THE DEVELOPMENT OF *CONOPEUM SEURATI* (CANU), AND SOME OTHER SPECIES OF MEMBRANIPORINE POLYZOA.

by

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Résumé

Les auteurs ont observé la fixation et la métamorphose des larves complètement développées de *Conopeum seurati* (Canu). L'astogénie précoce des colonies est décrite d'après du matériel fixé. Des comparaisons de types d'ancestrula et d'astogénie précoce sont faites pour 15 espèces membraniporines. Trois formes principales de bourgeonnement ont été vues. En gros, elles correspondent au groupement généralement admis de la majorité des espèces en trois genres : *Membranipora, Electra* et *Conopeum,* groupements basés sur les caractères des zoécies développées le plus tardivement. Les espèces de quelques autres genres, comme *Aspidelectra* et *Pyripora,* peuvent présenter, cependant, les mêmes modes de bourgeonnement.

The early development of the larvae of *Conopeum seurati* (Canu, 1928) has been observed (see Cook, 1962). These larvae were very small, and lacked a bivalve shell, which has been seen to develop in the larvae of *Electra crustulenta.* Further collections have shown that the larva of *C. seurati* continues a planktonic life, grows, and also develops a shell before settlement and metamorphosis. Larvae and adult, breeding colonies of *C. seurati* were collected from saline lagoons on the South bank of the River Crouch, Essex, on October 5th and 6th, 1965. The lagoons, situated between the old and new sea-walls, are approximately 100 yards long by 20 yards wide at the widest part, and range in depth from 3 inches to 3 feet 6 inches. The salinity of the water was found to be 28‰, but this probably varies considerably with rainfall (see Cook, 1961:260). Adult colonies were found growing abundantly in the lagoons on the stems of *Ruppia;* the polypides had well-developed intertentacular organs and eggs were present within the body cavities. Tow-nettings were taken over a wide area of the lagoons using a surface sampler of the type described by Willis (1963), and numerous, apparently fully-developed larvae were found. The samples were placed in tanks containing settling frames, and examined for settled and metamorphosed larvae after 24 hours.

The larvae from the tow-nettings had reached a considerably later stage of development than those described by Cook (1962). They

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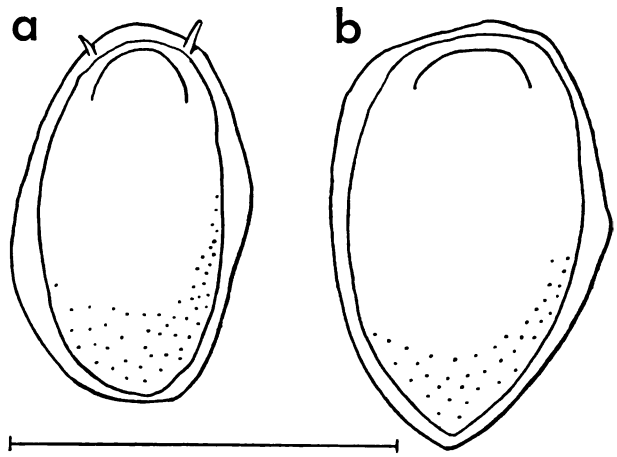
were larger (average dimensions 160 μ in height and 180 μ in length), more triangular in outline, and had developed a clear, light brown, bivalve shell. The sides were flattened and the posterior end was uptilted so that the basal groove between the two valves could be seen posteriorly. The apical region, smaller in proportion than in the younger larvae, was "mushroom" shaped (see Pl. I, 3, 4). There was no granular material on the surface of the valves, as seen in the larvae of *E. crustulenta* and *E. monotachys*.

Ten larvae settled succesfully and metamorphosed; the ancestrulae were watched for 3 days, but become moribund and no further development took place. The dimensions of the ancestrulae varied from La 200-220 μ and la 140-150 μ. The polypides of six of the ancestrulae were seen to have 7 tentacles, one had 8 and another, 6; the number of tentacles observed in polypides of adult colonies is 12-14.



Text-Fig. 1
Conopeum seurati (Canu). Ancestrulae.
a: with paired distal spines (1966.1.8.12.) - b: without spines (1966.1.8.14.). Scale=0.20 mm.

