MAGDA VINCX and CARLO HEIP

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LARVAL DEVELOPMENT AND BIOLOGY OF *CANUELLA PERPLEXA* T. and A. SCOTT, 1893 (COPEPODA, HARPACTICOIDA)

by

Magda Vincx and **Carlo Heip**

Laboratorium voor Morfologie en Systematiek,
Rijksuniversiteit (1), Gent, Belgium

Résumé

Développement larvaire et biologie de *Canuella perplexa* T. et A. Scott, 1893 (Copépode, Harpacticoïde)

Canuella perplexa T. et A. Scott, 1893 est un Copépode Harpacticoïde de la famille des Canuellidae du sous-ordre primitif des Polyarthra (Lang, 1948). Il est souvent très abondant dans les communautés méiobenthiques de la partie septentrionale du globe. La biologie (propulsion, nutrition, comportement précopulatoire et éclosion) et le développement larvaire de cette espèce sont examinés sur des animaux élevés au laboratoire.

Les caractères des nauplius, déterminants pour les Polyarthra (Lang, 1948), doivent être révisés d'après nos résultats sur *Canuella perplexa*. Les stades larvaires des Canuellidae sont morphologiquement différents de ceux des Longipediidae, autre famille des Polyarthra.

Introduction

Canuella perplexa T. and A. Scott, 1893 is an eurytherm, holeuryhaline, endopsammic harpacticoid copepod, which occurs mainly in brackish and marine waters of the northern hemisphere, preferring sandy or mud-sandy bottoms (Noodt, 1957). This large species (male: 0.96mm; female: 1.36mm) is present throughout the year and is dominant in the meiobenthic communities of two brackish water habitats in northern Belgium, which are currently investigated in our laboratory: the Divengat in Knokke (Heip, 1973) and the Sluice Dock in Ostend (Thielemans and Heip, 1977). It is also very common

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in the estuaries of Scheldt, Meuse and Rhine in the Netherlands, as well as in the North Sea proper (Van Damme and Heip, 1977).

Canuella perplexa belongs to the family Canuellidae which, together with the Longipediidae, constitutes the primitive suborder of the Polyarthra (Lang, 1948).

The post-embryonic development of harpacticoid copepods in general, and that of the Polyarthra especially, has been studied only occasionally. Nicholls (1935) made a complete study of the post-embryonic development of *Longipedia coronata, L. scotti* and *L. minor,* three representatives of the Longipediidae. In the Canuellidae, only the first nauplius stage of *Sunaristes paguri* was described by Lang (1948). Gurney (1930) made a drawing of a nauplius which may belong to the Canuellidae, as he suggested himself.

In this paper, the development of *Canuella perplexa,* reared in the laboratory, is described. Some observations on its behaviour will be discussed as well.

Material and methods

Gravid females of *Canuella perplexa* were obtained from the sediment of the Sluice Dock in Ostend, an almost marine basin in which *Canuella* represents on the average 89 percent of the copepod community (Thielemans and Heip, 1977). Each female was placed in a petri dish of 35mm of diameter, containing 4ml sterile water (pH: 8.05 and salinity: 18.6 permil Cl). The females, and subsequently the nauplii and copepodites, were kept at 20°C ± 1°C, in an illuminated environment and fed on a mixed diet of 0.1 ml *Phaeodactylum tricornutum,* Bacillariophyceae (± 31.8×10^6 cells/ml) and of 0.1ml *Dunaliella* spec., Chlorophyceae (± 7.9×10^6 cells/ml). Every two or three days, the animals were transferred to new cultures because a film of bacteria had been formed around the individuals. This film was removed from the older copepodites with a fine needle.

After hatching of the nauplii, the females were removed to a new petri dish. The exuviae of the different developmental stages were preserved in 4 percent formaldehyde. The exuviae are very suitable to draw because details of the external structures are clearer and the appendages are more easily removed. The exuviae were mounted in temporary vaseline-formol slides which enables displacement of the exuviae within the slide, so that as many setae as possible become visible. The length and width of the nauplii were measured as the greatest length and greatest width of the body (not including the appendages). The length of the copepodites was measured from the rostrum to the posterior end of the last abdominal segment. This length is rather variable, because the successive segments can be telescoped into each other.

The abbreviations used throughout the paper are: N1-N6: nauplius 1 to 6; Cop1-Cop5: copepodite 1 to 5; Ad: adult; A_1: antennule; A_2: antenna; Md: mandible; Mx1: maxillula or maxille 1; Mx2: maxille or maxille 2; Mxp: maxilliped; P_1-P_5: legs 1 to 5.

RESULTS

1. Development

a. Embryonic development

Contrary to most harpacticoid copepods, the Canuellidae carry the eggs in two egg sacs, attached to the genital segment. Each egg sac has an average length of 430μm and an average width of 256μm. The eggs are slightly ellipsoid and have average dimensions of 61μm by 76μm. The average number of eggs in two egg sacs is 33.

Johnson and Olson (1948) already noted that harpacticoids are iteroparous, i.e. that a female produces several egg sacs after one copulation. We observed that one female produced five times two egg sacs after one copulation (at 20°C) with the subsequent number of eggs: 55, 59, 41, 43, 29; or a total of 227 descendants. The last pair of egg sacs of a series always contains less eggs than the preceeding ones.

The nauplii develop within the egg sac and are very active just before hatching. We also noted that not all the eggs are in the same embryonic stage; some embryos develop faster than others and the nauplii are released at different times. Chua Thia Eng (1975) made the same observation in *Tisbe longisetosa.*

b. Post embryonic development

We distinguish six nauplius and six copepodite stages in the development of *Canuella perplexa* (the sixth copepodite being the adult). Each stage has a different duration and is separated from the following stage by a moult.

(1) Nauplius stages (Fig. 1).

N1: the average length is 79μm and the average width 43μm. The animal is swollen pear-shaped, not segmented and bears three pairs of appendages: A_1, A_2 and Md. The labrum (which covers the stoma) is very prominent, slightly convex and adorned with many spinules on the ventro-caudal side. The ventral plate is relatively well developed, bearing a rectangle of 'stout' spinules. The caudal appendages consist of two fairly long, hairy setae; these are the anlage of the furca. The animal is dorsally covered by the carapace. A great, red nauplius eye is situated dorsally at the base of the A_1. This eye is present till the adult stage.

N2: the average length is 110μm and the average width 64μm. The body form resembles that of the previous stage, but the posterior part is elongated. There is no segmentation at all. Four pairs of appendages are present: A_1, A_2, Md and Mx1, the latter as two long, plumose setae. The anlage of the furca bears two long setae. The carapace still covers the whole animal.

N3: the average length is 146μm and the average width 76μm. The animal is elongated with a greater differentiation of the caudal end; there is still no segmentation. Four pairs of appendages are present: A_1, A_2, Md and Mx1. The Mx1 is displaced more laterally. The labrum is more adorned; the further ornamentation is about the same in the following stages. The anlage of the furca shows a slight division into two parts at the posterior end. Each ramus bears one long and two much shorter plumose setae. Dorsally, the whole animal is still covered by the carapace.

