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Observations on living colonies of *Retiflustra* spp. (Cheilostomata : Anasca) from the central Queensland shelf, Australia

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Abstract : Two species of the sand-dwelling anascan bryozoan *Retiflustra* co-occurred on the central Great Barrier Reef shelf. *R. schoenaui,* reported for the first time from Australia, was found at the shallower sites (6-28 metres depth). *R. cornea* occurred along most of a transect (12.5-43 metres depth) across the central shelf, but most regularly at sites over 22 metres deep. *In situ* observations showed that, contrary to previous inferences, the conical colony was oriented apex upwards, supported 5-10 mm above the sediment by cuticular rootlets. The lophophores extended downwards toward the sediment and outwards into fenestrae which occured regularly on the spiral layers of the colony. The latero-frontal cilia on tentacles of many extended lophophores created a strong upwards current through the fenestrae. Limited gut content analyses suggested that food is phytoplankton (diatoms, naked and armoured phytoflagellates). The cuticular rootlets appeared early in colony development. Settlement and growth of the colony may not require hard substratum.

Résumé : Deux espèces de Bryozoaires Anasca du genre *Retiflustra* vivant sur substrat meuble coexistent sur le précontinent de la partie centrale de la Grande Barrière. *R. schoenaui,* signalée pour la première fois d'Australie, a été récoltée dans les stations les moins profondes (6-28 mètres). *R. comea* est présente le long de la plus grande partie d'une radiale de 12.5 à 43 mètres de profondeur sur le précontinent, mais est plus fréquemment récoltée dans les stations de profondeur supérieure à 22 mètres. Les observations *in situ* ont montré que, contrairement aux prévisions, la colonie conique était orientée l'apex vers le haut, surélevée de 5 à 10 mm au-dessus du sédiment par les racines cuticulaires. Les lophophores s'épanouissent vers le bas, en direction du sédiment, et vers l'extérieur par des fenêtres qui existent à intervalles réguliers sur les lames spiralées de la colonie. Les cils latéro-frontaux tentaculaires des nombreux lophophores épanouis créent un fort courant ascendant en direction des fenêtres. Une analyse préliminaire des contenus digestifs indique que la nourriture de ces Bryozoaires est constituée par du phytoplankton (diatomées, phytoflagellés nus et armés). Les racines cuticulaires apparaissent à un stade précoce du développement de la colonie. La fixation et la croissance de la colonie ne semblent pas nécessiter la présence de substrat solide.

INTRODUCTION

McKinney (1980) and McKinney and Raup (1982) have considered the mechanics and functional significance of spiral growth in erect bryozoans using observations on both living and fossil species, as well as computer simulations. As noted by McKinney and Raup, simulations allow an interpretation of the range of colony morphologies. However interpretation of function is often hampered by lack of observations on the bryozoan colonies themselves. In this note, one of the examples used by McKinney is discussed, the west Indo-Pacific sand-dwelling bryozoan *Retiflustra* (Cheilostomata : Anasca), based on the first observations of living material.

MATERIALS AND METHODS

Colonies of *Retiflustra cornea* (Busk, 1852) and *R. schoenaui* (Levinsen, 1909) were collected during an extensive survey of the epibenthos on the central Queensland shelf (Birtles & Arnold, 1983 ; Arnold, Birtles and Babcock, in prep). Distribution of the species and observations on morphology of the colony were based on preserved specimens.

Living specimens of *R. schoenaui* were collected from 18 and 20 metres depth in Pioneer Bay, Orpheus Island, Qld. The bottom at these collection sites was muddy sand, with scattered low, conical mounds (? of callianassid crustaceans) and numerous burrows, 1-2 cm in diameter, flush with the surface. The 20 m site had small stands of the sea grass *Halophila tricostata* (Greenway, 1979). Associated fauna included the pedunculate haplosclerid sponge *Cladocroce* sp, cnidarians *Morchellana* and *Scytalium* spp, gastropod *Strombus vittatus* (Linné, 1758), echinoderms *Astropecten* sp, *Heterometra crenulata* (Lamarck, 1816) and *Comatula Solaris* (P.H. Carpenter, 1882), ascidians *Herdmania momus* (Savigny, 1816) and *Cnemidocarpa stolonifera* (Herdman, 1899), and the burrowing gobioid fish *Oxymetopon* sp.

