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A CRITIQUE TO THE STUDY OF LARVAL DEVELOPMENT IN EUPHAUSIACEA

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The workers on the larval development in euphausiids the world over have noted variations in the combinations of larval characters present in the similar stages of development of different species or even in the same species. Subsequently there has been a lot of discussion on the correct classification and nomenclature of different larval stages in these animals. It is known that the larval development of the same species distributed in different ecological realms followed different courses towards their adulthood either by increasing or decreasing the number of stages or showing a difference in the combination of larval characters in particular stage in their life history. This has led to much confusion in the scientific world with regard to following any conventional method for tracing the developmental pathway of euphausiids. Some authors have developed formulae which could be applied for tackling the development of euphausiids but some of these formulae have become very vague due to over simplification. Phylogenetically the euphausiids being a less specialised group among the crustaceans it is to be accepted that probably any set formula cannot be applied to all the species uniformly.

In the light of the investigations carried out on the larval development of several tropical species of euphausiids from the Indian Ocean, a discussion reviewing the developments in the larval history of Euphausiaceae appears to be desirable.

INTRODUCTION

The nomenclature and classification of the different larval stages of Euphausiaceae have been subjected to discussion from time to time. Dana (1852) was the first to describe euphausiid larvae giving them generic and specific names unaware of their larval nature. Claus (1863) established that the three schizopodus genera of Dana namely, *Calyptopis, Furcilia* and *Cyrtopia* were different developmental stages in the life history of euphausiids. Metschnikoff (1869) described two early larval stages. In 1871 Metschnikoff described all the stages from egg upto calyptopis. With the classical work of Sars (1885) who worked on the very vast CHALLENGER collections, the euphausiid fauna became more familiar to the scientific world. He gave a well illustrated account on the developmental stages of the euphausiid larvae. This enabled him to fix the terminology of larval stages and give exact definitions to the various stages. This, along with consideration of the works of previous authors, allowed him to recognize and name each phase in the larval history. In order of development he called them nauplius, metanauplius, calyptopis, furcilia and cyrtopia. He also showed for the first time that species of different genera pass through the same developmental stages in their life history.

The term *cyrtopia* has been subjected to much discussion by earlier workers. As mentioned above it was first coined by Dana (1852) to describe a new genus.

Sars (1885) accepted this term to designate the larvae of the stage with "antennular flagella becoming elongate and distinctly articulate. Antenna transformed so as not to serve the purpose of locomotion. Posterior legs and gills successively appearing" (l.c.p. 150). According to Lebour (1925) the best way to distinguish a late furcilia from an early cyrtopia is by the flagellum of the antenna: this is unjointed in the furcilia and jointed in the cyrtopia. Macdonald (1928) described 12 cyrtopia stages in the life history of *Thysanoessa raschii*. His identification of the cyrtopia stages is quite vague as a combination of characters including luminescent organs, telson spines, and the length of the animal were used for the separation.

Fraser (1936), however, wanted to abandon the term cyrtopia and include the cyrtopia stage designates in the furcilia stages, as the cyrtopia stage placed too much stress on the alteration of form and function of the particular appendages. The cyrtopia are not recognizable from furcilia, he says, by any sudden increase in size as they change from old to the altered form. According to him the change in form and function of antenna which is the major criterion for recognising this stage did not necessarily coincide with equally significant changes in the form of other appendages. For example, in *Meganyctiphanes norvegica* there are seven terminal telson spines in the cyrtopia stage while five and three are present in *Euphausia krohnii* and *Nyctiphanes couchii* respectively, and only one in *Nematoscelis microps* and *Thysanopoda aequalis*. As Fraser (1936, p. 50-51) puts it "it is apparent, therefore, that the change in the antenna is not of the significance formerly attributed to it and the altered form does not merit the distinction of a division in the larval history".