The ancestrulae had no gymnocyst, but a pair of distal spines was present in all but one individual (see Pl. I, 2 and text-fig. 1, a, b). Bobin & Prenant (1962:376, text-fig. 2, IV) described and figured the paired spines, but based their figure of the early astogeny (fig. 2, V), on that given by Osburn (1944), for another, different species (see below).

The early astogeny of four colonies of *C. seurati* has been observed in preserved specimens, growing on glass, collected from the lagoons in 1963 (1963.12.30.3, Cook Coll.). The form of budding is basically the same in all four examples, although varying slightly in detail.

The ancestrulae (which are slightly smaller, on average, La 180-220 μ, than those which metamorphosed in the frames in 1965), each bud only one distal zooecium directly. This zooecium produces one further distal bud, and either one or two distal-lateral buds. Where two distal-lateral buds have been produced, they have both given rise

to a proximally directed zooecium, each of which grows over part of the lateral walls of the ancestrula, and originates the proximal series of zooecia. Where one distal-lateral bud has been produced, it gives rise to a proximal series of zooecia in the same manner on one side of the ancestrula. The proximally directed series on the other side derives from the distal-lateral bud of the second zooecium budded in the distal series from the ancestrula (text-fig. 2). This type of budding shows an interesting variation from that found in *C. laciniosum* and *C. reticulum* (see below).

In a series of papers, Waters (1924, 1925) stressed the importance of the study of ancestrulae and of the early astogeny of Polyzoan colonies. The ancestrula and early astogeny of some species of membraniporine forms have been compared. Three differing forms of growth are apparent and these show some positive correlation with other generic characters associated with the three genera, *Membranipora, Electra* and *Conopeum.*

1. *Membranipora.*

Twinned ancestrulae are known only in *Membranipora s.s.,* and are probably exclusively characteristic of the genus. They have been described in *M. villosa* by Robertson (1908:274) and O'Donoghue (1926), *M. tuberculata* by Hastings (1930:707), *M. savartii* by Marcus (1938:66), and *M. membranacea* by Atkins (1955:446).

In each species, a central distal-median zooecium is the first to be developed. Its rudiment is present soon after the metamorphosis of the larva in *M. villosa,* and it cannot be seen to originate exclusively from either of the twinned ancestrular buds. Each of the twinned buds then produces one distal and two lateral zoeccia. The most proximal-lateral zooecium on each side then buds in a proximal direction, thus forming a circle of zooecia around the twinned ancestrula.

2. *Electra.*

The ancestrula is always single, and the early astogeny is more variable.

In *E. pilosa,* a pair of primary lateral buds develops almost simultaneously, followed by a distal bud, as described by Atkins (1955, text-figs 2 B, C). Bobin & Prenant (1960) made an extremely full study of the characters of *E. pilosa* and of *E. verticillata* (which has frequently been considered a variety of *E. pilosa*), and concluded that these forms were specifically distinct. They found that the number of ancestrular spines was usually 5 in *E. pilosa* and 7 in *E. verticillata.* With one exception (a fragment of *E. verticillata* from Tenby, Cornwall, 1899.7.1.1286, Busk Coll.), specimens from Britain in the British Museum are all referable to *E. pilosa.* There are many specimens of *E. pilosa* from other localities, and a large number of colonies of *E. verticillata* from the French and Belgian coasts, and from west and south Africa, the Indian Ocean and Australia. One specimen of *E. pilosa* from Northumberland (1964.4.10.1), comprises nine young colonies growing upon algae. The number of spines on

the ancestrula varies from 5 to 10. 9 ancestrula have been seen in other British specimens and the number of spines varies from 4 to 8. 3 ancestrulae of *E. verticillata* from Natal (1899.5.1.203, Hincks Coll.) all have 5 spines. It therefore appears that the range of variation in number of spines reported in the ancestrulae of the two species is similar, and is not itself a distinguishing character between them. Waters (1924:598) noted the variability in spine number in the ancestrula of *E. pilosa.*

