

THE DEVELOPMENT OF *ELECTRA MONOSTACHYS* (BUSK)
AND *CONOPEUM RETICULUM* (LINNAEUS),
POLYZOA, ANASCA.

by

Patricia L. Cook

British Museum (Natural History).

Résumé

Deux formes de *Cyphonautes* récoltées dans le plancton de la Rivière Crouch en juillet et septembre, ont été reconnues comme identiques à celles trouvées dans les Rivières Blackwater et Tamar en juillet; aucune de ces formes ne semble avoir été décrite auparavant. L'une des larves, aux valves longues, gris foncé, très sculptées, munies de granules opaques le long du bord basal, se fixa et se métamorphosa en jeunes colonies d'*Electra monostachys* (Busk). L'autre larve, aux valves moins allongées, de couleur gris clair, à striations radiales avec une rainure diagonale et à granules opaques sporadiques, était plus grande et, par fixation, se développa en jeunes colonies de *Conopeum reticulum* (Linné). La période de reproduction des deux espèces, en Grande-Bretagne, se place entre juin et octobre ou novembre.

Bien que les deux larves ressemblent à celles de *Electra crustulenta* (Pallas), elles s'en éloignent par la couleur, la taille et la forme. Les colonies adultes diffèrent également d'*Electra crustulenta*, en Grande-Bretagne, par la date du début de la saison de reproduction.

The development of several membraniporine species of Polyzoa from the metamorphosis of *Cyphonautes* larvae is known. These larvae, which have a prolonged planktonic life, are produced by species which possess neither ovicells nor internal ovisacs, and which extrude small, yolkless eggs through a specially developed intertentacular organ. The *Cyphonautes* larvae of *Membranipora villosa* Hincks and *M. tuberculata* (Bosc) have been described respectively by O'Donoghue (1926) and Hastings (1930: 706); those of *Membranipora membranacea* (Linnaeus) and *Electra pilosa* (Linnaeus) by Atkins (1955); and those of *Electra crustulenta* (Pallas) and *Conopeum seurati* (Canu) by Cook (1961, 1962).

Neither *Electra monostachys* (Busk) nor *Conopeum reticulum* (Linnaeus) (1) develop ovicells or ovisacs, and small eggs were seen

(1) Full synonymies and descriptions of both *Electra monostachys* and *Conopeum reticulum* are given by Hastings (in a forthcoming paper), and *C. reticulum* has been discussed by Bobin & Prenant (1962: 383).

in *C. reticulum* Harmer (1926: 211), who also (pp. 199-201, 207) discussed the occurrence of *Cyphonautes* in the Membraniporidae.

Colonies of the two species, growing on shells and stones, collected from the River Crouch, Essex, in July and September, 1962, had well-developed intertentacular organs and contained from 5-9 eggs per zoecium. Unlike *E. crustulenta* and *C. seurati*, the colonies rarely extruded eggs in daylight, but many were found in the morning after colonies had been kept in dishes overnight. The eggs of *E. monostachys* were white when extruded, becoming pink within half an hour. They were oval in shape, with slightly truncated ends; their average dimensions were $L=100\ \mu$, $l=70\ \mu$. The eggs of *C. reticulum* were yellowish-white, more rounded, and slightly larger, their average dimensions being $L=110\ \mu$, $l=80\ \mu$. The eggs of both species developed as far as blastulae, but then became moribund, and the further development and release of young larvae from the containing capsule has not so far been seen.

