.

Branch intersections can be classified (text-fig. 7) as follows:

Type 1 (abutment). Here a zooid of a growing branch abutted the side of an existing branch. Generally the growing branch terminated soon after its first contact with the existing branch (type 1*a*), but sometimes it overgrew the mid-line summit of the existing branch before terminating (type 1*b*). In both cases the distal end of the growing branch is sealed to the exterior. It is not known whether resorption of the gymnocystal skeleton of the earlier branch occurred to permit soft tissue

connection between the two branches. The zooid in the growing branch usually had insufficient space to develop into an autozooid and is represented by a short length of cauda. Occasionally, however, space was available for the abutting zooid to become an opesiate kenozooid or even an autozooid. Intersections of type 1*b* have only been observed in BGS Yc 2708 where the growing branch met the cauda or distal gymnocyst of a zooid on an existing branch; overgrowth of opesia does not seem to have occurred. In this colony, 61 % of intersections are of type 1 (51 % of type 1*a* and 10 % of type 1*b*). *Herpetopora* colonies frequently overgrew obstacles higher than their own branches, suggesting that type 1 intersections involved a mechanism of self-recognition to halt branch growth.

Type 2 (overgrowth). Here the growing branch completely overgrew the existing branch and continued normal distal growth. This type of intersection in BGS Yc 2708 occurred only when a growing branch met parts of a zooid proximal or distal of the opesia, and never on meeting the opesia itself. Ten per cent of observed intersections in this colony are of type 2.

Type 3 (pore location). The most interesting type of intersection entailed branch growth towards a lateral pore window of a zooid in an existing branch (Pl. 43, fig. 5). As the second commonest type of intersection (25 % of observations), it is unlikely to have been a fortuitous occurrence. Furthermore, the growing branch often bent considerably in order to locate the pore window of the zooid in the existing branch. Branches growing away from or parallel to the existing branch began to bend towards the pore window at a distance of about 0·21–0·23 mm from the window in well-preserved type 3 intersections in *H. laxata* colony BM(NH) D.42361. In one example (Pl. 43, fig. 6) from this colony, a growing branch evidently approached the right-hand side of an existing branch, overgrew the distal gymnocyst of one zooid, and then turned sharply towards the left lateral pore window of the next proximal zooid in the branch (i.e. a type 2 followed immediately by a type 3 intersection). Significantly, the right lateral pore window of this zooid, which could have been contacted first by the growing branch, is lacking. Examination of type 3 intersections with an optical microscope reveals the precise alignment of the growing branch and the pore window of the earlier branch which is visible through the slightly transparent gymnocyst. Abraded type 3 intersections also show this alignment and the lack of any skeletal barrier to potential soft tissue linkage between the two intersecting branches. Sometimes an opesiate kenozooid provides the connection between two branches and it may be difficult to decide whether this was formed by a type 3 intersection or by the fusion of separate buds originating from each of the two branches.

Type 4 (collision). Rarely (4 % of observations in BGS Yc 2708) the distal growing tips of two branches collided. The probability of such 'head-on' collisions was undoubtedly small because of the narrowness of *Herpetopora* branches. Collisions occurred more often between branches constructing the dilated distal parts of zooids than branches constructing the narrow proximal caudae of zooids. The two colliding zooids are typically distorted in shape although they may have fully formed opesiae suggesting that they were able to function as autozooids.

Intersection types 1–3 were all formed as the result of a growing branch meeting an existing branch. However, it is unclear what factors determined which of the three would occur. For example, there is no obvious correlation between type 3 intersections and the close proximity of a pore window; some growing branches abutted the sides of existing branches very close to open pore windows without contacting the window, whereas others had to deviate considerably in order to locate a pore window. Intuitively, angle of encounter would seem to be a possible determinant of intersection type, but again no clear correlation is apparent (cf. the effects of encounter angle on interspecific overgrowth between multiserial cheilostomes, see Jackson 1979*a*). Another factor may have been the condition of the zooids on the earlier branch; perhaps zooids with cuticles in poor condition, dead or without a polypide were overgrown rather than abutted, and pore linkage was dependent upon a healthy zooid in the earlier branch.

As noted above (p. 532), intersecting zooids normally (88 % of observations in BGS Yc 2708) abutted, overgrew, or linked with pore windows of zooids of the same or lower generation number. This is to be expected if zooid generation number closely reflects the succession of zooidal budding.

All seven of the anomalous intersections in colony BGS Yc 2708 were type 1 intersections, i.e. branch abutments.

Type 3 intersections entail deviation in branch growth towards lateral pore windows which is strongly suggestive of tropism. Ryland (1977) has reviewed tropisms in living bryozoans but makes no mention of any examples resembling the type 3 intersections of *Herpetopora*. Soft parts which could provide a tactile tropism are not known to protrude from the open pore windows of living cheilostomes, and the most probable source of the tropism would appear to be a chemical released from the pore window. The growing branch commenced its response to this inferred chemical when it reached a distance of about 0·2 mm from the pore window. By causing the fusion of parts of the same colony, type 3 intersections are a form of autosyndrome (Knight-Jones and Moyse 1961).

Little comparative information has been published on branch intersections in runner-like bryozoans. Personal observations of the Recent species *Pyripora catenularia* have shown that most intersections are of type 1 (abutment), but a few type 2 intersections (overgrowth) also occur. No examples have been seen of growth towards lateral pore windows in *P. catenularia*, but Marcus (1949) observed 'interzooecial bridges' apparently linking lateral pore windows of zooids in adjacent branches of *P. audens*. Colonies of the runner-like cyclostomes *Corynotrypa* and *Stomatopora* exhibit predominantly abutment intersections, with occasional overgrowths (Gardiner and Taylor 1982; Carthew 1987).

BUD FREQUENCY AND SUCCESS

In common with other branching, runner-like bryozoans, the number of growing branches in a *Herpetopora* colony increased more rapidly than the space available at the perimeter of the expanding colony. Each zooid normally had the potential to bud three daughter zooids. Therefore, if all potential buds were to have formed, the number of zooids in successive generations would have increased in proportion to the cube of the generation number, whereas the area of substratum available for encrustation increased in proportion roughly to the square of generation number. As a result, the frequency of branch intersections and/or the density of zooids must increase in the younger, outer parts of colonies. However, most branch intersections (types 1, 3, and 4) resulted in the elimination of one growing branch (and all of the daughter branches which it may have subsequently formed), thus reducing the problem of crowding. Failure of one or more of the three potential zooidal budding loci to form an autozooid is a second factor which reduced crowding in *Herpetopora* colonies. This failure appears to correlate with the proximity of other zooids. To assess the effects of such crowding, frequency of bud formation and success (i.e. full development of the bud into an autozooid) have been studied in colony BGS Yc 2708 in relation to the branch order and polymorph type of the parental zooid.