Specimens were observed immediately after collection at the Orpheus Island Marine Station ; behaviour changed after only a few hours, as indicated by Winston (1978), and unless otherwise noted, observations on behaviour refer to these freshly collected specimens. Additional observations were made, based on videotapes of specimens collected at Pioneer Bay and returned to the aquarium system at James Cook University.

RESULTS

DISTRIBUTION

The distribution of the two species overlapped (Appendix 1), although on the central shelf, *R. schoenaui* was most commonly recorded at the nearshore shallow sites (Cleveland Bay, 6-7 to 19 m depth ; Pioneer Bay, 18-20 m), and one offshore site (28-28.5 m). *R. cornea* was distributed throughout most of the transect (12.5-43 m), but most regularly at the offshore sites (greater than 22 m).

MORPHOLOGY OF COLONY

The fully-developed colony of *Retiflustra cornea* and *R. schoenaui* consists of unilaminate, fenestrate sheets of lightly calcified zooids, growing out from a tight spiral around an open vertical axis (see McKinney, 1980 : Fig. 16 a). The sheets sloped obliquely downward from the central axis, with an apical angle of 110-120 degrees (in *R. cornea)* ; the growing edge was twisted further from the frontal surface of the sheets (see Harmer, 1926 : Fig. 8 ; McKinney, 1980 : Fig. 16 b) and generated the spiral from which the laminae arose by lateral outgrowth. Seven bifurcating branches were given off from each spiral. Each branch had four to six rows of zooids and alternatively bifurcated and anastomosed, creating open spaces or fenestrae within the unilaminate sheet. From the proximal angle of most fenestrae a cuticular rootlet arose, breaking up at its tip into fine tendrils to which sediment was attached. The successive sheets were of increasingly reduced diameter, forming a series of three to up to six nested cones, the abapical margins of which were flush with one another.

The smallest colony collected (species indeterminable) consisted of 51 zooids (Fig. 1). The ancestrula gave rise to a primary row of three autozooids. The next row contained three autozooids, and on either side of the row, a kenozoid, one with an intact cuticular rootlet. Successive rows of zooids created a fan-shaped colony which by the fifth row of zooids had bifurcated. At the axilla of this bifurcation was a developing cuticular rootlet. Each branch consisted of two to three rows of autozooids ; the left branch (as seen from the apex) had an incipient bifurcation but no rootlet.

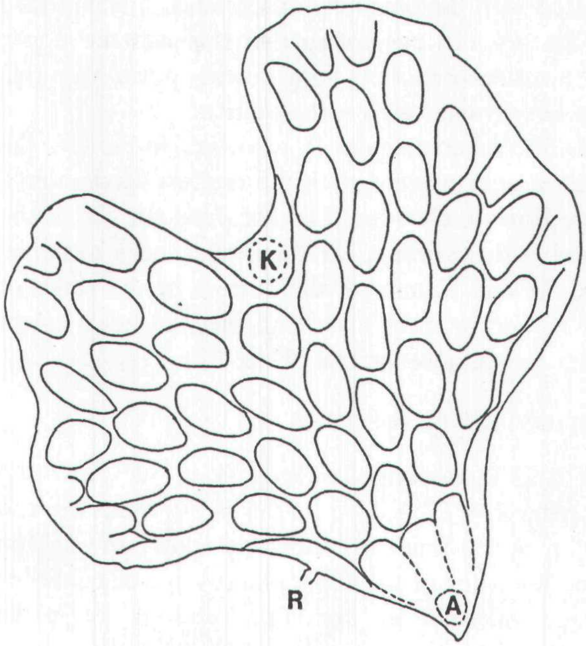


Fig. 1 - *Retiflustra* sp. Young colony, showing the ancestrula (A), lateral cuticular rootlet (R) and the axillary kenozooid with cuticular rootlet (K).

In a second, more fully-developed colony the apical region was damaged, but there was a terminal, apparently ancestrular rootlet and on either side of the colony a pair of cuticular rootlets arising at the level of the second and third autozooid rows and the fourth and fifth autozooid rows respectively.

