

STUDIES ON THE FAUNA OF CURAÇAO AND OTHER
CARIBBEAN ISLANDS: No. 136.

DEVELOPMENTAL STAGES OF SOME TROPICAL AND
SUBTROPICAL PLANKTONIC MARINE COPEPODS

by

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INTRODUCTION

Most planktonic marine copepods have nauplii which differ greatly from the copepodids so that it is difficult to relate them to the adult form. Rearing experiments are usually unsuccessful; only 8% of ca. 300 species of planktonic marine copepods have identified nauplii (see below cited list). To this 8% the following species are added in this work: *Acartia lilljeborgi*, *Calocalanus styliremis*, *C. pavo*, *Candacia* sp., *Clausocalanus furcatus*, *Centropages furcatus*, *Corycaeus amazonicus*, *C. giesbrechti*, *C. speciosus*, *Farranula gracilis*, *Labidocera fluviatilis*, *Microsetella rosea*, *Oithona oculata*, *O. ovalis*, *O. plumifera*, *O. simplex*, *Oncaea media*, *O. venusta*, *Paracalanus crassirostris*, *Pontellopsis* sp., *Pseudodiaptomus acutus*. They were reared from the egg to the first nauplius, or from the last nauplius to the first copepodid either at the Caraïbisch Marien-Biologisch Instituut (= Carmabi), Curaçao, during 1963, or at the marine station of the Instituto Oceanográfico, Ubatuba, Brazil, during 1966–1967.

Methods used have been described previously (BJÖRNBERG, 1965a, 1966, 1967). Other methods have often been used by other workers (BERNARD, 1963, 1965 a, b; BRESCIANI, 1960; CONOVER, 1965, 1966; CORKETT, 1966, 1967; CORKETT & URRY, 1968; FRASER, 1936; HAQ, 1965 a, b; JACOBS, 1961; JOHNSON & OLSON 1948; KOGA, 1960; LEBOUR, 1918; MATTHEWS, 1964, 1966; McLAREN, 1966; MURPHY, 1923; MULLIN & BROOKS, 1967; NEUNES & PONGOLINI, 1965; NICHOLLS, 1933; PROVASOLI *et al.*, 1959; ZILLIOUX & WILSON, 1966).

Because of the difficulty of rearing marine planktonic copepods, particularly the oceanic and the carnivorous species, many authors have identified nauplii tentatively by studying fixed plankton samples (CONOVER, 1956; GIBBONS, 1936; GIBBONS & OGILVIE, 1933; GRANDORI, 1912; JOHNSON, 1934 a, b, 1935, 1937, 1965, 1966; LINDQUIST, 1959; OBERG, 1906). Some nauplii mentioned in this work are also ascribed tentatively to the following species: *Acartia*

danae, *A. negligens*, *Calanoides carinatus*, *Ctenocalanus vanus*, *Eucalanus crassus*, *Eucalanus attenuatus*, *Farranula gracilis*, *Haloptilus longicornis*, *Nannocalanus minor*, *Pleuromamma* sp., and *Pontellopsis brevis*. The samples used were caught at CURAÇAO; off BRAZIL, from the research vessels "M. Lomonosov" (XIIth cruise to the South Atlantic), "Toko-Maru," "Almirante Saldanha" and "Emilia" and kept in the plankton collection of the Instituto Oceanográfico, University of São Paulo, Brazil; and off CHILE during the "Mar Chile I" expedition.

Various scientists (ANDREWS, 1966; CONOVER, 1956; CRISAFI, 1960a, b, c, d, 1962, 1963; DIGBY, 1950; FABER, 1966b; FISH, 1936a, b, c, 1955; GAUDY, 1962; GRAINGER, 1959, 1961, 1965; MACKINTOSH, 1937; MĂRGINEANU & ȘERPOIANU, 1961; MARSHALL, NICHOLLS & ORR, 1934; NICHOLLS, 1933; QUING-CHAO, 1964; VUČETIĆ, 1966; WIBORG, 1954) have deduced the seasonal variation of the cycle of development of a copepod species, its number of generations per year, its period or periods of reproduction, and the duration of each of its developmental stages from the study of fixed samples. Such investigations have not yet been carried out for the species herein described. The "ontogenetic migration" (BANSE, 1964, p. 77-78), the weight of each stage of development such as was calculated for other species of planktonic copepods (KANAeva, 1962), the internal anatomy of the larvae as studied by DUDLEY (1966) for the Notodelphyidae, is left for future investigations.

This publication describes only the external morphology of developmental stages of some species common in tropical and subtropical waters. Characteristic movements, data on the habitat and food habits of the larvae, when observed, and some suggestions on the possible evolution within the group, based on the morphology and movements of the nauplii, complement this study. Though incomplete, this work will, I hope, induce scientists to investigate the nauplii further and to expand the knowledge of this interesting and little explored field.

SARS' classification has been used for suborders, VERVOORT's for families. LEBOUR's nomenclature has been adopted when describing development stages.

SYMBOLS USED TO DESCRIBE THE SEGMENTATION AND THE SETATION OF THE APPENDAGES: numbers alone = number of setae; s = spine; mp = masticatory process; + indicates separate groups of setae; : separates setae belonging to different segments; 0 indicates the absence of setae on the segment; variation in number in parenthesis; b = balancer; ext = external; term = terminal; ms = minute spines; number in italics = very thin slender setae or spines.—Almost all symbols used taken from MARSHALL & ORR (1955).