Conspicuous differences are seen in bud frequency according to branch order (text-fig. 8). Whereas zooids in first order branches gave rise to an average of 2·67 daughter autozooids, those in second order branches produced only 1·51 autozooids, third order branches 0·62 autozooids, and fourth order branches 0·50 autozooids. The decrease is proportionally greater for lateral buds than distal buds; very few zooids in third and fourth generation branches gave rise to lateral daughter autozooids. The pattern of diminishing bud success with increasing branch order may be explained by the geometry of the *Herpetopora* colony. The two first order branches grew in opposite directions across free substratum space and could bud zooids unimpeded by the presence of earlier autozooids. The second order branches grew parallel to one another and, although they also crossed free substratum space, their buds developed in the close proximity of adjacent second order branches (and the two first order branches). In contrast, third order branches converged during growth with other third order branches arising from adjacent second order parents. Therefore, a considerable degree of interference occurred between each third order branch and other branches of the same or lower orders. Similarly, fourth order branches were also greatly

number of zooids

30   71   102   32

mean number of daughter autozooids

3 -

2 -

1 -

1st   2nd   3rd   4th
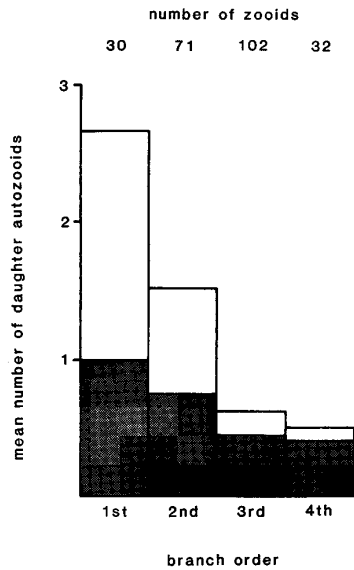
branch order

TEXT-FIG. 8. Frequency of autozooidal buds from parent zooids of different branch orders in *Herpetopora laxata* colony BGS Yc 2708. Stippled area represents distally budded autozooids, unstippled laterally budded autozooids.

disrupted by convergent growth with other branches, and zooids in these branches were prevented from budding the maximum possible number of daughter zooids.

There is a striking difference in the number of daughter buds produced by non-caudate and caudate autozooids. For lateral buds only, and summing the data across all zooid generations and branch orders, non-caudate autozooids produced an average of 0·43 buds, whereas caudate autozooids produced 1·54 buds. This difference may be related to the fact that the lateral budding loci of caudate autozooids are considerably more distant from their neighbours than the loci of the shorter non-caudate autozooids, and are therefore less prone to interference from other zooids.

ASTOGENETIC GRADIENTS

Gradients of changing zooid length have been quantified along branches of *H. laxata* colony BGS Yc 2708 for which the generation of each zooid (from the ancestrula) is known. These astogenetic gradients are more complex than is usual for bryozoans; individual branches exhibit a high degree of autonomy, and first and higher order branches demand separate treatment.

First order branches

The two first order branches are derived directly from the ancestrula and reveal astogenetic gradients of early colony development. Text-fig. 9 plots zooid length against generation along these branches. The astogenetic gradient of each branch has two phases: an initial phase (phase 1) of steadily increasing zooid length, separated by an abrupt increase in length from a later phase (phase 2) of fluctuating but generally increasing length. The slope of phase 1 is slightly steeper (0·19) in the distal branch than in the proximal branch (0·13), and the threshold between the phases occurs earlier in the distal branch (between zooid generations 5 and 6) than in the proximal branch (between generations 8 and 9). However, in both branches the zooid immediately preceding the threshold has a length of 1·23 mm. The first zooid after the threshold is 2·22 mm long in the distal

TEXT-FIG. 9. Astogenetic gradients of auto-
zooidal length in the two first order branches
of *Herpetopora laxata* colony BGS Yc 2708.
The changeover from non-caudate to caudate
autozooids occurs between generations 5 and
6 of the distal branch and generations 8 and 9
of the proximal branch. The abnormally long
zooid of generation 15 in the proximal branch
occurs in a damaged part of the colony and
may be spurious.
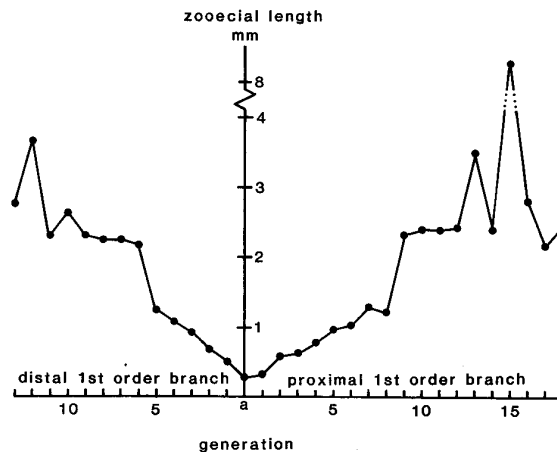
branch and 2·31 mm long in the proximal branch. Zooidal length generally increases with generation
in phase 2 but fluctuations are more pronounced than in phase 1.

The size–frequency distribution of autozooidal length in colonies of *H. laxata* (text-fig. 4)
demonstrated the existence of two types of autozooidal polymorph: non-caudate autozooids with
lengths less than 1·6 mm and caudate autozooids with lengths greater than 1·6 mm. The threshold
along the first order branches between phases 1 and 2 clearly corresponds to a changeover from
the budding of non-caudate to caudate autozooids.

Higher order branches

Thomas and Larwood (1960, p. 372) in their description of *H. laxata* remarked 'In any series of
zooecia successive caudae are commonly increasingly longer'. This tendency of zooids to become
progressively longer along each new branch is one of the most striking features of *H. laxata*
colonies (Pl. 42, fig. 2), and also occurs in *H. anglica*.