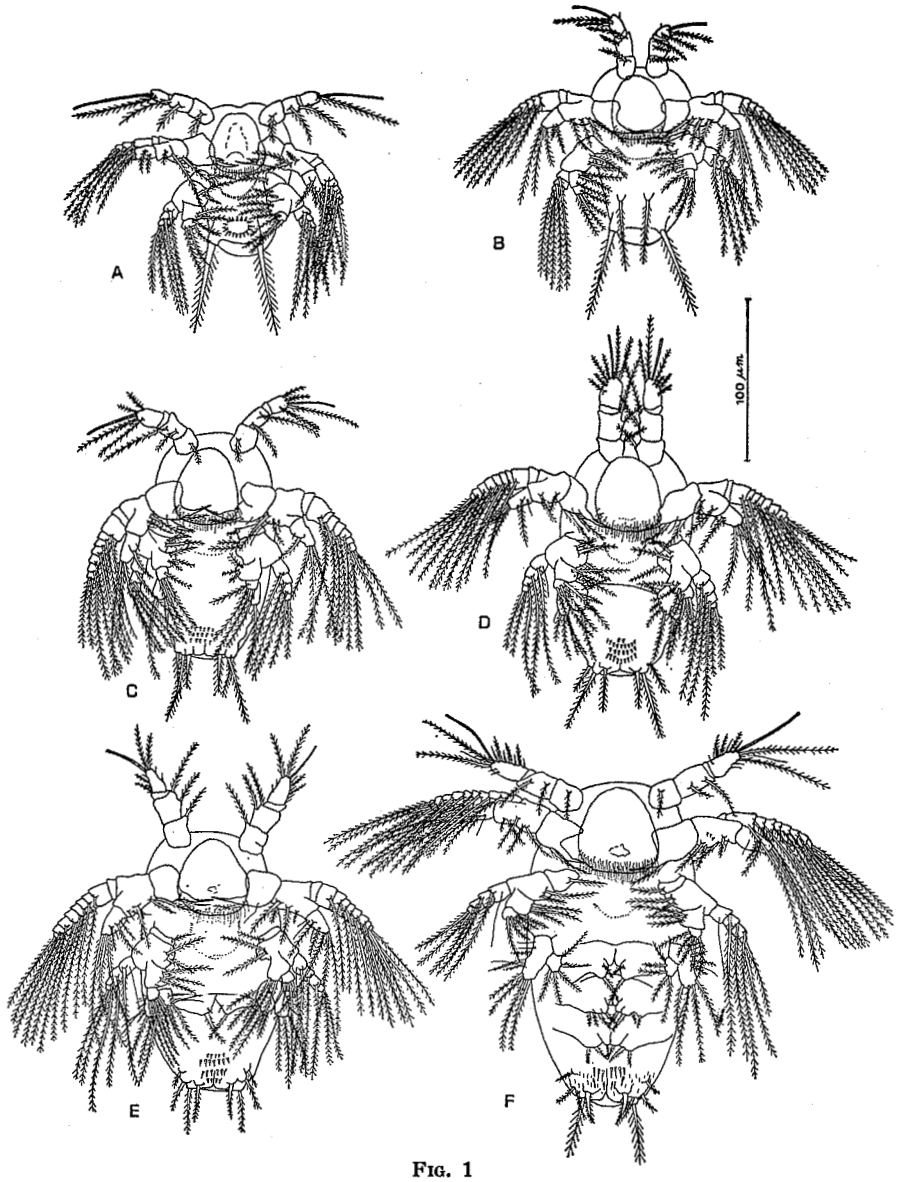

FIG. 1
Nauplius stages of *Canuella perplexa*, ventral view.
A-F: N1-N6.

N4: the average length is 149µm and the average width is 81µm. The general structure resembles that of the previous stage; four pairs of appendages are present: A_1, A_2, Md and Mx1. The body is two-segmented; the division is found behind the Mx1. The Mx1 has become biramous. The furca is no longer covered by the carapace. Its structure is comparable to the furca of N3.

N5: the average length is 164µm and the average width is 94µm. The body is prolonged and has two segments. Five pairs of appendages are developed: A_1, A_2, Md, Mx1 and Mx2. The Mx2 are two long, medioventral lobes, each with one long seta. The furca is distinctly bilobed with one seta and three spines on each lobe.

N6: the average length is 205μm and the average width is 117μm. Five segments are present and the posterior end is well developed. Seven pairs of appendages are present: A_1, A_2, Md, Mx1, Mx2, Mxp and P_1. The last three ones are rudimentary: only a few spines on lobes of the second, third and fourth segment. The furca is two-lobed with one long and four much shorter setae on each lobe.

(2) Copepodite stages (Fig. 2).

Cop1: the average length is 300μm. The body has the typical harpacticoid form; we distinguish a cephalothorax, a pereon and an abdomen. The cephalo-

