

OBSERVATIONS ON LIVING COLONIES OF *SELENARIA* (BRYOZOA, CHEILOSTOMATA). I.

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Résumé

Observations de colonies vivantes de *Selenaria* (Bryozoaires, Chéilostome). I.

Deux espèces du Chéilostome lunulitifforme *Selenaria* ont été observées à l'état vivant, dans les conditions du laboratoire. Le comportement des deux espèces rappelle celui des Cupuladriidae : les colonies sont maintenues par les mandibules des aviculaires périphériques et débarrassées des sédiments par les mandibules restantes. Au cours de l'alimentation, les deux espèces présentent des modes de comportement distincts, coordonnés pour l'ensemble de la colonie. Seules, les colonies de *S. maculata* sont capables d'un renversement d'orientation et d'une locomotion soutenue. Cette capacité se reflète dans la morphologie des aviculaires.

Introduction

Lunulitiform colonies occur among many cheilostome genera. The ancestrula or ancestrular complex derives from a larva which usually settles upon a sand grain or foraminiferan test and is encrusting, but later astogenetic generations of zooids grow free of any substratum. Colonies are unilaminar and discoid or domed. On the convex surface, zooids are arranged in radial or spiral series which grow from a central, ancestrular area. Zooids increase in size with astogeny until a zone of repetition is established, after which colony size is increased by the budding of intercalary zooid series. In some colonies, secondary zones of change occur peripherally which are related to maximum growth and colony maturity. The concave (basal) side of the colony is often filled during later astogeny by extrazoooidal or kenozooidal tissues but, in some species, consists only of zooidal basal walls. Frequently, heteromorphic zooids (avicularia), often with very long, setiform mandibles, are budded in regular patterns among the autozooids. Some colonies either have no avicularia (*Anoteropora inarmata*, see Cook, 1966) or have avicularia with short, curved mandibles (*Cyttaridium pulcherrimum*, see Harmer, 1957). Avicularia with setiform mandibles (often called vibracular setae) have been seen to function in two principal ways in living species of the lunulitiform family Cupu-

ladriidae. They dislodge deposits from the colony surface and support the colony on the sea bottom (see Marcus and Marcus, 1962 and Cook, 1963).

Lunulitiform colonies have often been abundant since the late Cretaceous (see Hakansson, 1975). Distribution and ecology of some forms, all of which are associated almost exclusively with sea-bottoms of fine calcareous or muddy sand has been described by Lagaaij (1963), Cook (1965 a and b), Tommasi *et al.*, (1972) and Buge (1975). The stratigraphical significance of lunulitiform colonies has been discussed by Lagaaij (1953).

Although the theoretical possibility of some form of locomotion has long been discussed (see Lagaaij, 1963 for a summary), observations of living colonies of Cupuladriidae has shown that regular, sustained lateral movement did not occur, although a high degree of colony-wide coordination of avicularian activity was present (see Marcus and Marcus, 1962, Cook, 1963, Greeley, 1967).

Colonies of *Setenaria* do not appear to have been observed alive before. Canu and Bassler (1929: 141, text-fig. 33A) refigured a photograph from Maplestone (1911: 118, pl. 34, fig. 3) of a colony of *Setenaria flagellifera*. They stated that it showed the vibracular setae "in movement". Actually, Maplestone made no such statement and the setae figured are spirally curled. From comparison with other preserved material, this indicates that the colony was dead and dried when the original photograph was taken.

The observations made here show that one species, at least of the genus *Setenaria*, is capable of locomotion and that this capacity is related to the morphology and probably to the innervation of the avicularia.

Material and methods

Colonies belonging to the genus *Setenaria* Busk, which had been collected alive by dredging and diving, were flown to London from New Zealand and Australia respectively. Colonies were packed in damp sea-weed or linen, enclosed in polythene bags, surrounded by freezer packs (to reduce bacterial action) and enclosed in expanded polystyrene boxes. In London, colonies were placed in closed, aerated and filtered sea-water systems. In 1975, it was observed empirically that colonies living directly on the crushed gravel filter bed at the base of the aquarium survived best and, in 1977, all colonies were therefore kept by this method.

Approximately 100 colonies (collected by Dr P.K. Probert) from the Otago shelf, New Zealand, all belonging to one species (here called "sp. 1"), were observed in May and June 1975. Activity then declined, but two colonies survived until November 1976, on the filter bed of the aquarium. The colonies were collected from a dredge haul in 25 metres (Mu 74/196 off Taratoa Head, 45°47'24" S, 170°46'36" E). The water temperature was 12.2 — 12.8°C and the sea bottom consisted of slightly muddy, fine sand (69.1 per cent by weight of grain size 125 — 250 μ).