Measurements of zooidal lengths in BGS Yc 2708 allows an analysis of the exact pattern of
these astogenetic gradients in second and higher order branches. As there are no detectable
differences between branches of different order, the data for all branch orders have been pooled.
Branches usually start with a series of one to three non-caudate autozooids, followed by a series
of caudate autozooids. Reversion to the budding of non-caudate autozooids has never been
observed in colony BGS Yc 2708 or any other colony of *H. laxata*, but sometimes (7 % of branches
in Yc 2708, all second order) new branches start with caudate autozooids instead of non-caudate
autozooids. Pairwise comparison of zooidal length between non-caudate autozooids and their non-
caudate distal daughters revealed that in seventy-three (99 %) of cases the daughter zooid was
longer than its parent. A similar comparison for pairs of caudate autozooids revealed a more
variable pattern with ten (63 %) examples of the daughter being longer than the parent, one (6 %)
of it being the same size, and five (31 %) of it being shorter. Values of length for non-caudate and
caudate autozooids according to their position along the branch are given in Table 4. The most
proximal non-caudate autozooid averages 0·90 mm long, the next 1·10 mm, and the next 1·22 mm.
The most proximal caudate autozooid averages 2·26 mm long, the next 2·62 mm, and the next
3·45 mm. Trends of increasing length within non-caudate and caudate series are depicted using
size–frequency histograms (text-fig. 10). An astogenetic increase in length is very clear from the
size distributions of non-caudate autozooids, but for caudate autozooids the trend seems to result
from the occurrence of some unusually long autozooids in later generations which cause a rise in
mean value.

TABLE 4. Autozooidal length (in mm) in *Herpetopora laxata* colony BGS Yc 2708 according to position within branches. For non-caudate autozooids the value of position is relative to the branch origin, for caudate autozooids it is relative to the point of transition between astogenetic phases 1 and 2. Zooids from first order branches have been excluded.

	Non-caudate			Caudate		
	1	2	3	1	2	3
Mean	0·90	1·10	1·22	2·26	2·62	3·45
S.D.	0·150	0·159	0·131	0·266	0·844	1·897
C.V.	16·6	14·5	10·7	11·8	32·2	54·9
Range	0·75–1·47	0·90–1·44	1·08–1·44	1·74–3·09	1·89–4·83	2·31–5·64
Determinations	157	74	11	30	11	3
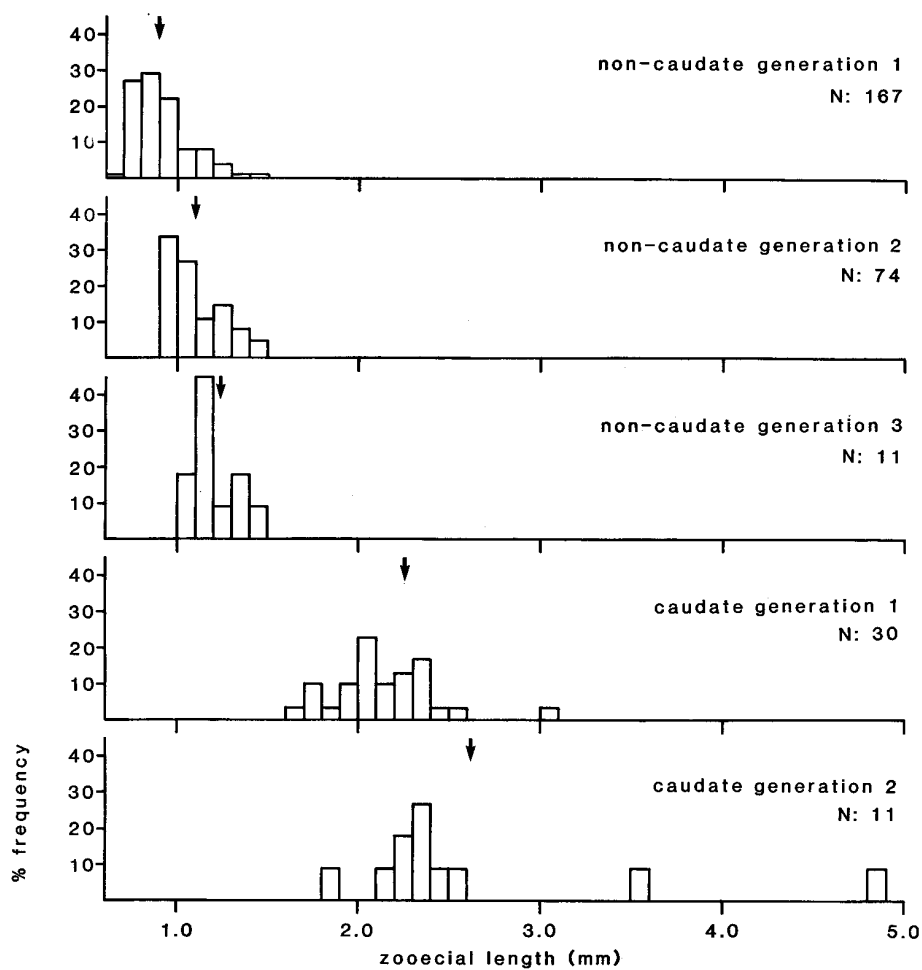
TEXT-FIG. 10. Size-frequency histograms showing astogenetic gradients of autozooidal length in non-caudate and caudate series of autozooids along branches of second and higher orders in *Herpetopora laxata* colony BGS Yc 2708. Arrows indicate mean length for each generation.

