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THE CYPHONAUTES LARVAE OF THE PLYMOUTH AREA AND THE METAMORPHOSIS OF *MEMBRANIPORA MEMBRANACEA* (L.)

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(Text-figs. 1–4)

Several cyphonautes larvae (Polyzoa Ectoprocta) have been distinguished and described (Lohmann, 1911; Marcus, 1940; Thorson, 1946), but few have been seen to metamorphose, thus linking the late larva with the adult. Three, belonging to the suborder Cheilostomata, which have been observed to do so, are *Cyphonautes compressus* into *Electra pilosa* L. (Schneider, 1869; Barrois, 1877; Kupelwieser, 1905–6), *Cyphonautes occidentalis* into *Membranipora villosa*, (Robertson, 1908; O'Donoghue, 1927) and an unnamed cyphonautes into *Nichtina* (= *Membranipora*) *tuberculata* (Hastings, 1929, pp. 706–7).[1]

Prouho (1892) found *Alcyonidium albidum* and *Hypophorella expansa* (Ctenostomata) to have cyphonautes larvae, but was unable to rear them to the stage when pyriform and adhesive organs were present, so that the appearance of the late larvae of these two species is unknown. He also reared the cyphonautes of *Electra pilosa* to a young stage, and took later larvae from the plankton (pl. 30, fig. 92). *Alcyonidium albidum* has not been recorded in the Plymouth area; *Hypophorella expansa* has been recorded (Marine Biological Association, 1931, p. 289), but the cyphonautes has not yet been recognized.

During work on the ciliary feeding mechanism of the cyphonautes larva (Atkins, 1955), two species were taken from the plankton in the Plymouth area, one large and one small, and both seen to metamorphose and give rise to colonies.

Inside Plymouth breakwater the common form in the tow-nets throughout 1953 was a small, rather opaque, cyphonautes, which developed into *Electra pilosa* L. and is evidently that known as *Cyphonautes compressus*.[2] It is about 440 μ broad at the base and 360 μ high when ready to metamorphose;

[1] For discussions on the validity of *Membranipora* as the name for the genus see Borg (1931) and Osburn (1950).

[2] In the autumn of 1953 a small number of the larvae of *Electra pilosa* were seen to be parasitized by young stages of a species of *Endodictyon*, probably close to *E. infestans* Gran, which is known to be endozoic in species of *Alcyonidium* (Newton, 1931, p. 128). It would seem probable that the colonies of *Electra pilosa* are parasitized and that the larvae carry the infection. The identification was kindly made by Dr M. Parke.

metamorphosis may, however, occur when the shell is only about 390 μ broad. Young forms with inhalant and exhalant chambers fully formed are no more than 160 μ broad and 130 μ high. The valves of the late larva are of a brownish tint, but are without ornamentation along their basal edges. Fig. 1 shows change in shape of the larva of *Electra pilosa* with growth. These stages have been taken from the plankton and not reared, but as there is considerable difference in size and transparency between the large cyphonautes and the larva of *E. pilosa* the young stages of the two are unlikely to be confounded and the late stages never (cf. Figs. 1 and 3 which are reproduced at the same magnification).

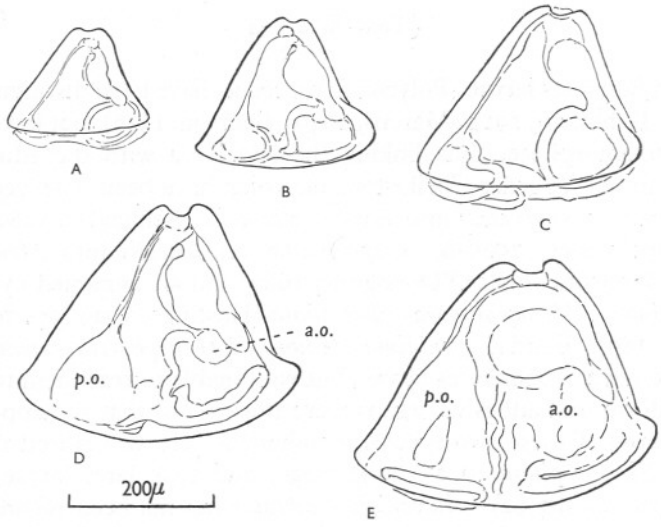

Fig. 1. *Electra pilosa* L. Cyphonautes larva (*Cyphonautes compressus*), to show change in the shape of the shell with growth, and the development of the pyriform (*p.o.*) and adhesive (*a.o.*) organs.