In intact, fully-developed colonies, the ancestrula was still visible at the apex, but the apical and lateral rootlets had disappeared and only the fenestral rootlets remained. In none of the colonies examined was there any foreign material attached to the apparent ancestrula.

Symmetry of the colonies from one site could be variable ; some specimens showing a left-handed spiral (as seen from the apex, Fig. 2 b), others a right-handed spiral, while some showed bilateral symmetry, with the right and left branches rejoining in midline of the colony (Fig. 2 c). The primary determinant of symmetry appeared to be the angle of the growing edge of right and left branches : the branch with the greater angle continued to spiral around the axis, while growth of the other branch became restricted to an outward infilling of the sheet. The symmetry could even change within a colony, with one example in which the first two laminae were symmetrical, while the third lamina was a left-handed spiral.

ORIENTATION OF THE COLONY IN LIFE (PLATE 1)

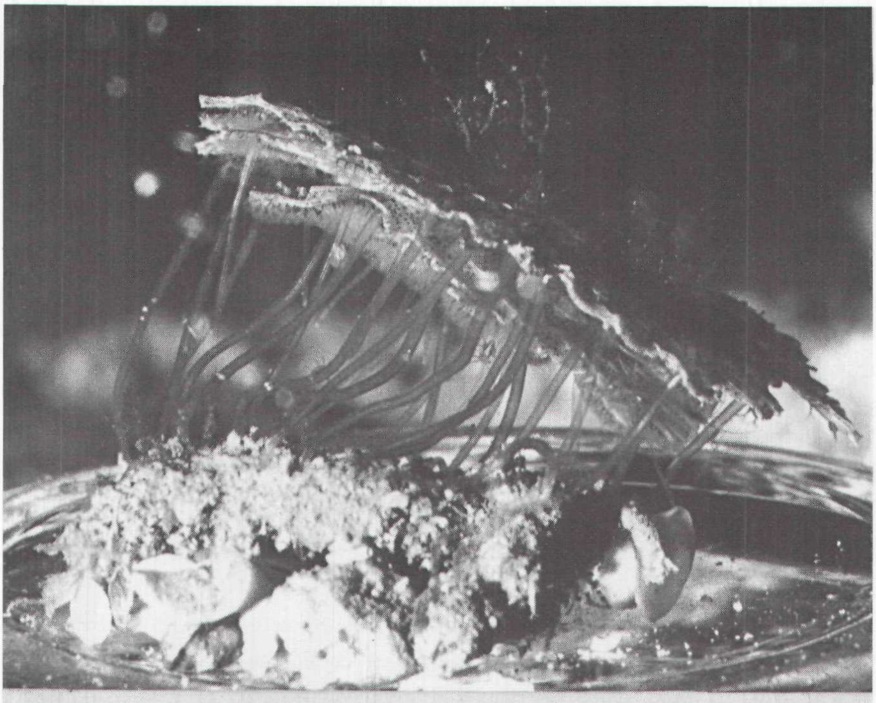
Specimens of *R. cornea* collected by the epibenthic sledge frequently had the abfrontal surface coated with diatoms, phytoflagellates, filamentous algae, foraminifera, serpulid polychaetes, etc. suggesting that this was the uppermost surface, subject to fouling. The cuticular rootlets hung directly down from the colony ; their tips and tendrils were heavily encrusted with sediment.