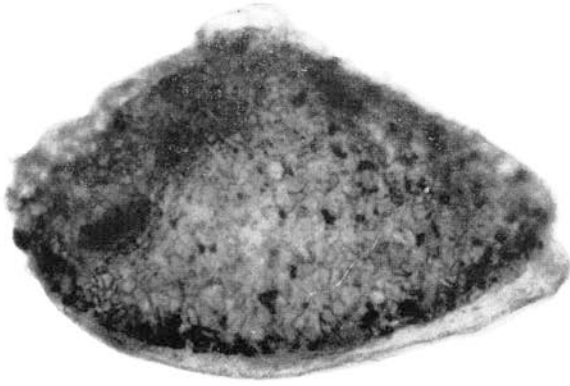
Collections of *Cyphonautes* larvae were made by trowel in the Rivers Blackwater (July, 1960) and Crouch (July and September, 1962, September, 1963). On the 3 forms of *Cyphonautes* found, one was the larva of *Electra pilosa* (see pl. I, fig. 5). Neither of the other 2 types of larva had apparently been described before. One, the more abundant, was dark gray, and had an elongated shell, with opaque granules concentrated along the basal edge of each valve. This larva was very similar to that of *E. crustulenta*, but differed slightly in size, shape and colour. On settlement and metamorphosis, it produced young colonies of *E. monostachys*. The other, rarer, larva was lighter gray in colour, larger, and not elongated; it differed from that of *E. crustulenta* in size and colour. It settled and, on metamorphosis, produced young colonies of *C. reticulum*.

C. reticulum and *E. monostachys* tolerate a wide range of salinity, from brackish river estuaries to sea water. However, the distribution of colonies of the two species collected from the River Crouch showed that *C. reticulum* was the more abundant in the higher, less saline parts of the river, and that *E. monostachys* was the more abundant in the lower reaches. Here, higher salinities are more frequent and prolonged, as a result of tidal changes in the estuary (salinity range 24 per mille - 36 per mille see Cook, 1961, 261).

The percentage of larvae found in both the Rivers Blackwater and

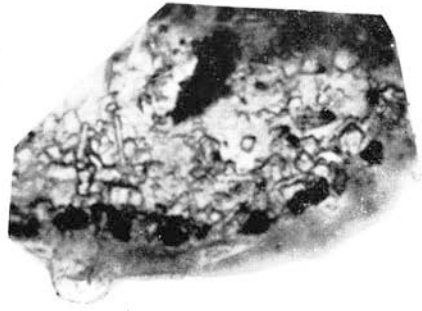
PLATE I.

1. *Electra monostachys* (Busk). Fully developed, live *Cyphonautes* larva, lateral view; showing elongated, sand-encrusted shell, with opaque particles along the basal edge. September, 1962.
2. *E. monostachys*. Part of the basal edge of one valve of a slightly younger larva; showing particles on the surface. September, 1963.
3. *Conopeum reticulum* (Linnaeus). Fully developed, live *Cyphonautes* larva, lateral view; showing valve surface with diagonal groove (*g*). September, 1962.
4. *Electra monostachys*. Lateral view of larva shown in Figure 2; showing thick, sand-encrusted shell. September, 1963.
5. *Electra pilosa* (Linnaeus). Fully developed, live *Cyphonautes compressus*, lateral view; showing transparent valves, gut, and pyriform and adhesive organs. September, 1963.



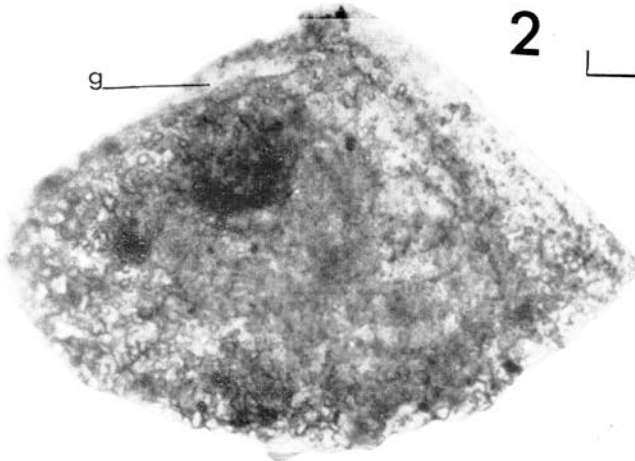
1

0.1mm



2

0.05mm



g

3

0.1mm

4



5



0.2mm

Crouch was the same, namely: 91 per cent *E. monostachys* form: 9 per cent *E. pilosa* form: 1 per cent *C. reticulum* form.