Einarsson (1945) argues that if there cannot be any marked difference between furcilia and cyrtopia as stated by Fraser then the same rule can be applied to the change from calyptosis to furcilia. as the distinction of a furcilia larva from a calyptopis larva is made on a single character, that is the carapace. To support his views Einarsson makes it clear that the change of the carapace *i. e.*, its withdrawal from over the eyes does not coincide with other important changes in the larval organism, such as the limbs, the telson or the antenna. As Einarsson (1945, p. 8) puts it "the change of form in the Euphausiid larval development is, on the whole, so gradual, that there is not at any point an actual "break" which manifests itself in a number of different parts of the larval organisms." In his opinion the changes in form from calyptopis to furcilia is more clear than from furcilia to cyrtopia, and that clarity alone made others to preserve the terms, calyptopis and furcilia, and discard the term cyrtopia. He suggests that in view of the gradualness in the euphausian development it would be better to discard all the larval names and designate the whole series as stage I, stage II, etc., beginning with egg as stage I. However, he adopted the system followed by Fraser (1936) for his account on the larval development of some species.

Gurney (1942, 1947) tried to re-establish the 'cyrtopia stage' in order to emphasise the common ontogeny of all decapods. Boden (1951), however, doubts whether the retention of the cyrtopia stage would help clarify the phylogenetic relationship among the decapods for the terms calyptopis and cyrtopia are peculiar to euphausiids. These terms emphasise little but division in the larval series of this group of animals.

Gurney (1942) synonymised calyptopis with protozoea, furcilia with zoea and cyrtopia with post larva of other decapod crustaceans. According to Boden (1951) the change in form of antenna in the cyrtopia stage is as important as the change in form of carapace in first furcilia or the change in the telson in

