OBSERVATIONS ON LIVE LUNULITIFORM ZOARIA OF POLYZOA.

by

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Résumé

Les observations sur les colonies lunulitiformes vivantes des Bryozoaires *Discoporella umbellata* et *Cupuladria doma*, draguées dans la baie de Funchal, Madère, semblent montrer que ces colonies ne sont pas capables de se mouvoir librement dans l'eau, comme on l'a suggéré. Les colonies se maintiennent juste au-dessus de la surface d'un substrat instable au moyen de leurs longues soies vibraculaires périphériques et sub-périphériques. La réaction automatique des soies à une excitation par pression sur la surface frontale du zoarium permet aux colonies de regagner la surface du substrat quand elles sont couvertes de vase ou de sable, d'éliminer les dépôts qui se font sur la surface frontale et, parfois, de réussir à renverser leur position quand elles sont tournées face basale en haut. La forme zoariale conique, chez les Bryozoaires, est à peu près toujours associée à un habitat sableux ou vaseux, mais les genres dépourvus de vibraculaires semblent être en général ancrés par des rhizoïdes sur le substrat et ne sont donc pas aussi vraiment libres que les colonies des espèces observées ici.

INTRODUCTION

The problem of the mode of life of Polyzoa with apparently free-living conical colonies has been discussed by many authors. The only published record (1) of observations on live conical zoaria is that of Whitelegge (1888:21), who examined specimens of *Bipora* [*Conescharellina*] *philippinensis* (Busk) from Australia. The zoaria of *Conescharellina* have rootlets on the convex ("frontal") surface (see Harmer 1957:722-6), and are probably anchored by them above a muddy substratum, perhaps with the flattened, non-zooecial ("basal") end upward. Maplestone (1910:3) first suggested this orientation. Several subsequent authors have assumed the same orientation for lunulitiform zoaria (see Harmer 1931: 150-151 for summary). The lunulitiform (2) zoaria, though conical, are not closely comparable

(1) Immediately before my sending this note to press, the observations of Marcus and Marcus (1962: 298) on lunulitiform species reached the Museum. Some of their results and conclusions are similar to those given here.

(2) Term defined by Lagaaij (1953 : 13) as follows :—"free, conical zoaria, equipped with vibracula, in genera like *Lunulites, Cupuladria, Discoporella, Selenaria,* etc.". These genera are probably not all closely related.

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with that of *Conescharellina*. They differ particularly in the concavity of the basal surface, the absence of rootlets (in most if not all of them), and the presence of vibracula.

Busk (1854:104,106) first suggested the possibility that the long vibracular setae of his "Selenariadae" (which then included *Selenaria, Cupularia* and *Lunulites*), were "subservient to locomotion". Hincks (1880:181 n.) stated that Busk had informed him that this "has been confirmed by actual observation". Canu & Bassler (1927:17; 1929:482) supposed that these conical zoaria (some with and some without vibracula), had the power of zoarial movement, and further postulated a hydrostatic mechanism, which had been first suggested by Canu (1915:21).

The lunulitiform zoarium consists of an ancestrula and circle of central zooecia which encrust the original substratum (usually a small sand grain or Foraminiferan). The zooecia subsequently developed have no substratum, and grow outward from this base which becomes the apex of the conical colony. The convex "frontal" surface of the zoarium consists of the frontal surfaces of the regularly arranged zooecia and vibracula. The more or less concave basal surface is secondarily thickened and bears furrows, ridges or porous sectors (see Lagaaij 1953, and Cook MS). In *Cupuladria* and *Discoporella* there is a vibraculum distal to each zooecium, with a large chamber, long seta, and powerful muscles. In any radial row the direction of asymmetry of the vibracula is alternate. No evidence of rootlets has been found in this type of zoarium.

Lunulitiform zoaria are almost invariably associated with sandy, silty or muddy bottoms, and their form is apparently correlated with this type of habitat. In 1881, 9 zoaria (belonging to 2 species, Cook MS), were taken at the surface of the Atlantic (27°16'N, 23°21'W); these were listed by Silén (1942:13) who remarked on the lack of any other similar record. This still remains a unique occurence, and the observations below do not tend to substantiate the possibility of zoaria being normally capable of free movement in the water.