PLANKTONIC COPEPOD SPECIES WITH IDENTIFIED NAUPLII
and the authors who described them

Acartia bifilosa (OBERG, 1906; GURNEY, 1931), *A. clausi* (GURNEY, 1931; CONOVER, 1956; SAZHINA, 1960), *A. longiremis* (OBERG, 1906), *A. tonsa* (CONOVER, 1956), *Calanus finmarchicus* (LEBOUR, 1918; OGILVIE, 1953; MARSHALL & ORR, 1955), *C. helgolandicus* (SAZHINA, 1961), *C. hyperboreus* (SØMME, in CONOVER, 1967), *C. tonsus* (CAMPBELL, 1934), *Candacia armata* (BERNARD, 1965 a), *Centropages abdominalis* (KOGA, 1960 b), *C. kroyeri* (SAZHINA, 1960), *C. typicus* (GRANDORI, 1925; GURNEY, 1931; OGILVIE, 1953), *C. hamatus* (OBERG, 1906; GURNEY, 1931; FABER, 1966 a; LINDQUIST, 1959); *Chiridius armatus* (MATTHEWS, 1964), *Corina granulosa* (BERNARD, 1965 b), *Corycaeus* sp. (HANAOKA, 1952 a), *Epilabidocera amphitrites* (JOHNSON, 1934 b), *Eucalanus attenuatus* (BJÖRNBERG, 1967), *E. elongatus* (GIBBONS, 1936, 1937; LOVEGROVE, 1956), *E. bungii* (JOHNSON, 1937), *E. pileatus* (BJÖRNBERG, 1967), *Euchaeta marina* (GAUDY, 1962; BERNARD, 1965 a), *E. japonica* (CAMPBELL, 1934), *Eurytemora americana* (FABER, 1966 a), *E. herdmani* (JOHNSON, 1966; FABER, 1966 a), *E. hirundo* (OBERG, 1906), *E. hirundoides* (DAVIS, 1943), *E. pacifica* (CHIBA, 1956), *E. velox* (GURNEY, 1931), *Euterpina acutifrons* (TESCH, 1915; RAMAMOHANA RAO, 1958 b; BERNARD, 1963; HAQ, 1965 b; EL-MAGHRABY, 1965), *Labidocera aestiva* (FABER, 1966 a), *L. bengalensis* (UMMERKUTTY, 1964), *L. brunescens* (SAZHINA, 1967), *L. jollae* (JOHNSON, 1935), *L. trispinosa* (JOHNSON, 1935), *Limnocalanus grimaldii* (LINDQUIST, 1959), *Longipedia coronata* (GURNEY, 1930; NICHOLLS, 1936), *L. helgolandica* (FABER, 1966 a), *L. minor* (NICHOLLS, 1936), *L. scotti* (NICHOLLS, 1936), *Macrosetella gracilis* (KRISHNASWAMY, 1949, 1950; BJÖRNBERG, 1965 a; TOKIOKA & BIERI, 1966), *Metridia lucens* (GIBBONS, 1938; OGILVIE, 1953), *Microsetella norvegica* (FISH, 1955; LOVEGROVE, 1956; OGILVIE, cited in LOVEGROVE, 1956), *Miracia efferata* (BJÖRNBERG, 1965 a), *Oculosetella gracilis* (BJÖRNBERG, 1965 a), *Oithona brevicornis* (FABER, 1966 a), *O. helgolandica* (GIBBONS & OGILVIE, 1933), *O. minuta* (SAZHINA, 1960), *O. rigida* (KRISHNASWAMY, 1950; RAMAMOHANA RAO, 1958 a), *O. similis* (OBERG, 1906; FABER, 1966 a), *O. spinirostris* (GIBBONS & OGILVIE, 1933), *Oithonina nana* (MURPHY, 1923; HAQ, 1965 a), *Oncaea mediterranea* (HANAOKA, 1952 b), *Paracalanus crassirostris* (FABER, 1966 a), *P. parvus* (OBERG, 1906; OGILVIE, 1953), *Paraechaeta norvegica* (NICHOLLS, 1934), *P. russelli* (KOGA, 1960 a), *Pontella mediterranea* (CLAUS, 1893; GIESBRECHT, 1893, SAZHINA, 1967), *Pontellopsis occidentalis* (JOHNSON, 1965), *Pseudocalanus minutus* (OBERG, 1906; OGILVIE, 1953; FABER, 1966 a), *Pseudodiaptomus aurivilli* (KRISHNASWAMY, 1950; UMMERKUTTY, 1964), *P. coronatus* (FABER, 1966 a), *P. euryhalinus* (JOHNSON, 1949), *Rhincalanus cornutus* (GURNEY, 1934), *R. nasutus* (GURNEY, 1934;

GIESBRECHT, 1893; GIBBONS, 1936), *R. gigas* (STEUER, 1935), *Temora stylifera* (GAUDY, 1961; BJÖRNBERG & MOREIRA, in press), *T. longicornis* (OBERG, 1906; OGILVIE, 1953; LINDQUIST, 1959), *Tortanus discaudatus* (JOHNSON, 1934 a), *T. gracilis* (KRISHNASWAMY, 1950), *Undinula vulgaris* (BJÖRNBERG, 1966), *Xanthocalanus fallax* (MATTHEWS, 1964).

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CALANOIDA

Family CALANIDAE

Calanoides carinatus (Krøyer, 1849)

(Figs. 1-9)

Material: Fixed samples collected with a fine net off Santos, BRAZIL, over the continental shelf.

Habitat: The nauplii and copepodids occur in small numbers on the shelf and sometimes in coastal waters off the southern coast of Brazil, in temperatures from 20.9-14.9°C, salinity 34.00-35.44‰, and oxygen content 3.44-6.12 ml/l. They were present also in samples from the region of the Subtropical Convergence in salinities exceeding 36.00‰.