Approximately 50 colonies (collected by Mr P. Arnold) from

Townsville, Australia, nearly all belonging to *S. maculata* Busk, were kept from January to April 1977. These colonies had already been kept in laboratory conditions for one month before being flown to London. The colonies were collected by diving in 2.5 metres (off West Point, Magnetic Island, Queensland, 19°36'30" S, 146°46'12" E). The water temperature was 24.6°C and the sea bottom consisted of coarse, well sorted sand. These waters were tidal, with a current of one knot and there were well defined ripples in the sand, parallel to the coast. Colonies occurred in small, scattered groups, usually between patches of the sea grasses, *Halophila ovalis* and *H. spinulosa*, together with alcyoneans.

Sophisticated apparatus for the maintenance of living bryozoan colonies has been described, particularly for estuarine species, by Jebram (1970). Methods of maintaining fully marine, specialized colonies are at present necessarily empirical. The following notes apply principally to the methods used in 1977.

Colonies were kept in glass sided aquaria of 70 litres capacity using filtered natural sea water, supplemented when necessary by Instant Ocean synthetic sea water. The system employed was essentially that used by aquarium enthusiasts, quantitatively described by King and Spotte (1974), where the constant aerating mechanism served to circulate the water through 50 mm of gravel filter bed with particle size between 3-7mm, via a 38mm airlift tube. Here physical and biological filtration occurred. The filter bed in addition served to maintain an alkali reserve for the system, with the pH remaining at a constant 8.1. Measurements of pH were taken using a Pye Ingold combined glass and reference electrode with standard glass membrane, silver / silver chloride reference electrode, KCl salt bridge with ceramic plug liquid junction and using phosphate buffer at pH 7 at 25°C and 3.5 per cent salinity (Hansson, 1973). Flow rate through the filter bed was estimated at 100 cu. cm per sq. cm filter bed per hour.

For colonies of Australian *Selenaria*, temperature was maintained at 24 °C, in a draught free environment, by a standard heater/thermostat arrangement, with a variation of $\pm 1^\circ\text{C}$ detected. This variation was attributed to the thermostat mechanism. Colonies of New Zealand *Selenaria* were kept at 12°C in a Constant Temperature room.

In an attempt to by-pass costly and time consuming culturing, the specimens were fed on a liquid suspension mixture of 50 per cent dried milk powder (particle size range 2-5 μ diam. with an average size of 3.29 μ) and 50 per cent Liquifry No 2 fish food (particle size range 7-15 μ diam. with an average size of 9.48 μ). 1ml of mixture was added approximately every three days. Each tank was illuminated for about 8 h a day, at one end, by a single, external 75 W tungsten reflector bulb.

Photographs of the colonies were taken using a Praktica LTL 1 in conjunction with a single Braun 42VC electronic flash gun:

- a) through the sides of the aquaria with a 55mm lens on 40mm extensions;
- b) in a shallow dish through a Wild M7 microscope.

Colonies were observed regularly for evidence of feeding behaviour, the presence of colony-wide water currents, avicularian irritability, behaviour and function, and colony movements.

It must be emphasized that all laboratory based reactions of bryozoan colonies should be interpreted in the understanding that little is as yet known of their behaviour under natural conditions. The contrast in the observed behaviour of *S. maculata* in the sea and in the laboratory is particularly interesting.

OBSERVATIONS

1. *Selenaria* sp. 1 from New Zealand.

Colonies were irregularly fan-shaped, and all had developed from regeneration of fragments. Preserved colonies from other, usually deeper-water Stations were, however, regularly and radially developed from an ancestrula which had budded one distal and one proximal avicularium and paired lateral zooids. The basal side of the living colonies was not much thickened and consisted of irregular units with scattered pores. Avicularia occurred only as distal lateral buds which originated intercalary zooid series. Zooidal opesiae were small and the horizontal cryptocyst well developed (Table 1).

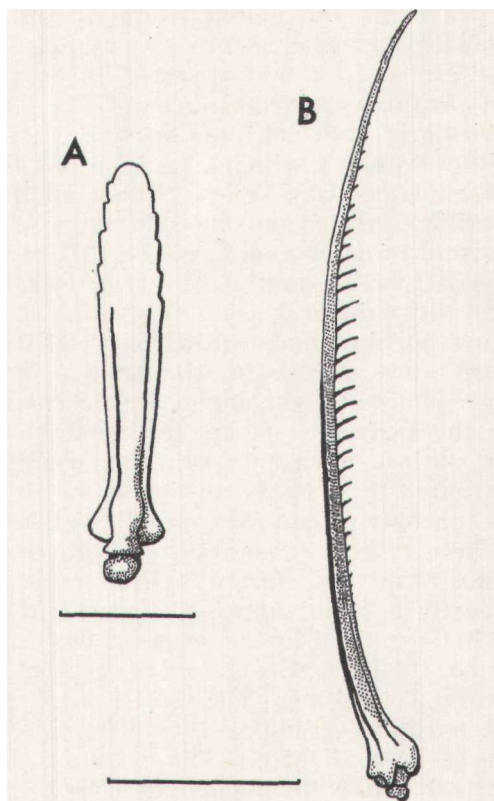
TABLE 1
Comparison of morphometrics of two species of *Setenaria*.