OBSERVATIONS

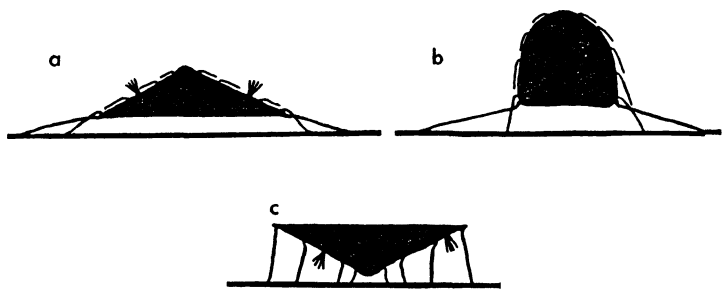
Live zoaria of *Cupuladria doma* (d'Orbigny) and *Discoporella umbellata* (Defrance) were dredged from 33m. and 50m. in the Bay of Funchal, Madeira, in March, 1963. The bottom consisted of very fine sand and stones weathered from volcanic rock. The numerous colonies of *D. umbellata* were small (largest diameter 9mm.); those of *C. doma,* which were obtained only from 50m., were comparatively large for this species (largest diameter 5mm.). Numbers of apparently dead colonies were found, but some of these were budding new groups of zooecia from the periphery, producing irregular zoaria. The proportion of living to dead colonies was higher in the shallower haul, the numbers being approximately equal. It is difficult to estimate the abundance of colonies in a given area, but in about 2-3 gallons of sand obtained from a 5-minute haul, during which time the dredge

moved very little, more than 250 colonies were found easily, and the total number present was probably far greater.

21 live zoaria of *D. umbellata* were successfully transported to the British Museum (Natural History) where they were kept on sand in a tank of aerated sea-water at an average temperature of 16°C. The photographs on pl. I, A-B and C-D, were taken respectively 16 days and 28 days after collection of the colonies.

Live zoaria were pink or brownish-pink in colour and the number of tentacles of the polypides of both species varied from 13-16. When released from the surface-film of the water the colonies sank immediately, and in spite of their shape, did not show any evidence of "planing" through the water. They did not use their vibracula for any swimming movements.

When placed in glass dishes those colonies which settled with the basal side downward assumed (within 3-10 minutes) a position slightly raised above the substratum, supported by the tips of the



TEXT-FIG. 1

Diagrammatic silhouettes of live lunulitiform zoaria on glass in lateral view. a. - *Discoporella umbellata*, basal side downward, tentacles of 2 polypides extruded. — b. - *Cupuladria doma*, basal side downward. — c. - *D. umbellata*, basal side upward, tentacles of 2 polypides extruded.

peripheral and sub-peripheral vibracular setae, which maintained an "open" position (i.e. directed radially and distally). The sub-peripheral setae touch the substratum at a more acute angle to the vertical axis of the colony than the peripheral setae (see text-fig.1,a). Colonies in this position on sand are extremely stable and are not shifted by agitation of the water. Colonies placed in close juxtaposition raise themselves temporarily higher on their setae, but do not appear to be capable of sustained lateral movement to disengage themselves. Those colonies which settled with the basal side upward appeared to make repeated attempts to right themselves. The setae all swung swiftly to a position at right angles to the frontal surface, and after 5-10 seconds gradually moved back to the open position. On a glass surface none of these movements were successful, but some of the zoaria placed on sand and gravel did turn over within 24 hours. Only one colony reversed its position while being watched and the success seemed to be quite fortuitous. The zoarium sank edge downward between two small stones as a result of gradual random shifting caused by the repeated movements of the setae. From this position the setae in contact

with stones at the lower edge swung repeatedly through 180°, while those in free water on the upper edge remained still. Gradually the zoarium shifted upward until nearly horizontal, whereupon the peripheral setae ceased to move, remained open, and maintained the colony above the stones. The entire process lasted approximately 40 minutes. The setae of the zoaria which remained with the basal side upward eventually ceased moving and then opened to a position at acute angles to the frontal surface and, thus raised above the substratum, the zooecia were able to extrude their tentacles (see text-fig.1,c).

Washed gravel placed in shallow trays of sea-water seemed at first to contain few living colonies, but within 1/2 hour several had appeared on the surface, and at least 50 colonies were evident within 15 hours, all with their basal side downward. These were removed and a further similar number more had emerged after 24 hours. Sand placed on top of the colonies was removed gradually by regular sweeping movements of the frontal setae, the peripheral setae remaing open. Small grains dislodged by the setae rolled down the sloping sides of the zoarium. The process by which the colonies regain the surface when buried is essentially the same. The surrounding substratum is gradually raised by the accumulation of detritus removed from the frontal surface by the frontal setae, and each slight upward movement is maintained by the peripheral setae. Comparably the same cleaning process maintains the solitary coral, *Fungia,* in its position on the surface of sand (see Marshall and Orr 1931). *Fungia* cleans itself by means of ciliary currents, but the Polyzoans were never seen to utilize the ciliary currents of their expanded polypides in this way, all the cleaning of the surface of the colony being effected by the setae. Infrequently and irregularly, all the supporting setae make a very small movement together, the resulting slight jerk causing sand grains to roll off the surface without any movement of the frontal setae.