TEXT-FIG. 11. Between-branch astogenetic gradient of autozooid length in *Herpetopora laxata* colony BGS Yc 2708. The points represent the lengths of laterally budded daughter autozooids (i.e. first autozooids of second order branches) of parental autozooids located in the first order branches. Non-caudate autozooids are shown as dots, caudate autozooids as triangles. Two regression lines have been fitted to the data from the proximal first order branch; the line of higher slope includes all autozooids, whereas that of lower slope excludes caudate autozooids.
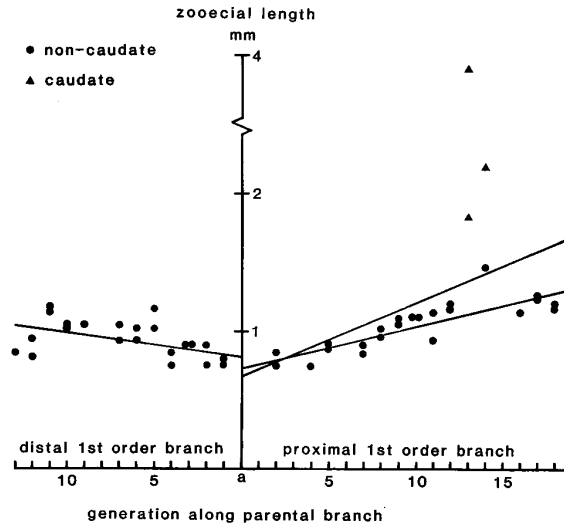

Between-branch gradients

The astogenetic gradients of individual branches have so far been treated separately as if each branch were entirely independent. However, the size of the first zooid of the second order branches bears a relationship to the position of the second order branches along the parental first order branch. This produces a between-branch astogenetic gradient (text-fig. 11). Length of the first zooid in the second order branches increases significantly in a distal direction away from the ancestrula, but values of the slope are low (0·017 along the distal first branch, and 0·053 along the proximal first order branch, but 0·031 if only non-caudate zooids are included in the linear regression). There is some indication of the slope levelling-out by about five zooid generations along the distal branch and ten along the proximal branch. Similar between-branch gradients are not obvious between branches of second and third, third and fourth orders, etc., though the comparatively short lengths of these higher order branches may hinder their detection.

Summary

Each separate branch in a colony of *H. laxata* exhibits an astogenetic gradient of zooidal length which consists of two phases: an early phase (phase 1) of non-caudate autozooids which steadily increase in length, followed by an abrupt rise in zooidal length into a later phase (phase 2) of caudate autozooids which also increase in mean length during branch growth. The threshold between phases 1 and 2 typically occurs after one to three generations of non-caudate autozooids have been budded, but a few branches omit phase 1 and bud caudate autozooids from the outset. Superimposed on these within-branch gradients there is a between-branch gradient, for first to second order branches at least, of increasing size of the first zooid in the branch depending on the position of origin of the branch distally along its parental branch.

For other species of *Herpetopora* the form of the astogenetic gradients may be different. Size-frequency distributions (text-fig. 4) of zooid length in *H. anglica* reveal only one autozooid polymorph and hence exclude the possibility of a two phase astogenetic gradient. However, zooid length does increase distally along branches. Quantification of astogenetic gradients in sixteen branches, each of three to six generations in length, from four colonies of *H. anglica* gave the following results: forty-five instances in which the distal daughter zooid was longer than its parent; two in which it was the same length; and six in which it was shorter. Text-fig. 12 shows the
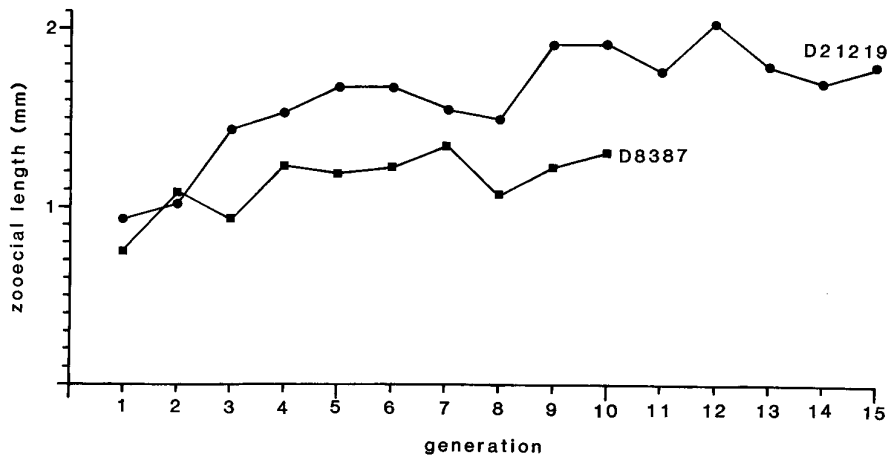
TEXT-FIG. 12. Astogenetic gradients of autozooidal length in long branches from two
BM(NH) colonies of *Herpetopora anglica.*

gradients in two exceptionally long branches of *H. anglica.* The overall trends seem to be of a
sustained increase in zooidal length throughout astogeny but with considerable 'noise' superimposed.

Astogenetic gradients of zooid size in most bryozoans are divisible into a primary zone of
astogenetic change, generally brief, which is succeeded by a typically extensive primary zone of
astogenetic repetition (Boardman and Cheetham 1973; Taylor and Furness 1978). Secondary zones
of astogenetic change and repetition occur in some taxa. However, application of this terminology
to *Herpetopora* is difficult as there is little evidence that a stable zooidal size, indicating a zone of
astogenetic repetition, is ever attained. Each branch (and the colony as a whole) may perhaps be
in perpetual astogenetic change.

REPARATIVE STRUCTURES

Use of the SEM to study colonies of *Herpetopora* reveals abundant evidence of damage and its
repair. Many specimens have zooids with extensively fractured skeletal walls. Sometimes all that
remains of the zooids are short, disconnected lengths of caudae. Distinguishing pre-mortem from
post-mortem damage is often difficult. Certain damage inflicted during the life of the colony can
be recognized in the various types of reparative buds which occur. The frequency of reparative
budding provides some indication of the extent of pre-mortem damage; however, this is a minimum
estimate because more subtle repairs may not be detectable, and unrepaired damage cannot be
distinguished from post-mortem damage.

Intramural reparative budding

Concentric, so-called regeneration rims are found within the opesiae of many *Herpetopora* zooids
(Pl. 43, figs. 5 and 6; Pl. 44, fig. 5). These rims may occur singly or in multiples of up to at least
three within each zooid. Use of the term 'regeneration' (Levinsen 1907 and most subsequent
authors) to describe these structures in cheilostomes is unsuitable as they are probably not related
to polypide regeneration, but are instead new zooids budded within the empty skeleton of an older
damaged zooid (Banta 1969). As such they are the daughter buds of zooids adjacent to the damaged
zooid and are presumed to have been budded through the open communication canals linking
zooids. Banta (1969) termed these structures 'reparative buds' but the additional term 'intramural'

is here introduced in order to avoid confusion with the other type of reparative bud described below.

