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

by

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Résumé

Observations de colonies vivantes de *Setenaria* (Bryozoaires, Cheilostome). II.

Nous avons continue, dans les conditions du laboratoire, nos observations sur les colonies vivantes de *Setenaria maculata* Busk d'Australie. Des algues rouges vivent en épiphytes à la surface supérieure des colonies et les formes épizoïques comprennent des vers en tubes, des éponges, des mollusques et un Bryozoaire cténostome, *Sudanella* sp. De petits Isopodes vivant dans des tubes servent de nettoyeurs symbiotiques. Les zoïdes des zones externes des colonies ndultcs sont polymorphes et sexuellement fonctionnels. Les zones subpériphériques des zoïdes aux parois distales concaves dressées qui portent des ovaires sont donc considérées comme femelles et couveuses. Les zones périphériques au système musculaire bien développé et aux lophophores modifiés (formés de longs tentacules nus accouplés et de fourreaux tentaculaires très allongés) renferment du sperme dans leurs coelomes viscéraux. D'après **leur** morphologie et leur comportement, ce sont donc des zoïdes mâles.

L'existence de telles zones de zoïdes polymorphes dans d'autres espèces de *Setenaria* et leur signification dans l'étude des populations fossiles sont brièvement discutées. Les colonies réagissent à la lumière visible bleu-vert et sont attirées par elle mais ne sont pas apparemment affectées par la lumière rouge ni par les radiations ultraviolettes ou infrarouges.

Introduction

Free-living lunulitiform bryozoans are found, sometimes in large numbers, in warm-water 'sand fauna' environments. Colonies are discoid or cup-shaped and live supported on the surface of the bottom sediments by long, setiform mandibles of the marginal avicularia, which arc budded in regular patterns among the other member zooids. The setae of earlier astogenetic generations, which no longer have a supporting function, clean sediments away from the colony surface and may be involved in the resumption of the "normal" position if the colony is reversed in orientation. Free-living colonies are without exception anascan cheilostomes, and include the families Cupuladriidae, Lunulitidae and Selenariidae.

Previous observations on living colonies established the locomotory potential of colonies of *Setenaria maculata* Busk, and compared them with colonies of another species of *Setenaria* which had relatively unmodified avicularia and which was not capable of locomotion (Cook and Chimonides, 1978).

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Material and methods

More than 100 living colonies of S. *maculata* collected in August from near Townsville, Queensland (19°08'S, 146°55'E, 11.5-12 metres), were maintained in a closed sea-water aquarium system, as previously described by Cook and Chimonides (1978). The structure and relationships of "soft parts" (muscles, viscera etc.) of colonies were examined from serial microtome sections of narcotized, fixed, decalcified material stained in haemotoxylin. Relationships of skeletons with "soft parts" were studied from thin-sections of material mounted in epoxy-resin. Skeletal structures were also examined from whole colonies treated with sodium hypochlorite, coated with gold-palladium and photographed using a scanning electron microscope. All observations of colony reaction to light were conducted with "mature" specimens (see p. 211) in sea-water at 25°C, in glass containers in a darkened room. Three sensor types were used where appropriate: a) a Weston lux meter with standardized photopic vision response, b) a Milliard CdS cell ORP 12 (see Milliard Technical Handbook, 1973:3) in conjunction with suitable ohmeter, and c) a Cambridge thermopile (see Longhurst, 1976:458; Turner, 1978: 9-8 and Szeicz, 1968: 177) in conjunction with a d.c. millivolt meter with microvolt resolution. All three sensors were calibrated against a standardized Kipps thermopile solarimeter using an Oriel diffraction grating raonochromator. Filter responses were calibrated against spectro-photometers from 360nm to 1000nm. Responses of colonies were recorded and graded subjectively as: a) setal movement (slow and fast), b) standing and moving, and c) "walking" (slow and fast). Measurements of electromagnetic radiation taken were incident readings at the edge of the container and were thus only a coarse assessment, taking no account of container and water absorption. The sources of greatest error were considered to be in maintaining a constant light level (due to supply-level control difficulties), and in presenting uniform illumination spread.

Tables 1 and 2 show the proportion of infra-red radiation present in the tungsten light source and the effect of additional passbands in photographic filters used. Table 3 indicates the typical transmission losses over the average path length from the edge of the glass container to the specimens being observed. The greatest losses occur over the red and blue. Blue has a highest loss due to the number of glass surfaces through which light was passed. Column a) gives the lux value, column b) gives the power incident calculated from the lux value (in watts per metre^2), and column c) gives the actual power incident as measured by the Cambridge thermopile (in W/m^2). We use a lumen as a unit of light measurement over the wavelengths 380 — 760nm only. Power from the lux value was derived according to the relationship