The first cyphonautes to be described, the *Cyphonautes compressus* of Ehrenberg (1838), was apparently lacking in ornamentation even in the late stage, for none is shown in his figure (pl. 44, fig. 2) of a late larva with well-developed pyriform and adhesive organs. He gave the size of this larva as '$\frac{1}{9}$ linie', which as the German line equals 2·18 mm, is about 242 μ. Schneider (1869) was quite possibly right in identifying his larva, which he found to develop into *Electra pilosa*, with *Cyphonautes compressus* Ehrenberg.

The settlement of *C. compressus* has been watched several times at Plymouth, for late larvae when taken from tow-nettings and placed in glass dishes tend to settle rapidly. A larva when about to settle glides over the substratum with the pyriform organ foremost, the vibratile plume clawing at the surface. The corona is extended, the cilia at first beating metachronally, although slowly:

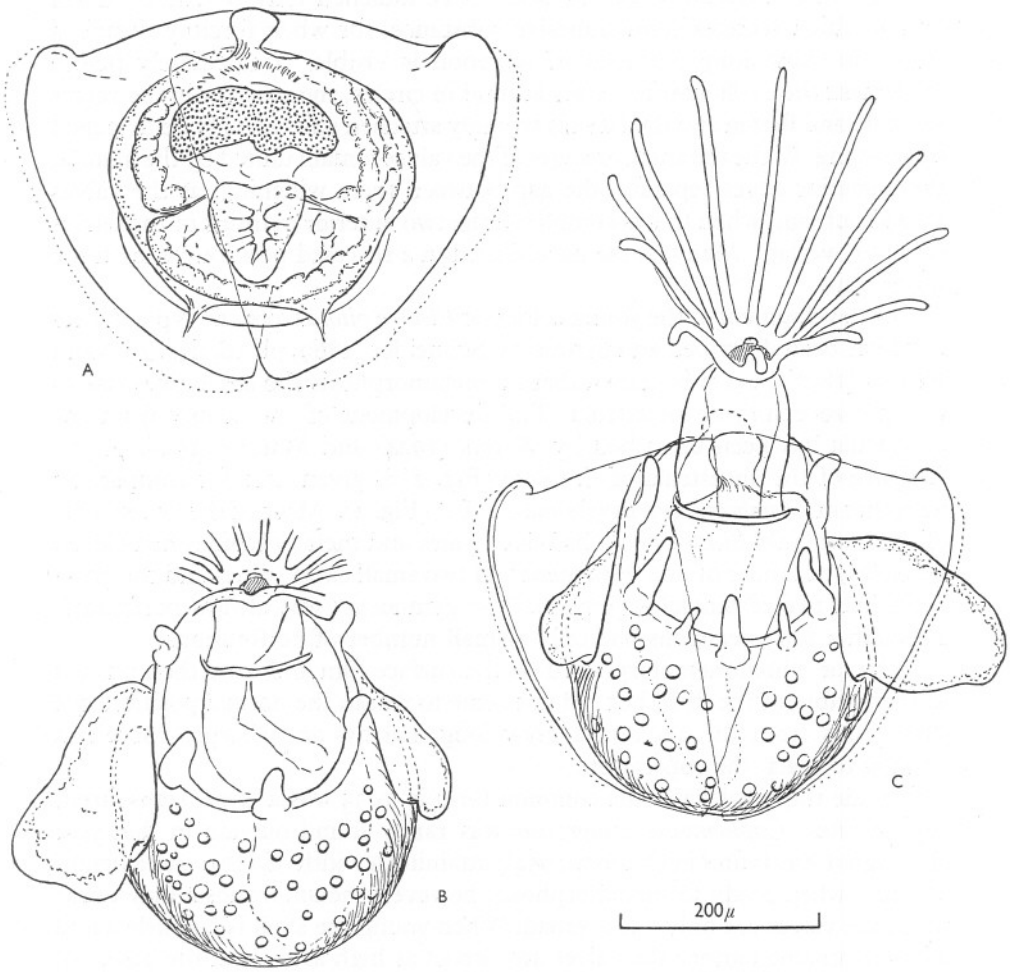

Fig. 2. *Electra pilosa* L. A, metamorphosing larva; B, ancestrula with five spines and the polypid with eleven tentacles; C, ancestrula with seven spines and the polypid with twelve tentacles. The shell is shown in position in A and C; it was removed from B for the figure to be drawn. Both ancestrulae have given rise to three buds, two being lateral and one distal (the latter is indicated by a broken line).

later the cilia become quiescent, extended almost horizontally. When gliding, if gently squirted at with a pipette, it heels over, but is not dislodged: when touched with a needle it can be seen to be attached only by the pyriform organ, which secretes some adhesive substance, for when forcibly detached from the substratum a thread of secretion is visible. Immediately before settlement the cyphonautes moves around in circles, then suddenly the valves separate and flatten and the larva is strongly attached and can only be detached by scraping. While the anterior edges of the valves remain united by the mantle, the posterior edges separate, the gap between them widening, as the valves spread out, and when this is completed the two anterior margins of the valves come to overlap. Many larvae have settled in a reversed position beneath the water film.