Only the mural rims surrounding the opesia of intramural buds are normally visible, but fractured examples indicate that at least some of the cauda is also calcified. Obviously, the opesia of the intramural bud is smaller than that of the zooid within which it occurs. In examples of multiple intramural budding, the youngest (innermost) buds can have severely reduced opesial dimensions, and it seems possible that diminishing size restricted the number of times that intramural budding could occur within a host zooecium. However, even the smallest intramural buds may have closure plates bearing opercular impressions suggesting the autozooidal nature of the bud. Intramural buds with closure plates can be distinguished from normal zooids with closure plates by the occurrence of a narrow gap around the closure plate which separates it from the mural rim of the host zooecium. In all but one out of many observed examples the opercular scar is located distally relative to the host zooid, showing that the reparative bud had the same polarity as the host zooid. A single example of a reverse polarity intramural bud (cf. Jebram 1978, fig. 4 (2)) has been found (Pl. 45, fig. 1) in which the bud is presumed to have originated from the zooid distal to the host zooid. Occasionally (Pl. 44, fig. 3), intramural buds are opesiate kenozooids, including one example (Pl. 44, fig. 2) of a reverse polarity intramural kenozooid occupying a severely damaged autozooid. Intramural buds appear to be more frequent in non-caudate autozooids of *H. laxata* than in caudate autozooids. This may correlate with the observation that caudate autozooids more often have closure plates (p. 524), the presence of which would prohibit intramural budding without first resorbing the closure plate.

Related structures, recognized for the first time in *Herpetopora*, are lengths of cauda-like skeleton visible within autozooids (Pl. 45, figs. 4 and 5). These 'intramural caudae' generally parallel the long axis of the host zooid, but can be oblique, can deviate laterally, and may even bifurcate. Intramural caudae could represent the proximal parts of autozooids, or alternatively they may be a type of non-opesiate kenozooid. Similar structures ('tubules') have been described by Marcus (1938, 1955) from two genera of living cheilostomes. Both intramural caudae and normal intramural buds potentially may provide a linkage between living zooids through the empty skeletons of dead zooids, thus maintaining physiological continuity of the colony despite mortality of intervening zooids.

Extramural reparative budding

Following destruction of entire zooids, or their very severe damage, 'extramural buds' were sometimes formed occupying the same site on the substratum as the damaged zooid. In reality, there is a continuum between intramural buds and extramural buds via original zooids which have suffered increasing levels of damage. Two types of extramural bud can be distinguished: buds having the same polarity as the original zooid and buds of opposite polarity. Buds of the same polarity (Pl. 44, figs. 1 and 4) may have their long axes slightly oblique to the original zooid, and can include remnants of the original zooid within their walls. The reparative zooids originate from budding loci almost but not quite coincident with the loci which gave rise to the original zooid. Lengths of original and reparative zooids are approximately the same. It is likely that extramural reparative budding is of commoner occurrence than is obvious but that its recognition is precluded by total removal of the original zooid or complete overgrowth by the reparative zooid.

Complete removal of one or more zooids from the middle of branches, or branch fracturing with removal of a portion of a zooidal cauda, sometimes resulted in the budding of reparative zooids from the proximal fractured end of the branch. These zooids grew in a proximal direction relative to branch growth direction (and that of the zooid they replaced). The reparative zooid and the parental zooid from which it originates have opposite polarities, and form a bipolar zooid pair (*sensu* Taylor 1986a). Comparatively few examples of bipolar zooid pairs have been identified in *Herpetopora*, possibly because branches of severely damaged colonies in which they should be most frequent are so badly fragmented that relationships between zooids are obscure. An example (Pl. 45, figs. 2 and 3) involving a caudate distal zooid shows only a small remnant of the mural

rim of its proximal maternal zooid within which is situated the reparative bud of opposite polarity. Although the reparative bud appears to be short (? non-caudate autozooid), its exact point of origin is unclear, and its distally budded daughter is a caudate autozooid. A second, unfigured example of a bipolar pair in colony BM(NH) D.42364 involves a distal zooid and a reparative zooid both of which are of similar size and are non-caudate autozooids.

Very similar bipolar zooid pairs have been previously described (Taylor 1986a) in colonies of the Recent cheilostome *Pyripora catenularia*, and also in the Palaeozoic cyclostome *Corynotrypa* (see Taylor 1985; Carthew 1987).

SUMMARY OF COLONY DEVELOPMENT

The sequence of development in colonies of *Herpetopora* can be summarized as follows:

1. Following settlement and metamorphosis of the larva on a firm substratum (e.g. an *Inoceramus* shell), the resultant ancestrula budded two daughter zooids, one distally and the other proximally, thereby initiating the two first order colony branches which grew in opposite directions.

2. These periancestrular zooids and subsequently budded zooids were normally capable of each producing three daughter zooids, one distally and two laterally on either side of the zooid. Distal daughter zooids extended the branch of the parent, whereas lateral daughter zooids initiated new branches of an order one higher than that of the parent zooid. The angle between branches averaged about 80° but varied between 50° and 105°, with higher angles occurring especially during early colony development. This pattern of branching resulted in a colony with two conjugate sets of parallel branches of odd and even number orders. However, variation in branching angle, branch curvature, and substratum irregularities typically obscures these relationships in actual specimens of *Herpetopora* (e.g. Pl. 44, fig. 5).

3. The length of successive zooids along the two first order branches in *H. laxata* increased steadily for six to nine generations from the ancestrula. Thereafter, length rose abruptly and subsequently continued to increase but more erratically. Similar two-phase gradients of astogenetic increase in zooidal size also occurred in each new branch of *H. laxata* formed by lateral budding, but the later phase (phase 2) followed an early phase (phase 1) comprising only one to three generations of zooids and sometimes missing altogether. The zooids budded during the two phases were autozooidal polymorphs distinguished principally by their lengths, the 'caudate autozooids' of phase 2 having longer caudae than the 'non-caudate autozooids' of phase 1. Caudate autozooids more often developed closure plates occluding their opesiae than did non-caudate autozooids. No autozooidal polymorphism is detectable in *H. anglica*, although astogenetic gradients of increasing zooidal length also occur along each branch.