In *D. umbellata* stimulation of the vibracula by light pressure with a fine camel hair brush resulted in closure of the setae. The effect was the same when only the frontal membranes of the zooecia were stimulated. Pressure on the central zooecia produced a wave of reaction, which started with the nearest setae and finally involved the peripheral setae if the pressure was maintained. Stimulation of only one side of the colony produced a similar reaction which was confined to that segment of the circle surrounding the focus of pressure. The closing movement of the setae over the hairs of the

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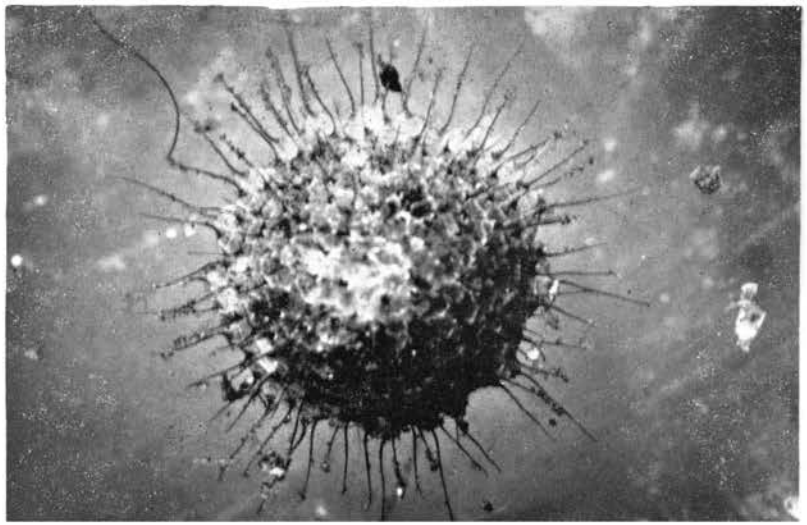
PLATE I

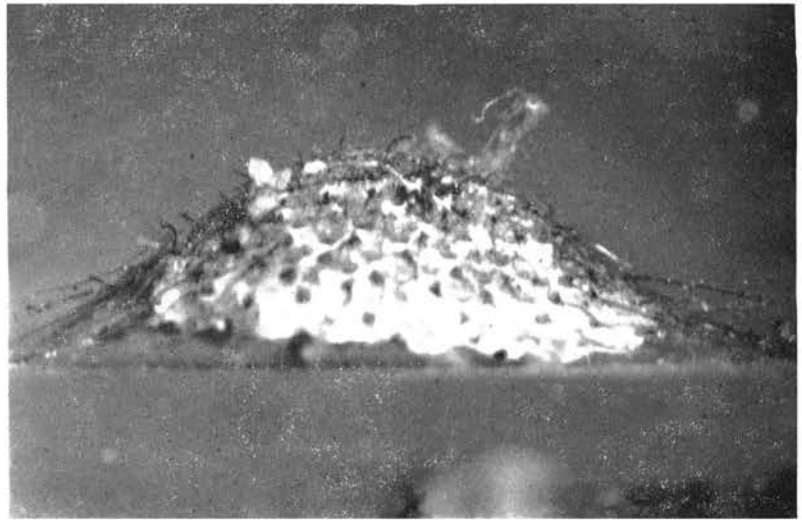
Live colonies of *Discoporella umbellata* (Defrance), photographed on a transparent, smooth substratum. Figure A approximately X 7, figures B, C and D approximately X 10,5.

A. - Frontal (upper) surface, showing vibracular setae in the open, supporting position. — B. - Lateral view, showing colony raise don the left side by open supporting setae. Sand grains (on the left) and filamentous detritus (on the right) being cleared from the surface by the erect frontal setae. — C. - Lateral view, colony with basal side upward; showing some setae half-closed, supporting the colony, others still in the open position. — D. - Lateral view, colony with basal side downward; frontal surface stimulated by hairs of a brush. Showing frontal setae (on the right) in the closed position over the hairs.