	<i>Selenaria</i> sp. 1	<i>S. maculata</i>
Colony diameter	3.0 — 7.0 mm	10.0 — 13.0 mm
No. of zooid generations	7 — 10	19 — 29
No. of zooids	70 — 200	1500 — 2300
No. of avicularia	25 — 80	120 — 160
No. of peripheral mandibles	11 — 30	30 — 40
L _z (zone of repetition)	0.35 — 0.40 mm	0.32 — 0.40 mm
L opesia " "	0.15 — 0.18 mm	0.26 — 0.28 mm
L av " "	0.25 — 0.27 mm	0.48 — 0.50 mm
L mandible (peripheral)	0.60 — 0.70 mm	2.70 — 4.00 mm
No. of tentacles	15 — 16	13 — 14
L tentacles	0.45 — 0.50 mm	0.50 — 0.70 mm
L t sheath	0.10 mm	0.15 — 0.20 mm
Diameter of spread of tentacles	0.50 mm	0.40 — 0.50 mm

The avicularia were smaller than the autozooids and the mandibles were relatively short, broad and slightly expanded and serrated terminally (Text-Fig. 1A). They were slung between symmetrical processes (see Plate II, D). Dr Probert noted that the mandibles frequently had a fringe of diatoms which may have actually increased their capacity for dislodging particles on the colony surface. The attached forms certainly did not impede mandible movement.

Colonies maintained themselves with the convex, zooidal side uppermost, raised approximately 0.50mm above the substratum by the closed peripheral and some subperipheral mandibles in a similar manner to that of colonies of the Cupuladriidae (see Marcus and Marcus, 1962; Cook, 1963). The movement of the mandibles, even when artificially stimulated by touch, was slow, one complete opening or closing taking 10-15 seconds. Movement was in one plane, at right angles to the colony surface. Individual mandible movements were made irregularly, with periods of quiescence of 30-120 seconds. Single peripheral mandibles also moved occasionally

TEXT-FIG. 1
 Avicularian mandibles in
Setenaria.
 A: mandible of *Selenaria*
 sp. 1. Scale = 0.25 mm ;
 B: seta of *S. maculata*.
 Scale = 1.00 mm.



and some concerted, apparently simultaneous movements of 2-3 adjacent setae were observed. This produced a "rocking" movement similar to that seen in the Cupuladriidae but the mandible movements were not colony wide (see Cook, 1963: 410). Colonies were able to uncover themselves when buried in sand (20-40 minutes), but were unable to reverse their orientation if placed upside down. In this position, they raised themselves on the half open peripheral and subperipheral mandibles. Dr Probert noted that colonies reversed on fine and sand made irregular lateral movements, leaving tracks in the sand (see also p. 152).

Single member zooids were often seen to feed (see Plate II, C). On a few occasions during May 1975, colony-wide, communal feeding was also observed. Approximately 75 per cent of zooids extended

their tentacle crowns but zooids in the central, ancestrular area did not feed. All the mandibles not engaged in supporting the colony swung to a vertical, half open position and then moved slowly to and fro while feeding continued. Tentacles were colourless; no obvious colony-wide water currents were observed.

2. *Setenaria maculata* Busk from Australia.

