*DEEP-SEA RESEARCH*

*Supplement to Volume 3*

# PAPERS IN MARINE BIOLOGY AND OCEANOGRAPHY



*It is suggested that references to this volume should appear in the following form*

*Pap. Mar. Biol. and Oceanogr., Deep-Sea Research, suppl. to Vol. 3*

Papers in Marine Biology and Oceanography, Suppl. to vol. 3 of Deep-Sea Research, pp. 239-241.

# Development and metamorphosis of the larva of *Agalma elegans* (Sars) (Siphonophora Physonectae)

By A. K. Totton
British Museum (Natural History)

Although Fewkes (1885) published a detailed and illustrated account of the holoblastic segmentation of the eggs of *Agalma elegans*, and of the subsequent development of the larva till it surfaces at the age of about seven days, he did not follow its metamorphosis into the adult. He had previously, however, given (1881, pl. IX, Figs. 1, 2) rather inadequate figures of a post-larval *Athorybia* stage, and a later one that he called the *Physophora* stage. The last is perhaps better called the "*Nectalia*" stage, as I have suggested (1954, p. 62).

Metchnikoff (1874) had, before Fewkes, watched segmenting eggs of this species without figuring them. He also gave an account, though not so good a one as Fewkes, of the development of the larva and the initial stage of its metamorphosis. But it is difficult to interpret Metchnikoff's later figures and to discriminate between the categories of buds that he figured.

Haeckel (1869) had been the first to describe the development of an Agalmid, after he had artificially raised about 60 larvae (one of them to the 27th day) of *Agalma okenii* (*Crystallodes rigidum*) at Lanzarote. He did not recognize the first gastrozooid or protozooid as such. It is labelled "d" (Dotter) and "dc" (Dotterhöle) in all his figures, whilst his Magen-polyp ("p") is really the second gastrozooid. He did not figure a larval tentacle for the protozooid, and I have never seen one either in *Agalma okenii*. In my *Discovery* report (1954, p. 66) I noted that the terminal gastrozooid—the primary zooid or protozooid—was smaller in *Agalma okenii* than its successors, and had a reduced basigaster. On page 69, however, I made the erroneous statement that such a protozooid was not formed. The sentence (lines 11–14) "The explanation . . . *okenii*" should be deleted.

Reduction of the protozooid in *Agalma okenii* has gone further than in *Agalma elegans*, whilst evolution of the bracts has progressed, giving the whole bud-colony a character of its own.

Adult specimens of *Agalma elegans* were not available except on one day during three visits that I have paid to Villefranche, and I was not able to secure any of the very youngest larvae, either by attempts at breeding or in the tow-net; but I did collect large numbers of post-larvae in various stages of development, and can now complete the account of growth and metamorphosis.

The fate of the larval bracts of the *Athorybia*-like stage has been unknown. Garstang (1946) several times suggested that they are dropped at metamorphosis. As a fact they, or at any rate the last-developed ones, are retained through life in their original very restricted position surrounding the proximal sides of the first and second gastrozooids to appear, where they can be seen figured by Fewkes (1881, pl. IX, Fig. 1) and by Totton (1954, frontispiece, Figs. A, D). But because of the secondary elongation of the area between the budding zone (blastocrene) of the siphosome and the

bases of the first two gastrozooids, the area which bears these bracts takes up a subterminal position at the end of a long stem. These larval bracts, so often figured, and their successors of similar though slightly modified shape, are quite distinctive; and differ from the definitive bracts, which arise in hundreds proximally to them in several ventro-lateral meridians of the stem. The contrast in bracteal types is best seen in early stages of metamorphosis, when the definitive bracts first make their appearance.

Information has been wanting in published reports on the position and time of first appearance of the nectophores. GARSTANG suggested that, as the nectophores appeared, so the bracts, which hitherto had served for locomotion, dropped off, but as we have seen this is not so. The oldest of METCHNIKOFF's figured specimens, in what might be called the *Melophysa* stage of development, shows two functional nectophores, but unless the reader is familiar with the animals it is not easy to orientate and interpret the figure. The little group of four rounded buds, seen through the uppermost bract, probably represent buds of gastrozooids and palpons. Close by, though not figured, is the nectostyle to which the larval bracts are attached by their muscular lamellae. The nectostyle can be seen in sagittal section (Fig. 1A) to be an elongated, hollow, cone-shaped diverticulum of the general cavity. The larval bracts are attached by muscular lamellae at different levels on many meridians on either side of the ventral line from which the cormidia are budded. From the opposite side of the pneumatophore spring the nectophores. As pointed out by GARSTANG (1946), delamination of tissues starts on one side (called ventral, on which the nectostyle is found), and proceeds gradually towards the opposite, dorsal side. This explains why the nectophores are late in appearing where they do on the dorsal side. METCHNIKOFF says that the pneumatophore has become free, in his figure 1, through the loss of one of the larval bracts. He draws attention to the beginnings of a stem; to the one-sided position of the nectophores; to the first definitive bract below them; to four palpons; and to the two (larval and first definitive) tentacles and a single gastrozooid. Evidently he was unaware of the smaller protozooid or confused it with a palpon. This is the only published account known to me of the beginnings of metamorphosis in a physonect siphonophore.