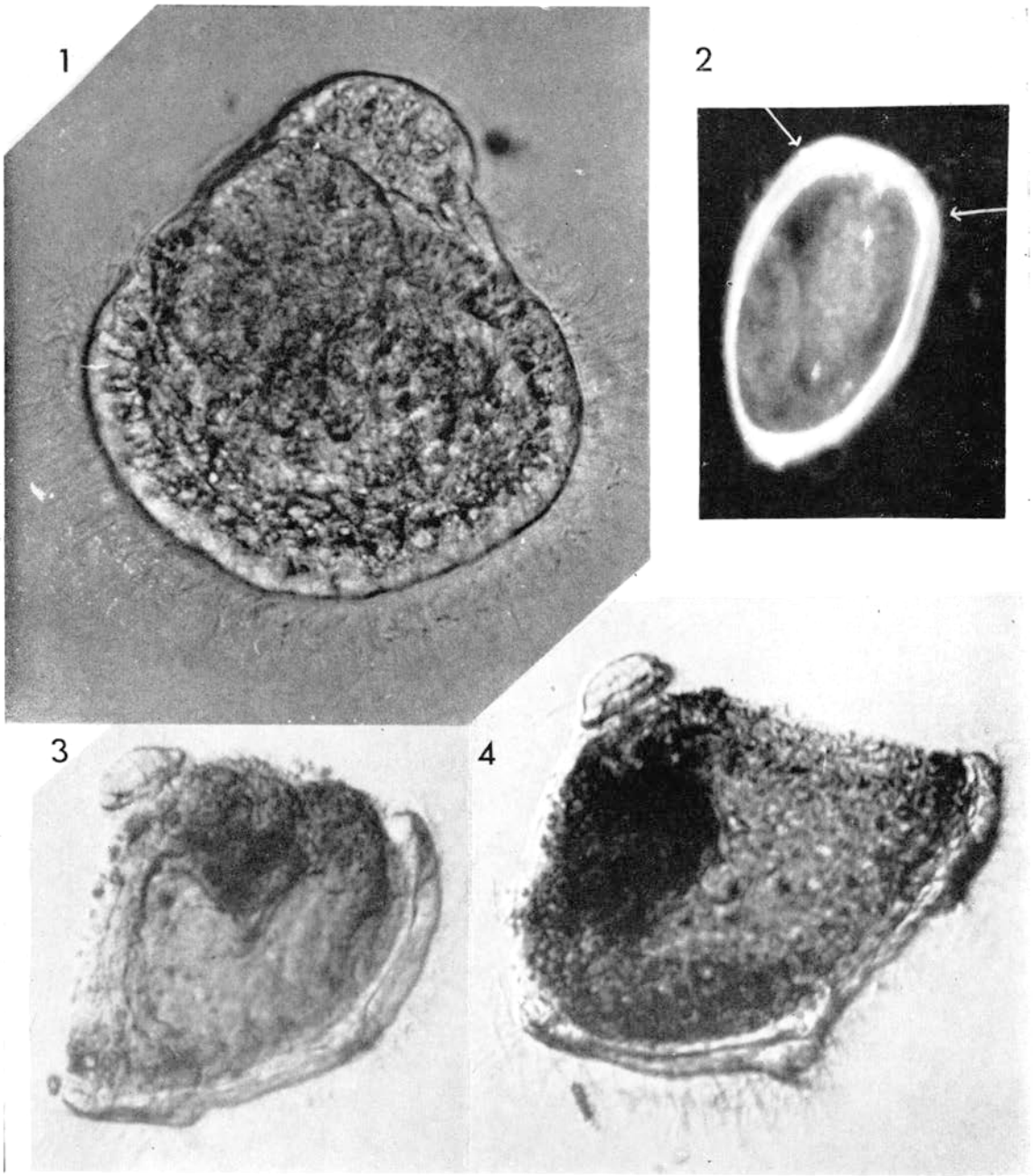
Electra posidoniae Gautier (1954), although very similar to *E. pilosa,* has an entirely different form of ancestrula and slightly different primary budding (text-fig. 4). The ancestrula of *E. pilosa* has a porous gymnocyst and a variable number of spines. That of *E. posidoniae* has an imperforate gymnocyst and spines are absent. The larva, ancestrula and early astogeny of *E. posidoniae* have recently been described by Ranzoli (1963). He found that the ancestrulae he studied produced one distal and one distal-lateral bud. Seven young colonies from Bahia de Palma, Mallorca (on *Posidonia,* October, 1957, 1958.7.30.1, Lagaaij Coll.) show a similar pattern of budding. In four cases the ancestrula has budded 1 distal and 1 distal-lateral zooecium, followed (apparently much later) by a proximal zooecium. In two cases only 1 distal and 1 distal-lateral zooecium had been budded. In one case 1 distal and 2 distal-lateral zooecia had been budded. All three of these zooecia were of equal size and appear to have originated simultaneously (text-fig. 4), thus differing from the budding of *E. pilosa.* The ancestrula of *E. posidoniae* was described (as *E. pilosa* var.), by Waters (1924:594-598, pl. 18, figs. 1-4), from a specimen growing on *Posidonia,* from Santa Margharita, Italy. He noted how this specimen differed from typical *E. pilosa,* both in the ancestrula and early astogeny, and in the character of the later-developed zooecia.