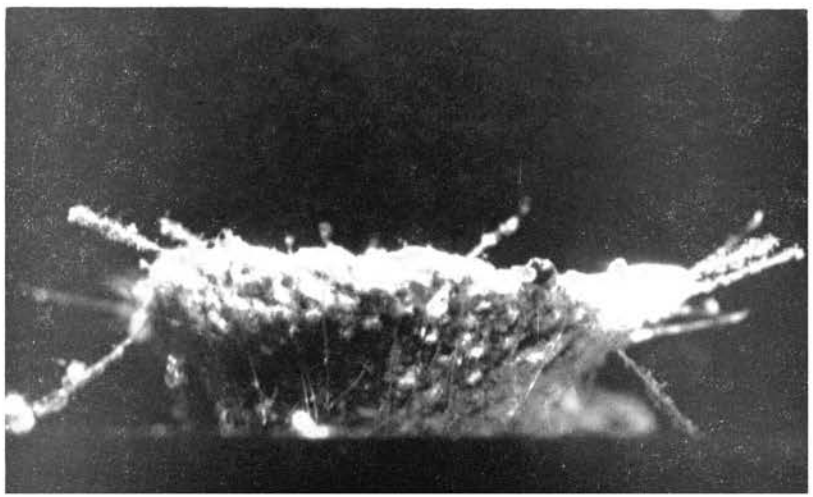
A



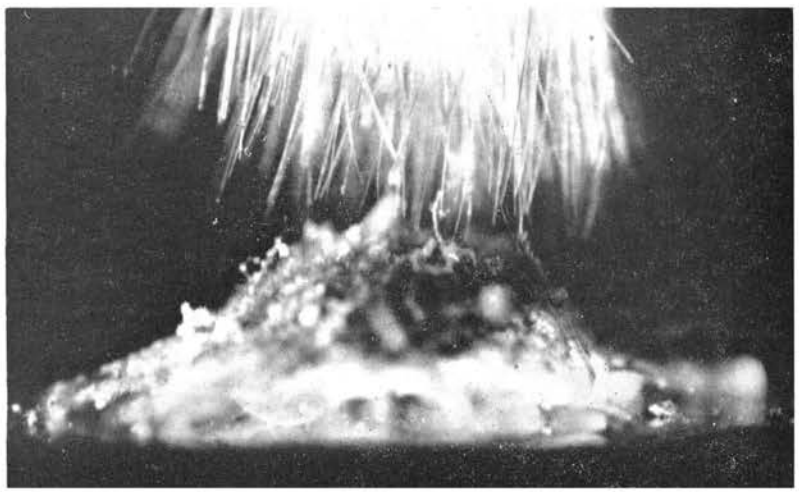
B



C



D



P. L. Cook

brush was rapid and powerful, and the colony could be lifted to, and occasionally above, the surface of the water, while the setae remained closed. The opening movement was more gradual, the setae moving individually and at random. When the brush was kept in one position for 2-3 minutes the more central setae remained closed over the hairs of the brush, but the peripheral setae gradually swung back to the open, supporting position. The frontal surface of the zoaria was frequently covered by filamentous fragments held by individual setae, but generally sand grains and solid substances were not held (see pl. I, fig. B). Some of the colonies kept at the British Museum showed evidence of sand grains being replaced on the surface when the colonies were exposed to strong light, but not all the colonies so treated reacted in this way. Frontal setae receiving no stimulation were normally in the open position.

Several zoaria had growing buds at the periphery. Those which had not developed the distal vibracular chamber were protected by the setae of the two next proximal-lateral zooecia from contact with the substratum. Those buds which had developed a vibraculum with a seta were seen to fold frontally when the seta closed, even though they were partially calcified basally.

The central zooecia of those colonies which were regenerating irregularly were often eroded, but those of other colonies were the same pink colour as the zooecia with polypides, and their frontal membranes were complete and glistening. No polypides were present in them, but the membrane had the convex appearance seen in ordinary zooecia when the frontal muscles are relaxed and the polypide retracted. The function, if any, of these zooecia is at present unknown, but it does not appear essential for them to be exposed, as several colonies evinced normal rections when the central area was covered by a Foraminiferan. Pressure stimulation of the surface of the Foraminiferan did not result in closure of any setae, however.

Small colonies of *Barentsia sp.* (Polyzoa, Entoprocta) were growing on several specimens of *D. umbellata.* The stolons ran between the zooecia, and the muscular peduncles twitched the calyces away from moving vibracular setae when they touched each other.