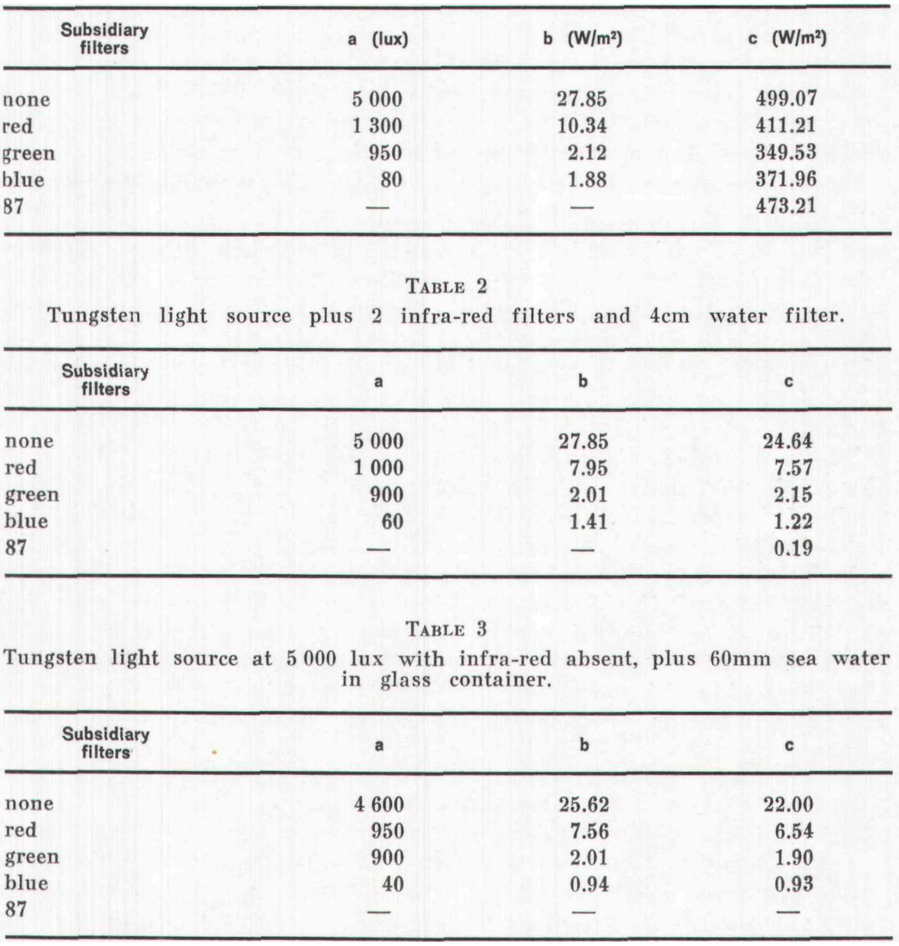
$$\varnothing = \mathrm{Km}\ \Sigma V\lambda E\lambda$$

where $\varnothing$ is the luminous flux in lumens, Km is taken as 630 lumens per watt, $E\lambda$ is the energy for wavelength λ expressed in watts, and $V\lambda$ are internationally agreed values for relative luminous efficiency of radiation for photopic vision at wavelengths λ (see Keitz, 1971:

244 and 414). The energy incident for the tungsten light source (using no filters) for the range of lux values used in observations was as follows: 5000 lux = 499 W/m^2, 2500 lux = 391 W/m^2, 1000 lux = 276 W/m^2, 300 lux = 160 W/m^2 and 50 lux = 75 W/m^2.

TABLE 1

Tungsten light source without filters (see text, p. 208)



Subsidiary filters	a (lux)	b (W/m²)	c (W/m²)
none	5 000	27.85	499.07
red	1 300	10.34	411.21
green	950	2.12	349.53
blue	80	1.88	371.96
87	—	—	473.21

TABLE 2

Tungsten light source plus 2 infra-red filters and 4cm water filter.

Subsidiary filters	a	b	c
none	5 000	27.85	24.64
red	1 000	7.95	7.57
green	900	2.01	2.15
blue	60	1.41	1.22
87	—	—	0.19

TABLE 3

Tungsten light source at 5 000 lux with infra-red absent, plus 60mm sea water in glass container.

Subsidiary filters	a	b	c
none	4 600	25.62	22.00
red	950	7.56	6.54
green	900	2.01	1.90
blue	40	0.94	0.93
87	—	—	—

OBSERVATIONS

1. Epiphytic and epizoic forms

Colonies ranged in size from 8-13mm, representing growth stages of from 13 to 27 astogenetic generations. Nearly all the larger colonies had a film of red algae growing from the central part of the upper surface and over the avicularian setae. Algae tended to proliferate during the months over which the colonies were observed, especially when they were exposed to sunlight for long periods. After the death of the cleaning isopods (see below), the algal growth increased so that in moribund colonies the movements of setae were affected.

All larger colonies also had a number of basal epizoic forms. These included small lamellibranch molluscs, orange sponges and more than one species of tube-worm, with either calcareous or sand grain-accreted tubes. These opened peripherally and the oral tentacles were protruded between the avicularian setae of the bryozoan. Other sand grain-accreted tubes housed small isopods, which were apparently cleaning symbionts. At low light levels, the isopods emerged almost wholly from their tubes and fed on algae and detritus removed from the upper surface of the *Selenaria* colonies.