The development of the young colony of *Electra pilosa* from the cyphonautes larva has been described and figured by Schneider (1869, pl. 16, figs. 2–7) and Barrois (1877), and it is known that on metamorphosis the larva gives rise to a single zooecium or ancestrula. The development of the colony from the ancestrula has been described by Waters (1924) and Marcus (1926, p. 31). A figure of the ancestrula of *E. pilosa* (Fig. 2) is given here for comparison with that of *Membranipora membranacea* (L.) (Fig. 4). Most of the ancestrulae of the Plymouth *Electra pilosa* had five spines and their polypides had eleven tentacles, but those of one settlement had two small extra spines and the polypides had twelve tentacles (Fig. 2). The gymnocyst was always perforated, although a few specimens had only a small number of perforations.

In larvae which metamorphosed on the surface film and were then pushed to the bottom of the dish, but did not come to rest in the normal position, the three buds from the ancestrula grew long, narrow and sharply curved in seeking to reach the substratum.

Outside the breakwater the common form in 1953 was a large, transparent cyphonautes (*Cyphonautes compressus* was rarely found outside in that year although it was found in October 1954), attaining a width of 840 μ and a height of 640 μ when ready to metamorphose; however, metamorphosis may occur when the valves are only 750 μ broad. When young the shell is colourless and without ornamentation; the valves are almost as high as wide at the base. At about 710 μ basal width the ventral edges of the valves become brownish, but there is still little or no ornamentation. With development of the pyriform organ (Fig. 3, *p.o.*), which is formed before the adhesive organ (*a.o.*), the anterior edge becomes increasingly longer than the posterior, and the greatest width considerably more than the height of the shell. With age also the basal edges of the valves take on a brown tint, and become progressively ornamented with refringent spots which in places appear to coalesce, forming ridges. The shell ornamentation is heavier in some metamorphosed larvae than in others. The posterior margin of the shell usually is almost invisible. Fig. 3 shows change in shell shape with age. These stages have been taken from the plank-