Nauplius II (Fig. 1): Length 0.23 and 0.22 mm. Body: undivided, pear shaped. Labrum or upper lip: oval. Caudal armature:

2 sensory setae ("feelers") and minute spines. Antennule, 0 : 1 + 1 + 1 : 4. Antenna: coxopod, 1s + 1; basipod, 2s; endopod, 2 + 3; exopod, 1 : 1 : 1 : 1 : 2. Mandible: coxopod, 1; basipod, 2; endopod, 3 + 2 + 3; exopod, 2 : 1 : 1 : 1.

Nauplius III (Fig. 3): Length (terminal setae included), 0.34 mm. Shape: body hook-like, anteriorly wider, tapering posteriorly from the margin of the dorsal shield. Labrum, oval with marginal and lateral minute spines. Labium, or inferior lip, hairy (hirsute). Body divided into anterior region and caudal region. Caudal armature: 2 sensory setae (1 dorsal, 1 ventral), ms (lateral, marginal, ventral); 2s (ventral), 2s term (dorsal). Antennule, (3 or 4 segments, first segment with incipient divisions) 0 : 3 : 2 + 3 + 1. Antenna: coxopod, 2s (setose) + 1; basipod, 1s + 2; endopod, 1 : 3 + 3 term; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 3. Mandible: coxopod, 1; basipod, 3; endopod, 4 + 2 + 3; exopod, 1 : 1 : 1 : 2.

Nauplius IV (Fig. 2, 5): Length 0.35, 0.39, 0.40 and 0.42 mm. Shape: body hook-like with anterior region widened. Labrum, oval with marginal, lateral and ventral minute spines. Inferior lip hirsute. Body divided into anterior and posterior regions. Caudal armature: 2 feelers, several minute spines (lateral, marginal, ventral), 2s (lateral on each side), 4s (ventral + 2s term (dorsal)). Antennule, 0 : 3 : 10 + 5 or 4ms. Antenna: coxopod, 2mp (setose) + 1; basipod, 1s + 1 + 1; endopod, 2 : 3 + 4 term + 5ms; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 3. Mandible: coxopod, mandibular blade + 1; basipod, 4 (5); endopod, 4 + 1 : 2 + 2 + 2 + ms; exopod, 1 : 1 : 1 : 2. Maxillule: 2 lobes, 4 : 3.

Nauplius V (Fig. 4, 6, 8): Length (terminal spines included) 0.45 mm. Shape: hook-like, dilated anteriorly. Labrum oval, hirsute. Inferior lip hirsute. Body with three segments. Caudal armature (Fig. 8): 2 sensory setae, ms (lateral, marginal, ventral) + 3s (lateral, on each side) + 4s (ventral) + 2s term (dorsal). Antennule, 0 : 3 : 13 + ms (pre-marginal). Antenna (Fig. 4): coxopod, 2s + 1 (long); basipod, 1s (spinous) + 2 (setose); endopod, 2 : 4 + 5 + ms; exopod, 0 : 0 : 3 : 1 : 1 : 1 : 1 : 1 : 3 term. Mandible: coxopod, with mandibular blade + 2 or 1; basipod, 5 + 1; endopod, 2 lobes, 2 + 2 + 1 : 2 + 2 + 2 + ms; exopod, 1 : 1 : 1 : 1 : 2. Maxillule: 4 lobes, 1 : 1 : 7 : 5.

Nauplius VI (Fig. 7, 9): Length, 0.59 mm (1 specimen), and 0.55 mm (2 specimens). Shape: hook-like. Labrum and inferior lip hirsute. Body with 4 or 5 segments. Caudal armature as in nauplius V. Antennule: 0 : 3 : 15 + ms. Antenna: coxopod, 2s + 1; basipod, 1 (spinous) + 2s; endopod, 3 (2) : 4 + 5 + ms (pre-marginal); exopod, 0 : 0 : 3 : 1 : 1 : 1 : 1 : 1 : 3. Mandible: coxopod, with mandibular blade, 3 teeth + ms + tuft of ms + 1; basipod, 6; endopod, (2 lobes) 2 + 2 + 2 : 2 + 2 + 2; exopod, 1 : 1 : 1 : 1 : 2. Maxillule: coxopod, 4-toothed; epipod I, 3-toothed; epipod II, 4-toothed; epipod III; basipod fused with endopod, 2 + 2 + 2 + 2; external epipod I, 1; exopod, 7. Maxilla: (6 lobes) 2 : 2 : 3 : 1 : 3 : 2. Maxilliped: (1 lobe) 1. Leg I: (2 lobes) 2 : 2 + 1. Leg II: (2 lobes) 2 : 2.

Copepodids I, II, III of *C. carinatus* have the following lengths: 0.73 mm, 0.94 mm, and 1.23 mm.

Discussion: Calanidae, Paracalanidae and Pseudocalanidae have similar nauplii, all hook-shaped when seen in profile, from stage III onwards. They have 4 ventral spines, pre-terminal, in the caudal armature from stages IV to VI. These spines are in the vicinity of the two terminal spines, and, laterally, there are 2 spines (in stage IV) and 3 small spines (in stages V and VI) besides numerous minute spines, ventral and marginal. Two long sensory setae are also present and there are no balancers. These setae therefore may have two functions, of "feeling" the environment and of balancing the nauplius.

To distinguish these larvae from each other the first criterion is size. Generally the adult females of these families are approximately 4 times longer than the last naupliar stage. The nauplii here described were considered as belonging to *Calanoides carinatus*, because they always occurred in low temperature conditions near the coast on the continental shelf off Santos. *C. carinatus* is the only calanid large enough to have the larval stages here described. In confirmation of this, a sample of these waters contained the whole series here described, together with the copepodids up to stage III. *Nannocalanus minor* may also have similar nauplii and is numerous in the same region, but not in the same waters.