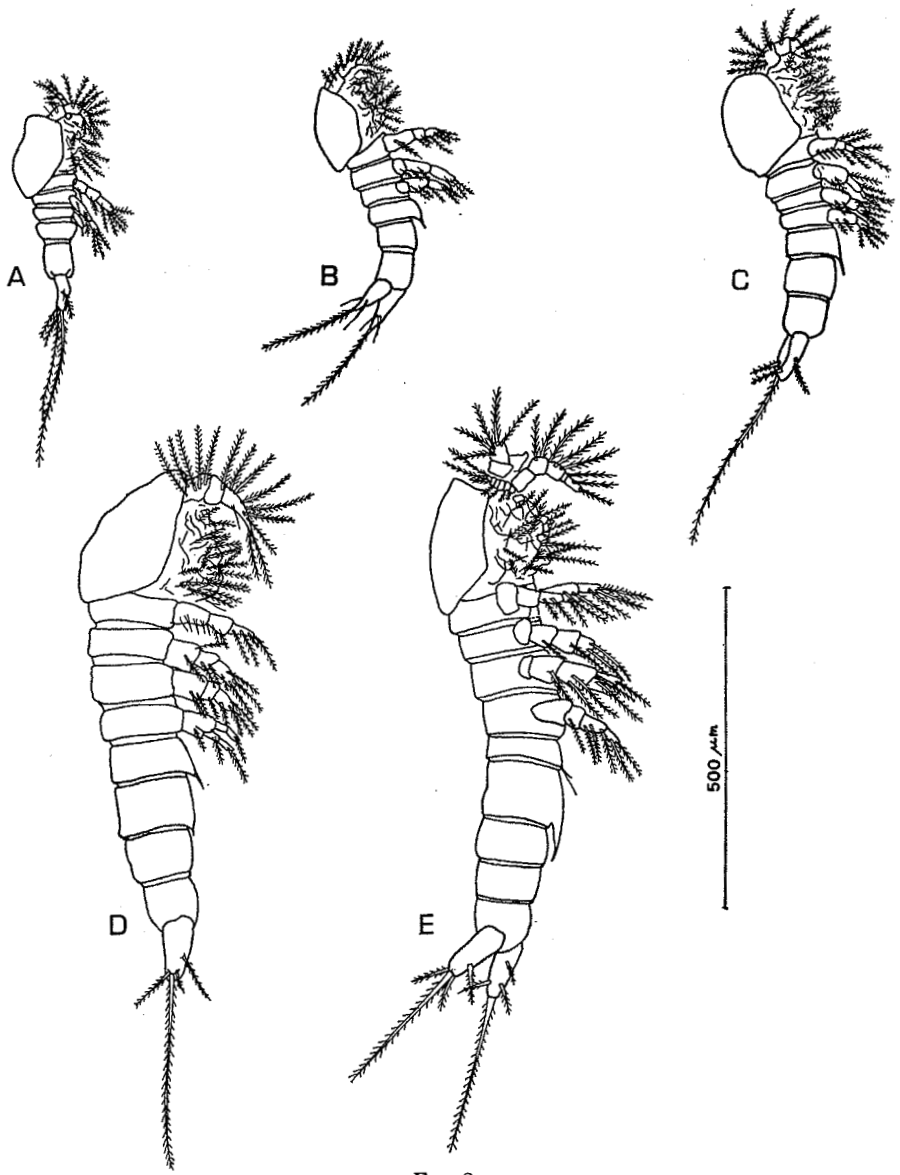

FIG. 2
Copepodite stages of *Canuella perplexa*, lateral view.
A-E: Cop1-Cop5.

thorax, with six pairs of cephalic appendages (A_1, A_2, Md, Mx1, Mx2, Mxp) is covered dorsally by the carapace. It does not change morphologically in the following stages. The pereon consists of three segments; the first and the second segment bear a pair of functional swimming legs (P_1, P_2); the third segment has rudiments of the third pair of swimming legs. The abdomen consists of two segments. The two branches of the furca each bear three long, plumose terminal setae and one short lateral seta.

Cop2: the average length is 344μm. The pereon consists of four segments, each bearing one pair of appendages. The fourth pair of legs is rudimentary. The abdomen consists of two segments. The branches of the furca have the same structure as those of Cop1; there is sometimes asymmetry in the length and the number of the lateral setae, here and in the following stages.

Cop3: the average length is 453μm. The pereon consists of five segments, each bearing a pair of swimming legs; the last pair is rudimentary. The abdomen consists of two segments. The branches of the furca have more setae.

Cop4: the average length is 698μm. The pereon consists of five segments, each bearing a pair of swimming legs. The abdomen consists of three segments; the genital segment (i.e. the first abdominal segment) is differentiated with some spines at the posterior end. We did not observe any sexual dimorphism.

Cop5: the average length is 860μm. The pereon consists of five segments, each bearing a pair of swimming legs. The abdomen consists of four segments; the genital segment of the males has two well developed, lobed appendages, each with three spines. The females have little lobes with shorter spines. It is thus possible to determine sex at the fifth copepodite stage.

Conclusion: in Table 1 the number of segments and swimming legs of each copepodite stage are given.

TABLE 1
Segments and appendages of the different copepodite stages.

Number of segments	Cop1	Cop2	Cop3	Cop4	Cop5	Ad
1	P_1	P_1	P_1	P_1	P_1	P_1
2	P_2	P_2	P_2	P_2	P_2	P_2
3	P_3r	P_3	P_3	P_3	P_3	P_3
4	+	P_4r	P_4	P_4	P_4	P_4
5	+F	+	P_5r	P_5r	P_5r	P_5r
6		+F	+	+	+	+
7			+F	+	+	+
8				+F	+	+
9					+F	+
10						+F

A segment with no appendages is indicated with +; r means: the appendage is present, but rudimentary; F indicates the segment that bears the caudal branches.

(3) Description of the appendages of the successive larval forms

Antennule (A_1) (Fig. 3).

N1: four segmented. The first segment with one, the second with two setae; the fourth segment bears one seta and an aesthetask.

N2: four segmented. The same as the A_1 of N1 except for the terminal segment which bears one short lateral and two long, terminal setae and an aesthetask.

N3: four segmented. The first segment with one, the second with two and the fourth segment with four setae and an aesthetask.

N4: four segmented. The same as the A_1 of N3, except for the six setae on the terminal segment.

N5: four segmented. The same as the A_1 of N3, except for the ten setae on the terminal segment.

N6: four segmented. The same as the A_1 of N3, except for the twelve setae on the terminal segment.

Cop1: four segmented. The first segment with two, the second segment with three, the third segment with one and the fourth segment with eight setae. The A_1 resembles the A_1 of an adult female. The second segment bears two aesthetasks: a long and a short one. These remain in the same position in the following stages. During the subsequent moultings, a great number of setae will be added and we refer to the figures for their position.

Cop2: four segmented.

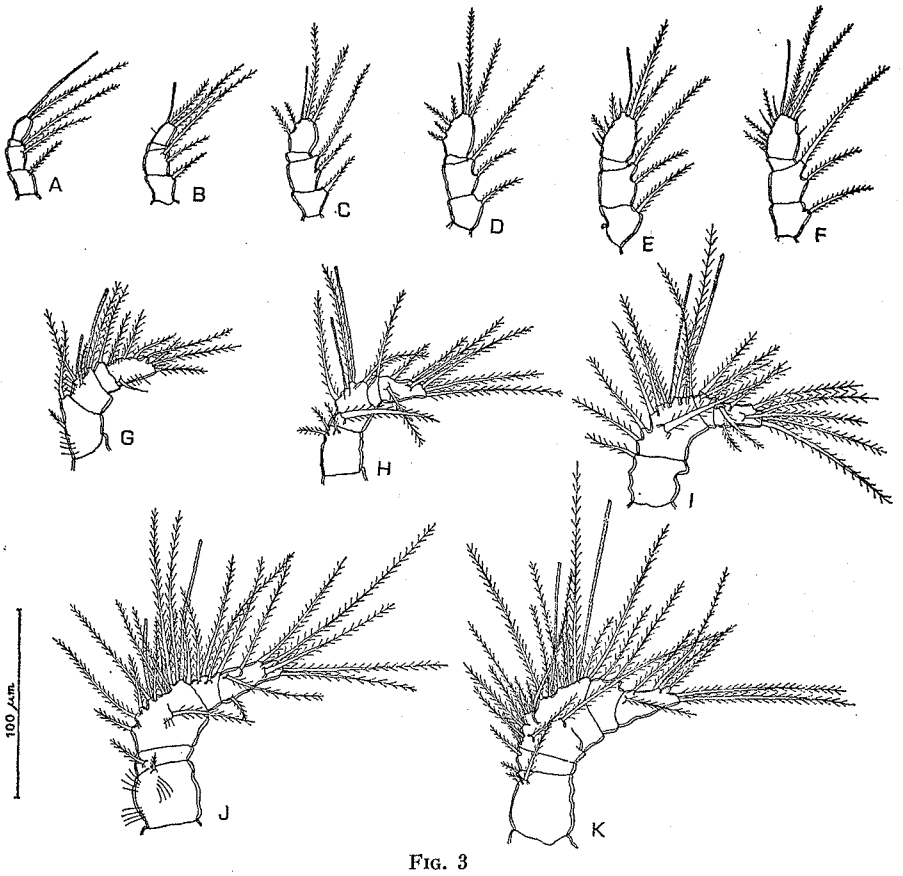

FIG. 3
Antennule of *Canuella perplexa,* lateral view.
A-F: A_1 of N1-N6.
G-K: A_1 of Cop1-Cop5.