EXPLANATION OF PLATE 45

Figs. 1 and 6. *Herpetopora anglica* Lang, back-scattered SEM images. 1, BM(NH) D.4189, reverse polarity intramural autozooid (arrowed) with a closure plate bearing an opercular scar, Coniacian or Santonian, Chatham, Kent, ×27. 6, BM(NH) D.29840, autozooids with open opesiae and opesiae occluded by closure plates, Turonian (*planus* Zone), Bridgewick Pit, Malling, Sussex, ×37.

Figs. 2–5. *H. laxata* (d'Orbigny), back-scattered SEM. 2–4, BM(NH) D.42375, Campanian (*mucronata* Zone), Webster's Pit, Norwich, Norfolk. 2, bipolar zooid pair involving an original caudate autozooid (left) which has an intramural bud with closure plate, and a reparative autozooid (right), ×23. 3, detail of the reparative autozooid of the bipolar pair showing the remains of the zooid which has been repaired, various segments of caudae external to and a possible oblique intramural kenozooid within the reparative zooid, ×87. 4, damaged autozooid with an apparently bifurcating segment of cauda within, ×61. 5, BGS Yc 2708, segment of cauda passing through a heavily worn autozooid, Campanian (*quadrata* Zone), Compton, Hampshire, ×72.
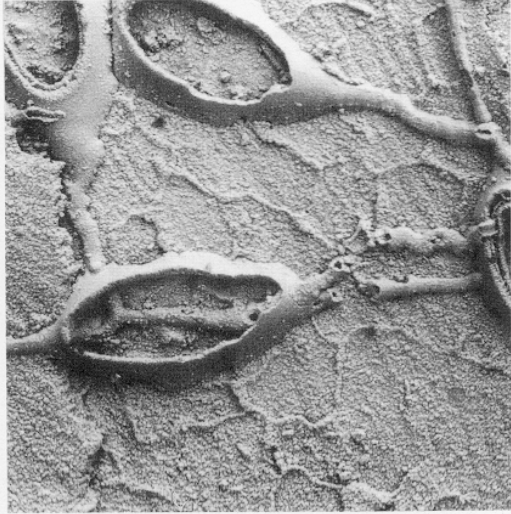
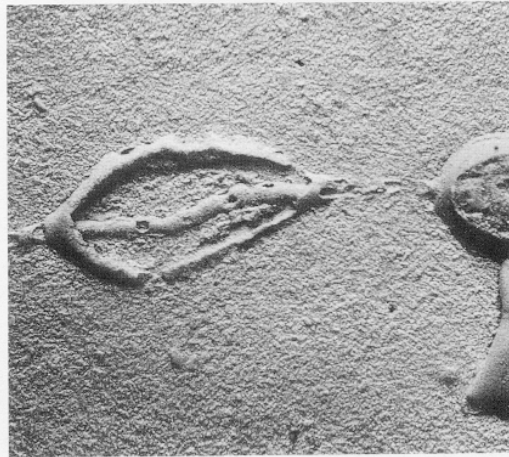PLATE 45
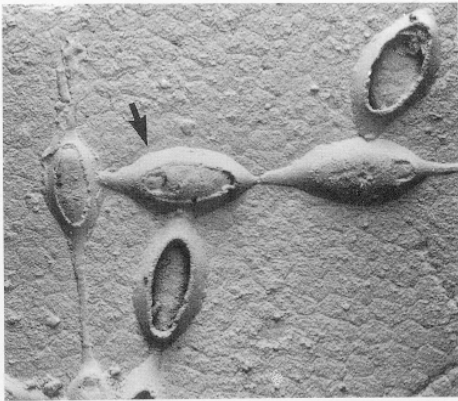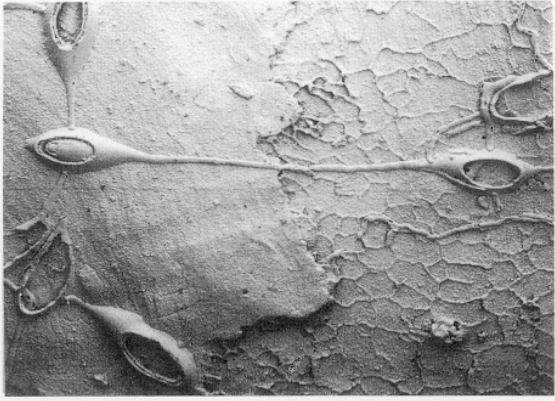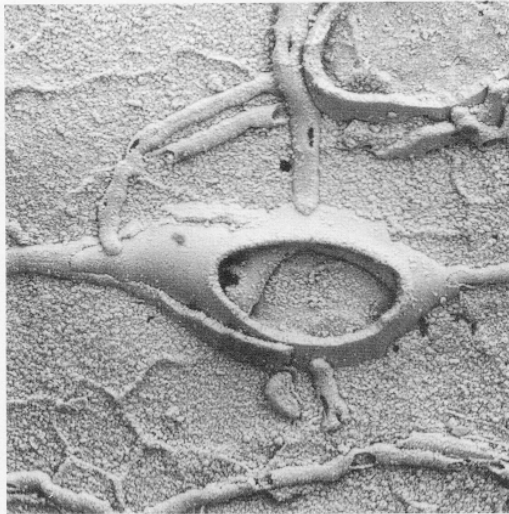
4. Lateral buds were possibly slightly retarded in their development relative to distal buds and often were not produced at all. Zooids located in branches of lower orders were more likely to bud all three potential daughter zooids, and caudate autozooids produced more buds on average than non-caudate autozooids in *H. laxata*. Caudal buds sometimes arose adventitiously from the caudae of zooids, and more rarely proximolateral buds were formed close to the opesiae of parental zooids.

5. Branches often intersected during colony growth. Most frequently the growing branch abutted the existing branch and ceased growth, but sometimes it overgrew the cauda of a zooid on the existing branch. Growing branches could also apparently respond to the presence of an open pore window of a nearby zooid and grow into it, probably chemotropically. Rarely, two growing branches collided and their terminal zooids became distorted.

6. Apart from autozooids, kenozooids were occasionally budded. These were either produced as lateral or distal buds, opesiate (but lacking an operculum) and with a subtriangular distal end, or produced as distal buds in long stolon-like branches, apparently non-opesiate with very long caudae and a slightly dilated distal end. A third type of kenozooid is the short portion of cauda remaining in a growing branch after abutment against the side of an existing branch.