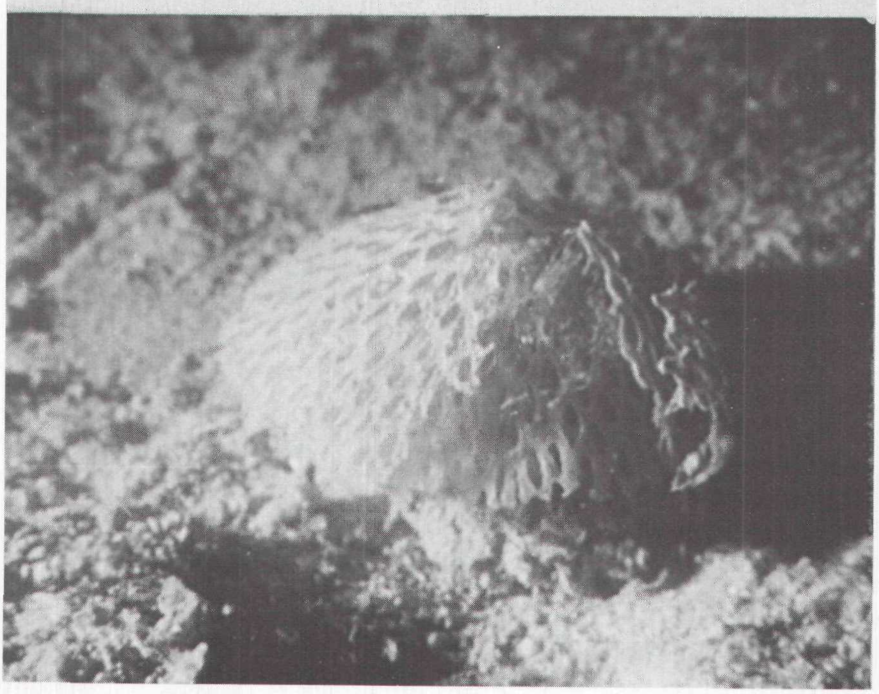
In situ observations of nine colonies of *R. schoenaui* in Pioneer Bay showed that all were oriented shallow apex upward, with the rootlets descending to the bottom, in which the tips were firmly embedded. The abfrontal surface of the colonies was always heavily covered with sediment. In three specimens examined *in situ*, the colony was supported 5,8 and 10 mm off the bottom by the series of rootlets. Diving observations of *R. cornea* have also confirmed an apex upward orientation (A. Birtles, pers. comm. ; pers. observations ; Plate 1 b).

MORPHOLOGY AND BEHAVIOUR OF POLYPIDES

R. schoenaui had 21-23 lophophore tentacles ($\bar{x}$ = 22.3, s.d. = 0.65, n = 11) with lophophore diameter $\bar{x}$ = 1.2 (s.d. = 0.12, n = 30) times the zooecium length, $\bar{x}$ = 2.6 (s.d. = 0.40, n = 30) times the zooecium width, and an approximate diameter of 0.7-0.8 mm. Tentacles of the lophophore were of equal length and bent inward, then strongly outward at the tip, resulting in a -bell-shaped or

PLATE I (1) *Retiflustra schoenaui*. Aquarium photograph of specimen collected in Pioneer Bay, Orpheus Island (18° 36' S, 146° 29' E), at about 20 m depth. Note shallow apex, with flattened form of zoarium, curicular rootlets supporting the colony above the substratum and downward orientation of lophophores. (2) *Retiflustra cornea*. *In situ* photograph at 18° 38' S, 147° 13' E, near Helix Reef, at 52 m water depth. Note conical form of zoarium, apex upward orientation, and elevation of the colony above the soft sediment. Photos : R.A. Birtles.





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campanulate lophophore funnel. The extroverted tentacle sheath was long and, when fully expanded, up to 1.3 times the length of the lophophore funnel. The digestive tract down to the pyloric whirl could be seen within the extroverted tentacle sheath at maximum expansion. The mouth was round, and set on a low cone at the base of the lophophore tentacles.

Lophophores of central zooid rows on the branches were oriented normal to the surface, but those arising from zooids bordering the fenestrae declined about 30-40 degrees from the vertical. The lophophore could be pivoted a full 360 degrees on the extroverted tentacle sheath and deflexed to almost a right angle to it. The extroverted tentacle sheath could be deflexed almost parallel to the zooecial surface, thus the mouth of the lophophore could be oriented directly upwards or downwards. The most common orientation, however, was the extroverted tentacle sheath and lophophore funnel in line and directed downwards at an angle, with occasional deflexions of the lophophore along the proximal-distal axis of the zooecium.

The length of the extended extroverted tentacle sheath, and its motility, allowed lophophores from the two zooid rows adjacent fenestrae to extend into the opening. Each side of the fenestrae was bordered by five to eight zooids, which in freshly collected specimens all had extended lophophores. The tentacles of adjacent lophophores overlapped and a single lophophore could extend from one half to two-thirds the width of a fenestra. Thus usually the whole fenestra was filled by extended lophophores. The concerted action of the latero-frontal cilia of the lophophore tentacles created a strong current upwards through the fenestra, and particles in the water could be seen to accelerate around a tentacle, exit at right angles to its long axis and be jetted upwards through the fenestra. Dye placed under the colony, however, was not seen to be carried upwards.