Cop3: four segmented with much more setae.

Cop4: five segmented with an increasing number of setae.

Cop5: five segmented. The A_1 is completely comparable to the A_1 of an adult female.

Antenna (A_2) (Fig. 4)

N1-N6: A_2 with a coxopodite, a segmented exo- and an unsegmented endopodite. The coxopodite is armed with a proximal, masticatory spine that lays under the labrum. There is a little seta associated with it. The basipodite has three till five median setae. The endopodite has three terminal and an increasing number of lateral setae on the inner edge. The exopodite is well developed with many segments: six in the first nauplius, increasing

by one segment with each moult to the maximum of nine in the fourth, fifth and sixth nauplius stage.

Cop1-Cop5: the coxopodite no longer bears a masticatory spine (cfr. Fahrenbach, 1962 and Rosenfield and Coull, 1974). The endopodite is two segmented. The exopodite has seven segments. Except for size and ornamentation, the A_2 resembles the A_2 of the adult and is therefore not figured.

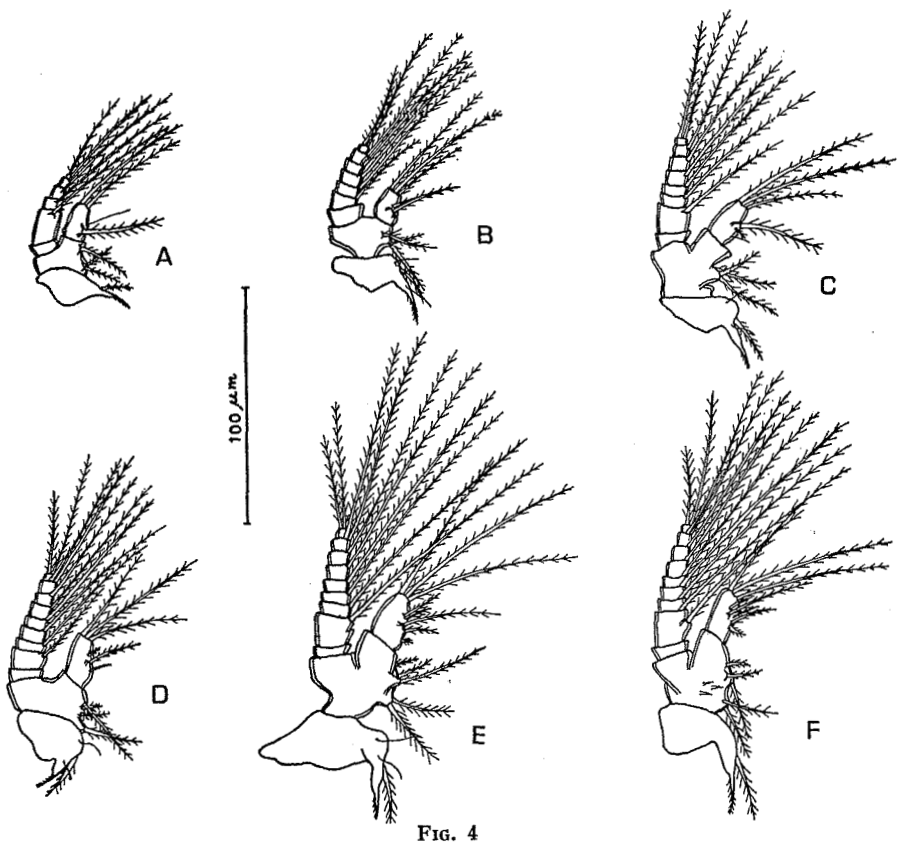

FIG. 4
Antenna of *Canuella perplexa*, lateral view.
A-F: A_2 of N1-N6.

Mandible (Md) (Fig. 5)

N1-N6: the mandible is biramous; we distinguish a coxopodite, a basipodite, an exo- and an endopodite. The coxopodite bears one median seta and the basipodite two median setae. The endopodite is two segmented with an increasing number of setae throughout the successive moults. The exopodite is four segmented with an almost constant number of setae.

Cop1-Cop5: the Md is very similar to the Md of the adult, except for size. Therefore it is not figured. The coxopodite bears strong denticles on the median side (masticatory function). The basipodite has two hairy setae. The endopodite is two segmented: the first segment has three, the second segment six setae. The exopodite consists of one segment and bears six plumose setae.

Maxille 1 (Mx_1) (Fig. 5)

N1: not present.

N2: an obvious anlage of the Mx1 is present as two medio-ventral, plumose setae.

N3: the two setae are shifted laterally.

N4: the Mx1 is bilobed: the endo- and exopodite have respectively four and five setae.

N5: the Mx1 is a two segmented appendage; the endopodite has five long and the exopodite has five long and three short setae.

N6: the endopodite has five long and the exopodite has seven well developed and three minute setae.

Cop1-Cop5: the Mx1 is very similar to the Mx1 of the adult, except for the size. Therefore it is not figured.

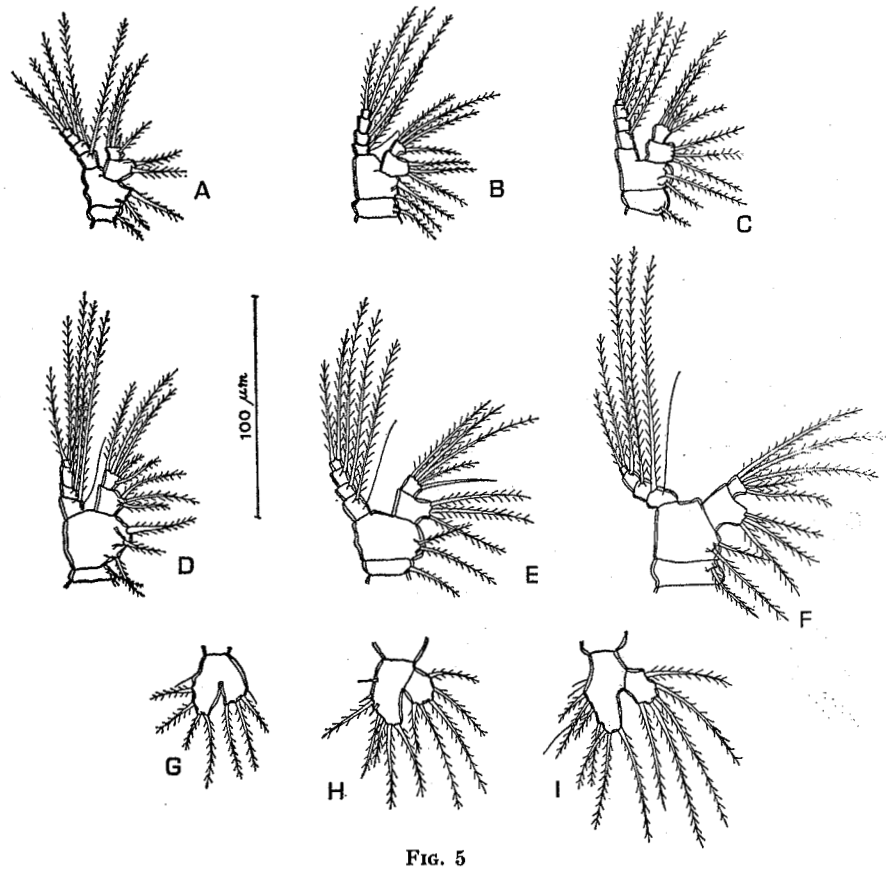

FIG. 5
Mandible of *Canuella perplexa*, lateral view.
A-F: Md of N1-N6.
Maxille 1 of *Canuella perplexa*, lateral view.
G-I: Mx1 of N4-N6.

