

A Note on Recapitulation in the Larvæ of the Decapod Crustacea. By G. E. H. FOXON, M.A., F.L.S. (From the Department of Zoology, University of Glasgow.)

FROM time to time many interpretations have been placed on the larval development of the decapod Crustacea, varying from the view of Brooks (1882), who held that the nauplius represented an ancestral creature, to that of Graham Kerr (1921), who maintained that it was merely a precociously developed head and that the developmental stages were entirely adaptations to early hatching and in no way recapitulatory. In addition there is the view of MacBride (1895), who held that, although there is no repetition of ancestral structure, the function is repeated.

It will probably never be quite certain where the truth lies; on the one hand, early hatching is an adaptation to the presence of less yolk in the egg, on the other hand, nobody would deny that the Megalopa stage of Brachyuran development does recapitulate a stage in which some ancestor carried the abdomen extended and may have used the abdominal appendages in swimming. But acceptance of some degree of recapitulation would appear to be assumed by the application, without qualification, of the names of lower groups, such as "*Mysis*" and "Schizopod" to certain larval stages of the higher decapods.

Recently attention has been given to the functions performed by crustacean appendages which in many cases have been found to be quite different from those inferred from their structure.

The object of the present note is to draw attention to some of those particulars in which larval Decapoda differ from those groups which they are alleged to resemble.

1. *The Thoracic Appendages.*

(a) *The Exopodite.*—In zoea larvæ and "*Mysis*" or "Schizopod" larvæ the thoracic exopodites are functional swimming organs, but in Mysids and Euphausids recent observations have shown their functions to vary considerably. These observations may be summarized as follows:—In primitive Mysids, such as *Gnathophausia*

(Manton 1928), the function of the thoracic exopodites is to cause a respiratory current, locomotion being effected by the pleopods. In higher Mysids, for example *Hemimysis* (Cannon and Manton, 1927), the thoracic exopodites are natatory and assist in filter-feeding. If we follow this

Fig. 1 a.

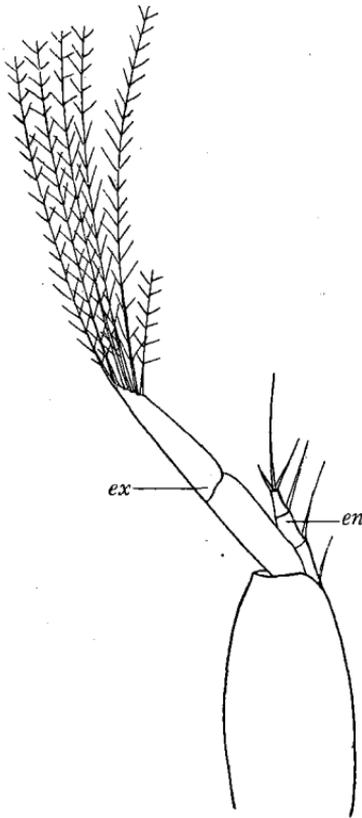
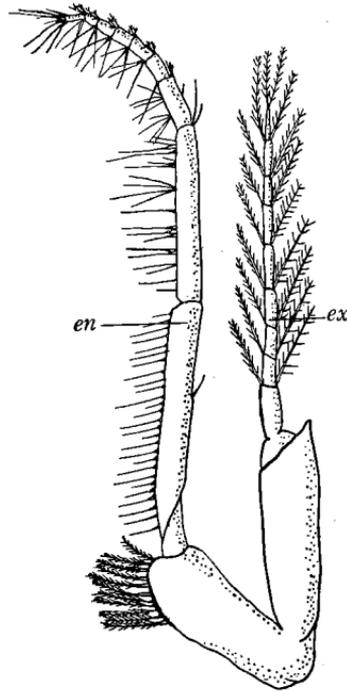


Fig. 1 b.