But curiously enough metamorphosing Physonects, probably of more than one species, have been figured unwittingly as adult representatives of a distinct genus "*Nectalia*". GARSTANG (1946, pp. 172–5) spent much time discussing "*Nectalia*" He quite correctly perceived that its long bracts were precormidial, or coronal as I prefer to call them, and homologous with the bracts of *Athorybia rosacea* and of *Melophysa melo*. But the reasons for his conclusion appear to be wrong in that he implied that these bracts would not be carried downwards with increase in number of the cormidia. The coronal (larval) bracts of Agalmids are in fact carried downwards with the first and second gastrozooids. They are "precormidial" in the earliest stages only. New bracts of this coronal type are formed for a long time after metamorphosis, but only in this restricted area, which comes to be terminal, and on the distal (oral) side of their predecessors. The later-formed bracts of this type are much longer than the first-formed ones, and gradually diverge from them somewhat in shape. But from the start they have a distal pocket of nematocysts at the end of the bracteal canal (misinterpreted by HAECKEL as a medusoid subumbrella), whereas the cormidial (definitive stem) bracts in *Agalma elegans* do not.

Fig. 1. Sagittal sections of two *Athorybia*-larvae of *Agalma elegans* taken with a plankton net at Villefranche. (*a*) (right) shows the bracts arising from the nectostyle, from the lower part of which are budded off the secondary gastrozooids. On the opposite side of the pneumatophore can be seen buds of the nectophores. Just below these is seen the small basigaster of the protozooid, and below this again the lower part of the pneumatosac, which at this stage is lodged inside the larval body. (*b*) A later stage. The pneumatosac is now outside the larval body. Between the latter and the second gastrozooid can be seen the larval tentacle and the budding zone of the first definitive tentacle.

Symbols used in figures throughout:

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Pn. | Pneumatophore | T. larv. | Larval tentacle | Nec. | Nectostyle | Pal. | Palpon |
| N. | Nectophore | Gz. 2, 3. | Second and third gastrozooids | Bg. | Basigaster | Pr. Z. | Protozooid |

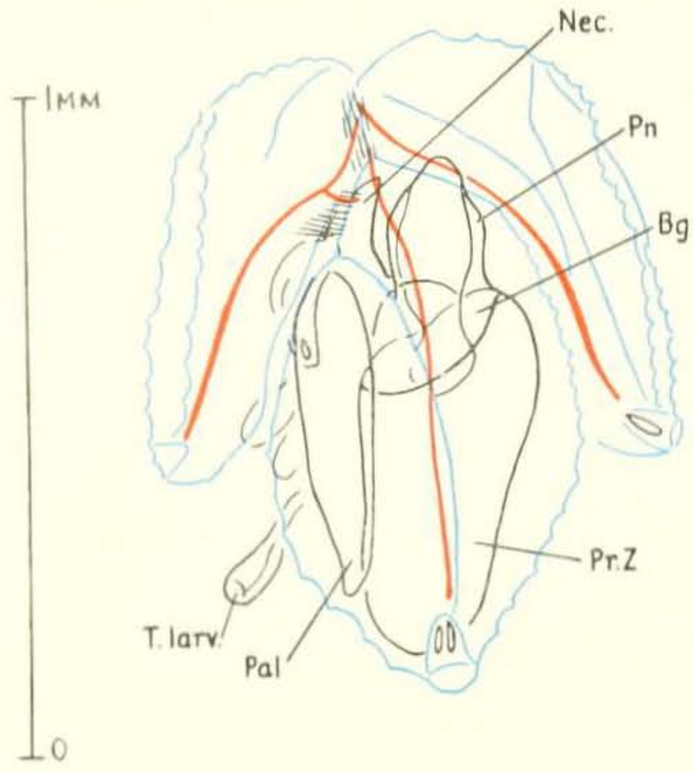


Fig. 2. An early *Athorybia*-larva of *A. elegans* showing attachment of larval bracts to the nectostyle and the first of a ring of palpons that come to surround the protozooid.