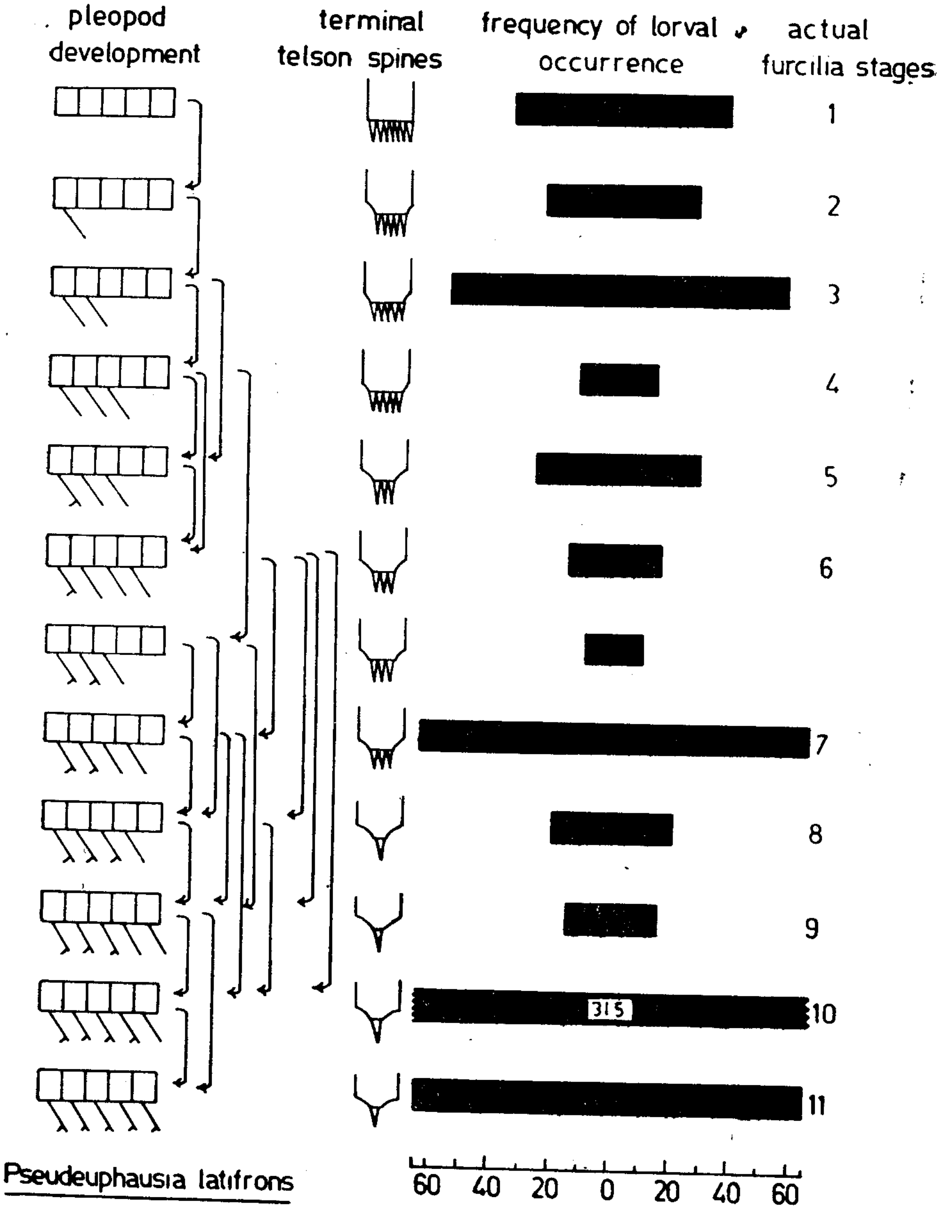

Fig. 1. *Pseudeuphausia latifrons*. The pathway of development and larval occurrence. The pleopods first develop as buds and subsequently become setose as indicated in the figure. The actual furcilia stages are determined on the basis of the theory of dominance and also based on morphological characters. The arrows indicate the possible route by which the larvae might pass through at times skipping some stages and at other times forming variant forms.