Associated bryozoans included one, small, basal colony of *Rimulostoma signatum* (Waters), comprising approximately 500 zooids (300 of which had ovicells, and 15 of which had large, spathulate avicularia), and numerous, smaller colonies of a ctenostome belonging to the genus *Sundanella* Braem. Unlike 5. *sibogac* (Har**mer),** which has large zooids (Lz 2-4mm) with over 20 tentacles (see Maturo, 1957:20), this species has small zooids (Lz 0.50mm) with 12-14 tentacles. Colonies of up to 50 zooids, showing the distinctive budding pattern of *Sundanella,* grew basally, peripherally and frontally on the *Selenaria* colonies, but did not markedly interfere with the setal movements or with colony-wide feeding. The ctenostome zooids fed more readily than those of the cheilostome, and at higher light levels. Several ancestrulae of *Sundanella* were seen on the avicularian setae themselves. Some colonies grew over the non-feeding apex of the *Selenaria* colonies, and their zooids occupied skeletons of the central zooids. In section, the ctenostome zooids show very thick, externally fimbriated cuticular body walls. Whether the zooids of *Sundanella* sp. are capable of boring into the young cheilostome zooids, or occupied the central zone after damage is not known.

2. Polymorphic sexual zooids

Elongated lophophores, consisting of paired, unciliated tentacles (2mm long) and extended tentacle sheaths (4mm long), were observed in living colonies. They were protruded, usually horizontally, for very short periods, from 2 to 10 seconds, and made rapid "flickering"

PLATE I

Sexual polymorphism in *Setenaria.* B, C an D, scanning electron micrographs. A. S. *maculata* Busk, Townsville, Australia. Living colonies, one climbing over the other. Two male lophophores almost fully extended at left and two partially extended above them. X6. Insert top right shows the same lophophores. X 12.

B. *S. maculata,* Townsville, BMNH 1980.1.20.2. Peripheral male zooids (m), subperipheral female zooids *(f)* and avicularia (av). X 50.

C. *S. bimorphocella* Maplestone, South Australia, BMNH 1928.9.13.80. Peripheral male zooids (ml, subperipheral female zooids (f), autozooids (z) and avicularia (av). X62.

D. *S. partipunctata* Maplestone, North West Australia, BMNH 1949.6.8.7A. Peripheral male zooids (m), subperipheral female zooids *<{),* autozooids (z) and avicularia (av). X 106.

