Syllogeus
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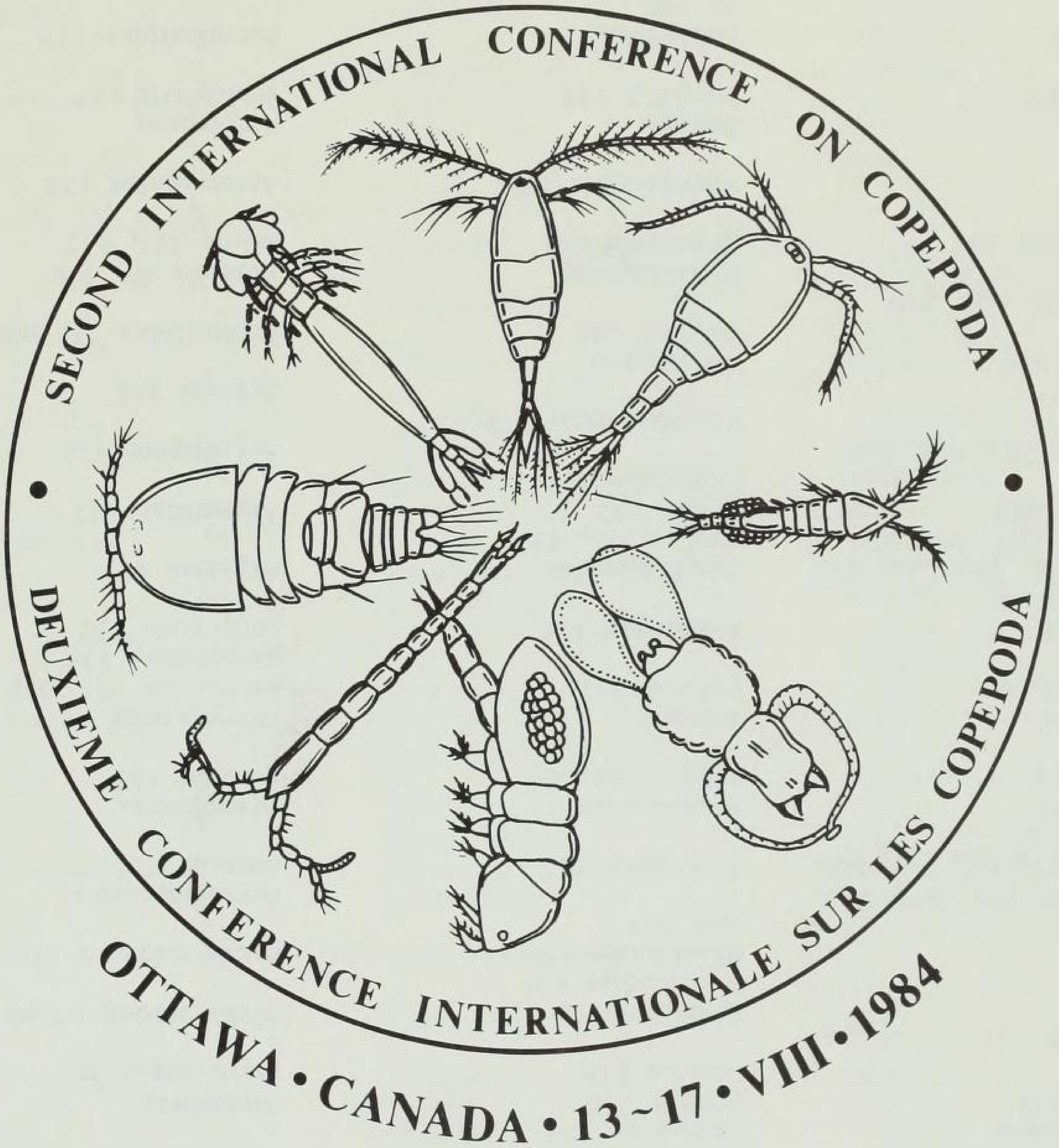
no.58(1986): https://www.biodiversitylibrary.org/item/111556

Proceedings of the Second International Conference on Copepoda
Ottawa, Canada, 13-17 August 1984

Edited by G. Schriever, H.K. Schminke, and C.-t. Shih



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Ottawa, 1986

ASPECTS OF THE APPENDAGES IN DEVELOPMENT

TAGEA K.S. BJÖRNBERG

Departamento de Zoologia, Instituto de Biociencias, Universidade de São Paulo, Caixa Postal 71 - São Sebastiao, SP. - Brasil

Abstract: Considerations are made on the morphology of the appendages, their muscle system and their function in the calanoid, cyclopoid and harpacticoid nauplii. The changes observed in their morphology and function in the copepodids are mentioned.

INTRODUCTION

From the perusal of the older authors (Gurney, 1931; Lang, 1948) and of the latest literature (Von Vaupel Klein, 1984) on appendages of copepods there are several problems related to this subject which are still to be solved and some still to be proposed. Among the latter there is the question of the origin of the first nauplius. Among the others there are the following: 1) the primitive number of podomeres on the appendages; 2) the question of which of the three orders, Cyclopoida, Harpacticoida or Calanoida, is the oldest; 3) the function of the appendages during the feeding process; 4) the most adequate nomenclature for each of the appendages and their respective parts. Some of these questions shall be discussed elsewhere during this Conference. The others, when pertinent, shall be commented upon here.

ON THE ORIGIN OF THE FIRST NAUPLIUS

Arthropodization started to exist when a trochophora-like larva acquired the capacity of producing an external carapace composed of a chitin-like material (Fig. 1). The first three pairs of jointed appendages of this nauplius-like larva appeared when the two pre-oral tentacles and the two first pairs of parapodia, produced by the posterior metamerisation of the larva, secreted the external covering of chitin-like material. The continuous movement of these appendages backwards and forwards, or up and down (Fig. 1b) may have insured at the point of flexure the development of a less rigid skeleton, and, thus, an articulation between the basis of the appendages and the body. Perhaps, by the same process or by undulating movements other articulations were maintained along the appendages, permitting motion.

Present day copepod nauplii show these same three pairs of functional limbs: the antennules, the antennae and the mandibles. The primordia of the other pairs of limbs, from maxillules to the second pair of legs, are present in the sixth naupliar stage, but, they are not functional (Fig. 2).