In *E. crustulenta* the primary buds are both lateral (see Bobin & Prenant 1962, text-fig. 1 V), and in *E. monostachys* the first bud is distal-lateral, and the second, which may be developed much later, is lateral or distal-lateral (see Cook, 1964:393, text-fig. 1 A).

The ancestrula of *E. bellula,* seen in 10 specimens from Pernambuco (on alga, 1888.4.16.25, Ridley Coll.), differs little from the later developed zooecia. It buds one distal zooecium (occasionally 2 closely apposed distal-lateral zooecia), which then produce distally directed series of zooecia. After 10-15 of these have been budded, a proximal series has been seen apparently budded directly from the ancestrula, in four cases.

The ancestrula of *E. tenella* gives rise to a pair of closely apposed distal zooecia, one of which buds a distal-median zooecium (see Marcus, 1938:67, pl. 15, fig. 37 B). A similar type of budding has been seen in *Aspidelectra melolontha* (Mouth of the Thames, 1899.7.1.1364, Busk Coll.).

E. multispinata (see Hastings, 1966:67) appears to develop in an entirely different manner. The ancestrula may be so small that it is rarely preserved, a possibility noted by Waters (1924:608, pl. 19, fig. 9). The specimen he examined (N. Australia, 1897.5.1.1491), shows



P.I.. Cook

Photographs: P.J. Warren (1); J. Brown (2) and M. Cullum (3 and 4).

PLATE I

Conopeum seurati (Canu).

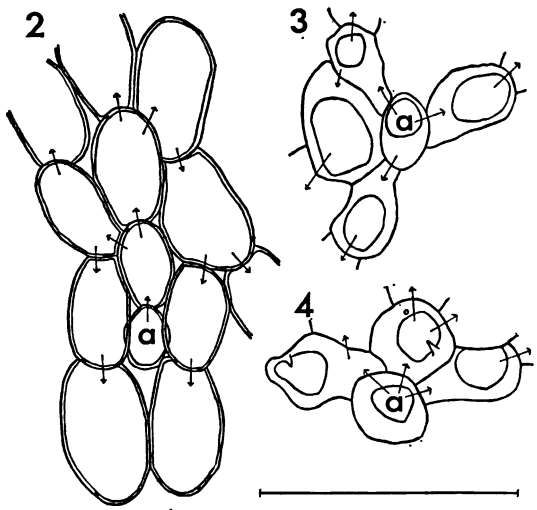
1: young, living larva, viewed from the apical organ. (Note the absence of shell.) ×790.

2: living ancestrula. (Note the position of the distal spines.) ×220.

3: an almost fully-developed, living larva, viewed from the side. (Note the shell.) ×480.

4: a fully-developed larva, viewed from the side. ×440.

2 zooecia of equal size, each apparently budded proximally from each other. A similar astogeny apparently occurs in *Pyripora catenularia,* seen in a specimen from Hastings, Sussex (1963.9.2.7).