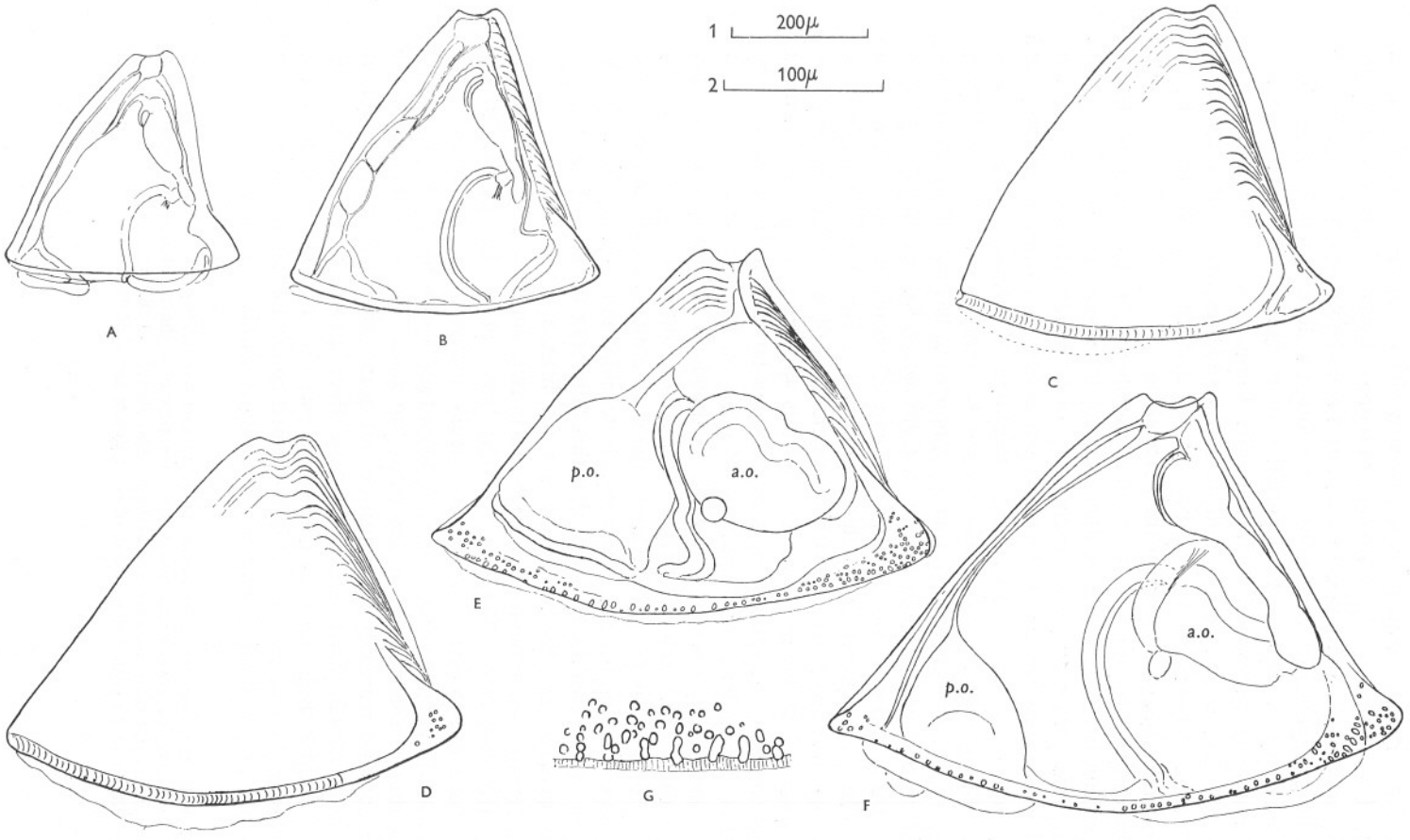

Fig. 3. *Membranipora membranacea* (L.). Cyphonautes larvae, to show change in shell shape with growth and the development of the pyriform (*p.o.*) and adhesive (*a.o.*) organs, and also the appearance of ornamentation along the basal edge of the shell with age. Both the larvae shown in E and F are about ready to metamorphose, although one is smaller than the other. G, small area of the basal edge of the shell enlarged to show the ornamentation and the almost transparent, faintly striated, extension of the shell edge. The valve only is shown in C and D, so that the growth lines are clearly visible. A–F to scale 1; G to scale 2.

ton and not reared.[1] This larva is probably the *C. compressus* of Claparède (1863, pl. xviii, figs. 15–18), if his figures represent stages in the development of one larva, which they appear to do, but it is certainly not the *C. compressus* Ehrenberg (1838) which Schneider (1869) found to develop into *Electra pilosa*. Lohmann (1911) separated Claparède's four figures into three species, *Cyphonautes compressus* Eh., *C. schneideri* Lohm. and *C. borealis* Lohm. Claparède did not give the magnification of his figures, but if all were drawn to the same magnification, then his figs. 15 and 16 are unlikely to be of *C. compressus* Eh. on account of their size alone.