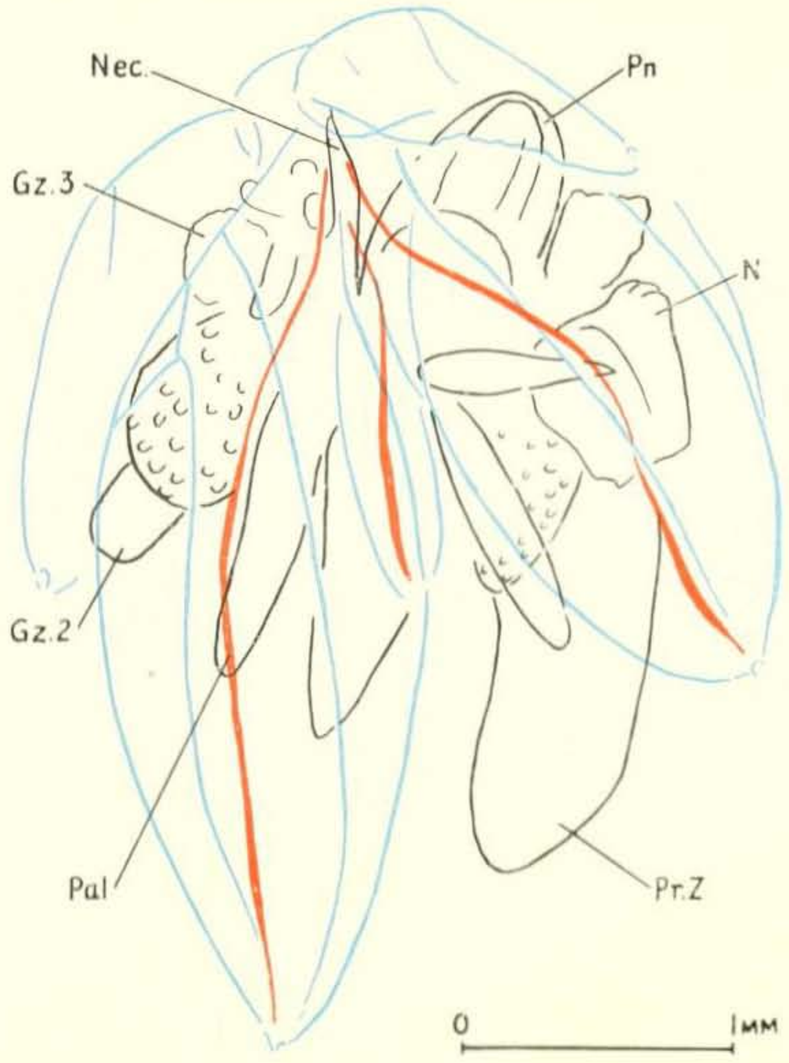


Fig. 3. The youngest larval bract still covers the pneumatophore. Palpons have increased in number, the nectophores are larger and the second gastrozooid has grown in size.