Tentacle flicking behaviour (especially fast flicking, see Winston, 1978) was frequent ($x = 0.48$ flicks/sec, s.d. 0.35). This figure is based on analysis of 7 bouts of 19-154 seconds recorded on videotape of colonies kept in an aquarium for four days. It probably is a minimum estimate as colonies held in aquaria for several days had fewer lophophores expanded and these quickly retracted in response to any vibration. Usually only the distal third of the tentacle was deflexed, but occasionally the whole tentacle would be brought rapidly inwards toward the mouth. On one occasion this clearly brought a particle on the tentacle in toward the mouth but it wasn't seen if this particle was subsequently rejected. Especially with colonies held in the aquarium for several days, protrusion of the lophophore was followed by rapid alternate expansion and contraction of the lophophore funnel, and frequent tentacle flicking.

Avicularia of *R. schoenaui* were usually protruding at almost right angles to the edge of the fenestrae, and were either held immobile or slowly moved through about a five degree angle.

FOOD

Nine polypides from two colonies held in the aquarium at Orpheus Island for four days were found to have armoured and naked phytoflagellates in the stomach. Several polypides had diatom frustules in the stomach as well as unidentified particulate matter. However none contained sediment or large particulate matter which would be expected if the zooids were nonselectively processing sediment as detritivores.

DISCUSSION

FAUNISTIC

The specimens from Pioneer Bay and nearshore stations off Townsville corresponded well to the description of *R. schoenaui* in Harmer (1926), especially in the presence of avicularia and vestigial ovicells. *R. schoenaui* has been reported from Singapore (Harmer, 1926; Marcus, 1921; Robertson, 1921), "China Sea", lat. 26°30'N, long. 121° 10' E (Levinsen, 1909), Sunda Strait (Mortensen, 1922*, in Harmer, 1926), Madura and Makassar Straits, Java Sea (Harmer, 1926) but this is the first report of the species from Australia. *Retiflustra cornea* has been frequently reported from Queensland, at least as far south as Cumberland Island (Busk, 1852, 1884; Hastings, 1932; Haswell, 1880; Livingstone, 1927); Torres Strait (Harmer, 1926 ; Kirkpatrick, 1890 ; Meissner, 1902) ; Darwin, Northern Territory (Levinsen, 1909), Admiralty Gulf, northwestern Australia (Harmer, 1926), west of northern New Guinea (Harmer, 1926) and off the Aru Islands (Harmer, 1926 ; Marcus, 1922).

Records of *"Carbasea cribiformis"* (= *R. cornea*, *fide* Harmer, 1926) from Taiwan (Kirchenpauer, 1869*, in Harmer, 1926), east of Sri Lanka, off the northeast Indian coast, and north of the Andaman Islands (Thornely, 1907) contain insufficient information to determine the species of *Retiflustra* treated. Further, the depths of collection for *"Carbasea cribiformis"* given by Thornely in the species account do not correspond to the depths of the stations at which the specimens were supposed to be collected, as given in the introduction to her paper.

Records from the literature summarized by Harmer indicate an overlap in depth ranges, with *R. schoenaui* reported from 15-82 m and *R. cornea* from 15-95 m. On the central Queensland shelf, *R. schoenaui* appeared to be more frequent at the shallow sites (6-19 m, one record from 28 m). *R. cornea* extended to the outermost sites along the transect (to 43 m), and has been collected even deeper at sites away from the transects (see caption, Plate I).