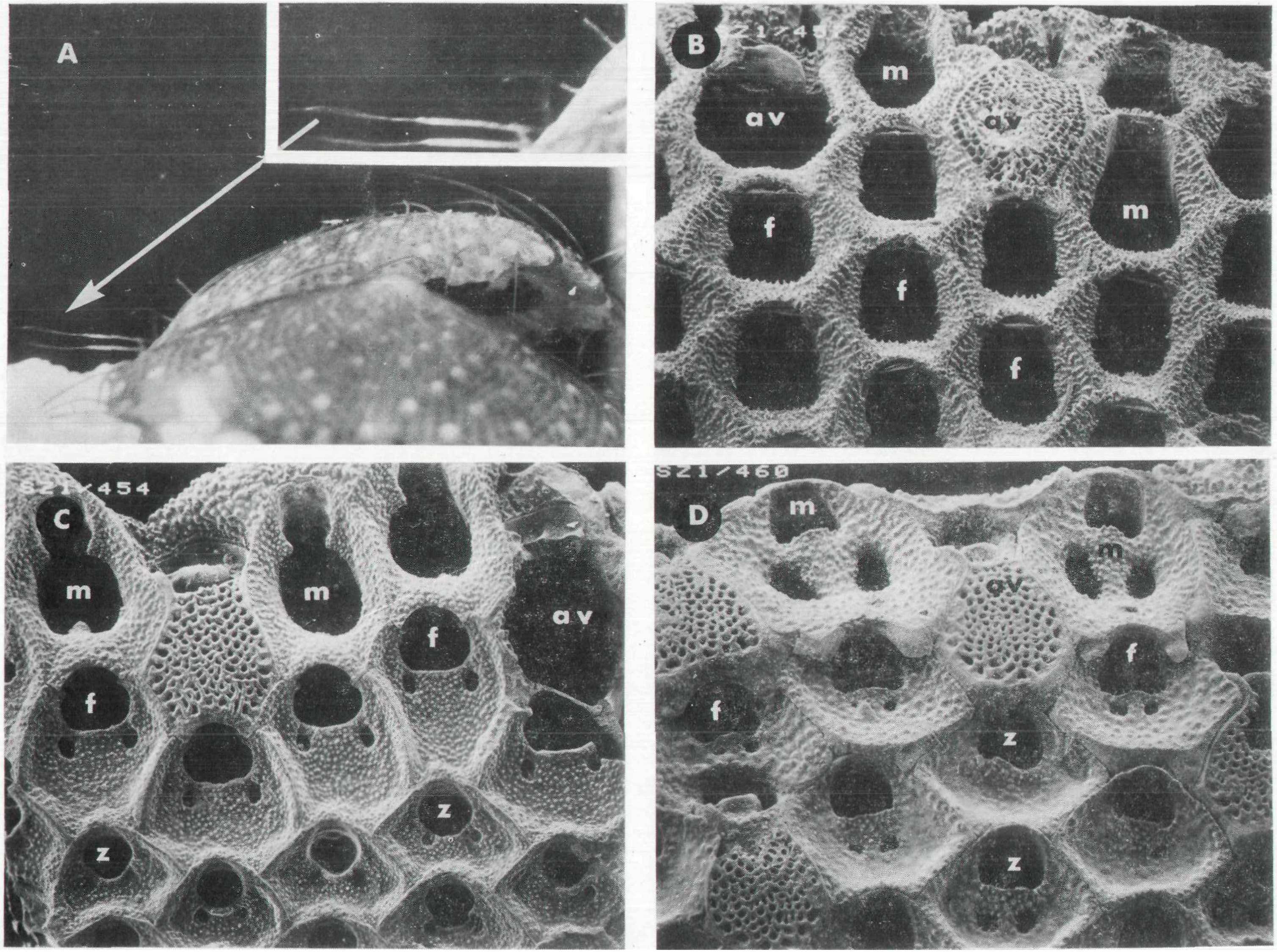


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PLATE I

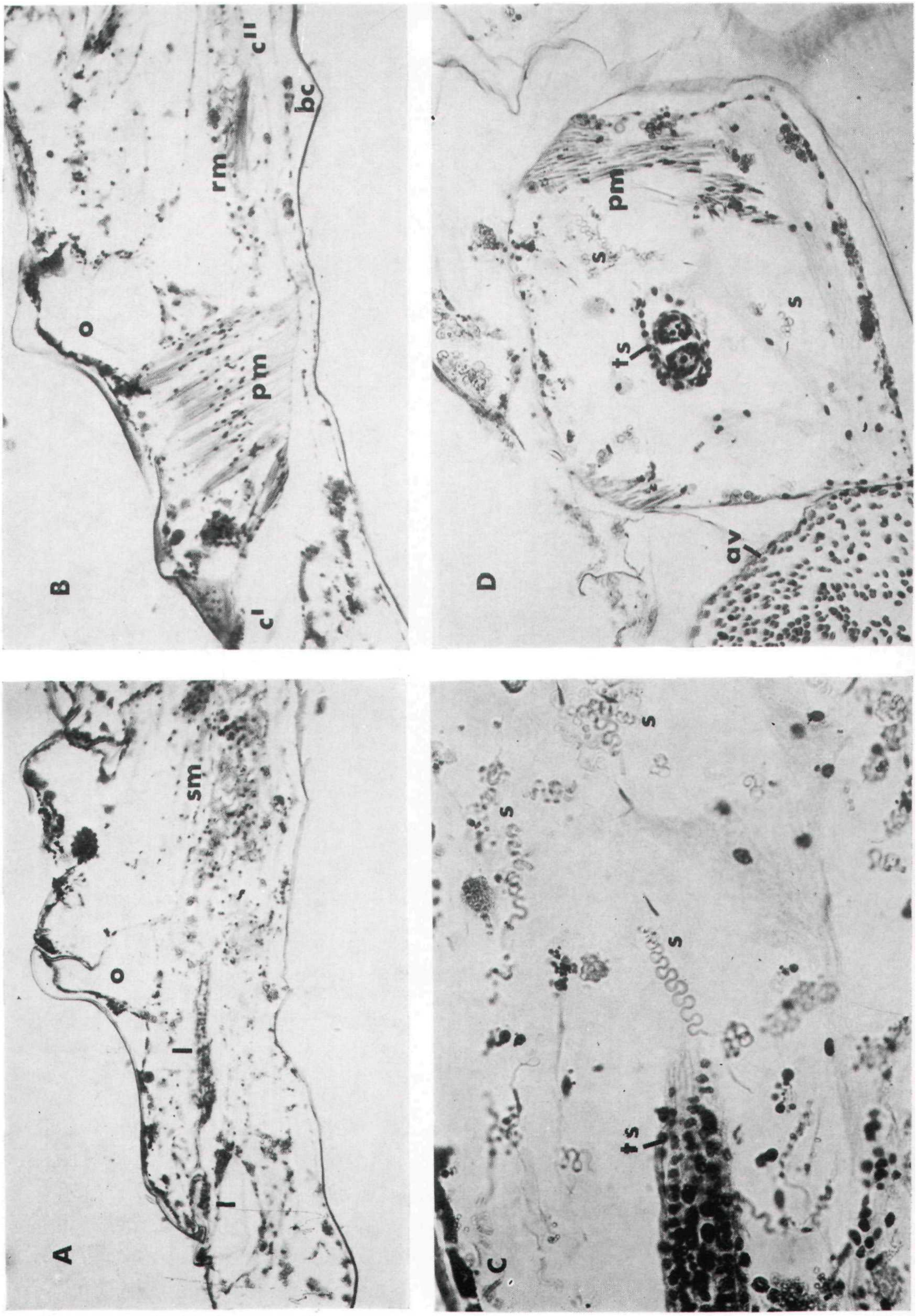

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PLATE II

movements (see Pl. I, A). Withdrawal was also rapid, but required several distinct muscular contractions. Elongated lophophores were protruded from 5 to 8 zooids simultaneously, but were confined to zooids occurring at, **or** up to three astogenetic generations from the growing margins (here called peripheral zooids). No correlation between protrusion and light level was obvious. Examination of decalcified, stained, serial sections revealed the presence of large quantities of sperm in the visceral coeloms of the peripheral zooids. This was correlated with the presence of lophophores with only two tentacles, and with very well-developed retractor and parietal muscles, quite unlike those of more centrally placed zooids. The cystid cavity of the peripheral zooids is unusually long and extends beneath 3 to 5 zooids of earlier astogenetic generations (see Pl. II, B). The sperm, recognized by their deeply stained, elongated heads and spirally contracted tails (see Pl. II, C), were absent from all autozooid coeloms. Zooids occurring from 2 to 6 astogenetic generations from the growing margin (here called subperipheral zooids) contain ovaries placed in the centre of the basal wall. Some of the larger ovocytes show heads of sperm, but no sperm was present in the visceral coeloms of subperipheral zooids. These zooids also show a small, distal concavity (see Pl. II, A, B) and it is inferred that they are female, brooding zooids and that the concavity could accommodate a developing embryo. Lophophores were present in some subperipheral zooids, their tentacle length and number appear to be the same as those of autozooids.

Examination of complete colonies and their skeletons reveals that there are small, but consistent differences in the size, proportions, degree of cryptocyst development and opercular dimensions among the autozooids, the subperipheral (female) zooids and the peripheral (male) zooids. Female zooids have slightly raised, concave distal walls and wide opercula; male zooids are longer, have reduced proximal cryptocysts