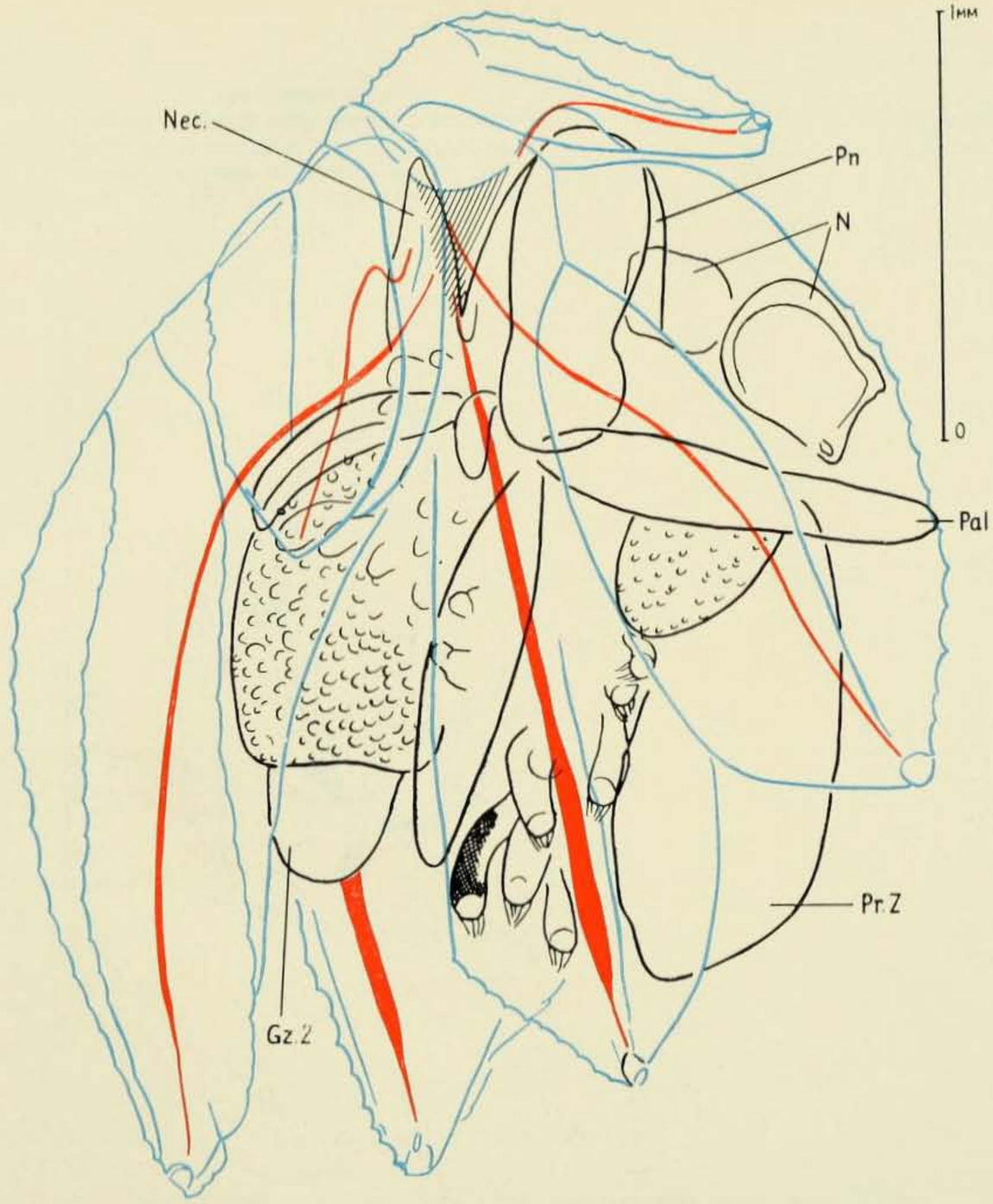


Fig. 4. The second gastrozooid is as large as the protozooid. Only one of the delicate muscularlamellae which attach the bracts to the nectostyle is indicated.


Fig. 5. An apical view of an anaesthetized larva to show that the buds of the nectophores are attached on the side of the pneumatophore opposite to the nectostyle.