As expected, the nauplii of *Calanoides carinatus* differ little from those of other calanids already described, such as *Calanus finmarchicus* (Lebour, 1918), *Calanus tonsus* (Campbell, 1934), *Calanus helgolandicus* (Sazhina, 1961), and *Undinula vulgaris* (Björnberg, 1966). *Undinula* has nauplii slightly smaller than those of *C. carinatus*; *C. tonsus* from cold waters, has larger larvae. *C. finmarchicus* from cold and temperate waters, has larger naupliar stages.

In aspect and external morphology, the nauplii of the four species are practically the same. *Calanus tonsus* differs in the more rounded shape of the labrum; *Undinula* has a smaller labrum and a very large maxillule. Though minute, the setae in *Undinula* are much larger than in *Calanoides*. *Calanus tonsus* has ventral and terminal spines in the caudal armature which are relatively longer than those of *C. finmarchicus*, of *Undinula* and of *Calanoides carinatus*. *Calanus helgolandicus*, and *C. finmarchicus* are very similar during naupliar life. They can be distinguished from each other because *C. helgolandicus* has smaller larvae.

Nannocalanus minor (Claus, 1863)

(Figs. 63–66)

Material: Fixed plankton samples collected on 6 March, 1960 off CHILE at 35°34' S and 74°07' W in an oblique haul from 150 m depth to the surface, during the Mar Chile I expedition.

Habitat: The net was hauled through a 150 m deep layer of water with temperatures between 18.65°C and 9.9°C and salinities between 33.96‰ and 34.46‰ in the Peru Current under influence of subtropical water. *Nannocalanus minor* usually occurs off Chile in waters with 17° temperature. It is also abundant off Brazil, in tropical and subtropical waters and off Curaçao during winter. It is a circum-tropical, subtropical species.

Nauplius VI (Figs. 63–66): Length, 0.45 mm (2 specimens). Body with several segments, pear-shaped, bent hook-like. Labrum and inferior lip protruding. Inferior lip hirsute. Caudal armature: 4 ventral serrate spines, 2 terminal serrate spines, and minute spines in between, 3 lateral spines on each margin. The two sensory setae, not present in the animals examined, were probably lost due to mishandling of the specimens. Antennule, 0 : 1 + 1 + 1 : 17. Antenna: coxopod 2mp + 1; basipod, 1 (long) + 2 (short); endopod,

2 : 3 (4) + 5 + 1 (very thin); exopod 10-segmented, 0 : 3 : 1 : 1 : 1 : 1 : 1 : 1 : 1 : 2. Mandible: coxopod, 1 + 3-toothed mandible blade; basipod, 4 (3); endopod, 4 + 2 + 3; exopod, 1 : 1 : 1 : 1 : 2. Maxillule, 1 : 1 : 2 : 8 (7) : 5 : 1. Maxilla, 1 : 2 : 1 : 2 : 2. Maxilliped, 2. Leg 1: 2-lobed, 2 : 2 + 1s. Leg 2: 2-lobed, 2 : 1 + 1s. Copepodids I, II, III of *N. minor* have the following lengths: 0.54–0.60 mm, 0.72–0.79 mm, and 0.94–0.99 mm.

Discussion: This nauplius was identified as a developmental stage of *Nannocalanus minor* because the whole series of copepodids, the adults and the nauplius occurred in the same sample. The adult *N. minor* female is about four times larger than this nauplius. Off Chile the other calanids which might have the same type of nauplius (*Calanus australis* and *Calanoides patagoniensis*) are much too large to have this small larva. *Paracalanus parvus*, also numerous in Chilean waters, is too small to produce a nauplius VI as long as 0.45 mm.

The number of setae of the various appendages of the nauplii mentioned, are compared on Table 1. A mistake in the description of the nauplius VI of *Undinula vulgaris* (Björnberg, 1966) is corrected in this Table. The rudiments of the maxilla and part of the setae had not been observed, because of the opacity of the material. A better study of the details is made here of the same material, now transparent. The maxilla in the nauplius VI is almost covered by the maxillule. The maxillule of *U. vulgaris* is larger than in the other larvae.

The following conclusions can be drawn from Table 1: *Calanus tonsus* is the species with slowest development of setae on the antenna and mandible, but it is relatively advanced in the development of the maxillule; *Undinula vulgaris* is also slow in the development of the antenna. *Calanoides carinatus* is sometimes backward and sometimes advanced in the development of certain appendages when compared to the other species. The same can be said of *Calanus finmarchicus*. No good description could be found in the literature of the first and second pairs of legs of nauplius VI of *C. finmarchicus*. *C. helgolandicus* has more developed legs and maxillae than maxillules and mandibles, when compared with the same stage of *C. finmarchicus*.

Family EUCALANIDAE

Eucalanus crassus Giesbrecht, 1888

(Figs. 10-16, 19-20)

Material: Fixed sample collected in shelf waters off Santos (24°24' S-45°53' W), BRAZIL.

Habitat: Larval stages studied, copepodids and adult were taken from waters of 14.90-22.40°C; salinity 35.55-35.44‰; and oxygen content 3.7-5.2 ml/l. The depth of the haul was 55 m, and the local depth 60 m.

Movement: The practically identical morphology of these larvae and those of *Eucalanus pileatus* leads to the conclusion that both move in the same way. *E. pileatus* glides slowly forwards keeping the antennules stretched with the setae opened like a fan. The sensory setae are continuously moving, "feeling" the environment, and also maintaining the balance of the nauplius. The antennae and the mandibles vibrate forwards and backwards performing a "breast-stroke," which pushes the nauplius on, maintaining it in an almost vertical position in the water (Fig. 16). It can also jump forwards occasionally.

Food: Phytoplankton, as shown by the colour of the gut of the larvae.