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* not seen

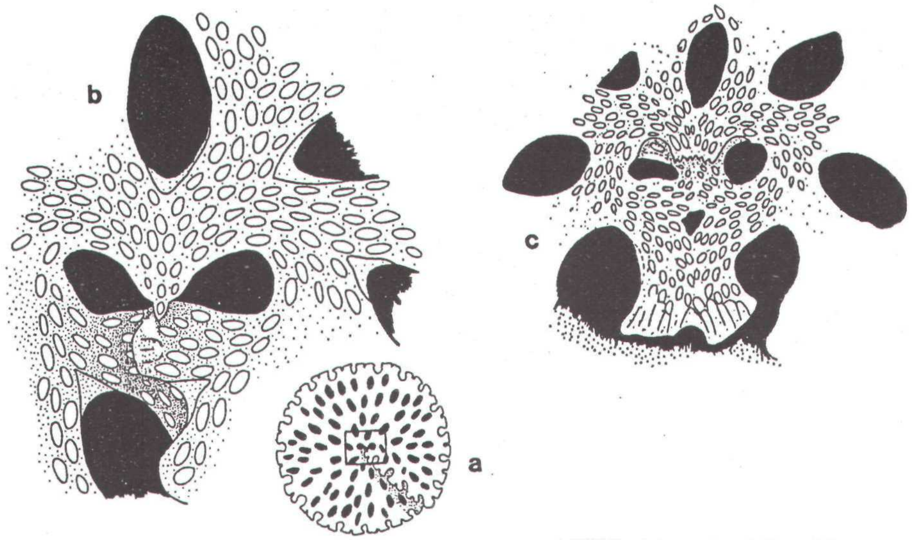

Fig. 2 - *Retiflustra cornea,* a. Schematic view of abfrontal surface of colony. Central rectangle encloses the area shown in b and c. b. Apex of colony. The ancestrula is still clearly visible, the right spiral overrides the left spiral, which continues to wind around the open central axis (i. e. the colony shows a left-handed spiral), c. Apex of colony. The ancestrula and first zooid rows are missing, as indicated by serrated free margin of apex. The two spirals are symmetrical and meet in mid-line on the colony from which both continue to spiral out from the open central axis. Figs. 2b and 2c from camera lucida sketches.

ORIENTATION IN LIFE

All authors (Busk, 1884 ; Harmer, 1926 ; Marcus, 1922 ; McKinney, 1980) who have discussed orientation have inferred an apex down position, in which the colony forms an inverted cone. Harmer considered that the rootlets held the colony in place as a set of "mooring ropes". This orientation apparently was assumed due to incrustation of the apical surface and possibly the reluctance to consider that the orifices of the zooids were directed toward the substratum.

The present observations show that apical incrustations and fouling resulted from the fact that this is the uppermost surface, freely available for settlement of debris and organisms from within the water column. The rootlets supported the colony off the bottom, raising it into the water column from which phytoplankton could be extracted. There was no indication from gut contents of aquarium held specimens that the zooids fed directly from the sediment surface, although probably the near bottom layer contains large amounts of resuspended sediment which must be handled by the lophophores. The active tentacle flicking and less frequent simultaneous contraction of all tentacles on a lophophore might help in rejection of such large particulate matter.

Particles in the water were brought into the lophophore funnel and expelled outwards between the lophophore tentacles as indicated by Winston (1977) for *Conopeum tenuissimum* and *Bugula* spp. by McKinney, Listoken and Phifer (1986). The lophophores were equi-tentacled, as shown for *Watersipora* by Winston

(1978: Fig. 2 d). The downward orientation of the lophophore resulted in the expulsion of such particles upwards through the fenestra. The combined action of the multiple lophophores expanded into the fenestra produced a strong vertical current. Thus the fenestrae appeared to be functional "excurrent chimneys" (see Banta, McKinney & Zimmer, 1974) although the incurrent pathways could not be determined by the use of carmine dye or milk droplets. The strong fenestral current and orientation of the lophophores into the fenestra resembles the pattern described for the reteporid *Reteporellina evelinae* by Winston (1978).

The presence of a cuticular rootlet system which anchors the colony in the sediment and raises it off the bottom is known for various unrelated soft-sediment bryozoans (Cook, 1979). Although including great diversity in colony structure, four out of six morphotype groups of bryozoans recognized from deep-sea sediments had anchoring rootlets (Cook, 1981). *Retiflustra*, which commonly reached 50-60 mm diameter at the base of the conical zoarium, is one of the largest of such rooted bryozoans, although the calcified zoarium of *Lanceopora* can reach 40 mm diameter (Cook, 1979). Lunulitiform zoaria supported by a rootlet system have been observed in *Anoteropora inarmata* Cook 1966 (Hayward & Cook, 1979) and *Mucropetraliella cotyla* Cook and Chimonides, 1981 (Cook & Chimonides, 1981 a), both from relatively deep water (300-800 metres). Off Townsville, a *Steginoporella* sp could co-occur with *Retiflustra* at sites less than 25 metres deep ; it had a conical zoarium with cuticular rootlets arising from the basal wall of most zooids. However, none of these lunulitiform bryozoans have the downward-oriented lophophores of *Retiflustra* nor the associated strong, vertical, colony-wide currents.