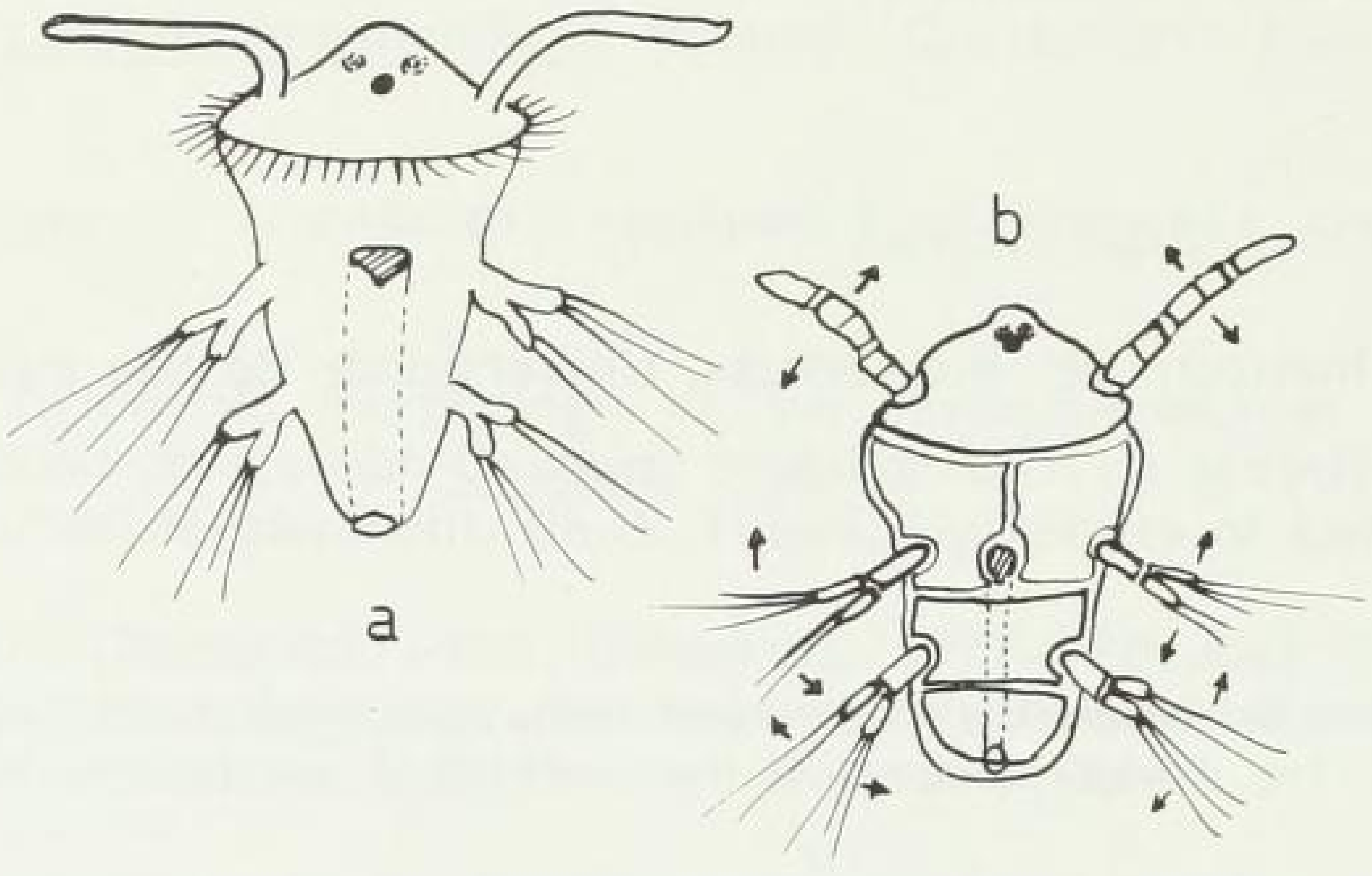

Figure 1. ***a.*** *Trochophora-like larva;* ***b.*** *The primitive nauplius, resulting from the arthropodization of a trochophora-like larva.*

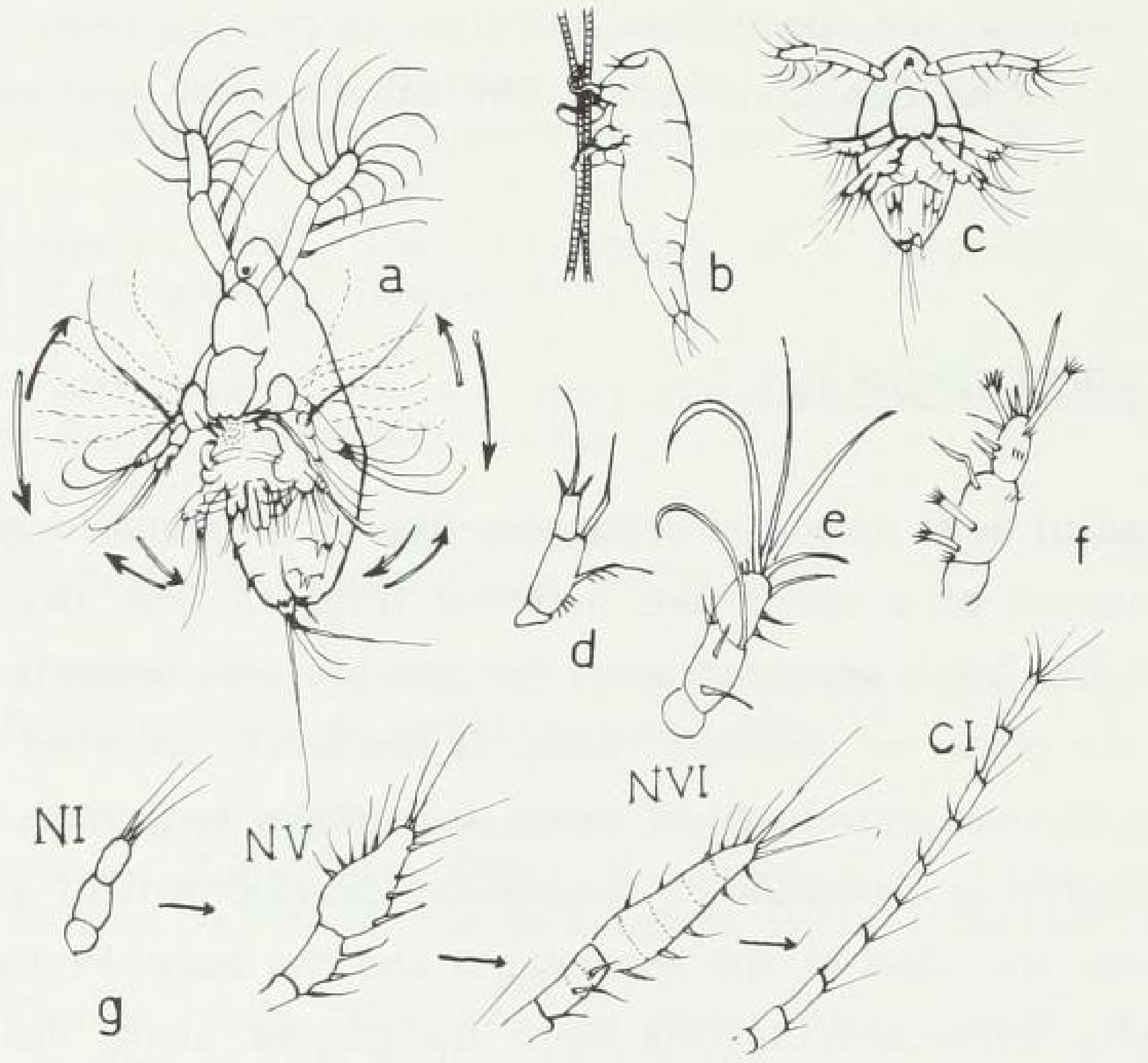

Figure 2. *The naupliar (NI,NV,NVI) and copepodid (CI) antennules:* ***a.*** *Eucalanus pileatus, the grazing nauplius, with antennules acting as keels;* ***b.*** *Macrosetella gracilis, with antennules hardly moving, because the nauplius is almost sedentary;* ***c.*** *Eucalanus nauplius (schematic) with antennule acting as a suspension organ;* ***d, e, f.*** *harpacticoid naupliar antennules with spines, spine-like and brush-ended setae (d after Gurney, 1931;* ***e*** *and* ***f*** *after Carter and Bradford, 1972);* ***g.*** *the changes undergone by the antennule from nauplius I to copepodid I in a calanoid copepod.*

THE ANTENNULES, THE ANTENNAE AND THE MANDIBLES

The antennules

They usually are three-jointed in the nauplius, but they may be one- or five-jointed, and they are always uniramous (Fig. 2). Besides specific characteristics they show others which vary with the naupliar stage and the general features of the order they belong to.

Their first function is locomotive. By moving backwards and forwards with paddle-like jerks, they pull the nauplius forwards. In some nauplii (Miracia, Macrosetella) they do not move or move very little, because the nauplius is almost sedentary. In other nauplii (Eucalanus pileatus) they act as keels, as they are maintained stretched out above the front of the nauplius, with their setae disposed fan-like around the last joint. In this case they may also aid in the suspension of the larva, when at right angles to the body (Fig. 2a, c).

At all stages of development they must have sensory functions, but studies of pores and sensillae in nauplii are unknown to me and should be investigated.

In some harpacticoids it is probable that the spines, the spine-like and the brush-ended setae of the naupliar antennule act as anchors for the larva living on algae or moss (Fig. 2d, e, f).

The first nauplius in Calanoida, Cyclopoida and Harpacticoida usually has cylindrical antennules. In Calanoida the last podomere of the antennule flattens out and becomes more paddle-shaped, with gradual addition of setae to the three terminal ones, as the nauplius grows older (Fig. 2g). The cyclopoid and harpacticoid antennule usually remains cylindrical throughout the naupliar stages. To the three terminal setae of the first naupliar stage other setae are added laterally. In the Harpacticoida instead of setae, spines or brush-like setae may appear. In the last (sixth) naupliar stage, when metamorphosis is about to take place, it is possible to see through the chitin of the last podomere of the antennule, the series of podomeres which will form the antennule of the copepodid (Fig. 2g).