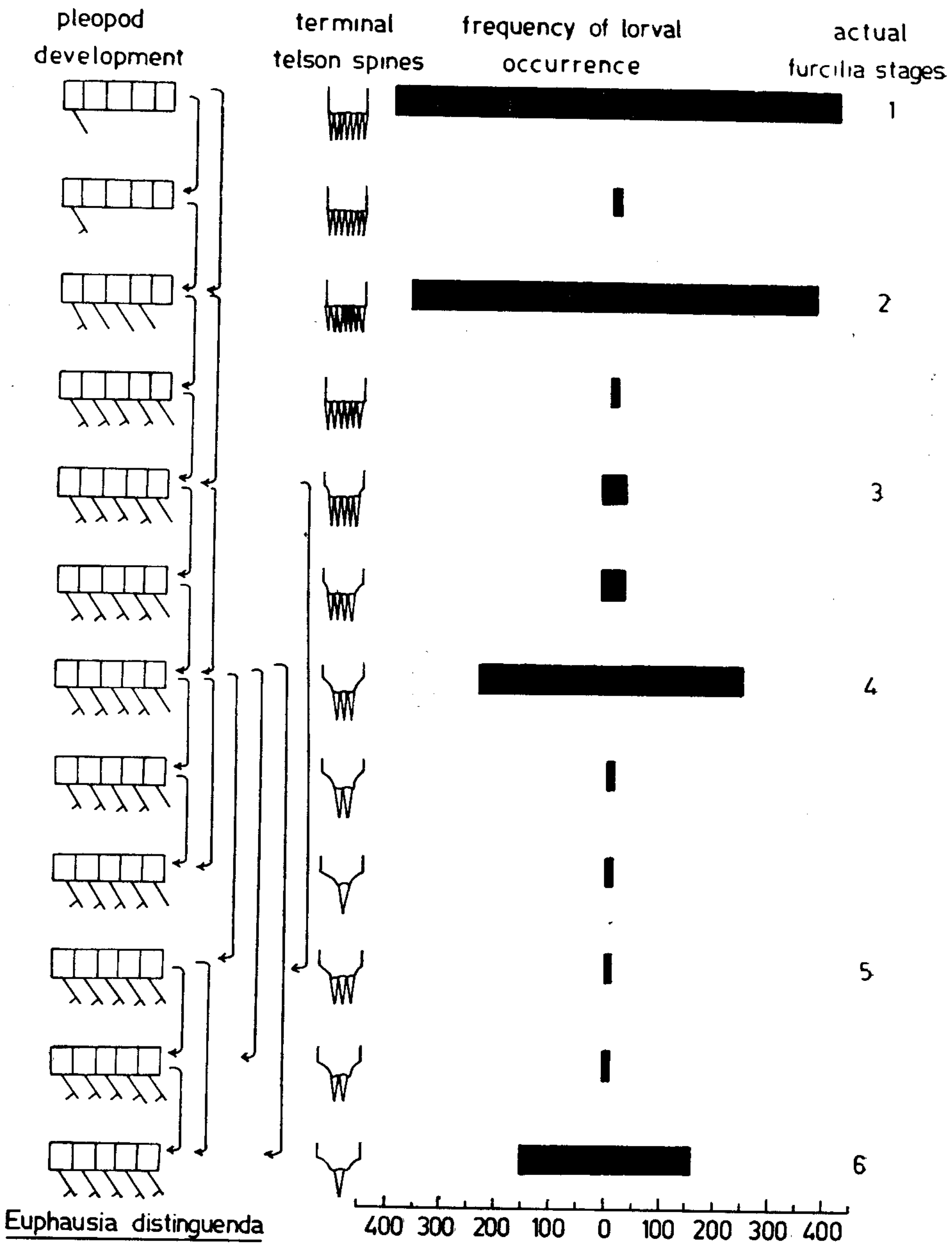

Fig. 2. *Euphausia distinguenda*. Other details as under Fig. 1.

the first juvenile. If the larva is to be characterised by function rather than form, he says, the division between furcilia and cyrtopia is a natural one and should be retained.

In spite of these facts put forward by himself, Boden (1951) tries to eliminate the term cyrtopia just to emphasise the continuity of a series in which dominant stages can be determined by statistical analysis. Therefore, he considered unlike Gurney, the so-called cyrtopia stages, larval rather than post larval stages because 'jumping of stages' and 'dominant stages', characteristic phenomena of furcilia, are found in the cyrtopia stage also. The authors also agree with the views expressed by Boden (1951) for the same reasons. The ensuing figures 1-6 are drawn based on ideas developed in these lines.

Grouping of furcilia larvae

The furcilia phase according to Sars' (1885) definition includes the larval stages in which "compound eyes more fully developed (than in calyptopis), mobile, and projecting beyond the sides of the carapace. Antennae still retaining their original structure, natatory. Anterior pairs of legs and pleopods successively developing" (Sars, 1885, p. 150). In euphausiids the attainment of the above characters is a gradual one and one larva has to undergo a number of ecdyses before reaching the final form. Attempts have been made to divide the furcilia phase into different stages mainly based on the pleopod development and reduction in number of telson spines. Among the furcilia larvae of *E. krohnii* (*E. pellucida* of Sars, 1885) Sars could recognise three stages, which he named

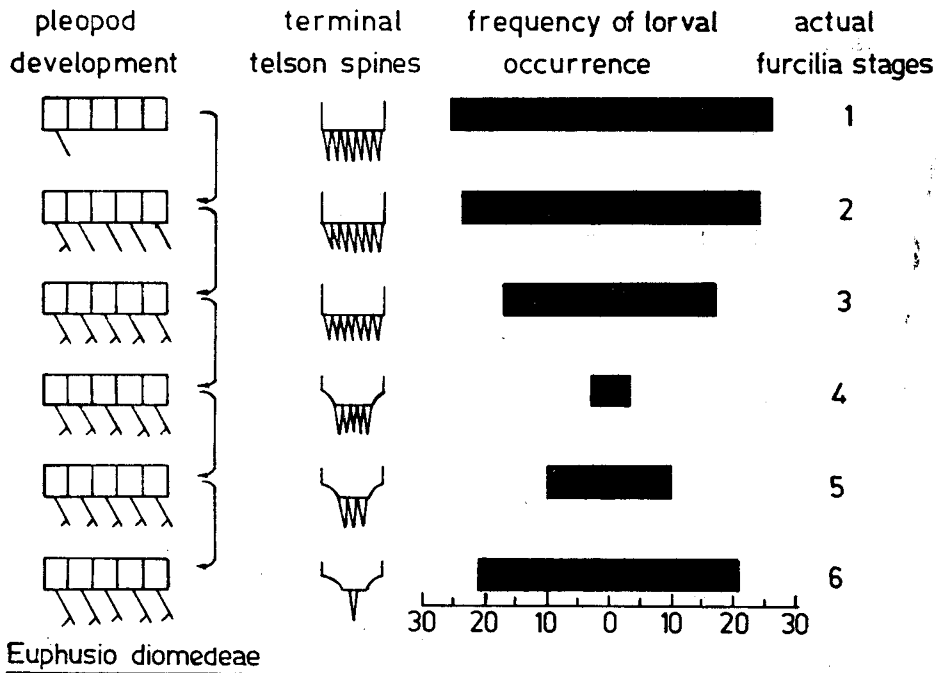

Fig. 3. *Euphausia diomedeae*. Other details as under Fig. 1.