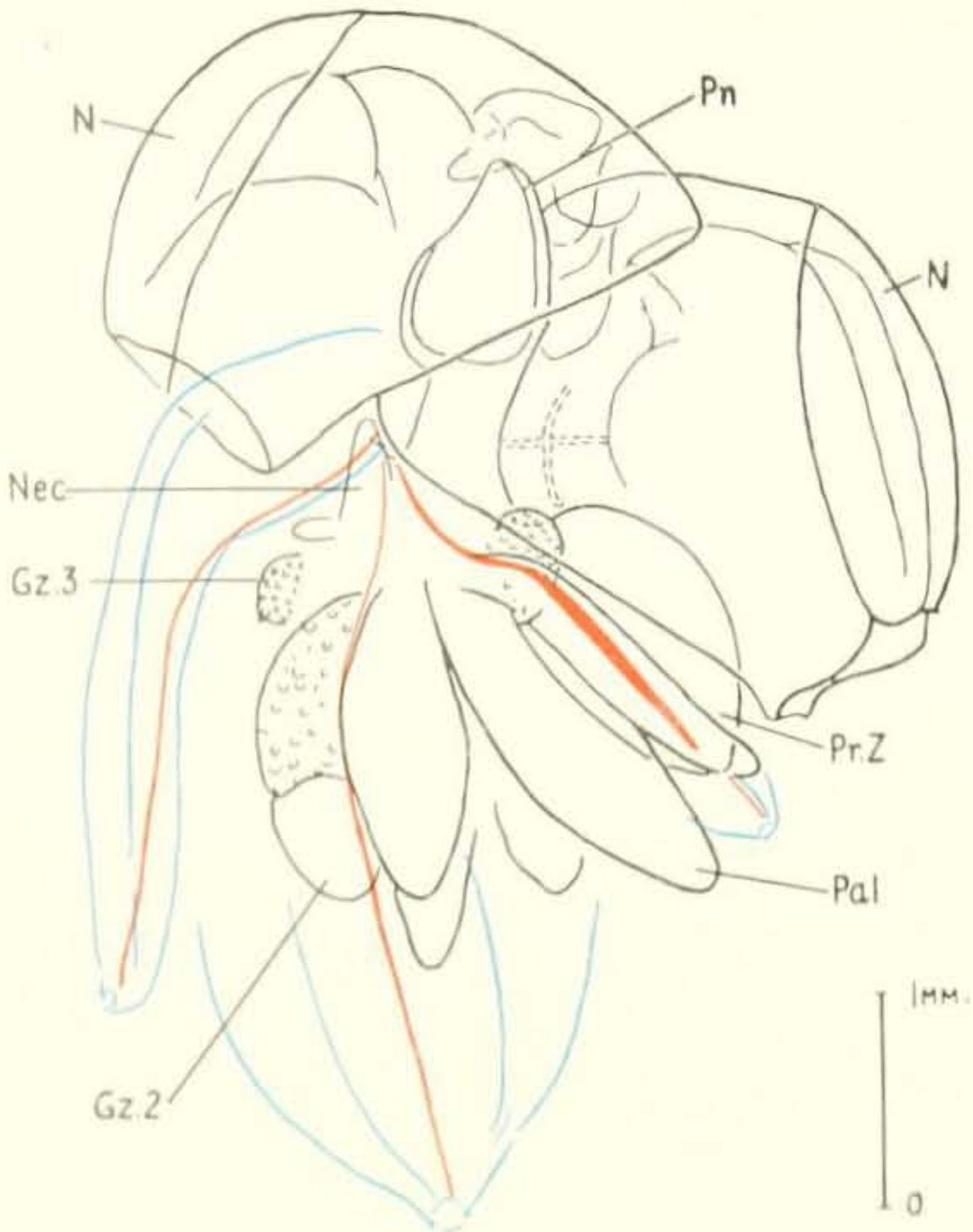


Fig. 6. An early stage in metamorphosis. That side of the upper end which carries the pneumatophore has elongated to carry the latter above the coronal bracts, and the nectophores have grown and are functional. The protozooid has taken up a latero-terminal position, leaving the second gastrozooid at the end.