Colonies were regularly budded from an ancestrular region consisting of an ancestrula, one distal and one proximal-lateral avicularium and paired lateral zooids. The basal side consisted of radially arranged, porous sectors. Zooids may have a spiral budding pattern at first, but appeared to be radially budded after the first two or three astogenetic generations. Zooids were much smaller than avicularia, and had large opesiae (Table 1). Avicularia were budded either within a primary, radial zooid series or as the second member of an intercalary series. The mandibles were very long, setiform, flexible, serrated on one side and each was slung from a complex, asymmetrical process (Text-Fig. 1B and Plate II, B). Colonies raised themselves 2-3 mm above the substratum by the closed peripheral and subperipheral setae (Plate I, C), the remaining setae making slow opening and closing movements, each taking 8-12 seconds, even when artificially stimulated. Movements ranged from sweeps in a plane at right angles to the colony surface to sweeps parallel to the surface, touching the frontal cuticle. Setae were frequently in contact during these movements and completion of a sweep appeared to be made by the strongest member. Colonies were able to uncover themselves rapidly when buried in sand or gravel, although there was great individual variation in the time taken. Fine sand was cleared by the setae in 6-25 minutes, gravel was cleared in 20 minutes — 3 hours. If placed upside down, colonies either remained in the reversed position supported by the half open setae (Plate I, E) or, more usually, made efforts to regain the "normal" position. The setae swung into the half open position and on irregular, granular substrata, this inevitably resulted in tilting the colony slightly. The setae on the lower edge then opened further, while the remainder closed. Some of the setae in contact with the substratum then closed, while others supported the colony. Colonies gradually became vertical, when further closing movements by the supporting setae and gravity caused them to regain normal orientation. Successful reversal depended entirely upon granularity and irregularity of the substratum and colonies placed on fine sand were unable to regain the normal position. These colonies also moved laterally in a random manner, leaving curved tracks in the sand (see above). Many colonies, kept on the coarse gravel filter in the aquarium, reversed their orientation at frequent intervals and, when not feeding, this was a regular activity in some cases, occurring as frequently as 2-3 times an hour. The most rapid reversal seen took 6 minutes to complete.

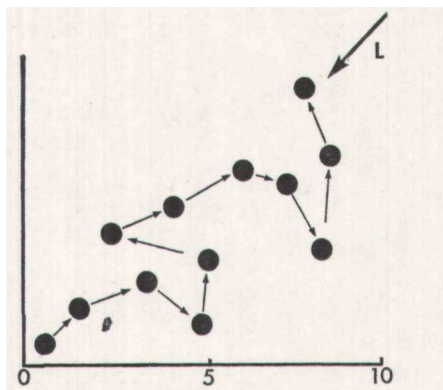
Colonies moved towards light. Mr Arnold, who observed them when first collected, noted that they moved away from a concentra-

ted light beam and observed no locomotion in their natural habitat, where in spite of the shallow water depth, light concentration was variable or even very low. The potential capacity for locomotion is definitely present however. Movement is complex and apparently requires coordinated, colony-wide behaviour patterns.

If a colony supported on its peripheral setae was lighted on one side, those setae facing the light began to make opening movements within 10 seconds. The setal activity proceeded in a clockwise direction round the periphery. During closing, the serrations of two adjacent setae often became locked together. Opening movements automatically unlocked the serrations because of their shape and position (Plate II, A). Setae on the unlighted side closed further, raising the colony on this side and acting as a fulcrum for lateral rotation movements caused by the successive opening and closing of the setae on opposite side. At intervals, several setae on the lighted side closed completely, raising this side high above the

TEXT-FIG. 2

Movement of colony of *S. maculata* towards light source (L) over 10 cm. Position of centre of colony after each "lurching" movement is shown by the black circles. Scale in cm.



substratum. These then all opened simultaneously accompanied by a partial opening of the setae on the unlighted side which, however, maintained contact with the substratum. The colony was thus propelled up to 3mm with a "lurching" movement. The movement was in part due to the flexibility of the setae which, particularly on the unlighted side, were often strongly curved by the pressure of the colony upon the substratum. This flexibility gave increased potential to the leverage exerted by the musculature, which resulted in rapid movement when the pressure was even slightly released.

Rotation was always clockwise but the direction of "lurching" formed a distinct pattern (Text-Fig. 2). Although individual colonies varied in reaction, most made sustained movements towards light and movement ceased if they were placed in darkness. The type of substratum influenced the speed of movement and colonies on fine sand moved very slowly (Table 2). The serrations on the setae possibly produced the most efficient frictional contact on gravel. There was some apparent periodicity in the frequency of "lurching" movements which was also correlated with substratum to some

extent, but the range of variation was considerable (Table 2). The fastest sustained movement of a colony on gravel over a distance of 50cm was at the rate of 1 metre per hour; the fastest movement on glass over 10cm was about 0.5 metres per hour. On reaching the lighted glass wall of the aquarium, many colonies raised themselves high on the completely closed setae of the lower side (3-4mm above the substratum) and supported themselves on the glass by the remaining peripheral setae, so that most illumination fell on the basal side of the colony. Some colonies maintained themselves in this position for 3-4 hours.

TABLE 2

Number of seconds elapsing between "lurching" movements of colonies on various substrata, over a distance of 10 cm.