and narrow opercula (see table 4). A preliminary survey of numerous specimens in the British Museum Collections shows that marginally placed zones of zooids with discontinuously different morhologies are present in the larger colonies of nearly every species. In S. *bimorphocella* Maplestone and S. *partipunctata* Maplestone, inferred male, female and autozooid zones are present (Pl. I, B, C, D). In S. *squamosa* Tenison Woods and *S. nítida* Maple-

PLATE II

Photographs of stained serial sections of decalcified colony of S. *maculata*, Townsville, Australia, BMNH 1980.1.20.2.

A. L.S. near periphery, showing brooding zooid with distal expansion (o), part of male zooid with lophophore (*l*) and sperm masses *(sm)*. X 90.

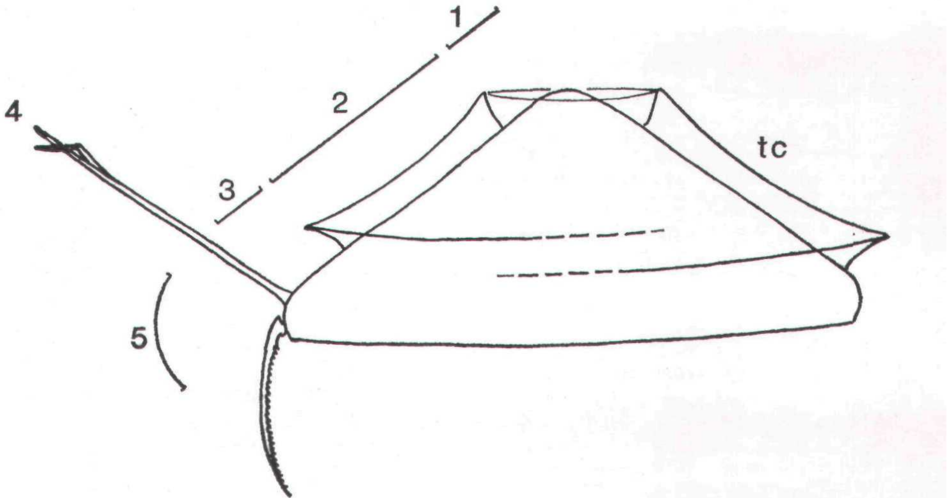
B. L.S. near periphery, another section near lateral wall of the same zooid, showing frontal membrane of male zooid depressed by parietal muscles *(pm)*, part of retractor muscle *(rm)*, distal expansion of brooding zooid *(o)*, and basal, colony-wide coelom *(bc)*. Note part of the elongated cystid cavity of the next, more peripheral male zooid *(c'-c")* ; approximately only half the full length is shown in this photograph. X 143.

C. L.S. part of male zooid, showing introverted tentacle sheath (*ts*) and sperm (*s*). X 400.

I). T.S. male zooid, showing paired tentacles within introverted tentacle sheath *(ts)*, and parietal muscles *(pm)* and sperm (s). Section of avicularian muscle at left *(av)*. X 180.

stone only two kinds of zooid, autozooids and large peripheral zooids of unknown function, have been recognized to date. In addition, in the larger colonies of all species, the marginal zooids are downcurved and the angle of their frontal walls is almost parallel to the vertical colony axis. The marginal avicularia are often significantly larger than those of the adjacent subperipheral zone. As observed S. *maculata* (and inferred for *S. bimorphocella* and *S. partipunctata)* the downcurved zone is positively correlated with the presence of male zooids with very elongated, centrally directed cystids. In some species (e.g. *Setenaria* sp. 1, see Cook and Chimonides, 1978), the zone of downcurved marginal zooids is followed by a zone of basal avicularia.