In the River Tamar, Devon, *C. reticulum* has been found in the higher reaches, where the salinity ranges from 21.5 per mille - 32.2 per mille (Neille Point and Cargreen, see Plymouth Marine Fauna, 1957, 348), but *E. monostachys* has not been reported. Notes and drawings made by the late Dr. D. Atkins, which are now preserved at the British Museum (Natural History), show that 2 types of larvae were present in the upper reaches of the river in July 1956. The form now known to be associated with *C. reticulum*, was the more abundant. Dr. Atkins considered that the rarer, more elongated form was *C. barroisii*, the larva of *E. crustulenta*, but her sketches and specimens show the size and distinctive shell shape of the larva of *E. monostachys*. The other, commoner, form she rightly considered to be probably undescribed. It is the larva of *C. reticulum*.

Development of *Electra monostachys*

The shells of young larvae from the plankton were higher in proportion to width than those ready to settle (L 140 μ , l 220 μ) and thus very similar to fully grown larvae of *E. crustulenta* in shape. The valves of fully developed larvae (L 150 μ , l 250 μ), had a rounded posterior end (near the exhalant aperture) and an elongated, more pointed anterior end (near the inhalant aperture, see pl. I, figs. 1 and 4). The valves were thick and sculptured, with accretions of sand grains, as in the larvae of *E. crustulenta*. Little of the gut could be seen (compare pl. I, fig. 4 with fig. 5, the larva of *E. pilosa*). There were also numbers of opaque granules, the majority of which formed a border to the basal edge of the valves. Although some of the granules on the surface of the valves were like those seen in *C. barroisii*, those on the basal edge were invariably black and regularly distributed (see pl. I, fig. 2). The larvae also differed from the fully grown larvae of *E. crustulenta* in their larger size (*C. barroisii*, L 150 μ , l 200 μ), more elongated shape, and dark gray colour (in *C. barroisii* the shell is yellowish - brown).

The ancestrulae which developed in September 1963 were complete 48 hours after settlement. They had a distinct, small gymnocyst and measured, on average, L=180 μ , l=100 μ . A pair of distal spines, and from 2-3 more proximal spines were present on some ancestrulae, others were spineless. The ancestrulae which developed in July 1962 were larger, measuring, on average, L=240 μ , l=200 μ . These were similar in size to those of preserved colonies in the British Museum, and to those sketched by Dr. J.S. Ryland, which had developed from larvae settled on panels in the Menai Straits, N. Wales, between October 3rd. and November 3rd. 1958. The ancestrulae from Menai had 2-3 proximal spines.

Subsequent zoecia usually had a well-developed gymnocyst, a pair of distal spines, and from 2-6 other spines. The number of tentacles seen in the ancestrular polypide was 7-9, and in the subsequent zoecia 9-10; polypides of yet older zoecia had 10-11 tentacles.

The zoecia of *E. monostachys* were smaller than those of *C. reticulum* at comparable stages of colonial development (see text-figs. 1 A-C), a difference also found in the zoecia of older, preserved colonies.