The first podomere usually remains the same in the copepodid while the second is subdivided into two or three podomeres in the Calanoida and in the Cyclopoida (for more details consult Dietrich, 1915; and Oberg, 1906).

The copepodid antennule, when fully distended, is not only a suspension organ in the Calanoida, but, mostly a sensory organ for food, gravity and predators (Strickler, 1982). It generally has aesthetes and other sensors (see Saraswathy and Bradford, 1980; Von Vaupel Klein, 1984). In Harpacticoida and Cyclopoida it only rarely acts as a suspension organ in planktonic species such as Oithona. It takes part in locomotion, according to Strickler (1975) in the Cyclopoida, by beating backwards and causing the copepod to start its "jump" forwards. All harpacticoid antennules have at least one aesthete (Lang, 1948) besides other setae probably sensory. In benthic specimens the antennule also helps in anchoring the copepod to the substratum. This same function was observed in some Calanoida (Pseudodiaptomus) in which the glandular setae of the antennule "glue" these appendages to the bottom and aid the animal in forming a feeding basket with its other limbs into which food is sucked by the movement of the buccal appendages (Fig. 3d, e, f). In some Calanoida, in some Cyclopoida and in most Harpacticoida one or both of the male antennules act as grasping organs during copulation. The differentiation of the antennules into the future female and male can be observed as early as in the fourth copepodid stage in the Calanoida. In the adult the antennules are then geniculated by fusion of some podomeres. Fusion is also observed in the antennular podomeres when there is no geniculation and the fused parts may be different in the male and in the female of the same species. Within the

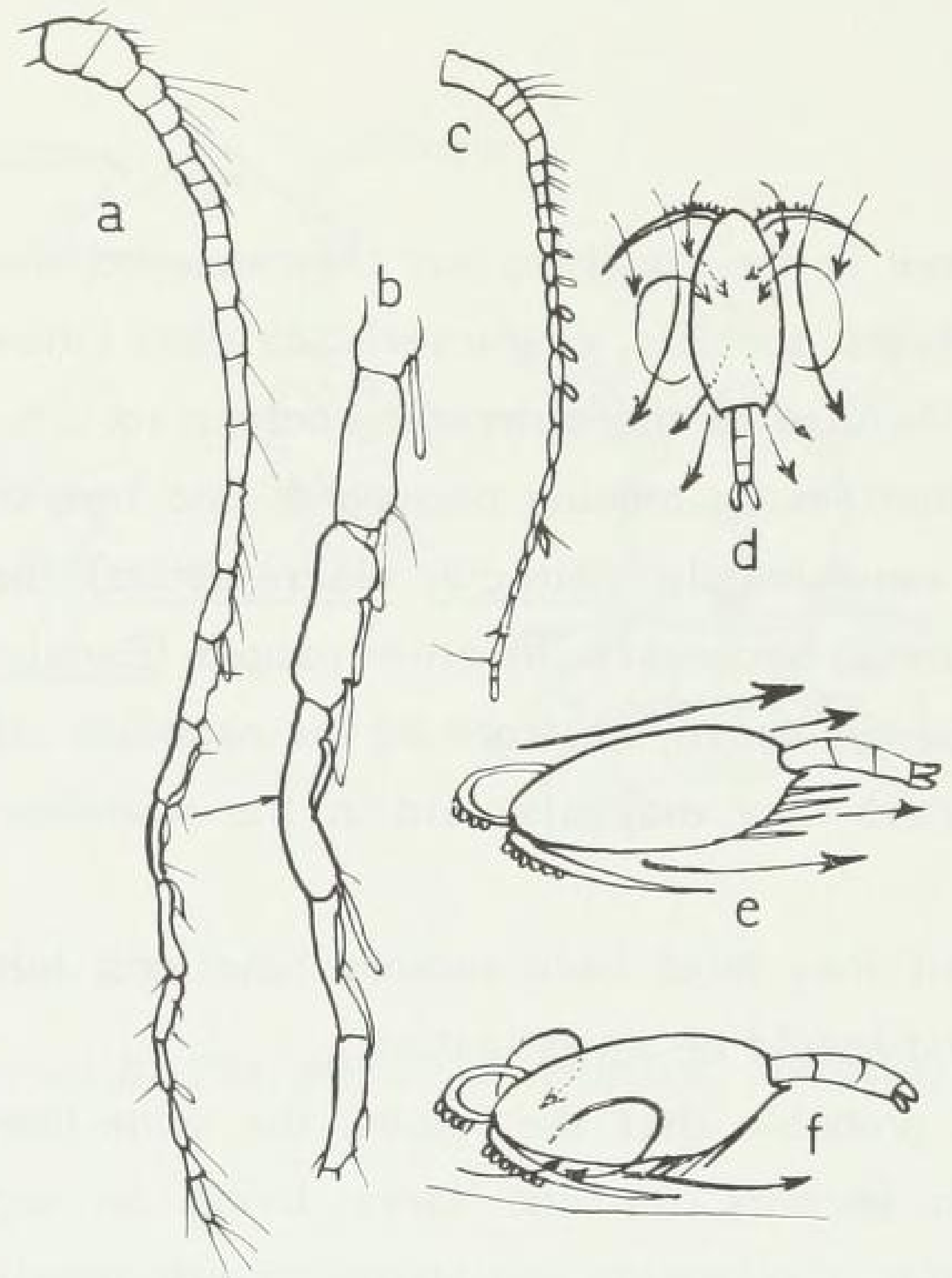

Figure **3**. *The copepodid antennule:* ***a.*** *(with detail in* ***b)*** *geniculate antennule of male Bathycalanus;* ***c.*** *non geniculate antennule of Bradycalanus male;* ***d.*** *Schematic representation of Pseudodiaptomus acutus with antennules glued to the substratum, and movement of feeding currents represented by arrows (seen in dorsal view) with legs forwards;* ***e.*** *the same, seen laterally, with legs stretched out backwards;* ***f.*** *the same seen laterally with feeding basket formed by legs and oral appendages*