According to Harmer (1926, p. 200) statements in the literature that a cyphonautes has been found in *Membranipora membranacea* (L.) (= *Nichtina telacea*) refer principally, if not exclusively, to *M. mülleri* Bidenkap (= *Electra pilosa* forma *membranacea*, and now known as *Electra crustulenta* (Pallas), see Borg, 1931, p. 11), and he had been unable to find evidence of its occurrence in the British species commonly known by that name. Thorson (1946, pp. 158–9, fig. 87B) mentioned that a cyphonautes, lacking ornamentation in the oldest stage, and which he referred to *Cyphonautes balticus*, metamorphosed in his dishes and was 'presumably the larva of *Membranipora membranacea* (L.)'. The present work shows this assumption to have been wrong, for the large Plymouth cyphonautes with ornamented shell was observed to metamorphose into *M. membranacea* (L.) and this appears to be the first definite observation that this species has a cyphonautes larva. The larva seems to be closest to Schneider's third species (1869, pl. 16, fig. 11), which Lohmann (1911) named *Cyphonautes schneideri*. Schneider's second species (pl. 16, fig. 10), also with an ornamented basal edge, which Lohmann named *C. borealis*, appears to have the posterior edge of the shell almost at right angles to the base, thus differing from the larva which develops into *Membranipora membranacea*. It is possible, however, that this difference in the angle is an individual variation, and the two species are not distinct.

The larva of *M. membranacea* gives rise to twin zooecia while still covered by the flattened valves (Fig. 4A). Nitsche (1871, pl. 38, fig. 3), and Waters (1925) have shown that 'a double ancestrula' occurs in this species, and the latter author figured a young colony of about twenty-two zooids (pl. 21, fig. 1), but neither of them found or described the larva. The twin ancestrulae of young colonies reared at Plymouth do not quite agree with the description given by Waters in that there may be fewer than '4 stout protuberances', but they also differ slightly among themselves (see Fig. 4). The paired proximal tubercles in the colony of seven fully-formed zooids have been pushed on to the undersurface of the colony and one only is visible (Fig. 4F).

[1] Dr A. B. Hastings has informed me by letter that in July 1930 she kept a few larvae of this species alive for a week and noted the development of the tuberculations (which were absent at first) and their increase in numbers. She also noted the increase in length of the anterior edge and associated sharpening of the anterior angle of the shell.