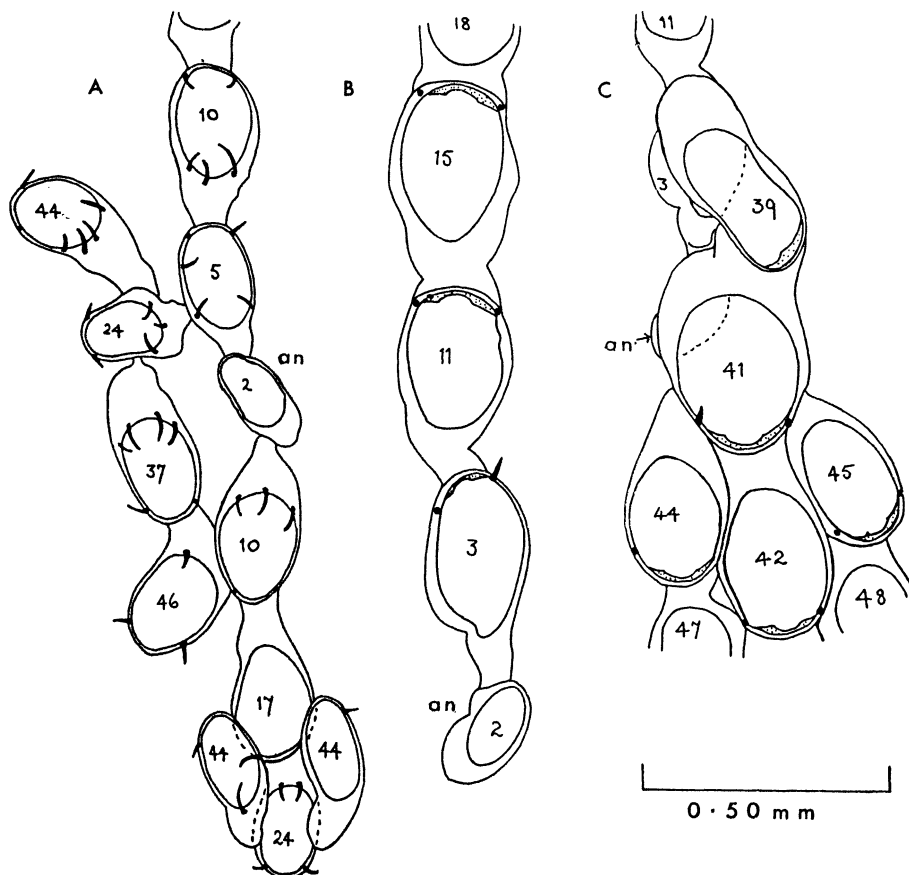


FIGURE 1.

- A. *Electra monostachys* (Busk). Ancestrula (an) and zoecia, showing proximal and distal spines.
- B. *Conopeum reticulum* (Linnaeus). Ancestrula (an) and 3 distal-lateral zoecia, showing distal spines and distal wall, with pore (stippled).
- C. *C. reticulum*. The same colony at a later stage, showing regeneration of primary ancestrular bud in a proximal direction, covering the ancestrula (an). The number of days elapsed after settlement of the larva is shown on each zoecium.

Development of *Conopeum reticulum*

The larvae were larger ($L=200 \mu$, $l=290 \mu$), and distinctly less elongated than those of *E. monostachys*, even when young ($L=140 \mu$, $l=180 \mu$). The valves were light gray, and less sculptured than those of the *E. monostachys* larvae, with faint radiating striations from the apical to the basal edge. A diagonal groove, running from the

apical organ towards the posterior edge of each valve, was seen in all fully developed specimens, and some younger larvae. This groove was also noted by Dr. Atkins in her sketches of larvae from the River Tamar. A few dark granules, similar to those in the *E. monostachys* larvae, were scattered over the surface, and although in some specimens these tended to be concentrated along the basal edge of the valves, they were not as frequent or as regularly distributed as in the *E. monostachys* larvae (see pl. I, fig. 3). Accretion of other particles was rare, distinguishing the larva of *C. reticulum* from that of *E. crustulenta*, from which it also differed in its much larger size, gray colour, and grooved valves.

Some of the larvae settled and metamorphosed. The ancestrulae had small gymnocysts, and measured, on average, $L=220\ \mu$, $l=130\ \mu$. No spines were seen. The number of tentacles in the ancestrular polypide was 9, and in the subsequent zooecia 8-9; polypides of yet older zooecia had 10-11 tentacles. The first zooecia to be budded all had distinct gymnocysts, but these were progressively smaller in subsequent zooecia (see text fig. 1, B, C). A pair of distal spines was present in nearly all these zooecia, but lateral spines were absent, although they may be present in zooecia of older colonies. A distinct pore, surrounded by a calcified flange, was seen in the distal walls of all zooecia. This pore, when present, is characteristic of *C. reticulum* (see Bobin et Prenant, 1962, p. 386, text-fig. 4, IX). The older zooecia were distinctly larger than those of *E. monostachys* at comparable stages of colonial development (see text-figs. 1 A-C).

Discussion.