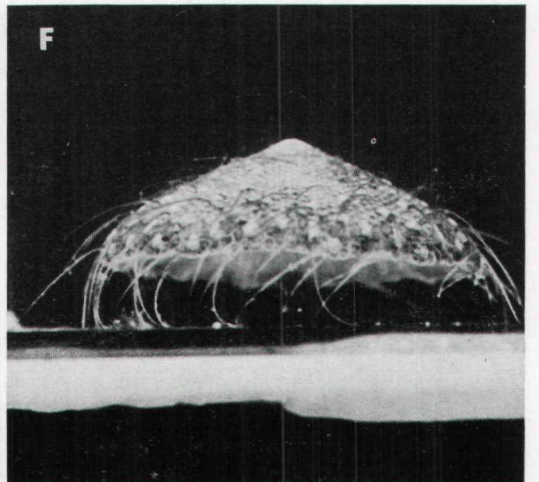
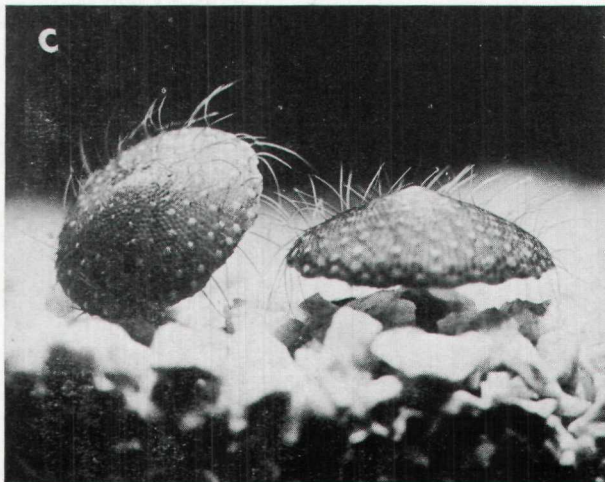
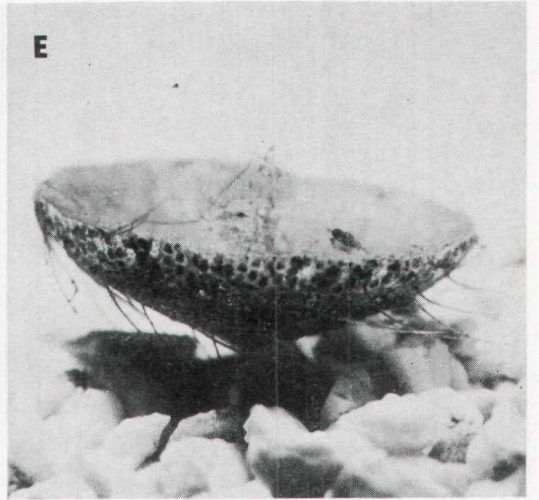
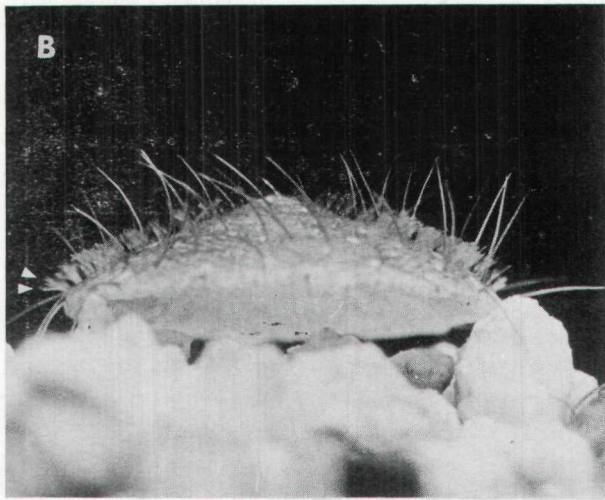
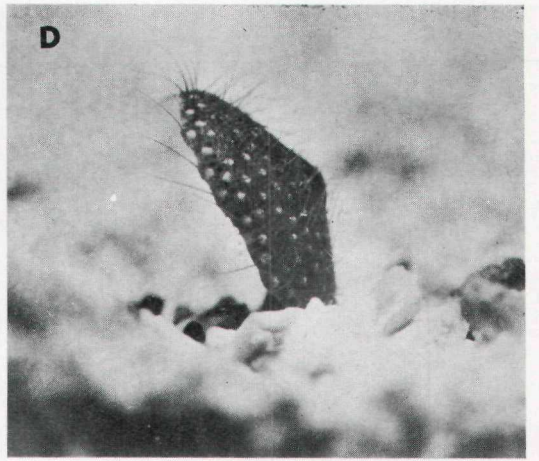
Substratum	No. of seconds	Total time in seconds	Total No. of movements	No. of rotations
Glass	12, 30, 55, 10, 33, 42, 53, 44, 45, 23, 36, 28, 75, 10, 33, 7, 23, 37, 80, 12, 36.	724	21	2
Gravel (3-7 mm)	A. 40, 38, 14, 16, 5, 4, 4, 21, 21, 33, 24, 16, 32, 8, 21, 9, 12, 24.	342	18	2
	B. 20, 40, 51, 31, 14, 21, 34, 30, 26, 52, 12, 26.	357	12	1
	C. 21, 37, 14, 26, 17, 22, 14, 32, 30, 8, 11, 13, 21, 14, 37, 29, 17, 50, 45, 10, 23, 33, 17, 24, 44, 25, 17, 26, 16, 12, 11, 28, 14.	758	33	2
Sand (0.10-0.25 mm)	A. 20, 50, 15, 43, 58, 35, 52, 65, 40, 35, 32, 21, 15, 57, 65, 19, 25, 32, 48, 33, 40, 35.	835	22	2
	B. 30, 57, 63, 123, 92, 58, 32, 80, 40, 62, 63, 21, 90, 69, 51, 23, 65, 23, 80, 31, 42, 65, 183, 13.	1456	24	3