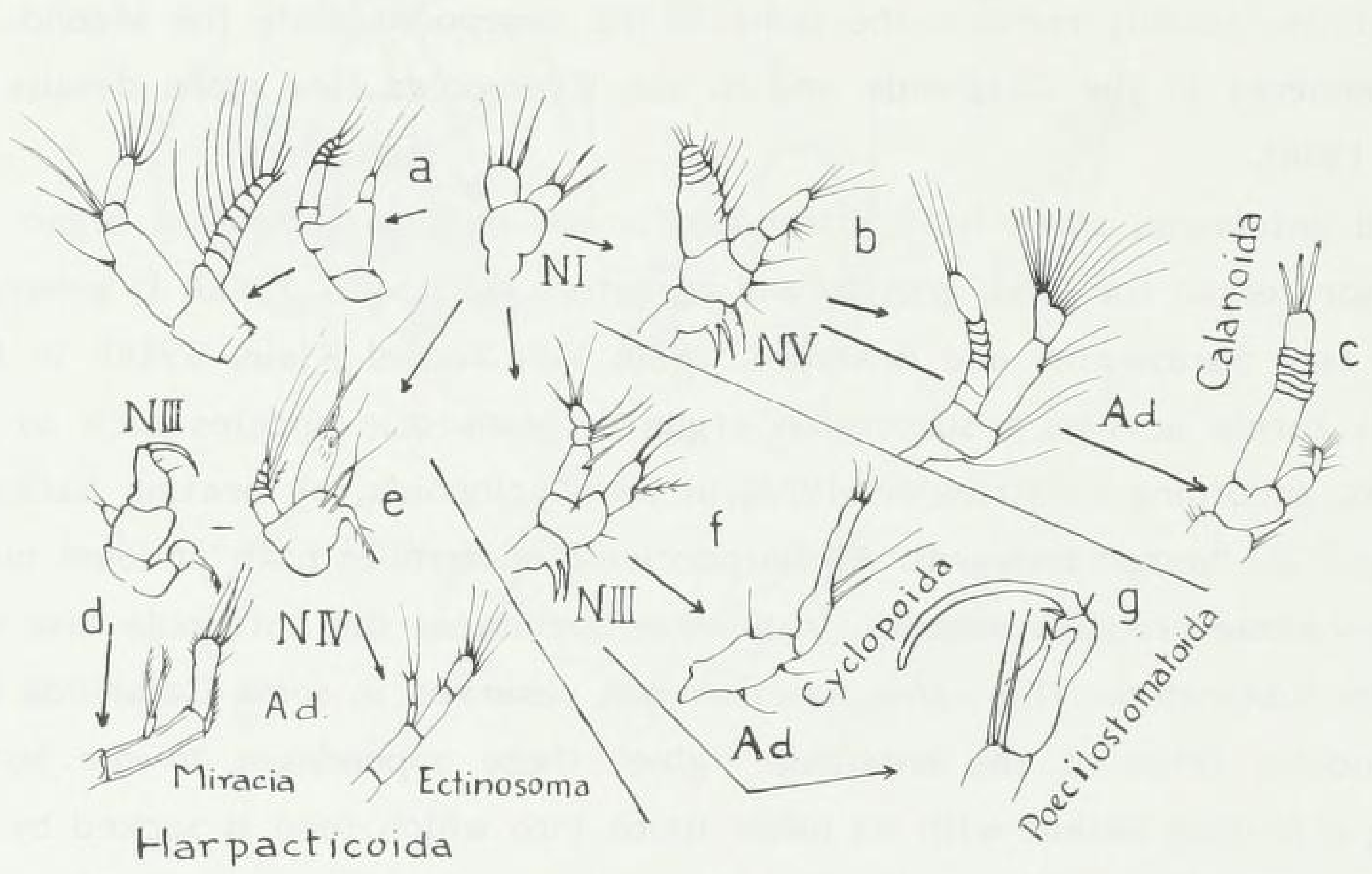

Figure **4**. *Antenna - The development of the antenna from the naupliar (N) stages to the adults (Ad.):* ***a.*** *canuellid naupliar (one-jointed endopod) antenna which metamorphoses into a copepodid antenna with a three-jointed endopod;* ***b.*** *the development of the Calanoida antenna from nauplius I (NI) through nauplius V (NV) to adult Calanid and Pseudochirella antenna* ***(c);*** ***d.*** *Miracia antenna of nauplius III and the adult antenna;* ***e.*** *Ectinosomid antenna of nauplius IV and the adult antenna;* ***f.*** *Antenna of Oithona nauplius III and of the adult;* ***g.*** *antenna of adult Corycaeus. (Antenna of Pseudochirella taken from Von Vaupel Klein, 1984).*

same family (Megacalanidae) there may be genera with and others without geniculation of the male antennule (Fig. 3a, b, c).

The antennae

The antennae are biramous in all nauplii of copepods studied up to now. They usually have a flat coxopod, which is provided with spines or setae or a blade-like projection aiding in pushing the food into the mouth. The basipod also has spines or setae and sometimes an endite with food pushing functions. The exopod generally is 2- to 5-jointed, but there are exopods with up to 10 podomeres. The exopod is locomotive. The endopod usually is one-jointed, sometimes two-jointed. The endopod of Longipedia and Canuellidae nauplii, the most primitive harpacticoid nauplii according to Lang (1948), is one-jointed, whereas in the adult it is three-jointed. This could be used as proof that the evolution can be accelerated in the nauplius and retarded in the adult. The endopod is ornamented with setae and sometimes spines or spinules. In the Harpacticoida it may have a terminal spine or hook (Fig. 4d) and is capable of hooking on to the substratum. Longipedia and Microsetella, planktonic harpacticoid nauplii, do not display this hook-like structure and are provided with simple plumose setae, like the other planktonic nauplii of the Cyclopoida and Calanoida (Fig. 4a, e).

During metamorphosis the basipod of the antenna suffers a small regression and sometimes the endopod is also reduced (e.g. Euchirella, Fig. 4c). In many copepodids there is a partial or even a total reduction of the exopod (as in Euaugaptilus and Oithona, respectively; Fig. 4f). In the last case the antenna becomes uniramous. In Corycaeus (Fig. 4g) it changes into a powerful grasping organ, less accentuated in other genera such as Oncaea. In the male Corycaeus this organ is used for holding the female, during copulation. In many Calanoida the biramous antenna has an important role in the gliding movement of the copepodid while grazing (Gauld, 1966). In the harpacticoid Miracia, from a grasping organ in the nauplius it changes into a simple setuled antenna with a very reduced exopod in the copepodid, and is then a suspension organ with possible sensory activities. A detailed comparative study of the reduction of the exopod of the antenna in the harpacticoids is found in Lang (1948).

The mandible

It is also biramous in all the first naupliar stages (Fig. 5a). In the orthonauplii (nauplius I and II) and usually in the first metanauplius (nauplius III) it is composed of a coxopod or coxa, a basipod, an endopod and an exopod. The coxopod has a spine or seta, which in the second and/or third metanauplius of the Calanoida changes into a mandibular blade (Fig. 5b) or into the rudiments of the gnathobase. The coxa of the Cyclopoida and of the Harpacticoida may be differently ornamented, but, it has no such blade or rudiment in the nauplius (Fig. 5c). In the majority of species a gnathobase only appears after metamorphosis.

The exopod usually is four- or five-jointed in the Calanoida nauplii and four-jointed or less, even one-jointed due to fusion of podomeres, in the Harpacticoida and Cyclopoida. The mandibular endopod is one-jointed in the Calanoida and alsp in the Harpacticoida (Fig. 5b, e), with the exception of Longipedia and Sunaristes (Canuellidae) where it is two-jointed. This is also the case in all the nauplii of the Cyclopoida (Fig. 5d) and of their nearest of kin, the free-living, parasitic and commensal