The types of larvae associated with *E. crustulenta*, *E. monostachys* and *C. reticulum* resemble one another, especially in the younger stages, and records of *Cyphonautes barroisii* must be examined in the light of this similarity. Colonies of *E. crustulenta* have been seen to breed from March to July in Britain (see Cook, 1962, 58), and from April to June in the Baltic (see Borg, 1947, 363). The occurrence of the larvae indicates that *E. monostachys* breeds from June to at least November in Britain. It is not found in the Baltic (see Marcus, 1940, 118, as *Membranipora (Electra) hastingsi*). *C. reticulum* apparently breeds from June to at least early October in Britain. It is also absent from the Baltic, although it is found in the Skagerak and the outer (i.e. seaward) Kattegat (see Marcus, 1940, 125). Thorson (1946, 159) did not find any larvae large enough to be of the type now known to be associated with *E. monostachys* or *C. reticulum* in the Baltic, and his records of *C. barroisii* from this area are certainly valid for *E. crustulenta*. Thorson found *C. barroisii* in the Baltic plankton from November to September, "with a maximum in winter". The observed breeding season of *E. crustulenta* recorded by Borg is therefore extended.

The description and figure of *C. barroisii* given by Lohmann (1911, p. 39, text-fig. 8) emphasized the small size of the sand-encrusted valves (maximum width $200\ \mu$). Lohmann also mentioned a record of a pair of sand-covered, flattened valves, in the tubes of *Terebella* sp., described by Ehlers (1876, p. 74, pl. I, fig. 5), from the

North Sea. Ehlers concluded that the valves probably belonged to the *Cyphonautes* of a Ctenostome, *Hypophorella expansa* Ehlers, the younger stages of which he had already observed. Prouho, who also reared larvae of *H. expansa*, commented (1893, 619) that there was no published record that the *Cyphonautes* valves described by Ehlers were, in fact, associated with *H. expansa*. Most of the few, known Ctenostome *Cyphonautes* are very small, and shell-less (see Marcus, 1940, p. 338-9, text-figs. 181-183). The width of the shells given by Ehlers was 240 μ , and his figure showed elongated valves, covered with sand grains, in the open, settled position. It is possible that the valves belonged to a membraniporine *Cyphonautes*, perhaps to *E. monostachys*. Dr. Atkins noted (1955, p. 441) that although *H. expansa* occurred at Plymouth, "the cyphonautes has not yet been recognized".

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Summary

Two forms of *Cyphonautes* larvae collected from tow-nettings in the River Crouch in July and September, were found to be the same as those found in the River Blackwater and the River Tamar in July; neither form had apparently been described before. One larva, which had dark gray, sculptured, elongated valves, with opaque granules along the basal edge, settled, and on metamorphosis developed young colonies of *Electra monostachys* (Busk). The other larva, which had light gray, far less elongated valves, with radial striations, a diagonal groove, and scattered opaque granules, was larger, and on settlement developed young colonies of *Conopeum reticulatum* (Linnaeus). The observed breeding season of both species, in Britain, is between June, and October to November.

Although both larvae resemble that of *Electra crustulenta* (Pallas), they differ in colour, size and shape. The adult colonies also differ from *E. crustulenta*, in Britain, in the onset of the breeding season.

Zusammenfassung

Zwei Formen von *Cyphonautes* Larven, die im Juli und September im Plankton des « River Crouch » gefunden wurden sind identisch mit denen, die im Juli im « River Blackwater » und im « River Tamar » gefunden wurden; keine dieser Formen scheint bisher beschrieben worden zu sein. Eine dieser Larven, welche dunkelgraue, gerippte, längliche Schalen besass, die an der Basalkante mit opaken Körnern besetzt war, setzte sich fest und bildete durch Metamorphose junge Kolonien von *Electra monostachys* (Busk). Die andere Larve, mit weniger länglichen, hellgrauen radialgestreiften Schalen, mit diagonalen Rinnen und sporadisch verteilten opaken Körnern, war grösser und entwickelte sich zu jungen Kolonien von *Conopeum reticulatum* (Linné). Die Fortpflanzungsperiode der beiden Arten liegt für Grossbritannien zwischen den Monaten Juni und Oktober oder November.