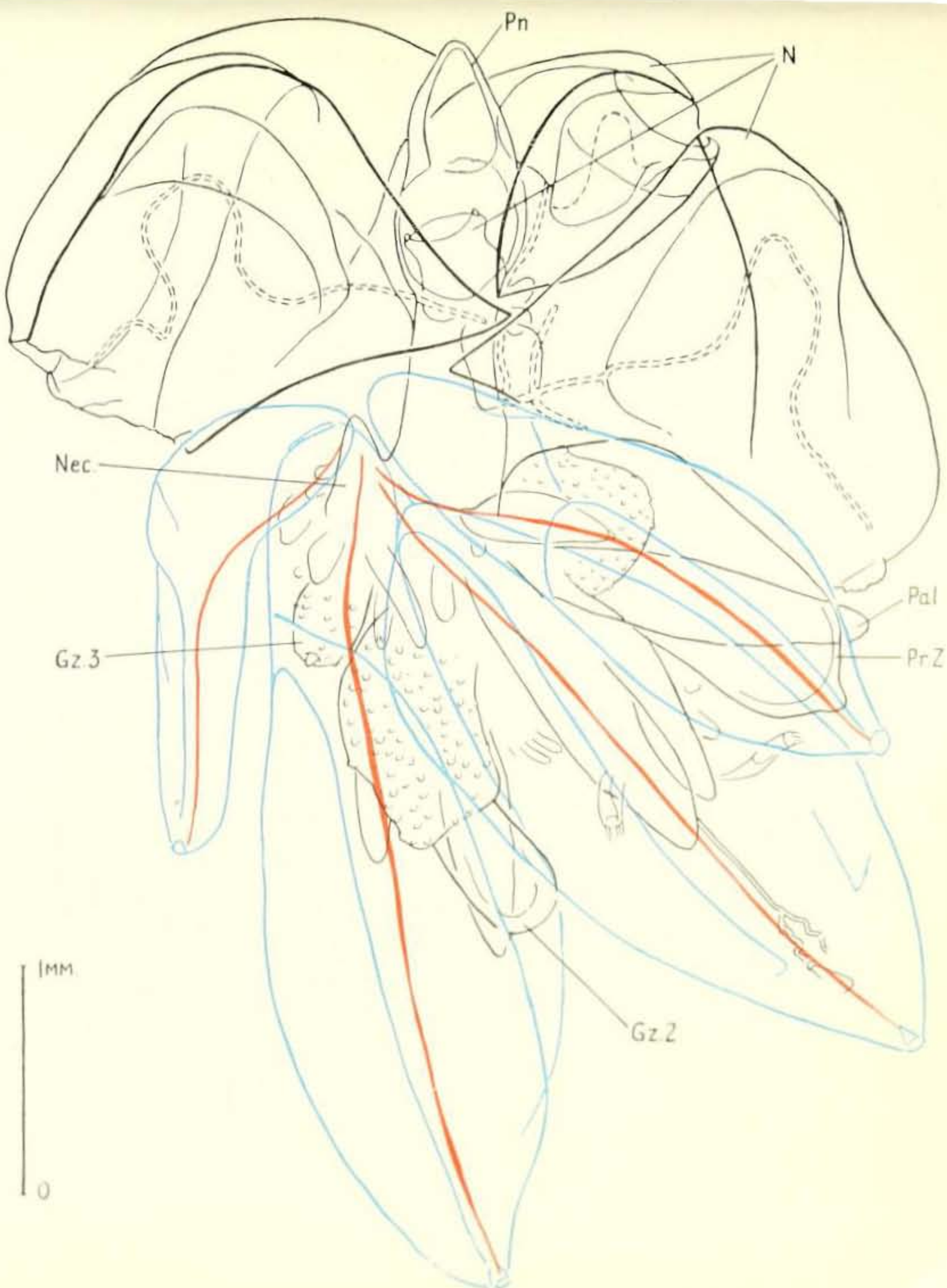


Fig. 7. The nectosome has elongated, but the siphosome has not. Note the small size of the basigaster of the protozooid compared with that of the second gastrozooid. The nectostyle can be seen clearly, still carrying the coronal series of bracts, and buds of stem appendages.