Only one live colony of *Cupuladria doma* was found, although 14 dead zoaria were present in the 50m. haul; its mode of life and reactions were essentially the same as those of *Discoporella umbellata,* but some slight differences were noted. Colonies of *C. doma* are small, high and steep-sided. Compared with those of other species the peripheral setae are extremely long in proportion to the size of the zoarium, with the result that the colony is raised further from the substratum than in *D. umbellata* (see text-fig.1,b). The movements of the setae on stimulation were more vigorous, and generally they all reacted to a stimulus anywhere on the surface, except at the extreme periphery where pressure caused only the setae in that segment to close. Zoaria of *C. doma* are frequently as high as they are wide, whereas those of other species are usually flatter; the proportionately longer setae of *C. doma* thus appear to be necessary for stability. The growing buds are directed almost vertically downward, and are protected by the greater raising of the zoarium above the substratum.

DISCUSSION

There is probably little turbulence at the depths at which lunulitiform zoaria occur, for none of them are found in shallow water. Thus their principal needs are to maintain a stable position just above an irregular and occasionally shifting substratum, and to clean their upper surfaces from settling deposits.

The colonies described above fulfil all these requirements. They achieve stability by means of two circles of setae which are in contact with the substratum at different angles, and are sensitive to the slightest variation on its surface. The setae increase the horizontal surface area of the colony without materially affecting its weight. Although they are presumably more efficient with the basal side downward, the zoaria observed can feed successfully when reversed. If covered by sand they can regain the surface of the substratum. It should also be noted that, when broken, they are capable of regeneration to a shape approximately that of a normal zoarium (see Dartevelle 1935:559-561, and many specimens in the Museum Collection).

Both at Madeira and at the Museum, the colonies were observed under abnormal conditions, the hydrostatic pressure being considerably less, and the light intensity greater, than in their normal habitat, although the temperature range of the water was similar. The extrusion of the tentacles, the continued feeding, and the general consistency of the reactions of the zoaria indicated that they had adapted themselves to this new environment, and their behaviour was probably similar to that at the depths from which they were collected.

Certain other lunulitiform zoaria (e.g. *Heliodoma* and *Setosellina*) also have large interzooecial vibracula, with long setae, alternating with the zooecia. In Recent *Lunulites,* the vibracula occur in radial rows which alternate with the radial rows of zooccia, and in *Selenaria* the vibracular individuals are truly vicarious and are comparatively sparsely distributed. It seems possible that these zoaria and their vibracula cannot all function in the same way as those of *Discoporella,* and observations on living material are very desirable.

Harmer (1957) described several Ascophoran species with conical zoaria, and concluded (p. 649) that the majority were attached by rootlets. Some of these species have avicularia, but none have vibracula.

Summary

Observations on living lunulitiform zoaria of the Polyzoa *Discoporella umbellata* and *Cupuladria doma* dredged from the Bay of Funchal, Madeira, have apparently shown that they are not capable of moving freely in the water, as had been suggested. The colonies maintain themselves just above the surface of an unstable substratum by means of their long peripheral and sub-peripheral vibracular setae. The automatic reaction of the setae to the stimulation of pressure on the frontal surface of the zoarium enables the colonies to regain the surface of their substratum when covered by mud or sand, to clean the frontal of deposits,

and in some cases to succeed in reversing their position when turned with the basal side upward. The conical zoarium of Polyzoa is almost invariably associated with a sandy or muddy habitat, but those genera not provided with vibracula appear generally to be anchored to the substratum by rootlets, and are thus not as truly free-living as the colonies of the species observed here.

Zusammenfassung

Beobachtungen an lebenden, mondförmigen, in der Bucht von Funchal (Madeira) gefischten Kolonien von *Discoporella umbellata* und *Cupuladria doma* zeigen, dass sie anscheinend nicht frei beweglich im Wasser leben, wie bisher angenommen wurde. Die Kolonien halten sich an der Oberfläche des beweglichen Untergrundes mit ihren langen, peripherischen und subperipherischen Vibraculärborsten fest. Die automatische Reaktion dieser Borsten wird durch Druck an der frontalen Fläche ausgelöst und ermöglicht es der Kolonie, sich wieder an die Oberfläche emporzuarbeiten, wenn sie von Schlamm und Sand bedeckt wurde ; sich zu reinigen, und sich umzudrehen und wieder aufzurichten, wenn dies nötig ist. Man findet die kegelförmigen Kolonien der Polyzoa fast immer an sand- oder schlammreichen Fundorten. Gattungen, die anscheinend keine Vibracularien besitzen, sind gewöhnlich durch Wuerzlein am Boden verankert und können deshalb nicht als echte, frei lebende Arten betrachtet werden, wie die beiden obigen Spezies.

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