Obwohl beide Larven denjenigen von *Electra crustulenta* (Pallas) gleichen, unterscheiden sie sich von den letzteren durch ihre Farbe, Grösse und Form. Die Adultkolonien unterscheiden sich von denjenigen von *E. crustulenta* in Grossbritannien durch das Datum des Beginns der Fortpflanzungsperiode.

REFERENCES

- ATKINS, D., 1955. — The *Cyphonantes* larvae of the Plymouth area and the metamorphosis of *Membranipora membranacea* (L.). *J. Mar. Biol. Ass. U.K.*, 34, pp. 441-449.
- BOBIN, G. et PRENANT, M., 1962. — Les espèces françaises du genre *Conopeum* Gray (Bryozoaires Chilostomes). *Cah. Biol. Mar.*, 3, pp. 375-389.
- BORG, F., 1947. — Zur Kenntnis der Ökologie und des Lebenszyklus von *Electra crustulenta* (Bryozoa chilostomata). *Zool. Bidr. Uppsala*, 25, pp. 344-377.
- BUSK, G., 1854. — Catalogue of Marine Polyzoa in the Collection of the British Museum, Part. II. London.
- BOSC, L.A.G., 1802. — Histoire Naturelle des Vers, III. Paris.
- CANU, F., 1928. — Trois nouveaux Bryozoaires d'eau douce. *Bull. Soc. Hist. Nat. Alger*, 19, pp. 262-264.
- COOK, P.L., 1961. — The Development of *Electra crustulenta* (Pallas) (Polyzoa, Ectoprocta). *Essex Nat.*, 30 (1960), pp. 258-266.
- COOK, P.L., 1962. — The early larval development of *Membranipora seurati* (Canu) and *Electra crustulenta* (Pallas), Polyzoa. *Cah. Biol. Mar.*, 3, pp. 57-60.
- EHLERS, E., 1876. — *Hypophorella expansa*. Ein Beitrag zur Kenntniss der minirenden Bryozoen. *Abhandl. Phys. Kl. d. K. Gesellsch. Göttingen*, 21, pp. 1-157.
- HARMER, S.F., 1926. — The Polyzoa of the Siboga Expedition, Part. II, Cheilostomata, Anasca. *Rep. Siboga Exped.*, 28 b, pp. 181-501.
- HASTINGS, A.B., 1930. — Cheilostomatous Polyzoa from the vicinity of the Panama Canal. *Proc. Zool. Soc. Lond.* 1929, pp. 697-740.
- HINCKS, T., 1880. — Contributions towards a General History of the Marine Polyzoa, II, Foreign Membranipora. *Ann. Mag. Nat. Hist.* (5), 6, pp. 13-24.
- LINNAEUS, C., 1767. — Systema Naturae, Ed. XII, 1, Holmiae.
- LOHMANN, H., 1911. — Die *Cyphonantes* der nordischen Meere. *Brandt. Nord. Plankt.*, 9, 13, pp. 31-40.
- MARCUS, E., 1940. — *Mosdyr* (Bryozoa eller Polyzoa). *Danmarks Fauna*, 46, pp. 1-401.
- O'DONOGHUE, C.H., 1926. — Observation on the Early Development of *Membranipora villosa* Hincks. *Stud. Biol. Stas. Can.* n.s. 3, 8, pp. 247-263. (= *Contr. Canad. Biol.*)
- PALLAS, P.S., 1766. — Elenchus Zoophytorum, Hagae Comitum.
- PLYMOUTH MARINE FAUNA, 1957. — *Mar. Biol. Ass. U.K.* Ed. 3. *Plymouth*.
- PROUHO, H., 1893. — Contribution à l'Histoire des Bryozoaires. *Arch. Zool. Exp. Gén.* ser. 2, 10, 4, pp. 557-656.
- THORSON, G., 1946. — Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Havundersøg., Kbh. Ser. Plankton*, 4, 1, pp. 1-523.