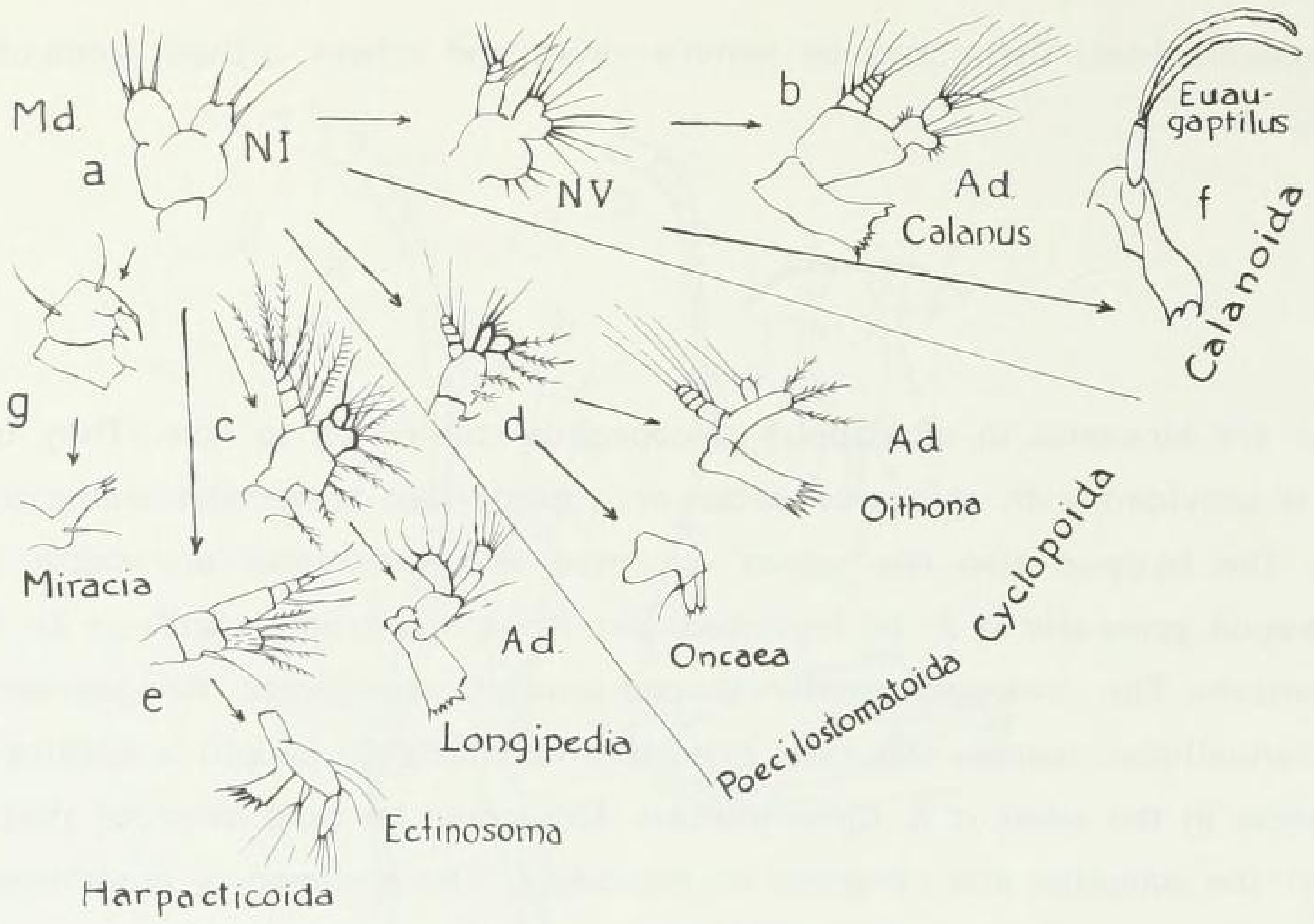

Figure 5. *Mandibles:* ***a.*** *Mandible of nauplius I (NI), nauplius V (NV) metamorphosing into* ***b.*** *adult (Ad.) mandible of Calanus and of Euaugaptilus* ***(f)****;* ***c.*** *mandible of Longipedia (with two-jointed endopod) in the nauplius and in the adult (Ad.);* ***d.*** *mandible of Oithona nauplius and of adult (Ad.), also with double-jointed endopod; the Oncaea mandible (copepodid);* ***e.*** *Ectinosomid mandible in the nauplius and in the adult;* ***f.*** *Euaugaptilus mandible (adult);* ***g.*** *Miracia mandible with hooks in the nauplius and in the adult without hooks.*

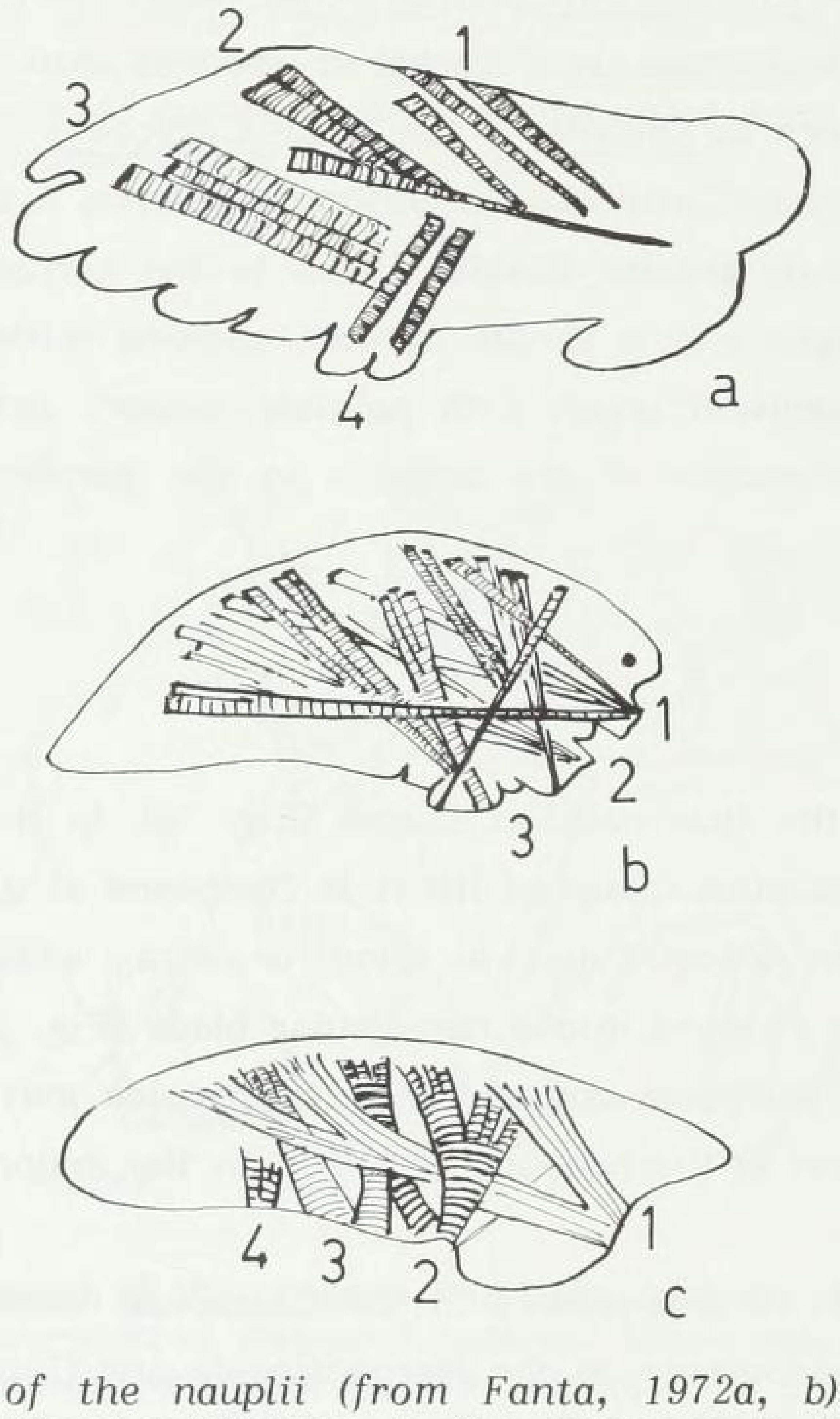

Figure 6. *The muscle system of the nauplii (from Fanta, 1972a, b):* ***a.*** *Oithona simple muscles, nauplius VI, insert without subdivision in the carapace;* ***b.*** *Euterpina, nauplius VI, muscles which cross, subdividing at insertion point in the carapace;* ***c.*** *Pseudodiaptomus, nauplius VI, with muscles which cross each other and subdivide, fan-like before insertion in the carapace.*

copepods, now classified in the order Poecilostomatoida (Bowman and Abele, 1982).

The naupliar mandible is a locomotive organ. In the Miracia nauplius it is a grasping organ (Fig. 5g), it fixes the specimen on to the substratum (a filament). The endopod and the exopod are fused and two strong spines and a seta permit the nauplius to hang on to the filament on which it lives.

During metamorphosis the mandible changes very little in the Calanoida - the mandibular blade widens or lengthens and forms the gnathobase with its indented border (Fig. 5b). It is probable that the crown of siliceous coating of the teeth is formed after metamorphosis, and this should merit an investigation. In the Augaptilidae the mandibular palp sometimes is very reduced (Fig. 5f). In the Arietellidae the endopod is reduced altogether.

In the Calanidae and nearest of kin, the vibration of the mandible plays an important role in the grazing movement. In the Oncaeidae and Corycaeidae the mandible is extremely reduced in the copepodids, which are carnivorous. The same happens with some mandibles of the Harpacticoida. The exopod usually suffers a stronger reduction than the endopod. In some copepodid mandibles the exopod and endopod are reduced to setae, but, in the Tisbidae and Porcellidiidae the contrary is the case: the mandible is well developed, especially the palp (see Lang, 1948). In the Canuellidae and Longipediidae the palp undergoes almost no change from the nauplius to the copepodid.

The first three pairs of appendages - general remarks and considerations

They are functional in the nauplius. While observing the nauplii, one is surprised at the variety of movements exhibited by the different forms (Fig. 7). The simplest locomotion is observed in Cyclopoida, Oncaea, and Corycaeus nauplii. Their three pairs of appendages move backwards and forwards, oar-like and the resulting movement is a jerk or impulse forwards or sideways in a more or less erratic fashion. The next simplest movements are those of some calanoid nauplii, such as in Acartia, which go round and round (Fig. 7b) in a continuous horizontal spiral or circle. Then there are the somersaulting movements or the movement in a vertical spiral of the calanid-paracalanid-clausocalanid hook-like nauplii (Fig. 7c). The Eucalanus pileatus nauplius has the most refined locomotion (Fig. 2a): it glides through the water very much like the adult calanoid when grazing. The Harpacticoida, apart from Longipedia and Sunaristes, exhibit very complicated naupliar movements (e.g. helicoidal) (Fig. 7d), or hardly any movements at all (as in Miracia when hanging on to a filament).