Maxille 2 (Mx_2)

N1-N4: not present.

N5: the anlage of Mx2 is present as two medio-ventral lobes, each with one long and one very short seta, situated posteriorly to the Mx1.

N6: two biramous medio-ventral lobes, each with two setae.

Cop1-Cop5: the Mx2 differs from the Mx2 of the adult only in size; therefore it is not figured.

Maxillipede (Mxp)

N1-N5: not present.

N6: the Mxp is an appendage of the second body-segment: two lobes each with four setae.

Cop1-Cop5: the Mxp differs from the Mxp of the adult only in size and is therefore not figured.

The first leg (P_1) (Fig. 6)

N1-N5: P_1 not present.

N6: P_1 is a little lobe with three setae situated on the third segment.

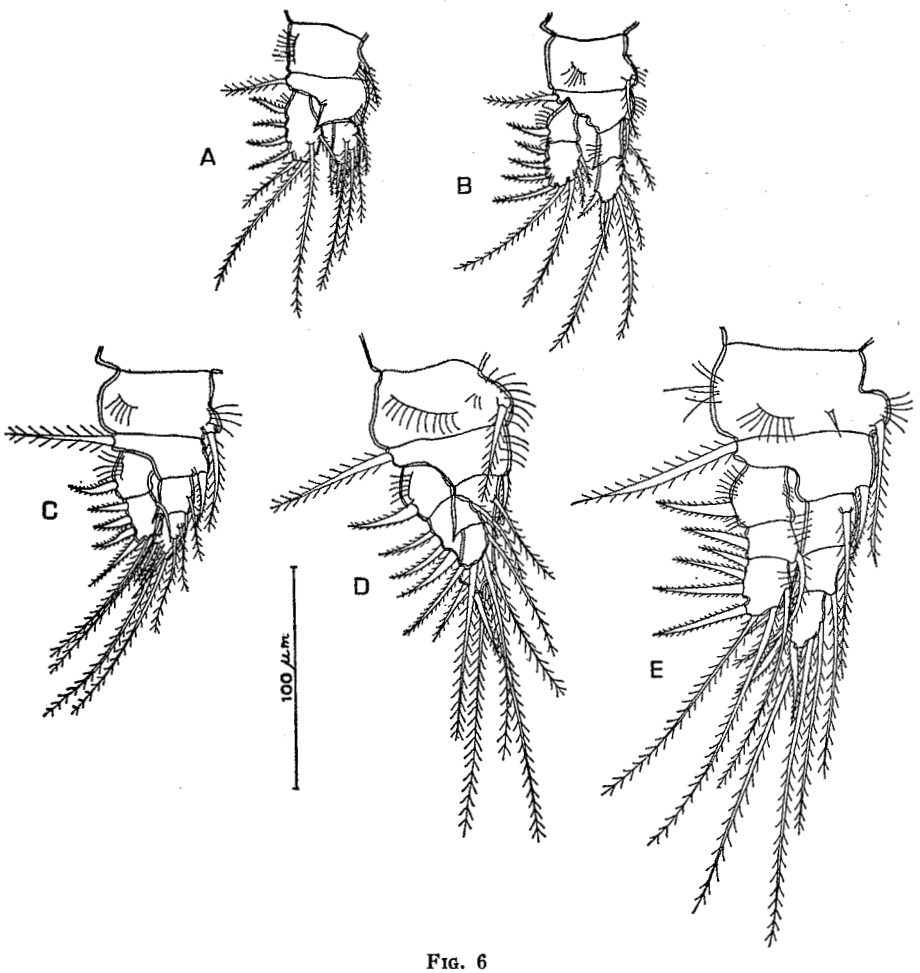

FIG. 6
First leg of *Canuella perplexa*.
A-E: P_1 of Cop1-Cop5.

Cop1: P_1 with coxo-, basi-, endo- and exopodite. The exo- and endopodite consist of one segment. The number and position of the setae is reproduced in the figures.

Cop2: the exo- and endopodite consist of two segments; the setation is similar to that in Cop1.

Cop3: except for size and setation, there is no change from Cop2.

Cop4: the P_1 is similar to the P_1 of Cop2, with a prolongation of the segments of the exo- and endopodite.

Cop5: the exo- and endopodite have each three segments. The P_1 is completely similar to the P_1 of the adult.

The second leg (P_2) (Fig. 7)

N1-N5: not present.

N6: the anlage of the P_2 is probably present as the most lateral setae on the furcal lobe.