'first, intermediate and last' furcilia. Brook and Hoyle (1888) based on comparative development of pleopods stated that in the development of one species (sp. not known) there are eleven moults and they designated each moult as one furcilia stage. According to their observations the stage I starts with larvae without pleopod rudiments and by the VIth stage all five simple nonsetose pleopods are established. From stage VIIth to XIth nonsetose pleopods become biramous and setose one after the other till all become setose.

Lebour (1926) recognised the following typical stages in general in the life history of euphausiids; nauplius, pseudometanauplius, metanauplius, calyptopis I to III, furcilia I to XIV and cyrtopia. The furcilias were recognised according to the successive development and setations of the pleopods. But this method of classifying the larvae is to be adopted with caution. Macdonald (1927) pointed out that the nonsetose pleopods in furcilia need not necessarily become setose in the subsequent moult. Gurney (1947) also found nonsetose pleopods of two different sizes among the larvae of the same species. He believed that the nonsetose pleopods simply increased in size during the subsequent moult instead of

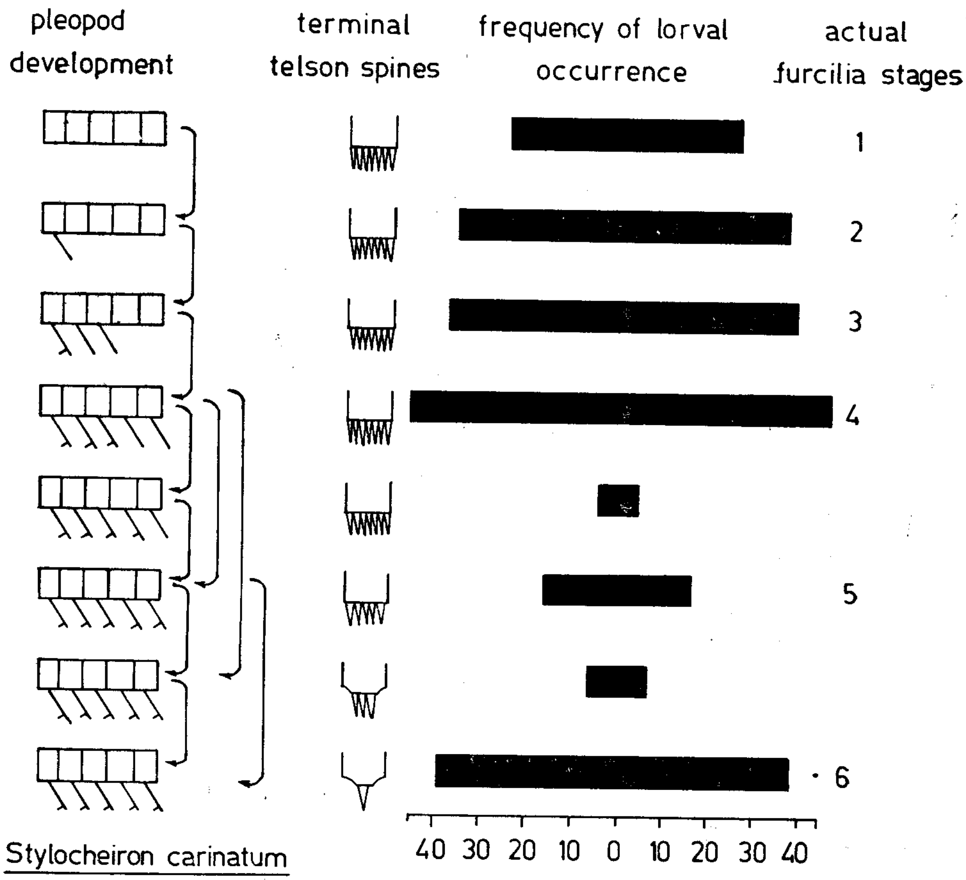

Fig. 4. *Stylocheiron carinatum*. Other details as under Fig. 1.

becoming setose. This condition of nonsetose pleopods of two different sizes has also been found in the Indian species.