7. Zooids and branches were often damaged during the lifetime of the colony and various reparative structures were formed. Particularly common was the intramural budding of zooids (usually autozooids) within the empty zooecia of dead autozooids. Intramural buds normally had the same polarity as their hosts and may have been derived as buds from the proximal neighbour of the host zooid. However, they occasionally had the opposite polarity. Severely damaged or entirely obliterated zooids were sometimes replaced by extramural reparative buds either of the same polarity or of opposite polarity to the zooids they replaced.

8. Partial colony mortality resulting from damage may often have caused the fission of colonies into spatially separated ramets (cf. Taylor 1985). However, through reparative budding and the ability of branches to grow towards open pore windows, colonies had the potential to reunite ramets.

DISCUSSION

Astogenetic gradients and their origin

Herpetopora, especially *H. laxata*, has a more complex pattern of astogenetic gradients than is usual in a runner-like bryozoan. Typically (e.g. *Stomatopora*, see Taylor and Furness 1978), a primary zone of astogenetic change, during which there is a progressive increase in size of the first few generations of zooids, is followed by a primary zone of astogenetic repetition when zooid size is astogenetically constant (though ontogenetic and microenvironmental variations may occur). All zooids budded at the same time, regardless of which branch they belong to and their spatial location within that branch, are morphologically similar in the zone of astogenetic repetition. Therefore, the astogenetic gradient is colony-wide. *P. catenularia* and *Pyriporopsis portlandensis* also have a primary zone of astogenetic change followed by a primary zone of astogenetic repetition (Taylor 1986a). However, each new branch formed by lateral budding in these pyriporids initiates a brief secondary zone of astogenetic change through which zooid size increases (e.g. Pohowsky 1973). This is followed by a series of zooids, similar in size to those in the primary zone of astogenetic repetition, which form a secondary zone of astogenetic repetition (text-fig. 13). At any one time during colony growth, therefore, zooids may be developing which belong to primary or secondary zones of change or repetition. Astogenetic gradients within the colony are subcolony-wide, each branch in the colony constituting a subcolony. In *Herpetopora*, similar subcolony-wide astogenetic gradients occur (text-fig. 13) but there is little evidence that zones of astogenetic repetition are ever formed in either *H. anglica* or *H. laxata*. Branches of *H. anglica* exhibit a single phase of generally increasing zooidal length, whereas those of *H. laxata* have a two-phase gradient beginning with a series of progressively lengthening non-caudate autozooids (astogenetic phase 1)
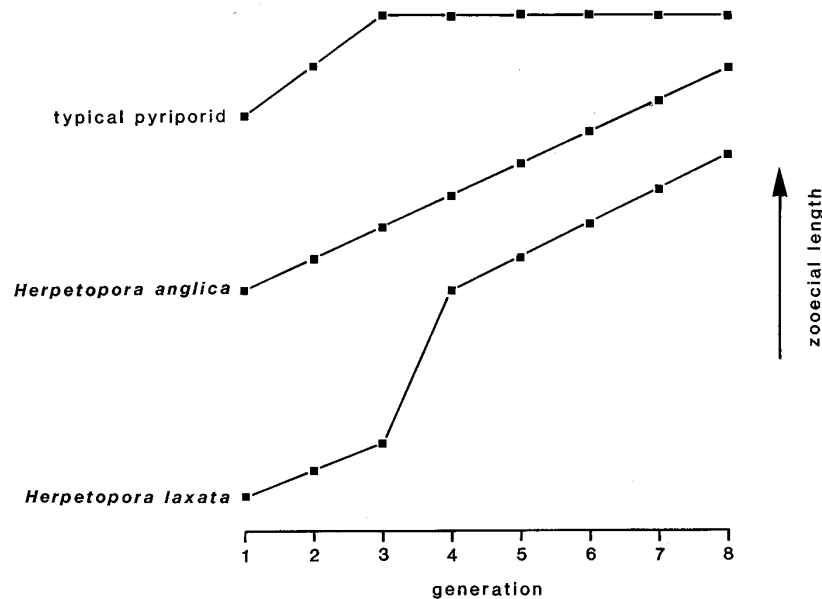
TEXT-FIG. 13. Simplified astogenetic gradients present in branches of typical pyriporid cheilostomes, *Herpetopora anglica*, and *H. laxata*.

which is followed by a series of caudate autozooids (phase 2) whose mean length increases with astogeny.

The physiological basis of astogenetic gradients is completely unknown in living bryozoans (e.g. Jebram 1978), and has formed a subject for speculation in fossil bryozoans. Two principal theories have been proposed:

1. In the trophic theory (Dzik 1975, 1981) the astogenetic gradient is controlled simply by the food resources available to the bud at the time of its growth. A juvenile colony has relatively few zooids and little energy to supply the growing buds and it is assumed that the zooids formed will consequently be small.

2. In the morphogenetic theory (Anstey *et al.* 1976) the astogenetic gradient is the result of diffusion through the colony or subcolony of a morphogenetic substance which determines zooid size. A similar theory has been applied to graptolites (see Urbanek 1973) in which the siculozooid is the presumed source of the morphogen. The equivalent of the siculozooid in bryozoans is the ancestrula, and it or, in the case of subcolony-based gradients in trepostomes, the monarchic zooid, is thought to be the source of the morphogen (Anstey *et al.* 1976; Podell and Anstey 1979). Autoradiographic evidence (Best and Thorpe 1985) of translocation of labelled carbon-14 towards the growing edge in living colonies of the cheilostome *Membranipora* is important in demonstrating the plausibility of morphogenetic control in bryozoans, although both the range of substances translocated and the mechanism of their translocation remain unknown in living bryozoans.

The trophic theory cannot be applied to the subcolony-based astogenetic gradients of *Herpetopora*, unless the unlikely assumption is made that new branches depend for their growth entirely on their own food resources. A morphogenetic theory is more easily applicable to *Herpetopora*. However, there is an alternative to the diffusion theory in which zooid size (and other characteristics) is

determined by the zooid's spatial position along a branch; zooid size may have been determined by the age of the branch at the time of zooid formation, older branches producing larger zooids. This alternative can be discounted in *Herpetopora* because extramural reparative buds (p. 541) are of a similar size to the zooids they replaced, despite having been formed later in branch growth. The source of the morphogens determining zooid size in each branch of a colony of *Herpetopora* was most likely to have been the parental zooid of the branch, through which the branch is connected via a canal-like interzooidal pore. In living cheilostomes strands of mesenchymal cells form the funicular system (see Bobin 1977) which links with the interzooidal pores and is thought to function as a system for the colonial transportation of metabolites (see Ryland 1979).