To explain these different types of locomotion the muscle system of the appendages has been investigated more closely by Fanta (1972a, b) and the results are compared in Figs. 6a, b, c, taken from Fanta (op.cit.). The simple movements of the Cyclopoida and other similar nauplii are thus explained by their simple almost parallel muscles which insert without subdivision in the naupliar carapace. The calanoid nauplii have a far more powerful muscle system, with intercrossing muscles, which insert in a fan-shaped (subdivided) manner in the carapace from the first naupliar stage onwards. The muscles of the harpacticoid nauplius, originally inserting without subdivision in the carapace (naupliar stages I to V), subdivide at the insertion point in the sixth stage, permitting a much more complicated locomotion than the one observed in cyclopoids, in Oncaea and Corycaeus.

From all the facts mentioned so far, we can arrive at some conclusions. It is generally accepted that the crustacean appendages were primitively more jointed. It is also a general belief that evolution

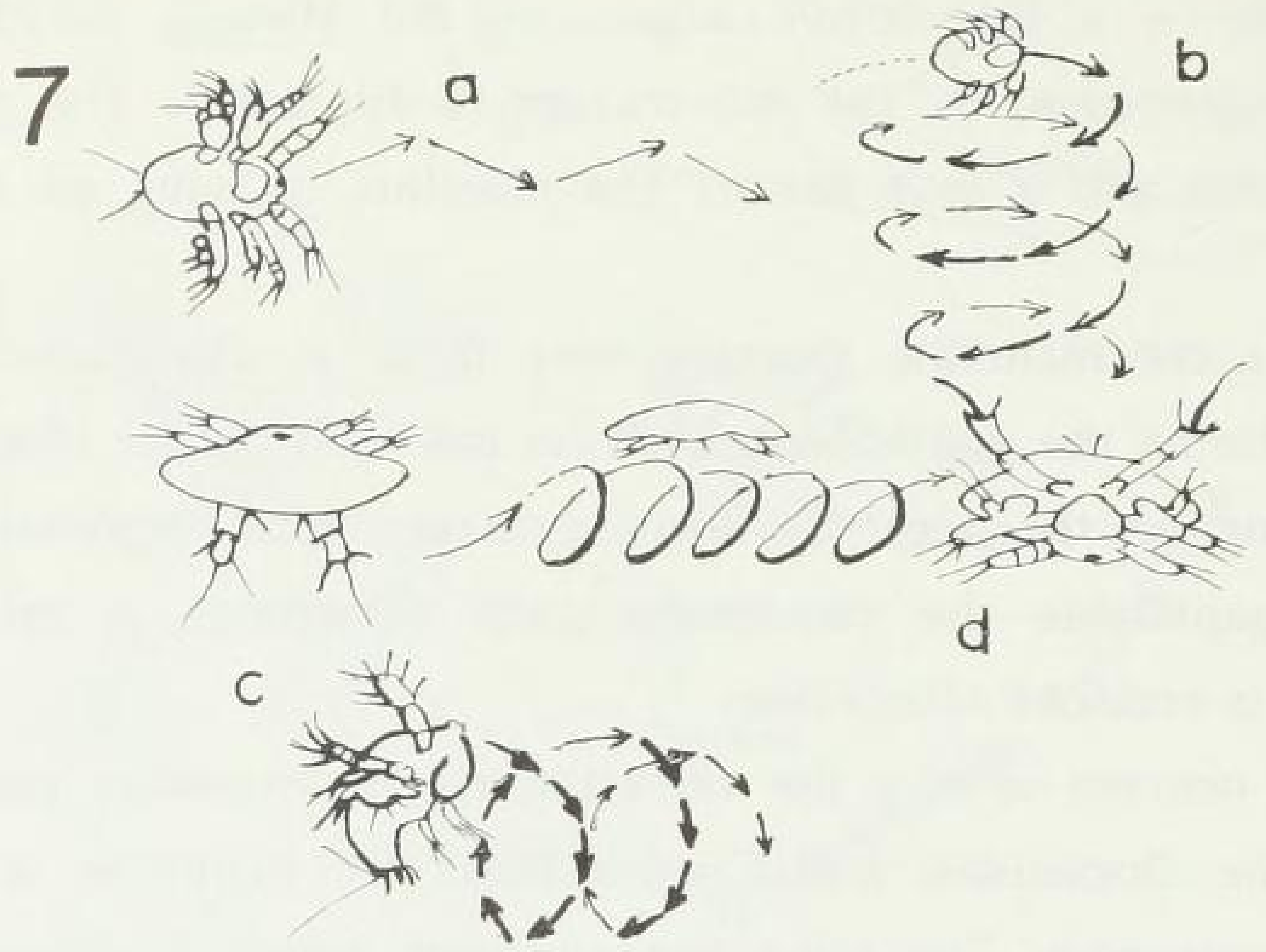

Figure 7. *Naupliar movements:* ***a.*** *Zig-zag motion of Oithona;* ***b.*** *Locomotion in circles of Acartia;* ***c.*** *Somersaulting Paracalanus;* ***d.*** *Helicoidal locomotion of an harpacticoid nauplius (taken from Bresciani, 1960).*

Figure 9. *Maxillae and Maxillipeds:* ***a.*** *naupliar maxillae (nauplius VI of Eucalanus pileatus), and copepodid maxillae of stage I and IV;* ***b.*** *maxillipeds of Eucalanus nauplius VI, copepodid I and IV;* ***c.*** *maxilliped of nauplius VI, copepodid I and IV of Pseudodiaptomus, in which the comb-bearing setae appear;* ***d.*** *the maxilliped of Acartia adult;* ***e.*** *the maxilliped of Oncaea adult;* ***f.*** *the same of Halicyclops adult (taken from Rocha, 1983);* ***g.*** *the same of Macrosetella adult;* ***h.*** *naupliar maxilliped of Chiridius (taken from Matthews, 1964).*

proceeds from simple and non-specialized forms to complicated and specialized ones in free-living organisms. If we compare the musculature of the nauplii, we find the simplest muscle system in the cyclopoids (Fig. 6e). The harpacticoid and the calanoid muscle systems are more complicated (Fig. 6d) and so is the locomotion of the nauplii. The primitive situation of appendages with several joints is also found in cyclopoids: the five-jointed antennule (Lescher-Moutoué, 1966), and the two-jointed endopod of the naupliar mandible. Interestingly the latter is present also in the most primitive harpacticoid nauplii (Longipedia and Sunaristes).

The only known nauplius which has an exopod of 10 joints on the second antenna (Fig. 4c) is a calanoid nauplius, judging from its general aspect and size. But, the other characteristics of the calanoid nauplii are not primitive.

If we compare the ornamentation of the appendages in the nauplii, we find the most elaborate type of spines and setae (Figs. 2d, e; 4d, e) in the Harpacticoida, the simplest again in the Cyclopoida. Thus, from the functional appendages of the nauplii we may conclude that of the three orders considered here, the most primitive copepods are the Cyclopoida, and, that the Harpacticoida and the Calanoida are derived.

The Harpacticoida Polyarthra (Longipediidae and Canuellidae) are either extremely primitive, or, they should constitute an intermediate order between the Cyclopoida and the Harpacticoida.

THE REMAINING APPENDAGES WHICH APPEAR AS RUDIMENTS IN THE NAUPLIAR STAGES (THE MAXILLULES, THE MAXILLAE, THE MAXILLIPEDS, THE FIRST AND THE SECOND PAIRS OF SWIMMING LEGS)

The maxillule

It is represented by a seta or spinule sometimes already in the third naupliar stage, or in the fourth stage by a heart-shaped, leaf-like structure (Calanoida) (Fig. 8, Pseudodiaptomus and Calanus). To the initial seta or spinule, more smaller spinules or setules are added in the next stage and the outline or the primordium of the future appendage. In the Oncaea nauplius V a rod-like structure with a long and a short seta develops from the rudiment present in nauplius IV. In the calanoid genus Acartia there are specific variations: the leaf-like rudiment only appears in the sixth nauplius in A. danae and A. lilljeborgi; in A. negligens it is not evident in nauplius IV. In the Harpacticoida the maxillule can also appear in the form of a simple seta, then a seta on an outlined lobe, and finally in nauplius VI, a lobe with a seta and several setules (Fig. 8, Microsetella). Longipedia and Oithona in the same stage have a maxillula rudiment similar to the heart-shaped structure of the Calanoida (Fig 8, Oithona).