In the furcilia stages there is no orderly development. Lebour (1926) noted that in some species of *Nyctiphanes* and *Meganyctiphanes norvegica* there is 'jumping of stages'. For example *Nyctiphanes* skips from a stage with three simple pleopods to one with two setose and two simple pleopods. If the developmental pathway of several species is tracked, it may be seen that jumping of stages is a rule rather than an exception.

Macdonal (1927) working on the larval development of *M. norvegica* recognised eleven furcilia stages of which some tended to be dominant and others suppressed. The term dominant is applied to those furcilia stages which are present in samples more frequently than other stages. The introduction and recognition of these two phrases, 'jumping of stages' and 'dominant stages' have had great influence on the classification of the furcilia phase. As a result of this influence a lot of confusion has arisen.

The basic reason for disagreement among authors regarding stages in the furcilia phase, says Sheard (1952, p. 56), is that "the stages of the furcilia phase are a matter of controversy, increased by the fact that experimental work on larval development is so difficult under land-based laboratory conditions that little has been carried out. In addition, the observed course of larval development from heterogenous samples has been based on inadequate material in the majority of species which have been examined". But these points do not make up the whole story. It has been noted by almost all workers that a number of variants occur in the furcilia stages of species (Fig. 1-6). The degree of variations has come to such a level that it is impossible to demonstrate any absolute or fixed relation in degree of development between the different organs (Rustad, 1930).

Theories of 'Jumping of stages' and 'dominant stages' in the furcilia phase have been accepted. Similarly in different species the pattern of development is different eventhough they follow the same course. This fact was established when Hansen (1908) stated that there is much difference between the development of three species of the same genus (genus *Euphausia*). When a set of organs are similarly developed in larvae of two species, other organs may be considerably more or much less developed in one of these larvae than in the other. Macdonald (1927) noted that out of the 26 larvae kept in aquaria, more than half moulted irregularly. This may or may not have been due to a change in environmental conditions.

For example when a larva may have three setose pleopods, one nonsetose pleopod and three telson spines, on the next moult it may retain the nonsetose condition of the pleopod and reduce the number of telson spines to two or one; or the same larva can also moult to a condition where the original three numbers of telson spines are retained, while all the pleopods become setose. The question of why there is such a large number of variants in the later developmental stages of euphausiids may now be examined.

Primitively, says Gurney (1942), development must have been a process of gradual growth, without metamorphosis or transformation. Metamorphosis is a characteristic of highly advanced forms. Because euphausiids are a very primitive group of animals Macdonald (1927) tried to apply this principle to this group of animals. He suggests that Gurney's observations are interesting as they suggest tentative steps in an evolutionary progress in the Order Euphausiacea towards reduction in the number of larval stages. It is true that in primitive development there is no well marked coincidence of ecdyses with a fixed degree of development. Fraser (1937) states that each variety of pleopod development found, indicates a larval stage and each stage is well marked and hence the idea of gradual development or continuous development is not altogether true with regard to them★. Hence we agree with Fraser (1937) that in euphausiids a continuous development is giving way to metamorphosis" and therefore, they come in between the primitive groups where continuous development is the rule and the more advanced forms where a distinct metamorphosis with a few pronounced stages is present. In euphausiids, nauplius, metanauplius and calyptopis stages are well defined and without variations while in the furcilia, the stages are less well defined by the presence of dominant forms and other variants.