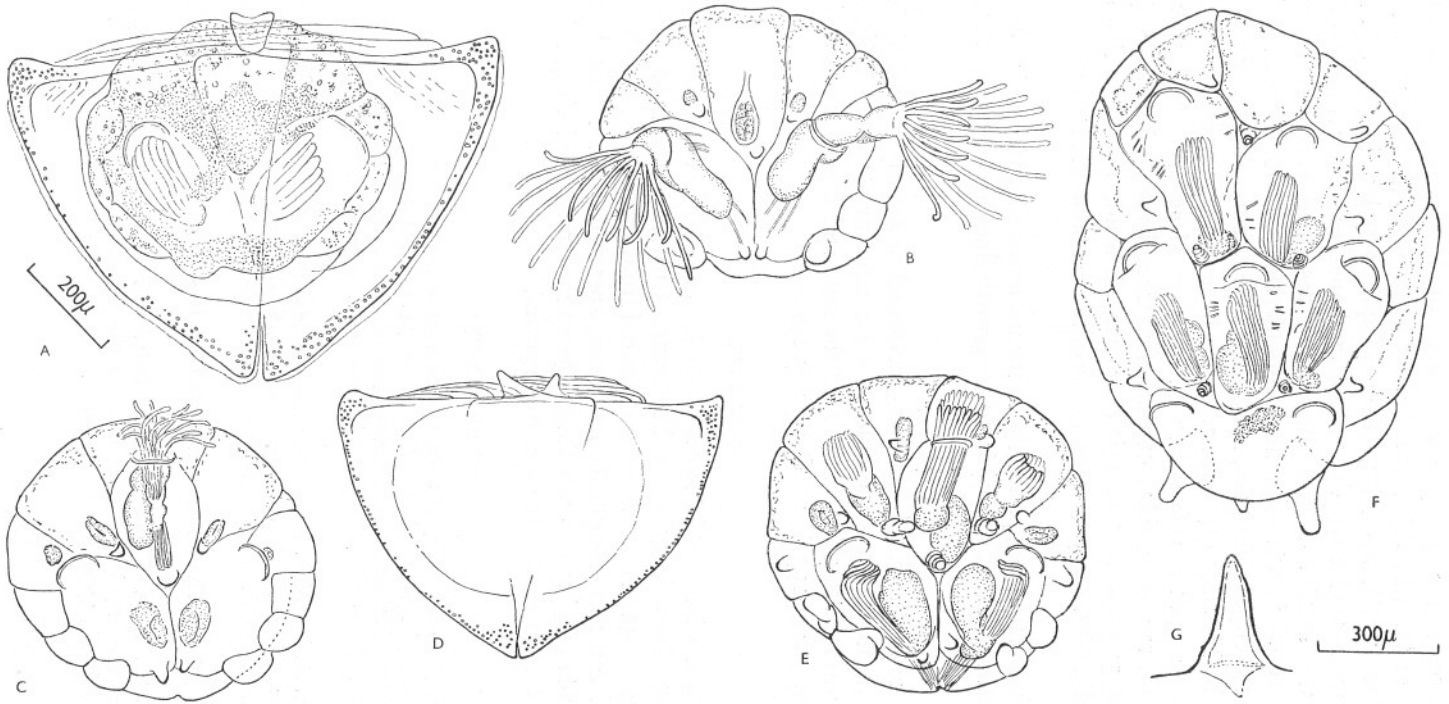

Fig. 4. *Membranipora membranacea* (L.). A, metamorphosing larva; B, C, E, F, development of the colony. G, spine in side view, enlarged. Shells were removed from colonies B and E before drawing; that from colony E is shown at D. The slight asymmetry of the colony shown in F is due to injury in removing it from the bowl in which it grew. B–F to scale in right-hand lower corner.

The development of the young colonies of *M. membranacea* closely resembles that of *M. villosa* Hincks as figured by Robertson (1908) and O'Donoghue (1927) and of *M. tuberculata* (Bosc) as figured by Hastings (1929). These two latter species are known also to have cyphonautes larvae with ornamentation along the basal edges of the valves, described variously as 'teeth' (Robertson, 1908), 'small spine-like denticulations' (O'Donoghue, 1927) and a 'tuberculated edge' (Hastings, 1929), and give rise to twin ancestrulae. As pointed out by Hastings (1929, p. 707) 'the occurrence of twin ancestrulae in three of the six species referred to *Nichtina* (= *Membranipora*) by Harmer (1926, p. 208), the ancestrulae of the other three being unknown, suggests that this may prove to be a generic character'; it would also seem that ornamentation of the basal edges of the valves of the cyphonautes may be a generic character.

The ribbing of the shell parallel with the posterior edge referred to by some authors (Hastings, 1929, p. 707) is due to growth lines and these are shown in Fig. 3C–E.

The work recorded in this note was incidental to a study of ciliary feeding mechanisms, undertaken while holding a Leverhulme Research Fellowship. Dr A. B. Hastings has most kindly read the note and drawn my attention to the papers by Borg (1931) and Osburn (1950).

Summary

The cyphonautes larvae of *Electra pilosa* L. and of *Membranipora membranacea* (L.) have been identified at Plymouth. Change in shell shape of both larvae during growth is described and figured from specimens taken from the plankton. Their metamorphosis has been observed, that of the larva of *M. membranacea* (L.) apparently for the first time, thus definitely proving the presence of a cyphonautes larva in that species.

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