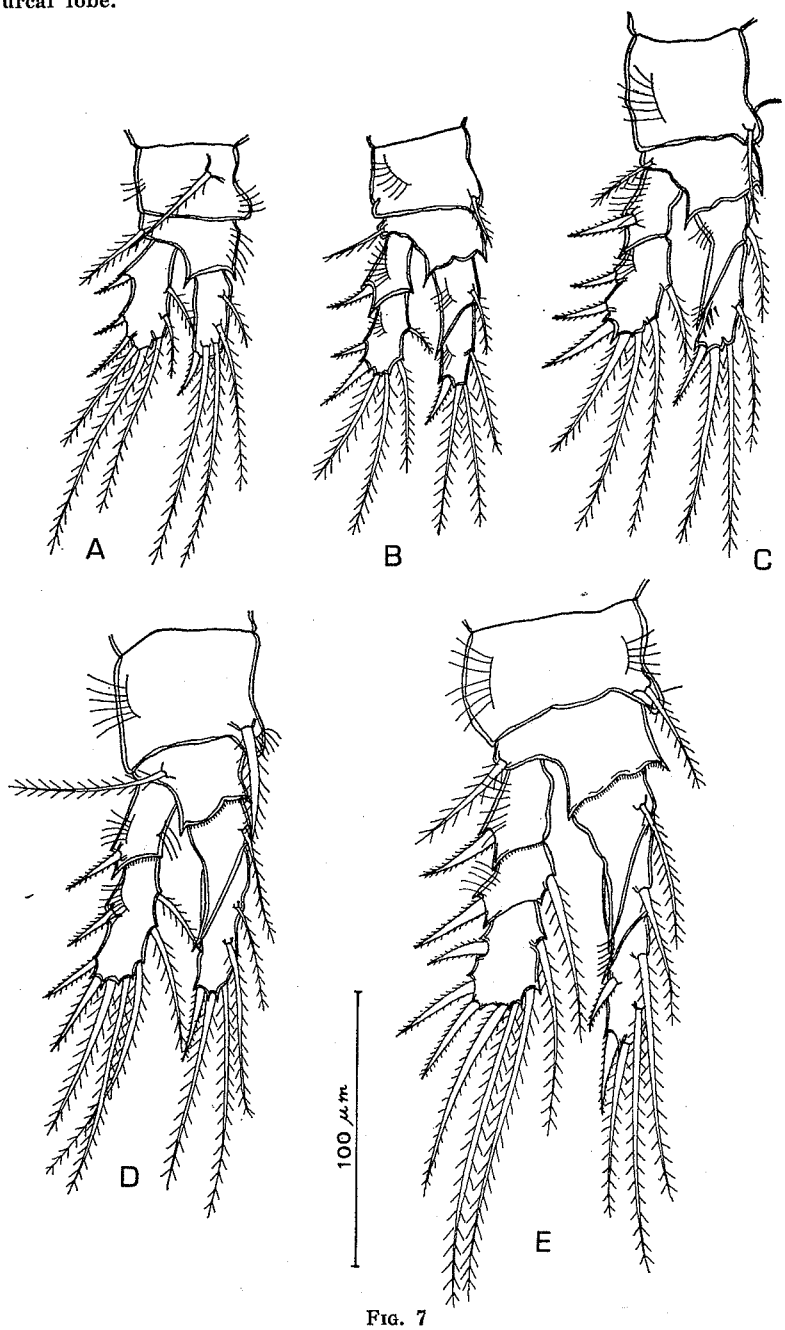

FIG. 7
Second leg of *Canuella perplexa*.
A-E: P_2 of Cop1-Cop5.

Cop1: the P_2 has a coxo-, basi-, exo- and endopodite. Exo- and endopodite consist each of one segment.

Cop2: exo- and endopodite consist each of two segments.

Cop3: except for size and for the addition of one lateral spine at the terminal segment of the exopodite, no change from Cop2.

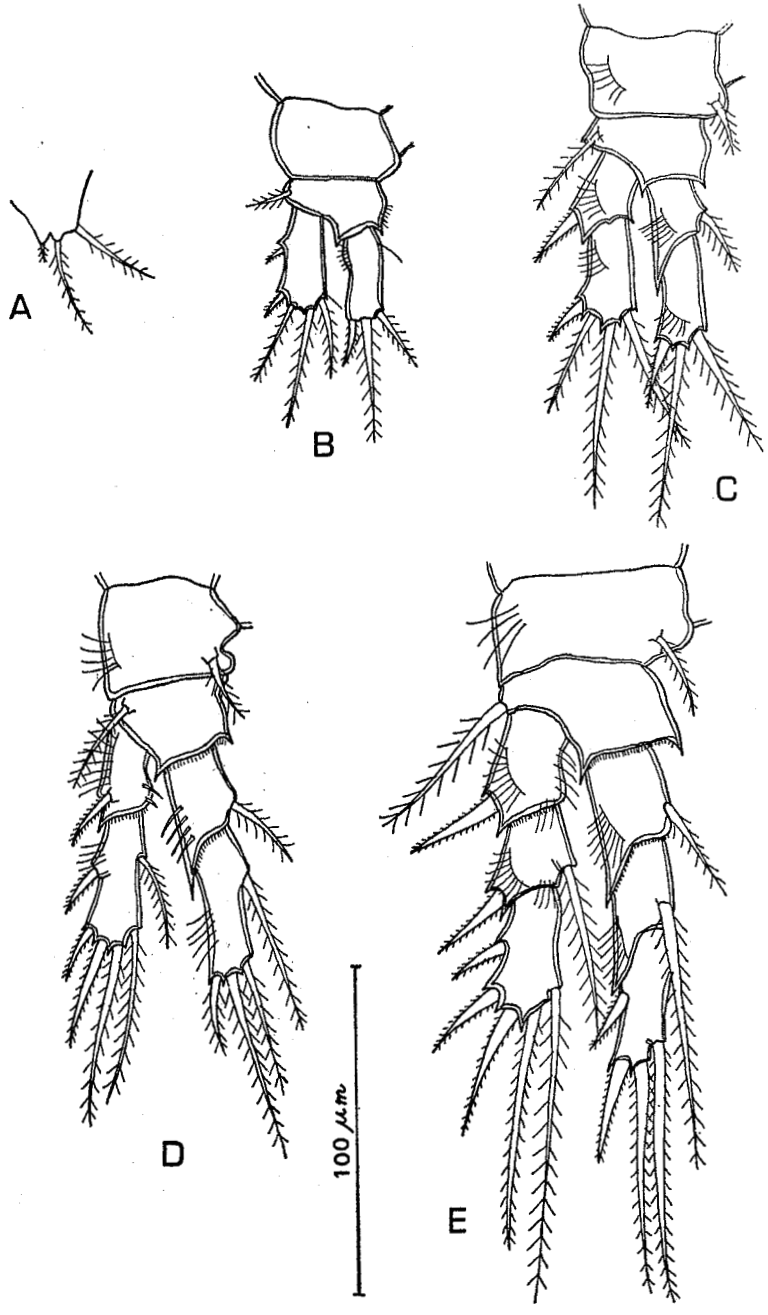

FIG. 8
Third leg of *Canuella perplexa*.
A-E: P_3 of Cop1-Cop5.

Cop4: the P_2 differs a little from the P_2 of Cop3: there is an addition of one proximal seta at the terminal segment of exo- and endopodite.

Cop5: the exo- and endopodite consist each of three segments (cfr. adult). The outer spines are much stronger than in the former stages.

The third leg (P_3) (Fig. 8)

N1-N6: not present.

Cop1: the P_3 is a lobe which bears three setae at the third thoracal segment.

Cop2: the P_3 has a coxo-, basi-, exo- and endopodite. The exo- and endopodite consist each of one segment.

Cop3: the exo- and endopodite consist each of two segments.

Cop4: the P_3 is similar to the P_3 of Cop1; there is an addition of a spine and of a seta at the terminal segment of the exopodite; also one supplementary seta at the terminal segment of the endopodite.

Cop5: the exo- and endopodite consist of three segments. The P_3 is equal to the P_3 of the adult.