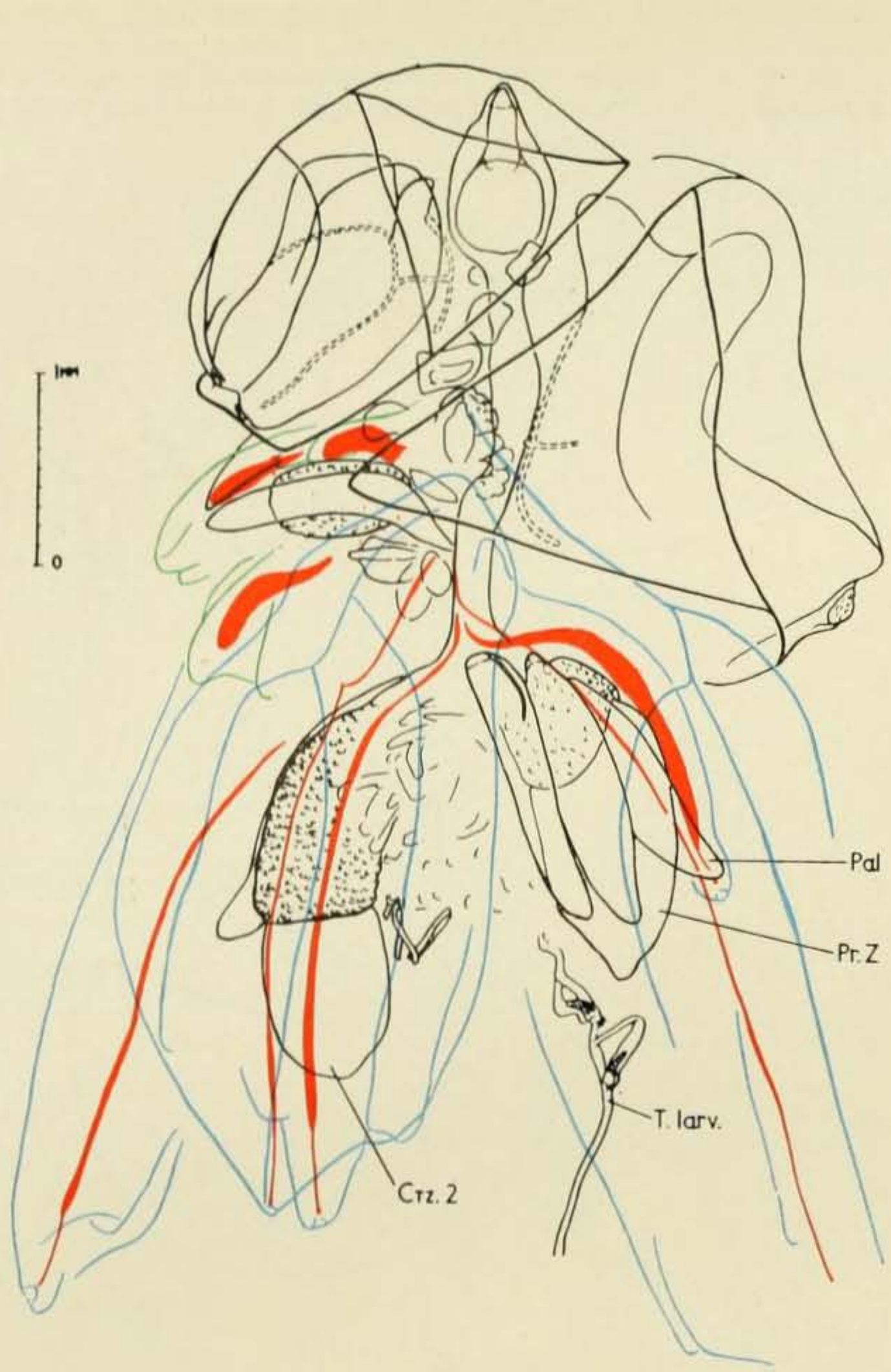


Fig. 8. The first of the definitive stem bracts coloured green can be seen on the elongating siphosome.