Nauplius III (Fig. 10): 4 specimens examined, measuring 0.50, 0.53, 0.54 and 0.55 mm in length. Shape: fusiform, Labrum, with minute setae in several ventral rows and marginally. Lower lip, strongly setose. Labrum and lower lip protruding ventrally, and anterior rostral region produced into an anterior, triangular and ventral dilation. Caudal armature: 2 ventral, pre-terminal spines; a longer and a shorter balancer, and 2 sensory setae, on the right caudal lobe. Antennule (Fig. 11), 0 : 2 : 7 term. Antenna (Fig. 12): coxopod, 2mp (spiny); basipod, 2 (short); endopod, 1 : 3 + 4 term; exopod, 0 : 2 : 1 : 1 : 1 : 1 : 1 : 2 term. Mandible (Fig. 15): coxopod, 1; basipod, 3; endopod, 2-lobed, 4 : 6; exopod; 1 : 1 : 1 : 1 : 2 term.

Nauplius IV (Fig. 20): 8 specimens, 0.60 to 0.68 mm in length (two 0.66 and two 0.64 mm long). Body with two divisions. Shape fusiform, with the ventral, anterior triangular dilation more pronounced. Labrum almost square, hirsute on the posterior margin and parallel to it; inferior lip also hirsute. Caudal armature: 4 ventral,

preterminal spines, on the right, preceded by a thin row of minute spines, 2 sensory setae and two unequally long balancers on the right lobe of the caudal region. Antennule, 0 : 2 : 9. Antenna: coxopod, 2mp (spiny); basipod, 2 (short); endopod 1 : 3 + 4 term: exopod, 0 : 2 : 1 : 1 : 1 : 1 : 1 : 2. Mandible: coxopod, with a 3-toothed masticatory blade + 1; basipod, 4; endopod, 2-lobed, 4 + 6 + setules; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 1 : 2 term. Maxillule: 2 lobes, 2 + 2.

Nauplius V (Fig. 13): 4 specimens examined, 0.77 mm (2 specimens), 0.80 and 0.81 mm long. 3 segments visible in the body. Shape fusiform. Labrum almost square with rows of minute setae near to, and on the posterior margin. Minute setae delimiting the inferior lip. Caudal armature: 4 ventral, pre-terminal spines, preceded by 2 rows of minute spines placed laterally and anteriorly to the caudal region. One short spine to the left of the ventral spines. The right ventral lobe bears 2 sensory setae and 2 balancers in the caudal region. Antennules: 0 : 2 : 11. Antenna: coxopod, 2mp (spiny); basipod, 2; endopod, 1 (long) + 1 (short): 4 (5) + 4 (5) term; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 1 : 3. Mandible: coxopod, with a 5-toothed mandible blade + 1 + 1; basipod, 5; endopod, 4 + 6; exopod, 1 : 1 : 1 : 1 : 1 : 2. Maxillule: basipod; internal lobe, 4; external lobe, 4.

Nauplius VI (Fig. 14): 3 specimens examined, 0.95, 0.98 and 1.00 mm long. 4 or 5 segments visible. Shape fusiform, longer and slenderer than nauplius V. Labrum and inferior lip with rows of minute setae parallel to, and on the posterior margin. Caudal armature: 4 ventral spines; a row of minute spines delimiting the caudal area; 1 thin and short seta, laterally on each side; 2. sensory setae and 2 balancers on the right lobe. Antennule: 0 : 1 : 2 : 14 (16). Antenna: like the antenna of nauplius V. Mandible: like the mandible of nauplius V, with one seta less on the exopod. Maxillule: basipod; anterior lobe, 5; internal lobe, 2 + 5; external lobe, 4. Maxilla: 5 lobes, 2 : 1 : 1 : 2 : 1. Maxilliped, one lobe, 2. Leg I: internal lobe, 4-toothed; external lobe, 2-toothed. Leg II: internal lobe, 2-toothed; external lobe, 2-toothed.

Remarks: In Table 2 the setation and the size of the larvae of *Eucalanus crassus* are compared to those of *Rhincalanus cornutus*,

R. nasutus (GURNEY, 1934), *Eucalanus elongatus* (GIBBONS, 1936; JOHNSON, 1937), *E. attenuatus*, and *E. pileatus* (BJÖRNBERG, 1967). Data are added on the nauplius V of *E. attenuatus* (Fig. 18), and the nauplius VI of the same species is re-studied (Fig. 17). These data correct the observations previously made (BJÖRNBERG, 1967). Nauplius IV of *R. cornutus*, collected in Curaçao, is figured for the first time (Fig. 59).

***Eucalanus attenuatus* (Dana, 1849)**

(Figs. 17-18)

Material: Nauplius V of the sample collected at 29°57' S and 73°38' W during the "Mar Chile I" Expedition, in waters off Coquimbo, EAST PACIFIC. Nauplius VI, collected off CURAÇAO, 1963.

Nauplius V (Fig. 18): 0.79 mm long. Shape of the body fusiform. Anterior region, triangular. Labrum, rectangular. Caudal armature: 1 lateral, short seta on each caudal lobe, 1 very thick, short sensory seta and 1 more slender one, with one seta on the right and two on the left. Antennule, 0 : 2 : 10 + 1 (thin). Antenna: coxopod, 2mp (spiny); basipod, 2; endopod, 1 + 1 (very long): 4 + 5 (6); exopod, 3 : 1 : 1 : 1 : 1 : 2. Mandible: coxopod with 4-toothed mandibular blade; basipod, 5; endopod, 2 + 2 + 5; exopod, 1 : 1 : 1 : 1 : 1 : 1 (2). Maxillule: 3 lobes, 1 : 4 (5) + 3.

Note: Nauplius VI of *Eucalanus attenuatus* was described briefly in another publication (BJÖRNBERG, 1967); it is described with more detail in Table 2. The nauplius V of the same species is described for the first time here. It also has the anterior region triangular in outline, like nauplius VI, and the posterior region less asymmetrical than in the other *Eucalanus* larvae. It is also characterized by the thickness of the sensory seta (Fig. 18).