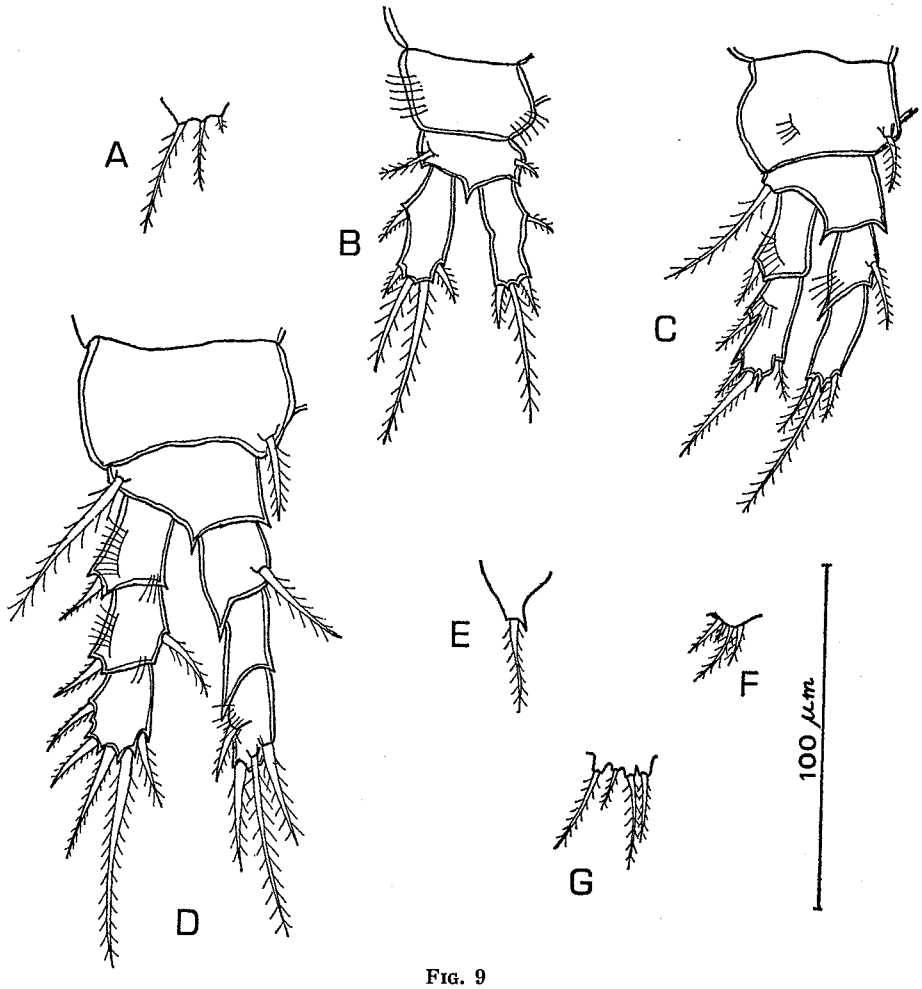

FIG. 9

Fourth leg of *Canuella perplexa*.
A-D: P_4 of Cop2-Cop5.
Fifth leg of *Canuella perplexa*.
E-G: P_5 of Cop3-Cop5.

The fourth leg (P_4) (Fig. 9)

N1-N6: not present.
Cop1: not present.
Cop2: the P_4 is similar to the P_3 of Cop1.
Cop3: the P_4 has a coxo-, basi-, exo- and endopodite. The exo- and endopodite consist each of one segment.
Cop4: the exo- and endopodite consist each of two segments.
Cop5: the exo- and endopodite consist each of three segments. The P_4 is similar to the P_4 of the adult.

The fifth leg (P_5) (Fig. 9)

N1-N6: not present.
Cop1-Cop2: not present.
Cop3: the P_5 is a lobate structure with one long and one short seta.
Cop4: the P_5 is equal to the P_5 of the adult, with four setae.
Cop5: the P_5 is equal to the P_5 of the adult.

Note: the legs of *Canuella perplexa* change according to the normal pattern in the Harpacticoida. When a leg appears, the two rami (exo- and endopodite) are one segmented. In the following stages, exo- and endopodite will consist of two segments. The exo- and endopodite of the legs P_1 to P_4 of Cop5 are three segmented (cfr. adult).

2. Biological notes

During the daily control of the cultures, some notes concerning the behaviour of *Canuella perplexa* were made.

a. Propulsion

Sars (1906) noted that the adults of *Canuella perplexa* are burrowing, endopsammic animals. In our cultures, the great mobility of the animals is very striking. The flexibility of the thoracal and abdominal segments towards each other allows the movement of the body segments in a lot of directions.

The nauplii are planktonic, hence the great nauplius eye in all the nauplius stages. The jerkey movements of the A_1, A_2 and Md propulse the nauplii. Just after hatching, they are already very active. A similar observation was made for *Euterpina acutifrons* (Fanta, 1972). In view of the typical harpacticoid habitus of the copepodites, it is evident that they will move as the adults do, yet with a slighter flexibility (they have less segments).

Contrary to what Monard (1928) states, the adults are probably negative phototactic. The following observations, though not very accurate, are indications of this:

(1) when a beam of light is pointed at a petri dish the animals concentrate as far as possible from the beam;

(2) when a petri dish containing substrate (sand-grains) and many *Canuella*'s is placed under a dissecting microscope and the source of light is beneath the petri dish, the *Canuella*'s leave the substrate after some minutes (this may be due to heating as well). At this moment, it is very easy to isolate them.

b. Feeding behaviour

Redeke (1948) distinguished two different types of feeding in the adults and copepodites of fresh water harpacticoids: the mordent and the turbulent type.

Marcotte (1977) distinguished three manners of feeding: 1. filter feeding (f.i. with *Calanus*); 2. raptorial feeding (f.i. with *Tisbe*); 3. mixed feeding (f.i. with *Centropages*).

Filter feeding corresponds to the turbulent type and raptorial feeding to the mordent type described by Redeke. We observed a mixed feeding with *Canuella perplexa*. When feeding is of the turbulent type, the animals are laying on their back (in that position, they can also move forward). A water current containing food particles is forced towards the mouth cavity by means of the mouth appendages. The food particles are taken up without being masticated. When feeding is of the mordent type, the animals scrape particles of the substrate (f.i. sand grains). In copepodites and adults, it is mainly the mandible, with its masticatory spines on the coxa, which is the active appendage; in the nauplii it is the second antenna. In dishes without sediment, we observed that *Canuella perplexa* bites the macroalgae (f.i. *Ulva*) in little pieces.

The Mx1 of the copepodites and of the adults bears proximally a lot of hairy setae, typical for a filter feeder, and is distally provided with masticatory structures suitable to grasp larger food particles, as does a raptorial feeder: *Canuella perplexa* is thus adapted to both feeding types.

c. Precopulatory behaviour

The copulation of harpacticoids is preceded mostly by a 'precopulatory-tandem' which may last for several days. Lang (1948) distinguished four types of precopulatory-tandems. The type of tandem of *Canuella* has never been described. It is formed as follows: the male, swimming with the ventral side downwards, catches the furca of the female with his club-shaped antennules. The female swims, in this position, with the ventral side upwards. It is mostly the right A_1 which holds on the left ramus of the furca of the female. The duration of this tandem varies between a few minutes and several days. The connection is very firm and such a couple crawls as easily through the substrate as a single individual.

The mating-process has not been observed.

d. Hatching

The female is extremely inactive when nauplii leave the egg sac. At the inner side of the egg sac is a little slit. The nauplii twist themselves one by one through the slit; they are instantly very active. It takes a few minutes to three days before all the nauplii are released. Once the egg sacs are empty, the female pushes them off with the P_4. We once observed that a female pushed off filled egg

sacs; the nauplii developed then further but never left the sac. This could be an indication that the female intervenes in the hatching-process.