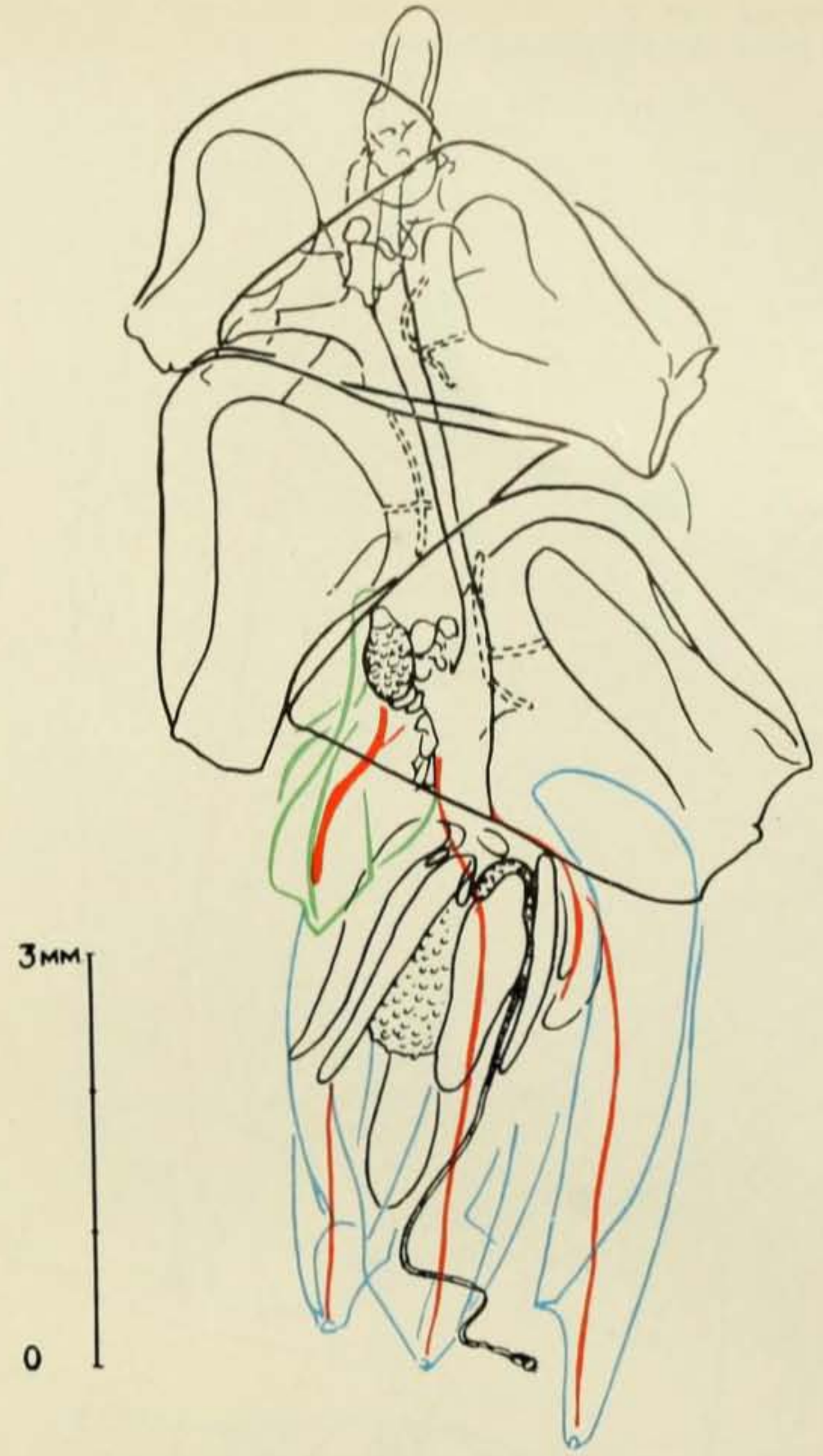


Fig. 9. The small size of the displaced protozooid is shown. The second gastrozooid now exceeds it in size. The nectostyle can still be seen opposite the pedicel of the first nectophore. Tentacles not indicated except for part of larval one.

Metamorphosis may be said to begin at the time when, the second gastrozooid being still smaller than the protozooid, and further cormidial buds having already made their appearance on the ventral side of the nectostyle (Figs. 3, 4), the stem of the future nectosome appears (Figs. 6, 7) as an elongation of that part of the oozooid that lies dorsal to the nectostyle. The nectostyle carries the larval bracts, rather like the tip of a man's umbrella with its bare ribs spread open, and also the cormidial buds. It remains at what may be called the nodal point of minimum growth, where it can be recognized at the side of the stem for some time, whilst the elongating stem of the nectosome carries the budding zone of the nectophores upwards and away from it in an aboral direction.

The second gastrozooid by now has overtaken the protozooid in size, and the adult type of tentilla on its tentacle can be seen (Fig. 8).

The upper end of the pneumatophore may have grown upwards as much as 4 mm above the nectostyle before there is a noticeable elongation of that part of the stem (siphosome) lying between the second and third gastrozooids. By the time that the nectosome, measured from tip of pneumatophore to nectostyle, is 5·5 mm in length, the siphosome, measured from nectostyle to base of first and second gastrozooids, may be 2 mm in length (Fig. 9).

An interesting point about the post-larva during this stage of metamorphosis is that the second gastrozooid comes to exceed the protozooid in size, and to assume a terminal position, leaving the smaller protozooid on the dorsal side. The protozooid too has a much smaller basigaster, which is partially divided on the outer, dorsal side. Its relatively small size can be seen in my frontispiece (1954, Fig. D. Gz. (rd)). At that time I had not studied the earlier developmental stages, which I have since collected in abundance, and confused the protozooid with the first definitive gastrozooid.

This side tracking of the protozooid is still more pronounced in *Nanomia bijuga*, where it becomes vestigial. The significance of this seems to be that it marks a new line of evolutionary experiment, an escape from the old line of specialization. This is all the more probable since the primitive type of tentacle found on the protozooid is replaced by a much more highly evolved type in the new series of gastrozooids. This " adult " trifid type of cnidosac demands more and bigger nematocysts. The basigasters of the secondary series of gastrozooids which supply the nematocysts are correspondingly better developed.

## REFERENCES

FEWKES, J. W. (1881), Studies of the jelly-fishes of Narragansett Bay. *Bull., Mus. Comp. Zool., Harvard Coll.*, **8** (8), 141–182.

FEWKES, J. W. (1885), Studies from the Newport Zoological Laboratory. XV. On the development of *Agalma. Bull., Mus. Comp. Zool., Harvard Coll.*, **11** (11), 239–275.

GARSTANG, W. (1946), The morphology and relations of the Siphonophora. *Quart. J. Micr. Sci.*, **87** (2), 103–193.

HAECKEL, E. (1869), Zur Entwickelungsgeschichte der Siphonophoren. *Natuurk. Verh. Prov. Utrechtsch, Genoots*, (1), **6**, 1–120.

METSCHNIKOFF, E. (1874), Studien über die Entwickelung der Medusen und Siphonophoren. *Z. Wiss. Zool.*, **24**, 15–83.

TOTTON, A. K. (1954), Siphonophora of the Indian Ocean together with systematic and biological notes from other oceans. *Discovery Repts.*, **27**, 1–162.