THEORY OF DOMINANT STAGES

The unorderly development in the euphausiids has been well discussed. Because of this unorderly development in the furcilia phase certain stages become

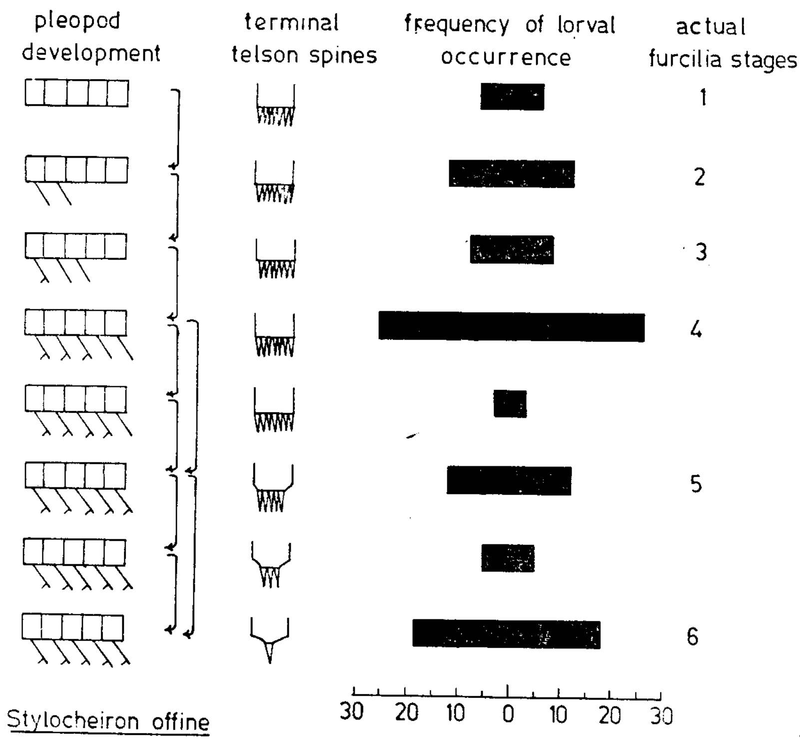

Fig. 5. *Stylocherion affine.* Other details as under Fig. 1

★ Fraser does not quite agree with the term 'continuous development' as applied to the primitive arthropod development because continuous development in its strict sense *i. e.* numerous ecdyses at which slight morphological changes occur, does not present at all in this group of animals. In arthropods the course of development is in all cases marked off into stages by the occurrence of ecdyses between which no marked change in form usually occurs.

numerically dominant over others, *i. e.*, in number (Fig. 1-6). Fraser (1937) stated that only the dominant stages in furcilia should be considered as actual stages of that part of the life history and other intermediate stages which are less dominant as variants. So, according to him the numerous number of furcilia stages can be brought down to a reasonable number by direct evidence of moulting and quantitative analysis of the material.

Macdonald (1927) was the first to trace the larval development on quantitative basis (in *M. norvegica*) and he found that of all the eleven furcilia stages only two stages were represented by a good number of specimens (20% and 26% of the total number of 302 larvae examined) and he described those two stages as 'tending to be dominant'.

Boden (1950, 1951) classified the furcilia instars into a total of six stages based on the theory of dominance. For different species the number of furcilia types or instars were different. For example *N. couchii* had 15, *N. simplex* 16, *N. australis* 24, and *N. capensis* 25. His six furcilia stages based on the development of *N. capensis* are as follows:-

F I Pleopods nonsetose, second antennal endopod simple, seven terminal spines on telson.

F II Pleopods mixed, second antennal endopod simple, seven terminal spines on telson.

F III Pleopods setose, five terminal spines on telson, second antennal endopod simple.

F IV Pleopods setose, three terminal spines on the telson, second antennal endopod simple.

F V Pleopods setose, three terminal spines on the telson, second antennal endopod segmented.

F VI Pleopods setose, one terminal spine on telson, second antennal endopod segmented.

Sheard (1953) classified the furcilia larvae into three phases, according to the changes in the morphological characters. The major changes thereby occured were:-

F I Eyes developed and free of the carapace, pleopods absent or present as nonsetose rudiments. Terminal telson spines generally 7, sometimes reduced in number. Lateral spines three in number, the central spine always present.

F II Some or all pleopods setose, terminal spines sometimes reduced in number, lateral spines three in number, the central spine always present. The pair of long lateral spines are unaltered at the base.

F III All pleopods setose and functional, the pair of long lateral spines are altered at the base, the terminal spines are progressively reduced to one.