Rhincalanus cornutus (Dana, 1849)

(Fig. 59)

Material: Collected off CURAÇAO, from coastal water of high salinity in January and August, 1963. Nauplii III, IV, V, VI and young copepodids were present in the same sample.

Note: The living nauplius is transparent and reddish. Stage IV is figured completely for the first time. Details on the morphology of the various stages are given in Table 2. The data are taken from GURNEY (1934) and from the observation of the Curaçao material. Pigment is concentrated in the posterior region of the nauplius.

DISCUSSION OF THE LARVAL STAGES OF THE EUCALANIDAE

The nauplii of *Eucalanus crassus* differ from those of *E. pileatus* in that they are much larger. The adult *E. crassus* is also larger than the adult *E. pileatus*. The presence of very large nauplii called my attention to a sample, where besides the larvae, all the copepodids and female *E. crassus* occurred. Female *E. pileatus* are about 2.1 mm long, *E. crassus* is 2.9 to 3.3 mm long. *E. monachus* is also larger than *E. pileatus*, but does not occur off Brazil in the upper layers of the sea. The specimens which I had identified as *E. monachus* (BJÖRNBERG, 1963) were young *E. pileatus*. In the other samples collected in the same area on the same day but with a coarser meshed net, large numbers of adult *E. crassus* were found, but neither *E. pileatus* nor any other species of *Eucalanus*. In tropical and subtropical waters mature females occur along with all the developmental stages of the species. This also brings me to the conclusion that the *Eucalanus* larvae present in the region belonged to the mature species found there. *E. pileatus* is very numerous in waters off Brazil and Curaçao, but it is smaller than *E. crassus*; the larva is consequently also smaller, and slightly different from the one described here (see Table 2).

Several corrections of the description of nauplius VI of *Eucalanus pileatus* (BJÖRNBERG, 1967) appear in Table 2. The description of *R. cornutus* based on Curaçao material confirms GURNEY's (1934)

data. The number of setae on the appendages of the larvae of *E. pileatus* is usually the same as or larger than in *E. crassus*.

If the nauplii of the Eucalanidae are compared (see Table 2), the following can be noted:

- 1) the nauplii of *Eucalanus elongatus* and *Rhincalanus* have lateral spines (s) in the posterior region and two terminal spines (s term) like the larvae of the Calanidae, Paracalanidae, Pontellidae, and others;
- 2) the nauplii of *E. attenuatus*, *E. pileatus*, *E. crassus* do not have posterior terminal lateral spines (the spines are restricted to the ventral pre-terminal region);
- 3) there is a tendency to specialization of the anterior region in larvae which have lateral cephalic protuberances at the height of the antennule's articulations (*Rhincalanus*), or have a pointed forward prolongation in the cephalic region (*E. attenuatus*);
- 4) there is a tendency to the lengthening of the nauplii (*Rhincalanus*, *E. attenuatus*, *E. elongatus*);
- 5) *Rhincalanus* is further differentiated by the antenna, which has a masticatory blade resulting from the fusion of the 2 masticatory spines usually present in the coxopod of the antennae of the Calanidae, and in the strong asymmetry of the terminal posterior spines;
- 6) the nauplii of *E. crassus* and *E. pileatus* differ from the other *Eucalanus* larvae in having a rounded body and caudal region, and the asymmetry of the caudal armature is accentuated as in *Rhincalanus*;
- 7) the nauplii of *E. attenuatus* and *E. elongatus* have a less asymmetrical caudal armature.

Two hypotheses to explain these facts are possible:

- a) That *Eucalanus elongatus* is the most primitive form of Eucalanidae, because it has a less asymmetrical nauplius, which is most similar to the calanid larvae. From *E. elongatus* two evolutionary trends lead to:
 - a) *Rhincalanus*, with nauplii which have not lost the posterior terminal spines, with terminal spines which became setose and asymmetrical, and with fused spines of the antennal coxopod forming a scythe-like blade (Fig. 59) very similar to that of the Harpacticoida;
 - b) the *Eucalanus attenuatus* group with nauplii in which the termi-

nal spines lose their setose and spiny characteristics, and are asymmetrically inserted in the posterior right lobe. *E. attenuatus* would be the basis of this trend of evolution because its larva is elongate, like that of *E. elongatus*, instead of more rounded, and the asymmetry of the terminal setae is less pronounced than in the nauplii of *E. pileatus* and *E. crassus*.

2) That *Eucalanus elongatus* and the species of *Rhincalanus* belong to the Eucalanidae directly related to the Calanidae, and the *Eucalanus attenuatus* group of species is related rather to the Pseudodiaptomidae than to the Calanidae because of the absence of lateral terminal spines, the very strong asymmetry of the nauplius, and the different type of locomotion.

Family PARACALANIDAE

Paracalanus crassirostris F. Dahl, 1894

(Fig. 21–32)

Material: Nauplii I and II, reared in Ubatuba, BRAZIL. Remaining stages taken at Piscadera Inner Bay, CURAÇAO, or near to the marine station at Ubatuba, and in Santos bay, near the beach.

Colour: Transparent body with orange pigment near the digestive tube anteriorly and strongly concentrated in the caudal region.

Nauplius I (Fig. 21): 3 specimens examined, 0.06, 0.07 and 0.08 mm long. Shape: oval or rounded, when alive; pear-shaped, plump, when fixed. Labrum: oval, very large in relation to the size of the nauplius. Segmentation indistinct. Caudal armature: 2 short filaments. Antennule, 0 : 0 (3?) : 3. Antenna: basipod and coxopod partly fused, 1 + 1 mp; endopod, 2; exopod, 5. Mandible: coxopod; basipod, 1s; endopod, 2; exopod, (6) 2.