The leaf-like structure protrudes from a ridge on the ventral shield of the naupliar carapace. The presence of this prae-coxa is not as evident in all naupliar stages as it is in Eucalanus pileatus, Metridia sp. and Pontellopsis sp. (Björnberg, 1972) where it takes the form of a basal plate.

The retarded development of the maxillule in some Harpacticoida (Phyllognathopus, Euterpina) is reflected in the development of the muscles which should move this appendage. Thus, in the sixth naupliar stage of Euterpina no muscles for the maxillule are present (Fig. 6b). In Oithona and Pseudodiaptomus small muscles are already visible in the nauplius VI to move the maxillary leaf-like structure (Fanta, 1972a). In the harpacticoid Tisbe the maxillules are relatively well developed in the

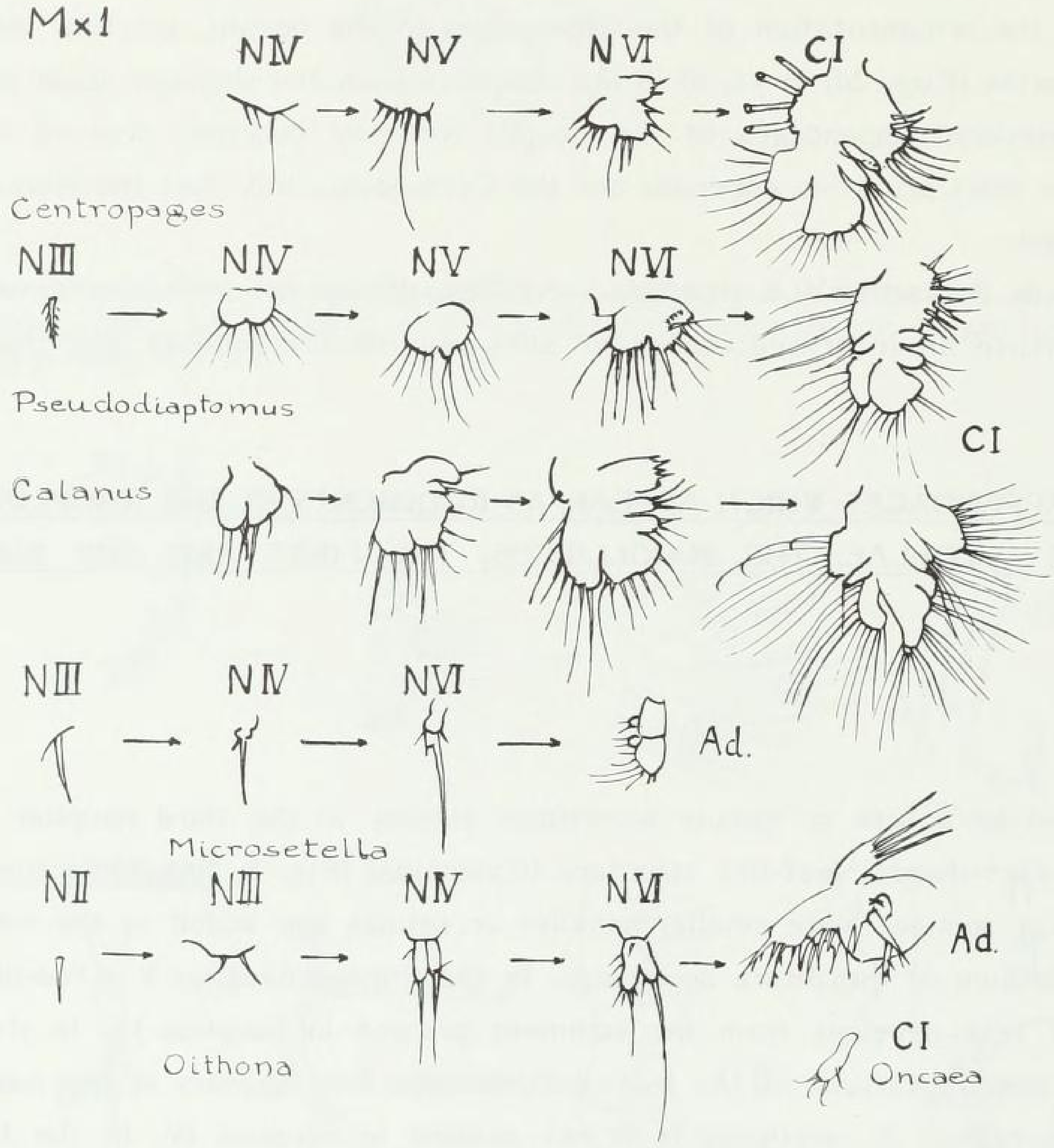

Figure **8**. *Maxillule - the Centropages maxillule of nauplius IV (NIV), nauplius V(NV), nauplius VI (NVI) and of copepodid I (CI); the Pseudodiaptomus maxillule of nauplius III (NIII), IV, V, VI and of copepodid I (CI); the Calanus maxillule of nauplius IV, V, VI and of copepodid I; the Microsetella maxillule of nauplius III, IV, VI and of the adult; the Oithona maxillule of nauplius II, III, IV, VI and of the adult (abbreviations as in the remaining figure); the maxillule of the first copepodid (CI) of Oncaea.*

nauplius V with two setae on each of the two podomeres which form the rudiment of the appendage (Johnson & Olson, 1948).

During metamorphosis the maxillule usually changes into its definite shape, but, with a smaller number of setae and spines than in the sixth copepodid. The internal lobes, as well as the exopod and the endopod of the maxillule are sometimes already outlined in the last nauplius stage of the calanoids (as in the Calanidae) (Fig. 8, Calanus). The maxillule can be very reduced in the first calanoid copepodid (Pontellopsis, Acartia, Euaugaptilus) and in some harpacticoid copepodids (Macrosetella, Nitocrella) in which, according to Lang (1948), two setae represent the endopod and the exopod. A greater involution of the maxillule is observed in Oncaea (Fig. 8, Oncaea).

It is usually believed (Gauld, 1966) that the function of the maxillule is to help in the feeding process. In the suspension feeders it composes the feeding chamber through which feeding currents pass leaving particles. These are swept off the setae by maxillary spines which also push the food particles into the mouth cavity. From Strickler's, Koehl's, Paffenhöfer's and Alcaraz' study of suspension feeding in copepods with microcinematography (the animal studied was Eucalanus pileatus) it was concluded that there is no filtering of water with retention of particles, nor circular currents by the beating of the mouth appendages. The second maxillae "actively capture parcels of water containing food particles" (Koehl and Strickler, 1981). "The endites of the first maxillae have an important role in pushing into the mouth the food particles obtained mostly by movement of the second maxillae". Unfortunately the authors last mentioned have not yet studied suspension feeding in copepods such as Calanus finmarchicus, Centropages, Temora and Diaptomus. In large containers I have observed circular feeding currents generated by Pseudodiaptomus (Fig. 3d, f). It would be interesting to know what microcinematography could reveal when applied to genera which have already been studied with other methods. From my own experience I find that each species has its own way of feeding.

The maxilla

It is also present in the fifth naupliar stage of some Calanoida, and, in the sixth naupliar stage of the Harpacticoida as a seta (or two setae) inserted on a ridge of the ventral shield, below the rudiment of the maxillule. In the next stage of the Calanoida it is composed of a crenulated ridge sometimes provided with minute spines or setules. During metamorphosis it acquires its definite shape and becomes functional, aiding in the feeding process. In Candacia, a carnivorous copepod, its setae are transformed into five strong spines (Gauld, 1966). Von Vaupel Klein (1984) summarizes the discussions about the interpretation of the composition of this mouth appendage.

Koehl and Strickler (1981) ascribe to it an important role in the catching of algae during the feeding process of Eucalanus. The outward fling of the maxillae creates a gap between them filled by the inrushing water and by the alga. Then they rapidly close in over the alga and water, which is squeezed out between the setae of these appendages and is pushed posteriorly by the first maxillae.