Colonies frequently came into contact with one another during lateral locomotion and reversal movements. Although mutual movements of the setae tended to "space" colonies, because the setae ceased movements once the pressure stimulation was absent, the more active colonies frequently climbed over the less active (Plate I, C) or turned them over. In one case only, it was observed that a very active colony appeared to "pursue" another, even when it had moved out of contact. This was almost certainly fortuitous, but

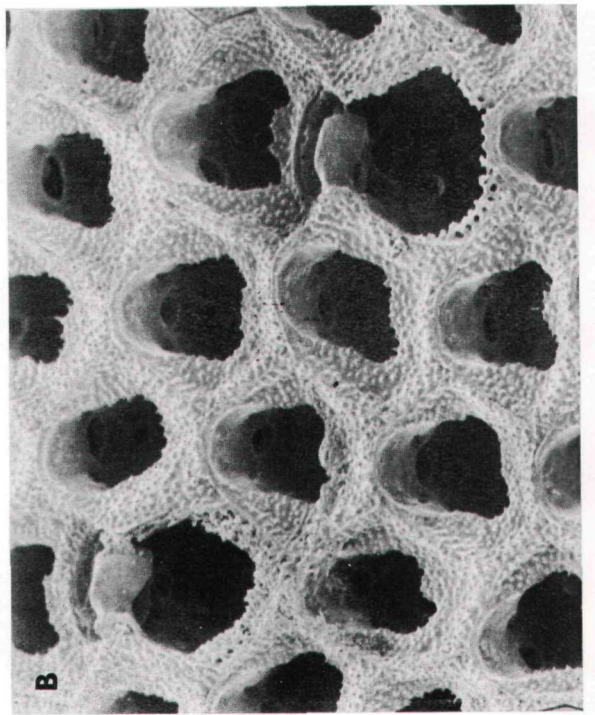
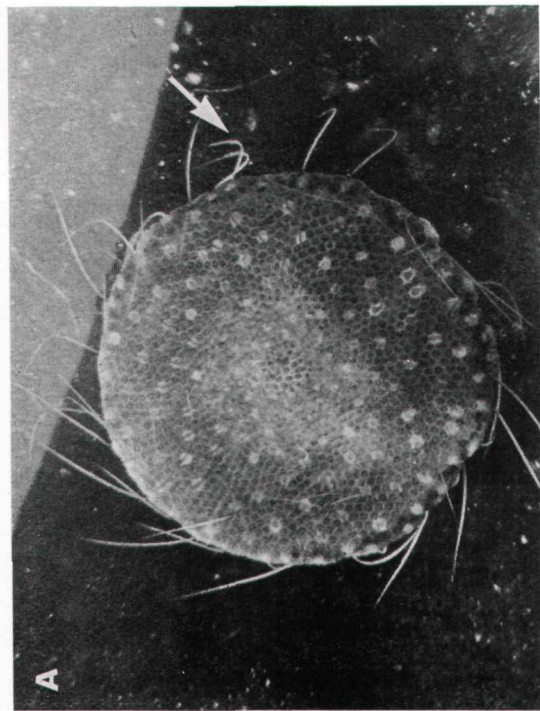
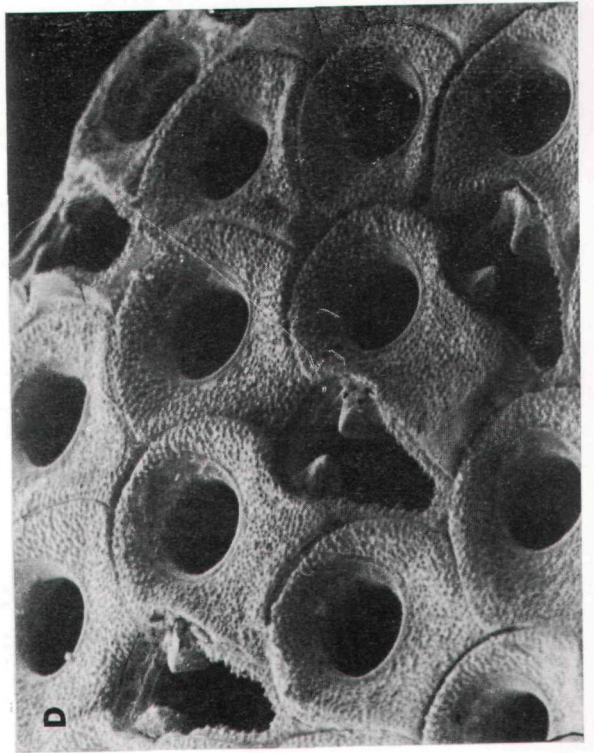
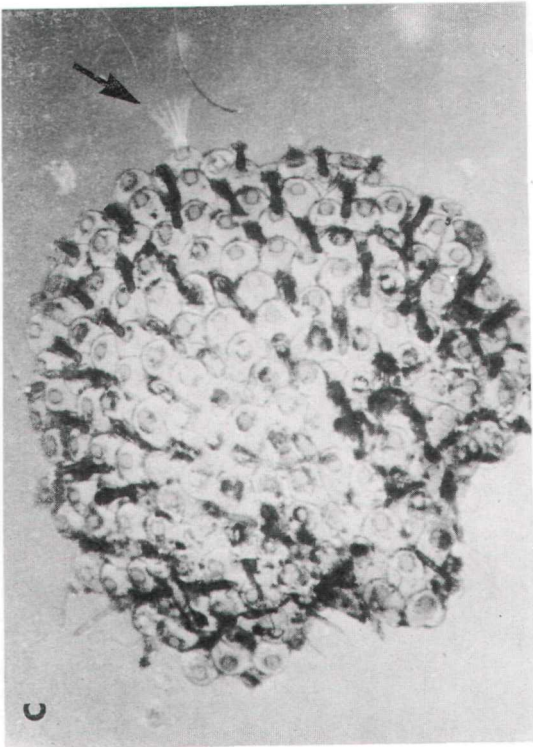
PLATE I