It appears that colony growth does not continue after development of the downcurved, marginal series, and that "mature" colonies may be regarded as being composed of as many as five concentric zones, each with different zooid morphologies and functions. The extent and occurrence of these zones have not yet been recognized and defined in all species, but in *S. maculata, S. bimorphocella* and *S. partipunctata* they comprise: 1) a central disc of circumancestrular and other zooids (primary zone of change), which have opesiae occluded by calcification and do not feed, although they may function as a passive, excurrent chimney (see Cook, 1977, 1979); a similar zone exists in the larger colonies of the Cupuladriidae (see Cook, 1965a). 2) A zone of feeding autozooids. 3) A zone of female zooids with a preliminary feeding, and subsequent brooding function. 4) A zone of non-feeding male zooids. 5) A mature zone of downcurved zooids (many of them males) and very large, supportive avicularia and/or basal avicularia (see Fig. 1).



TEXT-FIG. 1

Zonation in colonies of *S. maculata.*

1. Circum-ancestrular zone of non-feeding zooids **(excurrent** chimney ?). 2. Zone of feeding autozooids with outline of everted tentacle crowns shown diagramatically (tc). 3. Zone of feeding and non-feeding brooding zooids. 4. Zone of non-feeding male zooids. 5. Final zone of downturned male zooids and/or enlarged avicularia.

3. Colony reaction to light

Previous observations (see Cook and Chimonides, 1978) showed that colonies of *S. maculata* from a depth of 2-3 metres moved towards light, using the peripheral avicularian setae as a means of locomotion. When species from slightly deeper water (11.5-12 metres) were obtained, the first question arising was, would these colonies also respond to light, and if so, what would be the quality of response and to what levels of illumination. The second question was whether any part of the electromagnetic spectrum in, and immediately adjacent to the visible region, would have any particular effect on colonies.

The original observations used tungsten light and a similar source was used in these observations. As before, colonies were positively responsive to light. The time of onset of response and its level was related to the illumination level, and the direction of movement was most distinct when the incident light was nearest to 90° on one side of the sloping colony surface (taking into account refractive effects). Setal movement was produced on the other side of the colony if a) the angle of the light was raised to shine on the whole surface, and b) the light was directed through the colony, as under strong illumination, colonies are semi-transparent. The ratio of illumination, as expected, is important in directional response.

At 5000 lux (499 W/m^2), the quickest initial responses in active specimens were: setal movement within 2 minutes, standing within 4.5 minutes, and walking towards the light source within 8 minutes. Lethargic specimens did not begin to respond for 10 minutes, but all colonies walked after 30 minutes illumination. At 2500 lux, all responses took about twice as long as before.

These colonies were then kept in darkness for 30 minutes to halt activity with the intention of repeating the experiments. It was found subsequently that response times had diminished noticeably: setal movement occurring after 30 seconds, standing after 2.5 minutes and walking in 5 minutes. When colonies were kept in darkness for 1 hour, the initial response times were repeated. When colonies were first activated at 5000 lux it was possible to maintain all activity for at least 1 hour while reducing illumination levels to approximately 1000 lux. This pattern of response suggested that some form of short-term sensitization was occurring.

Colonies were sensitized in sunlight (2 hours in excess of 5000 lux, measured at 650 W/m^2) and then kept in darkness for 15 minutes until motionless. Two lamps were then positioned at 90° to the colony surface on opposite sides. One side was illuminated at 300 lux and setal movement occurred after 2 minutes on that side. When the direction of illumination was reversed the setae on the darkened side stopped activity and movement began on the lighted side within 30 seconds. This response was readily repeatable. Illumination on one side was then decreased progressively in an attempt to find the light level at which movement would cease. A period of 15 minutes was allowed for each level. Slowing of setal movement, but not cessation, was detected at 50 lux, the lowest controllable level of lighting. After 30 minutes at this level, the light was turned off; activity ceased within 7 minutes. When again illuminated at 50 lux, setal movement was resumed within 30 seconds. These observations were repeated several times with different colonies with the same results.

The tungsten light source showed negligible emission in the ultra-violet frequency range. As sunlight contains ultra-violet (290nm) and water transmits to below 200 nm, a soft ultra-violet source (Thorn Blacklight blue) was used on sensitized specimens. No reaction was apparent. It was already known that colonies were indifferent to the broad spectrum infra-red heaters used in the aquarium, as limited by water absorption. Tungsten light has, however, a high proportion of infra-red radiation (see Tables 1-3). The effects of infra-red radiation were therefore further tested by using sunlight sensitized specimens and the tungsten light source with a Wratlen 87 filter which occluded the visual spectrum to about 760 nm. Without the filter, emission of the source was measured at 5000 lux. The filter was introduced and the position of colonies was marked and they were observed using background illumination of an estimated 5 lux only. No response was apparent.

The visible spectrum was then investigated. This was divided into the three primary light colours using photographic filters, Ilford Tricolour Blue (380-500nm), Kodak Wralten 58 Green (480-605nm) and Red (similar to Kodak Wratten 25 red/stereo red 26, which showed transmission from 600nm onwards). It was known that none of these filters would have 100 p. 100 transmission in their respective passbands. As in the case of the visual blocking filter (87) used previously, an illumination of 5000 lux without filter was used in the anticipation that with a filter sufficient light would still be present to initiate a response. As all the filters showed an addilional passband from 760nm onwards, a series of infra-red absorbing filters was also introduced, limiting transmission to below 700nm.