It is interesting to note that *Canuella perplexa* sometimes pushed off the egg sac and eats her own nauplii, while they were still in the egg sac. Whether this phenomenon occurs in natural conditions as well, remains an open question. Mullin and Brooks (1967) observed cannibalism by the female of *Rhincalanus nasutus* on her nauplii.

DISCUSSION

The post-embryonic development of *Canuella perplexa* consists of six nauplius stages and six copepodite stages (the sixth being the adult).

Partially based on the common structure of the nauplii of *Longipedia* (Longipediidae) and of *Sunaristes* (Canuellidae), Lang (1948) proposes a deep systematic gap between the Longipediidae and the Canuellidae (Polyarthra) on the one side and the other Harpacticoida (= Oligoarthra) on the other.

The developmental stages of some Longipediidae were described by Gurney (1930) and by Nicholls (1935), namely those of *Longipedia scotti, L. minor* and *L. coronata*. The Canuellidae are treated only occasionally. Gurney (1930) described two nauplii that he found in a plankton sample from the mouth of the Lynher. He interpreted these forms as representatives of the Longipediidae, which included at that time also the genera *Canuella* and *Sunaristes*. He described these larvae as "Longipediidae, Genus II. Nauplius, Stage I and Nauplius, Stage V". He commented on these forms as follows: "The resemblance to the larva of *Longipedia* in the structure of the appendages is so close that a near relationship is obvious, and there is also in Stage I the pair of large maxillular spines, which is so characteristic. On the other hand, the body lacks altogether the conspicious posterior median spine, and there is a pair of long furcal setae in Stage I. The body has, otherwise, the same form as in *Longipedia,* with a very arched dorsal contour. In Stage V the resemblance to *Longipedia* is still more marked. There are now three pairs of furcal spines, but no median spine. The larva is in fact simply a *Longipedia* without a posterior spine". Gurney also described another "*Longipedia,* Genus II. Nauplius Stage III" and he suggested that Genus II as well as Genus III are the larvae of *Canuella* or *Sunaristes*.

Lang (1948) described the first nauplius of *Sunaristes paguri* and stated that the specimen, described by Gurney (1930) as "Longipediidae, Genus II. Nauplius, Stage I" must be the second nauplius stage of *Sunaristes paguri,* instead of the first.

From these three descriptions (Gurney, 1930; Nicholls, 1935; Lang, 1948), Lang listed the general characters of the nauplii of the Polyarthra as follows: "The body form is swollen pear-shaped; the

anlage of the first maxilla is present in the first nauplius stage". All these characters are unique among the Copepoda.

It is obvious that *Canuella perplexa* deviates from this scheme; the first nauplius has two large, caudal setae and the anlage of the first maxilla appears in nauplius stage II. These two characters are typical for the suborder of the Oligoarthra (Lang, 1948). In the suborder of the Oligoarthra, the larval development of many more species has been investigated. Hirakawa (1974) noted, in the rather primitive Ectinosomidae, that the nauplius stage I of *Microsetella norvegica* is very similar to that of *M. rosea* (Björnberg, 1972) and of *Longipedia:* all these nauplii bear rudimentary first maxillae and a median caudal spine which is lacking in *Canuella.* From all these considerations, it follows that the larval criteria in the subordines Polyarthra and Oligoarthra should be revised.

As already mentioned, knowledge of the developmental stages of the Canuellidae is limited to the nauplius stage I of *Sunaristes paguri* (Lang, 1948) and to a nauplius belonging to the Canuellidae, described as *Longipedia,* Genus II by Gurney (1930). There is a striking resemblance with nauplii of *Canuella perplexa.* This indicates the homogeneity of the species within the Canuellidae. The two caudal setae of the nauplius I of *Sunaristes paguri,* which Lang (1948) interpreted as the first maxillae, are in our opinion, the furcal setae.

The post-embryonic development of *Canuella perplexa* has some characters in common with that of *Longipedia coronata:* 1) the A_1 consists of four segments throughout the naupliar development; 2) the coxo- and basipodite of the A_2 are armed with strong masticatory spines and plumose setae; the endopodite has some rigid terminal setae and a few lateral setae on the inner edge; the exopodite is well developed and consists of many segments, each with one long, plumose seta; 3) the mandible is also very similar: a small coxopodite bears one seta; the basipodite is more developed; the important masticatory function of this mouth appendage is reflected in the presence of the rigid spines on the first segment of the endopodite. The exopodite consists of four segments in all the naupliar stages; 4) the maxille 1 of the nauplius stages III to VI is bilobed with corresponding lateral and terminal setae; 5) the evolution in the development of the copepodites is similar.

Although the two species resemble each other structurally, it is nevertheless remarkable that the general body form of the nauplii is very different. The nauplii of *Longipedia* have a prominent mediocaudal spine that is absent in the larvae of the Canuellidae.

Nicholls (1935) noted the resemblance between the nauplii of *Longipedia coronata* and the cirripede larvae in habitus and in the structure of the masticatory spine on the coxopodite of the second antenna. The nauplii of the Polyarthra, with four segments in the antennule, occupy and intermediate position between the majority of the copepods with three segments and the cirripedes with five segments in the antennule. Both the nauplii of the cirripedes and those of the Canuellidae are planktonic. This may be a primitive situation. Swimming of the nauplii of the Polyarthra is uncomplicated, by "paddle-strokes" of A_2 and Md. They are incapable of any

other motion, owing to their simple muscle system (Björnberg, 1972). The setae on the segments of these appendages are of the simple type, i.e. thin and spine-like or plumose; thus well adapted to planktonic life. The nauplii of all the other harpacticoids have well developed masticatory cutting processes, hooks and other very specialized features on both A_2 and Md. These are adaptations to their life on a substratum. Another primitive character of the *Canuella*-nauplii is the bimerous endopod (i.e. with two segments) on the mandible, which become unimerous in the higher developed forms.

From all this we conclude that:

(1) the Longipediidae and the Canuellidae are primitive Harpacticoida. This is also striking with regard to the post-embryonic development;

(2) the Ectinosomidae are very close to those primitive forms. The nauplii of stage I of *Microsetella* have a median, caudal spine, which indicates the affinity with the Longipediidae;

(3) the characters which determine the Polyarthra as apart from the Oligoarthra, described by Lang (1948), should be revised.

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Summary

Canuella perplexa T. and A. Scott, 1893 is an harpacticoid copepod belonging to the family Canuellidae of the primitive suborder Polyarthra (Lang, 1948). It is often a dominant species in meiobenthic communities of the northern hemisphere. The biology (propulsion, feeding behaviour, precopulatory behaviour, and hatching) and larval development of this species were examined on animals reared in the laboratory.

Characters of the nauplius which were considered by Lang (1948) to be diagnostic of the Polyarthra will have to be reexamined in the light of our results on *Canuella perplexa*. The post-embryonic stages of the Canuellidae are morphologically different from the larval stages of the also primitive Longipediidae.

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