Setenaria maculata Busk — living colonies

A: lateral view of colony feeding; note curve produced by tips of tentacle crowns in silhouette (marked). (X 5); B: as A; note position of frontal setae and compare with F. Peripheral tentacle crown (arrowed). (X 5); C: two colonies; left hand colony beginning to climb over right hand colony which is in the "pre-feeding" position. (X 2.75); D: lateral view of colony 2 seconds before regaining "normal" orientation after reversal. (X 2.75); E: colony in reversed position; note position of setae and epizoic forms on basal surface. (X 5); F: lateral view of colony in locomotion on glass; note sequential movement of peripheral setae. (X 4.6).



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the movements were away from the light, towards which both colonies had originally been travelling and the behaviour was maintained for 20 minutes.

Member zooids fed sporadically at any time, which ever way the colonies were orientated. Tentacles were colourless (see also Table 2). At relatively low light levels, particularly in the evening, an entire zone of zooids, from the 10th to the 28th astogenetic generations, and comprising about 75 per cent of the total number of zooids, fed together communally. The tentacles of the earliest astogenetic zooid generation seen to feed were apparently longer than those of the next few generations but as long as those of the subperipheral and peripheral generations. The tips of the tentacle crowns thus formed a shallow, concave curve above the slightly convex curve of the colony surface (Plate I, A). The peripheral tentacle crowns were held almost horizontally (Plate I, B). Communal feeding was only observed in the aquarium, where there was a fairly strong water current passing over the colonies and distinct excurrent movements were not seen. It is possible, however, that the non-feeding centre of the colony forms a passive excurrent "chimney" and that peripherally directed currents are also initiated by the peripheral tentacle crowns (see Cook, 1977). Before, during and after communal feeding, colonies exhibited distinct behaviour patterns. First, all lateral locomotion ceased and colonies raised themselves high on the peripheral setae, which made no further movements. The remaining setae all swung to a nearly vertical, half open position and nearly all remained motionless during feeding (Plate I, B). After 15-20 minutes feeding, all the tentacle crowns were withdrawn, apparently simultaneously. All the frontal setae then opened and closed simultaneously, moving across the frontal membranes parallel to the colony surface, in a cleaning movement. To the naked eye, this movement was very similar to the opening of a spirally arranged iris diaphragm. After this, the setae swung into a half open, vertical position again, the tentacles were extended and feeding recommenced.