Colonial integration

Colonial organisms can be arranged in hypothetical series from poorly integrated to highly integrated. In poorly integrated colonies, the colony behaves in the manner of a simple aggregation of clonal solitary individuals, whereas in highly integrated colonies it behaves as a 'superindividual' whose constituent zooids can have no independent existence. Although this is a useful conceptual way of viewing colonial animals, integration is a rather nebulous concept; it is impossible to quantify integration in a consistent way because the various morphological features (e.g. presence of polymorphism, extrazooidal tissue, astogenetic variation, etc.) which have been used for estimating integration in the absence of any firm physiological data, cannot be combined into a single measure of integration along a linear scale. Integrational states for particular morphological parameters can, however, be estimated, and may potentially (as in *Herpetopora*) yield conflicting results.

The runner-like colony form of *Herpetopora* is poorly integrated along the spectrum of colony forms found in bryozoans (see Boardman and Cheetham 1973; Jackson 1979*b*). The absence of extrazooidal parts, of shared interior skeletal walls, or marked ontogenetic changes in zooid morphology, are also features of a poorly integrated bryozoan. Set against these are indicators of high integration in the several types of polymorphs and their often predictable positions, the subcolonial organization into branches with autonomous astogenetic gradients, the apparent chemotropic growth of branches towards open lateral pore windows, and the abundant reparative structures.

The last two features are particularly noteworthy. *Herpetopora* colonies were clearly able to survive substantial damage and mortality of zooids which often led to fission of the colony into several spatially separated ramets (*sensu* Harper 1977), as in the Palaeozoic cyclostome *Corynotrypa* (Taylor 1985). However, repair of damage, and the ability to grow towards pore windows, presumably by chemotropism, gave the potential for re-establishing communication between ramets, and multiplying communications within ramets. What functional value might there have been in this 'replumbing'? *Herpetopora* colonies do not seem to have possessed active heterozooids such as avicularia whose energy requirements must presumably be supplied by nutrients gained from autozooids. However, it was probably advantageous for previously disconnected parts of the colony to be re-linked in order that all feeding zooids could contribute energy to the formation of new buds in growing regions of the colony.

Functional morphology

Colony growth pattern in runner-like bryozoans determines how the zooids, and most importantly their feeding tentacle crowns, are distributed over the area of the substratum. In *Herpetopora*, astogenetic gradients of increasing zooid length along each branch meant that tentacle crowns of successive zooids were progressively more distantly spaced along the branch, and new branches were spaced at increasing intervals. The density of tentacle crowns would therefore have diminished outwards from the colony origin. Such a distribution is functionally advantageous if the colony origin is located on the optimal area of the substratum. As location of the colony origin depends upon the settlement behaviour of the larva, a highly selective pattern of larval settlement might be predicted in *H. laxata*. This prediction is not currently testable, however, in view of the scarcity of colonies preserving their origins.

Conversely, colonies with runner-like growth (equivalent to the 'guerilla' growth strategy identified in plants, Lovett-Doust 1981) have a high probability of locating spatial refuges where chances of mortality are diminished (Buss 1979). This is because these straggly colonies spread rapidly from the point of colony origin per zooid budded in comparison with compact, sheet-like colonies. Therefore, *Herpetopora* colonies should have been good at locating refuges on a patchy substratum. One important source of substratum patchiness may have been caused by the activities of grazers and other predators. Abundant evidence of colony damage often followed by repair supports the notion that predators had a significant impact, abiotic damage seeming a less likely option in the relatively tranquil habitats colonized by *Herpetopora*. While some parts of colonies may have been destroyed or severely damaged by predators, there is a high probability that others would have survived relatively unscathed because of the wide 'dispersal' of zooids across the substratum.

The refuge-locating abilities of colonies would have been further enhanced if, as seems possible, branches with caudate zooids had high rates of linear growth. Coates and Jackson (1985) predicted that uniserial colonies should have relatively elongate zooids to maximize their ability to locate spatial refuges, and were able to support this prediction with data comparing zooid elongation in uniserial and multiserial encrusting bryozoans. Caudate zooids of *Herpetopora* have very narrow, tube-like caudae which may have grown rapidly. If so, the rates of linear extension of distal parts of branches would have been great, resulting in enhanced ability to explore areas of substratum distant from the colony origin.

From the point of view of colony feeding, the disorderly arrangement of tentacle crowns in colonies of *Herpetopora* was probably of little importance. The runner-like colony form is normally associated with colonies whose zooids feed autonomously (Winston 1978) rather than co-operating in the formation of colony-wide or subcolony-wide feeding currents (e.g. Cook 1977). Furthermore, calculations suggest that overlap of tentacle crowns may not have occurred even between closely spaced zooids at branch intersections. There is a good correlation between the width of the zooid orifice and the diameter of the tentacle crown in cheilostomes (Winston 1981). Orifice width in *Herpetopora* can be measured from zooids with closure plates bearing impressions of the operculum. Operculum (and orifice) width is about 0·07 mm in *H. laxata*, giving an estimated tentacle crown diameter of 0·18 mm using the regression data of Winston. As this value is less than the width of the zooid (0·24–0·45 mm, *fide* Thomas and Larwood 1960), the extremely small tentacle crowns of *Herpetopora* probably did not even overlap the edges of the zooids. Boardman *et al.* (1983, fig. 4) give a reconstruction of a primitive cheilostome zooid of similar skeletal morphology to *Herpetopora* showing the very small size of the tentacle crown.

There is considerable scope for further work on the functional morphology of *Herpetopora* and its relationship to the ecology of the substrata encrusted. Using the branching parameters already determined from fossil colonies, it would be particularly instructive to simulate model colonies (cf. Bell 1986) for the purpose of ascertaining:

a, the exact distribution of zooid tentacle crowns across the substratum;

b, the rate of change of zooid numbers during colony growth (assuming either constant linear growth rate or constant budding rate);

c, the effects of obstacles and areas of partial mortality on growth pattern and ultimate size of the colony.

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P. D. TAYLOR

Department of Palaeontology
British Museum (Natural History)
London SW7 5BD