In the erect, rooted bryozoans *Sphaeropora* and *Lanceopora* the larva is interstitial and the rootlet develops from the ancestrula (Cook and Chimonides, 1981 b ; pers. comm.). Considerable growth of an ancestrular rootlet before budding of the primary autozooids has been documented for other genera, e.g. *Selenariopsis*, *Parastichopora* and *Conescharellina* (Cook, 1981). The lack of foreign material attached to the ancestrula of young colonies and at the apex of old colonies of *Retiflustra* suggests that their larva can also settle directly on a soft-substrate. Only one damaged colony showed an apical, apparently ancestrular, rootlet but lateral rootlets definitely appear in *Retiflustra* by the second autozooid row. Cook and Chimonides (1981 b) implied a similar pattern of settlement and development for bryozoans rooted in soft-sediments. The present observations on *Retiflustra* provide support for their suggestions.

Initially the lateral rootlets probably hold the fan-shaped colony of *Retiflustra* erect, as in *Lanceopora* (Coleman, 1977 ; pers. observations). With subsequent bifurcations of the branches and development of more fenestral rootlets, colony orientation would shift to that of the adult. The apical and lateral rootlets may disappear at this stage.

Although the growth model of McKinney and Raup (1982) clearly describes the *Retiflustra* from, the functional significance attributed by McKinney (1980) such as maximizing the filtering area for the minimum of substratum contact clearly assumed an apex downward position and an association with hard substratum. *In situ* observations showed that the orientation was opposite to that generally inferred and that *Retiflustra* at all stages appeared to be associated with soft unstable sediments, where space for settlement is unlikely to be limiting. The sheetlike morphology with multiple rootlets may in fact maximize the area of attachment points, maintaining the colony in shallow shifting sediments. The efficacy of this system is indicated by the occurrence of both species at sites off Townville less than 20 metres deep, in which the bottom is unstable and subject to resuspension by wind-generated waves (Belperio, 1983).

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APPENDIX

Collection sites for *Retiflustra* spp. First entry is the site code (see Birtles & Arnold 1983, Fig. 1 for location of sites), followed by station number and depth, uncorrected for tidal range. Based on collections in 1981 and 1983.

Retiflustra schoenaui

OA : 882 (7 m) ; OB : 903 (7.5-8 m), 905 (6-6.5 m) ; 1b : 1097 (11.5-12 m) ; 1B : 1106 (15.5-16 m) ; 2b : 1133 (18-19 m) ; Pioneer Bay, Orpheus Island, 3 dives (18, 18, 20 m) ; 5A : 863 (28-28.5 m).

Retiflustra cornea

1A: 878 (12.5-13 m) ; 1B: 898 (15-15-5 m) ; 1104 (17-18 m) ; 2A: 870 (22.5 m) ; 2B : 891 (20.5 m) ; 2B : 1113, 1114, 1115, 1116 (22-24.5 m) ; 2b : 1133 (18-19 m) ; 3A : 876 (21 m) ; 3B ; 895 (24-24.5 m) ; 3b : 1125 (24 m) ; 4A : 864, 865, 866, 867 (23.5-25 m) ; 4B : 885, 886, 887, 888 (24-26 m) ; 5A : 860, 861, 862, 863 (28-30 m); 5b: 1162, 1164, 1165 (29-30.5 m); 6A: 958 (35-36 m); 6B: 1172 (35.5-36 m); 7A: 949, 950, 952 (37-38 m) ; 7B : 940, 941, 942, 943 (38.5-40 m), 1175 (40-41 m) ; 8A : 954, 955, 956, 957 (40-42 m) ; 8B : 945, 946, 947, 948 (41-43 m).