This is a rather simple classification, in the sense that it is applicable to all euphausiids. But in tracing the developmental stages of individual species further subdivision of the stages and their description are necessary. As for example to represent the furcilia stages of *E. diomedeae* (Fig. 3) a classification following Sheard can be adopted as under:-

F I of Sheard to represent F I of *E. diomedeae.*

F II of Sheard to represent F II, F III and F IV of *E. diomedeae.*

F III of Sheard to represent F V and F VI of *E. diomedeae.*

In order to get a picture of development in its sequential manner it is really necessary to follow a system based on the theory of dominance as it was followed by many workers (Fraser, 1936; John, 1936; Boden, 1950, 1951; Mauchline, 1959, 1965).

Mauchline (1959) adopted a new system for tracing the larval development. He measured all larvae within a stage without eliminating the variants. With the data he made length-frequency histograms. He could find in each stage a point at which the maximum number of larvae occurred. He suggested that instead of taking such dominant forms alone for studies, all the instar forms must be described and where there is much variation as many larvae as possible should be presented either as range or size within an instar, the mean size and

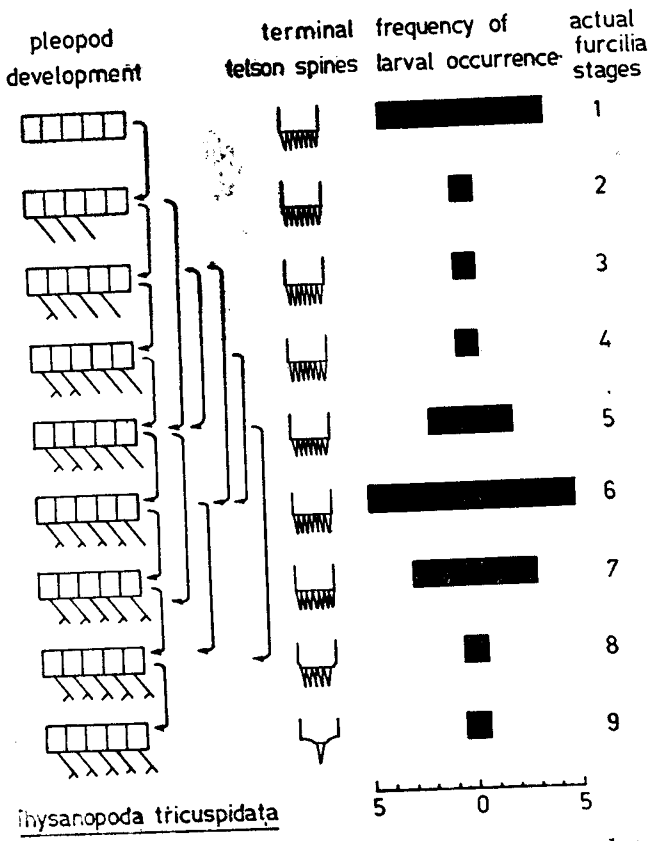

Fig. 6. *Thysanopoda tricuspidata*. Other details as under Fig. 1.

number of specimens measured being indicated, or in the form of length-frequency histograms for each larval form or instar. But this system is practicable only when a large number of larvae of all stages are available at hand.

The euphausiids in the neritic and oceanic environments have been found to behave differently with regard to their larval stages. Usually a greater number of variants and actual stages are found among the neritic species. In the oceanic forms the developmental pathway appears to be more or less rigid. The obvious reason for such a difference is that the ecological conditions in neritic areas are subjected to more frequent changes than oceanic areas. Hence the developing larvae would also react to such changing conditions and one way in which they could respond is through irregular moults at frequent intervals resulting in more variant forms (Eg. *Pseudeuphausia latifrons*, a neritic form (fig. 1).

With good number of larvae on hand it has become possible to trace the life history of five species of euphausiids of the Indian Seas. A schematic representation of the different furcilia stage of these is shown in figs. 1-5. The larval history of *Thysanopoda tricuspidata* (Fig. 6) appears to be incomplete since material available was meagre. The arrows in the figures indicate the possible mode of moulting to the subsequent stages in which process some stages may be avoided. The observed variant forms are also shown. The actual furcilia stages are determined on the basis of the theory of dominance on one hand and the larval features on the other.

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