RELATIONSHIPS BETWEEN BEHAVIOUR AND MORPHOLOGY

The general patterns of behaviour of all the colonies of *Selenaria* observed here resembles those seen in the Cupuladriidae.

PLATE II

Selenaria maculata Busk and *Setenaria* sp. 1

A: *S. maculata*. Living colony viewed from upper (zooidal) side. Two setae in process of unlocking serrations (arrowed). (X 4); B: *S. maculata*. Skeletons of zooids and two avicularia. Note large, asymmetrical process for slinging of mandible. The frontal wall of the avicularium is very thinly calcified in life, concealing the process. (X 50); C: *Selenaria* sp. 1. Living colony viewed from upper side; one zooid feeding (arrowed). (X 15); D: *Selenaria* sp. 1. Skeletons of zooids and three avicularia. Note paired, symmetrical processes for slinging mandible. (X 65).

B and D taken using Scanning Electron Microscope.

Although avicularia are less plentiful in *Setenaria*, the regular astogenetic pattern of zooids and hetromorphs, the reactions of mandibles to pressure and their functions of cleaning and support are almost exactly the same as those seen in *Discoporella umbellata* and *Cupuladria doma*.

Although the asymmetrically slung setae of the Cupuladriidae apparently resemble those of *S. maculata*, they are functionally more like the mandibles of *Setenaria* sp. 1, as they are capable of movement in one plane only (see Cook, 1963). The function of the mandibles of *Setenaria* sp. 1 allows the inference that colonies of Recent *Lunulites*, which have somewhat similar, relatively short, stout mandibles arranged in radial rows, behave in a similar manner.

Differences between the two species of *Setenaria* in the action of the avicularia is entirely reflected in their morphology. In *Setenaria* sp. 1 the avicularia are small, with short muscles, and the mandibles are short and slung between symmetrical processes (Text-Fig. 1 A and Plate II, D). Movement is in one plane and two directions. The mandibles are thus similar to some of those discussed by Hastings (1963). Although sustained lateral locomotion is theoretically possible, it would require much more colony-wide, coordinated behaviour than that apparently possessed by this species. In *S. maculata*, the avicularia are very large, as are the long muscles controlling the mandibular setae, which are long and flexible. The basal setal attachments and the calcified process from which the mandible is slung are complex and asymmetrical (Text-Fig. 1 B and Plate II, B). Setae are capable of movements in nearly all planes and directions above the colony surface. In addition, combined thrust of two setae with locked serrations is frequent during locomotory closing movements. Sustained lateral locomotion involves reaction to light as well as to pressure and a high degree of coordination of setal movement, particularly during "lurching" where half the supporting setae open and the other half make a thrusting movement, simultaneously.

CONCLUSIONS

These observations have emphasized many problems inherent in lunulitiform structure which will require much further study by workers in several fields.

First, there are differences between field and laboratory observations which need study of colonies in their natural habitat and monitoring of physical conditions and behaviour patterns in the laboratory. In this way, a relationship between "normal" and "potential" behaviour and function may be established. Second, the high degree of morphological integration of lunulitiform colonies (see Boardman and Cheetham, 1973) seems almost certain to be

accompanied by a relatively sophisticated nervous organisation. For example, both species of *Setenaria* exhibit colony-wide, coordinated behaviour patterns during communal feeding. These involve avicularian movements which are not the result of pressure and which show distinct episodes before, during and (in *S. maculata*) after feeding. Third, there is a complex relationship between avicularian morphology and behaviour. Although colonies of *S. maculata* have not been seen to make extensive lateral movements in the natural state, the potential capacity to do so may be of advantage in the very shallow waters in which they have been found. There may be other correlations between ecological conditions, avicularian structure and colony form generally. These may eventually show series of character states which can be progressively related to the genetic structure of populations.

Acknowledgements

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Summary

Two species of the lunulitiform cheilostome genus *Setenaria* have been observed alive under laboratory conditions. The behaviour of both species resembled that of living Cupuladriidae in that colonies were supported by peripheral avicularian mandibles and cleaned of sediments by the remaining mandibles. Both species exhibited distinct, coordinated colony-wide behaviour patterns during feeding. Colonies of *S. maculata* alone were capable of reversal of orientation and of sustained locomotion. This capacity is reflected in the morphology of the avicularia.

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