Nauplius II (Fig. 23): 1 specimen examined, 0.09 mm long. Shape: pear-shaped and bent like a hook or comma, plump, wider anteriorly, posteriorly rounded. Labrum, oval. Caudal armature: 2 filaments as long as the mandibles. Segmentation of the appendages, indistinct. Antennule, 0 : 3 : 4. Antenna, coxopod, 1 mp; basipod, 1s; endopod, 3; exopod, 1 : 1 : 3. Mandible, coxopod, 1; basipod, 1; endopod, 4; exopod, 1 : 1 : 1 : 2.

Nauplius III (Fig. 24): Length 0.11 and 0.13 mm, with caudal spines included. Hook or comma-shaped. Labrum, oval. Caudal armature: 2 ventral serrate spines; 2 terminal serrate spines; 2 sensory setae; minute spines on the lateral margins. Antennule, 0 : 3 : 7. Antenna: coxopod, 2mp; basipod, 2; endopod, 1 : 1 + 3 term; exopod, 2 : 1 : 1 : 1 : 1 : 3 term. Mandible: coxopod, 1; basipod, 3; endopod, 4 + 2 + 4; exopod, 1 : 1 : 1 : 3.

Nauplius IV: 4 specimens examined, 0.14, 0.16, 0.16 and 0.17 mm long. Shape: pear-shaped, slender, bent like a hook, wider anteriorly and tapering towards the caudal region. Labrum: oval. Caudal armature (Fig. 25): 3 spines on each lateral posterior margin, with minute spines in between; 4 posterior, pre-terminal, ventral spines; 2 terminal posterior spines; 2 sensory setae. Segmentation much more distinct. Antennule: 0 : 3 : 11. Antenna: coxopod, 1s; basipod, 1; endopod, 1 + 3; exopod, 2 : 1 : 1 : 1 : 3. Mandible: coxopod with 3-toothed blade; basipod, 4; endopod, 9; exopod, 1 : 1 : 3.

Nauplius V (Fig. 28): Lengths of specimens examined 0.18–0.19 mm. Shape: pear-shaped, bent like a hook. Labrum, oval. Caudal armature (Fig. 27): 6s (lateral); minute lateral spines; 4 pre-terminal, ventral spines; 2 terminal posterior spines; 2 sensory setae. 3 distinct segments (ventral view). Antennule: 0 : 3 : 13. Antenna: coxopod, 2s + 1; basipod, 2; endopod, 2 : 3 + 3; exopod, 3 : 1 : 1 : 1 : 1 : 2 + 1. Mandible (Fig. 31): coxopod, with 2-toothed blade; basipod, 4; endopod, 5 + 5; exopod, 1 : 1 : 1 : 2. Maxillule (Fig. 30), 2 : 2 + 2 + 3 : 5.

Nauplius VI (Fig. 29): Length of specimens examined 0.18, 0.20 and 0.21 mm. Shape of an inverted cone, with caudal region much longer relative to the remaining body than in nauplius V. 6 or 7 segments visible ventrally. Labrum, oval. Inferior lip, protuberant. Caudal armature: setation, spines and feelers as in nauplius V. Antennule, 0 : 3 : 13. Antenna: coxopod, 2s + 1; basipod, 2; endopod, 2 : 3 + 4; exopod, 3 : 1 : 1 : 1 : 1 : 2. Mandible (Fig. 32): coxopod, 2-toothed mandibular blade; basipod, 4; endopod, 4 + 6; exopod, 1 : 1 : 1 : 2. Maxillule (Fig. 22): 3 lobes, digital protuberance: 6 : 5 (6).

Movement: The nauplius swims by active successive strokes of the antennules, antennae and mandibles, as if running a short distance, caudal region down, naupliar eye up. Sometimes it turns a somersault, then it runs a short distance again in a straight line, it stops, it runs again, turns a somersault, etc.

Paracalanus aculeatus Giesbrecht, 1892

(Figs. 54–55, 57)

Material: From plankton samples collected over the continental shelf off Santos, BRAZIL.

Habitat: *Paracalanus crassirostris* is very numerous in coastal and inshore waters, off Brazil and Curaçao. In samples taken over the continental shelf off Santos, in salinities between 34.00‰ and 35.00‰ there were three different series of nauplius of *Paracalanus*: the very small nauplius of *P. crassirostris*; the medium sized nauplii of *P. parvus*; and the larger nauplii tentatively ascribed to *P. aculeatus*, the remaining species of *Paracalanus* occurring in the area. *P. aculeatus* and *P. crassirostris* also occur in large numbers off Curaçao in very saline waters. They are circum-tropical and circum-subtropical species. When adult they are correspondingly larger than the larvae: *P. crassirostris* is about 0.5 mm long, *P. parvus* between 0.75 and 1.10 mm; and *P. aculeatus* about 1.20 mm long. This species also lives in oceanic waters, in salinities between 35.00‰ and 37.00‰. The nauplii may occur in salinities in which the adults do not thrive.

Nauplius IV: Length 0.21 mm. Pear-shaped, bent like a hook. Labrum oval. Caudal armature (Fig. 55): 6s (lateral), ms (lateral), 4s (ventral, pre-terminal), 2 feelers, 2s term. Antennule, 0 : 3 : 11. Antenna: coxopod, 2s; basipod, 2; endopod, 2 : 2 + 3; exopod, 6 segments, 10. Mandible: coxopod, mandible blade, 2 teeth; basipod, 4; endopod, 8; exopod, 1 : 1 : 1 : 2. Maxillule: not observed.