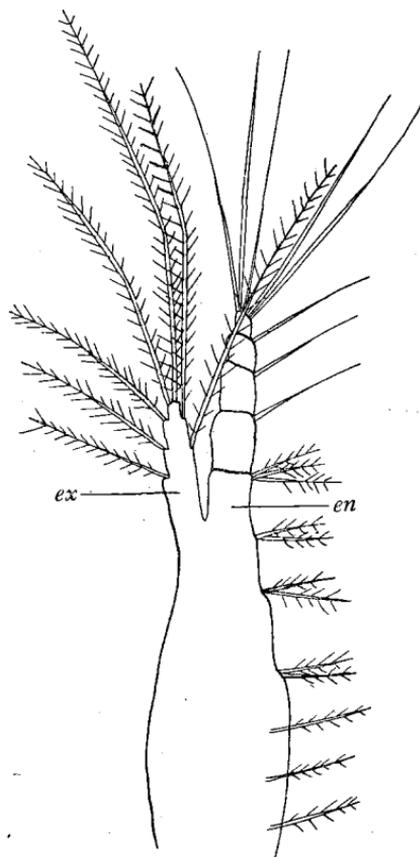
Fig. 1 a.—Second maxilliped of the zoea of *Portunus* sp.Fig. 1 b.—Third thoracic appendage of *Mysis*. (After Sars, from Calman.) *en*, endopodite; *ex*, exopodite.

line of evolution, the next group are the Cumacea, where these appendages are entirely locomotory and do not assist in filter-feeding. I also wish to record my doubts as to whether the pleopods of male Cumacea, even in those species in which they are best developed, are ever

functional, for in the males of *Iphinoë trispinosa*, in spite of many attempts, I have so far failed to observe any movement in these appendages.

In Euphausiids Manton (1928) has observed that in *Meganyctiphanes* the thoracic exopodites are concerned

Fig. 2.



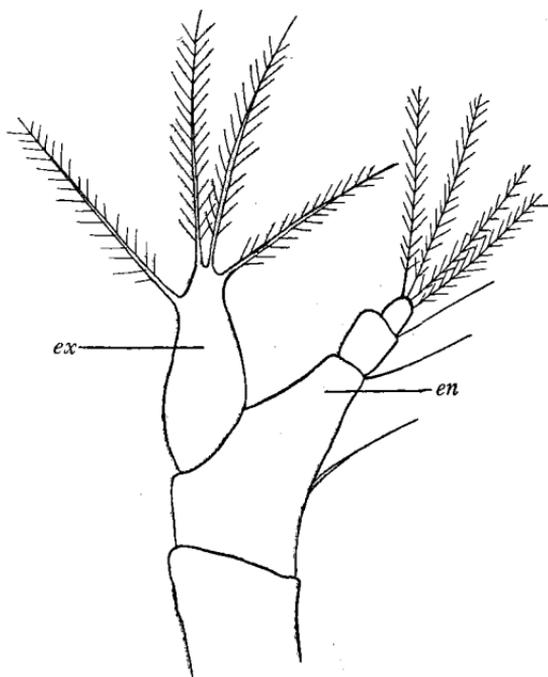
First maxilliped of the last protozoa of *Acetes*.
(After Brooks.) Lettering as before.

solely with respiration and feeding, the pleopods being the swimming organs. Turning to Euphausiid larvæ, there is some contradiction between the accounts of various workers (see Foxon, 1934), but it would seem most likely that the exopodites are not used for swimming.

Anaspides has also been observed by Manton (1930); here the pleopods are again the swimming organs, they may possibly be aided by the thoracic exopodites, whose main function is the production of a respiratory current which does not assist in filter-feeding.

(b) *The Endopodite*.—Both in Mysidacea and in the larvæ of the higher Decapoda the exopodite and endo-

Fig. 3.



Second maxilliped of the last protozoa of *Lucifer*.
(After Brooks.) Lettering as before.

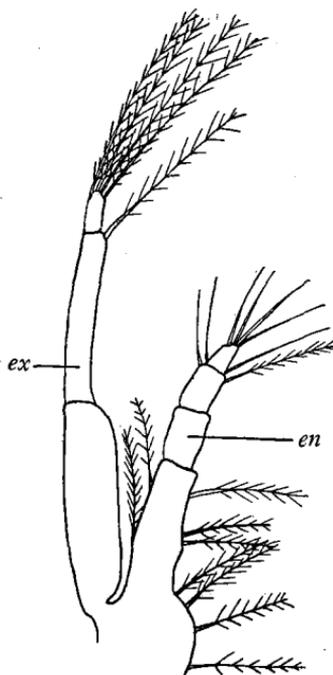
podite show considerable structural differentiation. These differences are, of course, correlated with function. In Mysids, for example *Hemimysis* (Cannon and Manton, 1927), while the thoracic exopodites are the swimming organs which assist in filter-feeding, the endopodites are used to hold the food when they are feeding on large masses.