All observations used sensitized specimens. Those illuminated with blue or green light responded as if no colour filtration had been present, showing setal movement within 30 seconds, standing within 3 minutes and walking after 6 minutes. When placed in the dark, all activity ceased. In red light most colonies showed little or no response, although some showed setal movement which soon ceased. One colony everted three lophophores but showed no setal movement. When the specimens were placed in sunlight (660 W/m^2) all immediately showed activity culminating in walking. Some colonies were then "shaded" using a red filter. Within 15 minutes they became inactive, but resumed activity rapidly when the filter was removed.

Subsequent trials using daylight-sensitized specimens involved transfer of colonies from one colour to another in various combinations, in order to confirm responses. Feeding was seen in two cases only, on transfer from blue to red light. Cook and Chimonides (1978) noted that daylight-illuminated colonies fed readily in lower light intensities during the evening. This would correlate with decrease in overall intensity of light and a shift towards the red end of the spectrum. No feeding responses could be elicited to order, however. In one case of red-to-blue, and one of green-to-blue, transfer, specimens remained inactive until again exposed to sunlight (626 W/m^2). Again, this response could not be produced to order, nor was there any other evidence suggesting that red light was actually antagonistic to activity.

An interference wedge monochromator, band width 20nm, was used to measure the threshold response wavelength. This was recorded at 560 run, emission being held at 2 W/m^2 over the band 460nm to 660nm. At each stage the colonies were given 15 minutes to show response, with progression in 20nm steps. Wavelengths below 560nm were correlated with activity of colonies, wavelengths above 560 nm were correlated with inactivity.

DISCUSSION

Epizoic forms are frequently found on the basal side of lunulitiform colonies (see Cook, 1965b). The frequency of occurrence of tube-worms in this population of *S. maculata* may be merely a function of the general lack of solid substrata in a "sand fauna" environment, or may be a specific, symbiotic association. The cleaning symbiosis of the small isopods may also be obligatory rather than specific, but both animals benefit from the association. Somewhat similar crustacean-lunulitiform bryozoan cleaning associations, involving small pagurids and colonies of Cupuladriidae, are known from "sand faunas" in west Africa (see Cook, in press). The orientation of the mouths of the tubes of all these epizoic forms, which extend in a peripheral direction as the bryozoan colony grows larger, suggests an organized response to their substratum. In the case of the isopods this response is also correlated with its food supply and methods of feeding.

It is inferred that several species of *Selenaria* exhibit a high degree of sexual polymorphism. In *S. maculata,* the observed correlations of specialized morphology, behaviour, and the presence of sperm and ovaries, allow confident inference that the rôle of the more marginally placed zooids in mature colonies is sexual. This inference is supported by the absence of polymorphic zooids in astogenetically young colonies, and by the presence of similar, concentric zones of polymorphic zooids in the larger, mature colonies of other species. *S. maculata* exhibits relatively slight skeletal polymorphism; the subperipheral and peripheral zooids of *S. bimorphocella* and *S. partipunctata* are much more distinctive (see Pl. I, B, C), and were first described by Maplestone (1904). It is interesting that in these two species, the inferred large, male zooids have elongated opesiae or opesiules which may be correlated with the occurrence of well-developed parietal muscles like those observed in S. *maculata.* These are presumably required in order to protrude the extremely elongated male lophophore. Inferred brooding zooids are all raised distally, and have wider opercula than those of male zooids and autozooids. These kinds of dimorphism are frequently found in cheilostome brooding zooids and are presumably respectively correlated with the accommodation, and eventual release, of the larvae. Brooding zooids were briefly described by Levinsen (1909) in an un-named species of *Setenaria,* but they were not figured.

TABLE 4
Average measurements (in mm) of zooids of A) *S. maculata,* B) S. *bimorphocella* and C) S. *partipunctata.*

	Autozooids			Female zooids			Male zooids		
	A	B	C	A	B	C	A	B	C
Lz	0.30	0.24	0.21	0.35	0.40	0.21	0.50	0.42	0.32
lz	0.33	0.35	0.19	0.37	0.36	0.21	0.45	0.30	0.24
L opesiae	0.24	0.09	0.09	0.22	0.16	0.09	0.30	0.28	0.08
L opesiules	—	0.02	0.02	—	0.05	0.02	—	—	0.08
l opesiae	0.16	0.12	0.09	0.19	0.18	0.09	0.23	0.21	0.09
l opesiules	—	0.02	0.02	—	0.04	0.02	—	—	0.06
l opercula	0.12	0.10	0.06	0.16	0.16	0.10	0.12	0.10	0.05