Text-Figs 2-4

2. - *Conopeum seurati* (Canu). Ancestrula (a) and subsequent zooecia. Note establishment of the proximal series by budding from derivatives of the primary distal zooecium (1963.12.30.3.).

3. - *Conopeum reticulum* (Linnaeus). Ancestrula (a) and primary zooecia. Note the distal-lateral and proximal budding (1962.2.14.1.).

4. - *Electra posidoniae* Gautier. Ancestrula (a) and three primary zooecia (1958.7.30.1.). Scale=0.80 mm.

3. *Conopeum.*

The ancestrula is single and the development is principally distal and proximal, but differs in the 3 species in which it has been observed.

In *C. reticulum* the primary buds are distal-lateral and proximal as seen in specimens from the R. Blackwater, Essex (1961.6.26.1 and 1962.2.14.1, see text-fig. 3). In one colony observed during growth, the proximally directed series of zooecia were the result of regeneration of the primary distal zooecium over the ancestrula in a proximal direction (see Cook, 1964, text-fig. 1 C). This is somewhat similar to the development seen in *C. seurati* which has been described above. A species with similar zooecial characters to *C. seurati* has been described from the eastern coasts of North America, as *Membranipora crustulenta* (see Osburn, 1944:31, text-fig. 20 E). Here the primary budding is distal and proximal, and the ancestrula was figured without spines. A copy of Osburn's figure was used by Bobin & Prenant (1962, text-fig. 2, V) to illustrate the early astogeny of *C. seurati,* but the American species appears to be distinct. The same type of budding has been described by Maturo (1957:37, text-fig. 30) for a species described as *Electra crustulenta.* This is almost certainly the same species as Osburn's, and both forms greatly resemble *Electra laciniosa,* recently described by Shier (1964:612), which should be

referred to *Conopeum*. Specimens of *E. laciniosa*, from Galveston Bay, Texas (1966.2.16.1, shore, on mussels, Shier Coll.) have ancestrulae with one minute pair of distal spines. In each of the seven young colonies examined, the ancestrula buds one distal zooecium, followed by one proximal zooecium, exactly as figured by Osburn and by Maturo. Each of these zooecia then produces 2-3 distal buds, which originate the distal and proximal fan-shaped series of zooecia.

Many more observations will be required of the ancestrula and young, preferably living, growing colonies of species belonging to these genera. The degree of variation in budding pattern and the effects of different ecological conditions must be established. At present the indications are as follows:

Membranipora, twinned ancestrulae may be regarded as diagnostic.

Electra, the preponderant form of budding is lateral and distal-lateral.

Conopeum, the direction of budding, by various methods, is distal, and proximal.

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Summary

The settlement and metamorphosis of the fully-developed larva of *Conopeum seurati* (Canu) has been observed. The early astogeny of colonies is described from preserved material. Comparisons have been made of the type of ancestrula and early astogeny of 15 membraniporine species. Three principal forms of budding have been seen. These correspond broadly to the accepted grouping of the majority of the species into three genera, namely, *Membranipora, Electra* and *Conopeum*, based on the characters of the later developed zooecia. Species of some other genera, e.g. *Aspidelectra* and *Pyripora*, may have, however, similar budding patterns.

Zusammenfassung

Es wurde eine Kolonie von *Conopeum seurati* (Canu) und die Metamorphose von völlig entwickelten Larven beobachtet. Die junge Stockbildung wurde an präpariertem Material beschrieben. Die Ancestrula und die junge Stockbildung von fünfzehn Membranipora Spezien wurden verglichen. Wir stellten drei Hauptformen von Knospenbildung fest. Diese können in drei Genera, wie dies bei der Mehrzahl dieser Spezien üblich ist, gruppiert werden, nämlich : *Membranipora, Electra* und *Conopeum*. Diese Vergleichung fusst auf den Merkmalen der sich später entwickelten Zoöcien.

Es ist aber möglich, dass auch andere Spezien, wie z.B. *Aspidelectra* und *Pyripora* gleiche Knospenbildungsmuster zeigen.

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