The habits of the zoea larvæ of the Brachyura have been described by Lebour (1928, p. 500), and I have observed them myself; here there is a differentiation of structure

similar to that found in Mysids. The exopodites are swimming organs and the endopodites assist in feeding by holding the food against the mouth-parts. In structure, however, the thoracic appendages of such a zoea are remarkably different from those of a Mysid (see fig. 1, p. 118).

Turning to the larvæ of the lower Decapoda, we find that the thoracic appendages differ remarkably in struc-

Fig. 4.



Second maxilliped of the first larva of *Crangon* sp.
Lettering as before.

ture from both those of Mysids and of higher decapod larvæ. In the lower decapod larvæ the structure of exopodite and endopodite appears very similar, see for example the first maxilliped of the last protozoa of *Acetes* (fig. 2, p. 119). In the absence of precise observations it is impossible to say whether the apparent absence of structural differentiation is reflected in function, but it may be significant that the second maxilliped of the last

protozoa of *Lucifer* is shown by Brooks (fig. 3, p. 120) to have swimming setæ on both exopodite and endopodite.

Whatever interpretation may be placed upon this it is clear that in Mysids, on the one hand, and in higher decapod larvæ on the other, we have differentiation of function of exopodite and endopodite accompanied by differentiation of structure which has proceeded along two different lines. The structure of the thoracic appendages of the larvæ of the lower Decapoda seems very much less specialized, but differentiation increases as the higher members of the group are approached, as, for example, in the larva of *Crangon* (fig. 4, p. 121).

Thus we may say that the structure of the thoracic appendages of Mysids is not reflected in those of decapod larvæ.

2. *The Mode of Respiration.*

Most Malacostraca respire by gills over which a current of water is drawn, but attention should be directed to the variations in the methods by which this current of water is caused.

In Decapoda the strong current of water which flows forward over the gills is caused by the exopodite of the second maxilla. In both Mysids and Cumaceans there is a similarly directed current, caused, however, by the epipodite of the first trunk-limb. Euphausiids have a respiratory current which assists in filter-feeding, caused by the thoracic exopodites, which, as stated above, are not natatory. Respiration has also been shown by Manton (1930) to be the function of the thoracic exopodites in *Anaspides*, although they may assist the pleopods in swimming.

Thus it is clear that larval Decapoda, which have a strong respiratory current created by the exopodite of the second maxilla from early stages, do not recapitulate conditions found in other groups of Malacostraca.

To conclude, Manton (1928) has suggested that the utilization of the thoracic exopodites for swimming is secondary, this function formerly having been carried out by the pleopods; and we may suggest that their former function was respiratory. If this is so, we may regard the ancestral Malacostraca as carrying out their functions in a similar way to *Anaspides*. With the

adoption of new methods of producing a respiratory current the thoracic exopodites became released from this duty, and two courses of evolution were open to them—either to disappear, as in higher Decapoda, or to assume the swimming function, this alternative resulting in reduction of the pleopods (Mysids). *Gnathophausia* is especially interesting as standing near the base of the Mysid stem, and Manton (1928) has suggested that it still receives assistance from the thoracic exopodites in respiration. The Euphausiids remain more primitive in that the respiratory current is caused by the thoracic exopodites, but the high degree of efficiency here reached is really a third line of specialization.

Thus the larvæ of the Decapoda do not in their ontogeny pass through either a typical Euphausiid or Mysid stage, and neither their structure nor function is recapitulated.

Finally, it may be pointed out that Calman (1909) includes a natatory exopodite to the thoracic limb as a characteristic of the caridoid facies. As recent observations show that this appendage performs various functions it may be as well to revise the definition, so that function is not stated or implied; perhaps some expression such as "whip-like" exopodite would meet the case.

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