The highly modified, non-feeding lophophores of the male zooids of *S. maculata* (see Pl. I, A) resemble those already known in the genera *Hippopodinella* and *Hippoporidra,* both in morphology and behaviour (see Cook, 1977, 1979). Distinctive behaviour during emission of sperm in unmodified male zooids has been described for several species by Silén (1972). In some species, only the distal pair of tentacles is involved in emission. Skeletally polymorphic male zooids are known in several other genera, notably in *Hippothoa* (see Ryland and Gordon, 1977), but the behaviour of their protruded lophophores has not been recorded. In the absence of such observations, it is perhaps premature to correlate that of the elongated lophophores with colony mobility. However, it is interesting that although species of *Hippopodinella* and *Hippoporidra* may encrust sessile substrata, they are most frequently (in some cases exclusively) associated with living molluscs, or with mollusc shells occupied by living pagurid crabs, and are therefore secondarily mobile (see Cook, in press). In addition, if the highly modified avicularia of *S. maculata* and similar species are indicative of potential colony mobility, as inferred by Cook and Chimonides (1978), it may be very significant that the species with this type of avicularia are also exclusively those which show zones of inferred male and female polymorphic zooids (see Pl. I, B, C, D).

Colonies congregate under the influence of light, and are often in contact with one another (see PL I, A and Cook and Chimonides, 1978, PL I, C). As yet, however, the nervous system of *Setenaria* has not been investigated, and no sensory system or organs are immediately apparent. Attention is drawn to a similar problem in recognizing photoreceptors in echinoderms (Millott, 1966, 1975). The extreme elongation of the male lophophores of *S. maculata,* which extend outwards 6mm from the edge of the colony (a length approximately equal to its radius), makes it unlikely that the colonies are self-fertilized. The excurrent patterns of water flow are probably centrifugal at the periphery and vertical at the centre of feeding colonies (see Cook and Chimonides, 1978, and Fig. 1), so that even if a male lophophore was directed centrally, it is unlikely that many sperm would be caught in the feeding current of the subperipheral, female zooids. Fertilization is apparently internal. Some female zooids have been seen to possess lophophores early in ontogeny, and sperm are therefore inferred to have entered there visceral coeloms via a coelomopore placed at the base of the distal pair of tentacles, a position which it is generally assumed to have throughout the Cheilostomata. The presence of sperm heads in immature ovocytes has been reported for several species by Marcus (1938:81, 119), who described precocious fertilization, followed by ovocyte growth before eventual cleavage. The brooding of embryos has not been observed in S. *maculata;* presumably they develop in an interior ovisac in a similar manner to those of the Cupuladriidae.

Initial response rate of colonies to light appears to be proportional to the level of incident illumination and indicates some type of photobiochemical reaction. Sensitization occurred, and lasted up to one hour, during which low light levels stimulated response within 30 seconds. The component of light which produced sensitized response was identified as blue-green of wavelength 400-560nm. Behaviour indicated that the response may be two-staged, the first stage involving energy accumulation leading to sensitization, the second stage involving a trigger mechanism in the blue-green part of the spectrum. Colonies became lethargic and moribund before the wavelengths involved in energy accumulation could be defined, but as sensitization could be induced by tungsten light passing through glass, the ultra-violet portion of the spectrum can be ignored. Spectral response in sea water shows a drop in transmission towards the red with increasing depth (see Richter, 1968:387, Fig. 2), so there is a possibility that blue-green light may be the source of energy accumulation as well as he trigger of response.

That light should act as an attracting agent to a mobile marine animal implies a danger of "marooning", and it is to be expected that an upper limit of response exists. It was noticed that some standing colonies showed a reversal of behaviour in sunlight, setal movements occurring on the side away from the light and ceasing on the lighted side. It was not possible, however, to reproduce this behaviour with tungsten light. The significance of the thin film of red algae on setae and frontal membranes of freshly collected colonies is not known, but it may be correlated with attenuation of blue-green light.

In conclusion, it is obvious that S. *maculata* has one of the most integrated forms of bryozoan colony known at present. Much further work is needed, including field observations, on the behaviour and functional morphology of this and other lunulitiform species. The presence of skeletal evidence which may be correlated with function makes such observations highly significant in the study of fossil assemblages. *Selenaria, Lunulites* and related genera have a long fossil history, and in addition, colonies are often found in large numbers and are of stratigraphical and palaeoecological value (see Lagaaij, 1953 and Hakansson, 1975). The recognition of locomotory potential and of astogenetic stages of sexual maturity may make it possible to analyse growth series in fossil populations and to infer environmental parameters with much greater confidence.

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Summary

Observations under laboratory conditions have continued on living colonies of *Selenaria maculata* Busk from Australia. Red algae are epiphytic on upper colony surfaces, and epizoic forms include tube-worms, sponges, mollusca and a denostome bryozoan, *Sundanella* sp. Minute tube dwelling isopods act as cleaning symbionts. Zooids of the outer zones of mature colonies are polymorphic and sexual in function. Subperipheral zones of zooids with concave, raised distal walls have ovaries and are inferred to be female, brooding zooids. Peripheral zones of zooids with well-developed muscle systems and modified lopophores (consisting of long, paired, unciliated tentacles and greatly elongated tentacle sheaths) contain sperm in their visceral coeloms. They are inferred from morphology and behaviour to be male zooids. The occurrence of similar zones of polymorphic zooids in other species of *Selenaria,* and their significance in study of fossil populations is briefly discussed. Colonies respond to blue-green visible light and move towards it, but are apparently unaffected by red light or by ultra-violet and infra-red radiation.

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