The maxilla in the carnivore Candacia is of greater importance than the maxilliped to hold the prey (Wickstead, 1959). In Centraugaptilus (Krishnaswamy et al., 1967) the maxilla has two rows of small buttons, non sensory, cuticular structures, which probably function as adhesive plates to hold the prey. In Oncaea the maxilla is reduced to a pincer-like structure which must be very efficient in grasping and holding the victim, even in piercing it for later sucking. Wickstead (1962) described a similar behaviour for Corycaeidae. In Oithona the maxilla of the copepodids is provided with long stout, spiny spines or thick spiny setae which together with the maxillipeds, similarly structured, grasp the food from the surrounding medium (Gauld, 1966). In Macrosetella the maxilla is very much reduced and also ends in the form of a pincer, thus being an effective grasping organ with which the animal holds the Trichodesmium filaments on which it lives. Vermiform and brush-like setae of the maxillae of several families of Calanoida and Harpacticoida are probably sensory and attachment organs.

The maxillipeds

They usually are present in the sixth naupliar stage in the form of a pair of long tongue-like bands, disposed laterally to the midventral line, and, situated between the maxillules (Fig. 9b). At their tip they carry 2 or more setae. During metamorphosis the maxilliped acquires its almost definite shape. It is uniramous from the naupliar stages. In the Pseudodiaptomus first copepodid it has three podomeres (Fig. 9c); in the second, five; and, in the third, it already displays the seven podomeres of the adult. The specialized setae of the endopod, which carry little comb-like structures for scraping the substratum or for cleaning the other appendages, are present from the fourth copepodid stage to the sixth of Pseudodiaptomus (Fig. 9c).

The maxilliped is formed by the praecoxa, the coxa or coxopod, the basipod and the endopod. In Macrosetella (Harpacticoida) the endopod is represented by a hook (Fig. 9g). In Sunaristes and Cerviniopsis, considered primitive Harpacticoida, the four podomeres are also present (Lang, 1948). In their nauplius there is no indication of a praecoxa or of any other podomeres in general. Some nauplii, those of Eucalanus attenuatus, show a suture across the tongue-like flap which is the rudiment of the maxilliped in nauplius VI (Fig. 9b). In Chiridius armatus, Matthews (1964) found a well developed minute appendage with four podomeres and a terminal seta in the last naupliar stage (nauplius IV in this species)(Fig. 9h). The maxilliped may be very reduced relative to the maxilla, in both the nauplius and the copepodid (Acartia, Pontellidae)(Fig. 9d). Euchaeta has the longest naupliar maxilliped known (Sazhina, 1982) and one of the most developed copepodid maxillipeds.

The function of the maxilliped, when reduced in size, is to shut the feeding basket in calanoids such as Acartia, and in cleaning the other appendages. In Euchaeta, a carnivore, the combined action, first of the maxillipeds, grasping the prey, then of the maxillary setae closing up below its body, holding it against the underside of the head, permit the tearing off of pieces of the prey by the maxillulary endites and the toothed edges of the mandibles (Wickstead, 1962; Gauld, 1966).

In the Cyclopoida of the genus Halicyclops Norman (Fig. 9f), and in Graeteriella Brehm, as well as in commensal genera, which do not need this appendage for feeding, the maxilliped is very reduced. It is very developed in the genus Oithona where it is used for catching food, and in the Poecilostomatoida, chiefly in the males, where it is prehensile for holding the female during copulation (Fig. 9e).

The swimming legs

The first pairs of legs usually are present in the last naupliar stage as a pair of foliaceous structures situated posteriorly to the outline of the maxillipeds and carrying spines and/or setae on their posterior border. In Cyclopoida and Harpacticoida there sometimes is a pair of simple foliaceous structures or just a pair of ridges from which setules or spinules protrude. In the last nauplius stage of Chiridius armatus the first swimming leg is distinctly composed of four podomeres, two basal ones, an endopod and an exopod. The spines and setules mayx or may not be present in the nauplius. In none of the observed primordia of legs was it possible to find any indication of a praecoxa.

During metamorphosis the foliaceous structures of the nauplius change into the legs proper, which usually have a coxa or coxopod, a basipod and endo- and exopod, generally undivided, or composed of two podomeres as in the exopod of the second leg. The first copepodid already shows the rudiments of the third pair of legs; the second copepodid, of the fourth pair of legs; the third copepodid, of the fifth pair of legs. The fourth copepodid and the fifth copepodid (sometimes as early as the third copepodid) show differences in the fifth pair of legs which permit the distinction between males and females in the Calanoida. The Harpacticoida, judging from Euterpina acutifrons, show a differentiation of the male and female appendages only the moult of the fifth copepodid (Haq, 1965). The sixth pair of legs appears in the fifth copepodid stage of the Harpacticoida, but, disappears in adult females. In the Oithonidae the copepodid V shows sexual dimorphism; the male already has a fifth and a sixth pair of legs represented by setae; the female has the fifth pair only, according to Uchima (1979).

Specific differentiation of the swimming legs is easily observed in the first pair of the Harpacticoida and in the fifth pair of the Calanoida, from a taxonomist's point of view. The sixth pair of legs also presents specific features in the Cyclopoida. The fifth pair suffers changes in the females of the Calanoida, Harpacticoida and Cyclopoida to facilitate the attachment of eggs or of egg sacs in those species which do not lay their eggs directly into the sea water, or on the bottom of the sea. In the males of the Calanoida the fifth pair of legs is considerably changed in some species, undergoing a differentiation on the left and on the right side in order to grasp the female with one leg while the other places the spermatophore on the genital segment of the partner. Among the Calanoida and the Harpacticoida there are species which retain their fifth legs or their first legs respectively, hardly unchanged (some Calanidae, Megacalanidae, Canuellidae, Longipediidae and Cerviniidae). These are undoubtedly more primitive than those which show numerous adaptations.

In those copepods which lay their eggs freely there is a great reduction, even to complete absence of the fifth pair in order to facilitate the swimming movements (see Von Vaupel Klein, 1984).

The remaining legs from the second to the fourth pair usually are composed of a coxa or coxopod, a basipod, an endopod with three podomeres and an exopod of also three joints. In the Calanoida there may be a reduction in the number of podomeres of the endopod of the first and second legs (Aetideidae, Phaennidae) and in others the exopod may also suffer a reduction of podomeres (Euchaetidae). In Paroithona the endopods of all legs are reduced to two podomeres.

As for the ornamentation of the legs there are also great variations, but, usually the coxopods and the basipods bear one or two setae, the endopods have plumose setae, one on the first, two on the second and generally five or more on the last podomere. There may be reduction of these setae or they may be substituted by spines, partially or totally. The exopod in most species is ornamented with spines (five or six) externally, a terminal spine of various shapes and there are plumose setae (six or more) internally. There can also be a reduction in the number of these setae. Pores of glandular cells (such as mucus glands, luminous glands, and others), patches of fine hair-like setules, tufts of bristle-like spines, perforations, scale-like structures, etc. may also be present on the face of the several podomeres which compose the swimming legs (Clarke et al., 1962; Campaner, 1978; Verdinelli, 1981; Von Vaupel Klein, 1984). Generally, the most complicated and varied ornaments of the appendages are found in the benthic or plankto-benthic Calanoida and Harpacticoida (excepting the Longipediidae and the Canuellidae).

CONCLUSIONS

From the study of the naupliar appendages, one has to agree that, by the accepted standards of primitiveness, the cyclopoid nauplius presents the greatest number of primitive features. It is also a fact those the Poecilostomatoida the nauplii of which are known, have cyclopoid nauplii. The next most primitive nauplii, judging from the appendages, are the Longipedia and the Canuellidae nauplii, among the Harpacticoida. All the other nauplii of the Harpacticoida are far more advanced in their most developed stage (the fifth) than any of the known Calanoida or Cyclopoida nauplii.

To decide whether a group of animals is older or younger than others the adaptive radiation can also be used. A group which is found in the greatest number of environments, with the greatest number of most diverse species occupying the most varied niches has the probability of being older, or of having inhabited the world for a longer period of time than the other groups.

If we look at copepods we find the Harpacticoida with a greater number of species in the marine benthos, with one or two terrestrial species, and with several in freshwater. The Calanoids have most species concentrated in the marine plankton, some in the planktobenthic community, a few almost benthonic, and few species in freshwater. The Cyclopoida are well established in the marine environment and in freshwater where they have invaded the benthos, the plankto-benthos and the plankton, and there are many commensals, parasites and species associated with other animals (which have now been separated into different orders). From the naupliar evidence and the adaptive radiation it seems that of the three groups considered in this paper the Cyclopoida is the oldest group of copepods established in the world.

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