Nauplius V (Fig. 57): Length, 0.22 mm. Pear-shaped. Labrum oval. Caudal armature: 6s (lateral), ms (lateral), 4s (ventral, pre-terminal), 2 sensory setae, 2s term. Antennule: 0 : 3 : 14. Antenna: coxopod, 2s; basipod, 2; endopod 2 : 2 + 3; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 1 : 2. Mandible: coxopod, with mandible blade, 2-toothed; basipod, 4; endopod, 9; exopod, 1 : 1 : 1 : 2. Maxillule: 3-lobed, 1 : 6 : 5.

Discussion: One of the first planktonic, marine nauplii described was that of *Paracalanus parvus* Claus. The Paracalanidae nauplii are so much alike that the only distinctive characteristic is

size. The nauplii of *P. crassirostris* are 0.06 to 0.08 mm long in stage I, 0.17 mm in stage IV and 0.18 to 0.21 mm in stage VI. Nauplius I of *P. parvus* is 0.09 mm long, nauplius IV is 0.21 mm and nauplius VI is 0.25 mm long. *P. aculeatus* (Fig. 57) is 0.21 mm or more in stage IV and 0.31 to 0.33 mm in the larval stage VI.

Family CALOCALANIDAE

Calocalanus pavo (Dana, 1849)

(Figs. 33–34, 36–37)

Material: From fixed plankton samples collected in Piscadera Bay, CURAÇAO. The metamorphosis of the nauplius VI into the first copepodid of *C. pavo* was observed at the Caraïbisch Marien-Biologisch Instituut.

Habitat: *Calocalanus pavo* is frequent and numerous in warm waters (temperature above 17°C), with high salinity (above 36‰). It is therefore very common in waters of the Brazil Current and off Curaçao, Colombia, Peru and north of Chile. Its nauplii were frequently present in Curaçao waters, but not in inshore waters.

Nauplius IV (Fig. 36): Length 0.17 and 0.19 mm. Body long, dilated anteriorly, hook-shaped. Labrum oval, long. Caudal armature: 4 long ventral serrate spines, 2 long terminal, serrate spines, 2 lateral small spines on each side, 2 sensory setae, very minute spines along the lateral margins. Antennule, 0 : 3 : 11. Antenna: coxopod, 2mp; basipod, 2 + 1mp; endopod, 2 : 3 (4) + 4; exopod, 1 : 1 : 1 : 1 : 1 : 3 (2). Mandible: coxopod, mandible blade, 2-toothed; basipod, 4 (3); endopod, 8; exopod, 1 : 1 : 2. Maxillule: 3 lobes, 3 : 3.

Nauplius V (Fig. 33): Length 0.21 and 0.20 mm. Body pear-shaped, 4-segmented, bent hook-like. Labrum, oval. Caudal armature a row of 4 ventral, serrate spines; two very long, serrate spines lateral to the ventral row, one on each side; 2 lateral smaller spines on each side; 2 terminal, long spines; 2 sensory setae; numerous minute spines on the margins. Antennule, 0 : 3 : 15 (14). Antenna: coxopod, 2mp; basipod 2; endopod, 1 (2) : 4 + 4; exopod, 1 : 1 : 1 : 1 : 1 : 3. Mandible: coxopod, mandible-blade, 2-toothed +

1; basipod, 4; endopod, 9; exopod, 1 : 1 : 1 : 2. Maxillule: 3 lobes, 2 : 7 : 5.

Nauplius VI (Fig. 37): Length 0.22 mm. Body fusiform, 4-segmented. Labrum oval. Caudal armature (Fig. 37): a row of 4 ventral spines, 2 terminal spines, 2 long lateral spines (one on each side), 2 small lateral spines on each side and many minute spines; 2 sensory setae. Antennule, 0 : 3 : 14. Antenna: coxopod, 2mp; basipod 2; endopod, 2 : 4 + 4; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 3. Mandible: coxopod, 2-toothed mandible-blade + 1; basipod, 4; endopod, 9; exopod, 1 : 1 : 1 : 2. Maxillule: 3 : 1 : 1 : 1 + 3 : 5. Maxilla: 5 lobes (Fig. 34). Maxilliped: 1. First leg: 2 lobes, 2 : 2 + 2s. Second leg: 2 lobes, 2 : 4s.

***Calocalanus styliremis* Giesbrecht, 1888**

(Figs. 35, 38–39)

Material: Nauplii collected with a very fine net at Ubatuba, BRAZIL, and reared in the Instituto Oceanográfico.

Habitat: *Calocalanus styliremis* is frequent in coastal and shelf waters off Brazil, Chile and Curaçao. It is a circum-tropical and a sub-tropical species. The nauplii are quite abundant in coastal waters.

Movement: Locomotion of this nauplius is very similar to that of the *Paracalanus crassirostris* nauplii, but it seems to somersault less often.

Nauplius IV: Length 0.16 mm. Shape of the body, labrum, setation of the appendages similar to nauplius IV of *C. pavo*. Colour: orange in the caudal region and in appendages other than the antennules. It differs only in the caudal armature (Fig. 39) and in the setation of the mandibular palp (Fig. 35). This has 3 setae on the basipod instead of 4, and 10 setae on the endopod. The caudal armature lacks two longer lateral spines: there are on each lateral margin 3 small equally long teeth, with minute spines in between. The terminal caudal spines are not as long as in *C. pavo*.

Nauplius VI: Length 0.21 mm. Although smaller, this larva has the same setation as the nauplius VI of *C. pavo* except in the caudal armature. There are 3 small, caudal lateral spines on each

side, and minute spines in between; 2 sensory setae; 2 terminal dorsal spines; 4 ventral, almost terminal, caudal spines (Fig. 38). The last pairs of appendages, maxillules, maxillae, etc., are difficult to see because of the opacity and small size of the nauplius.

Discussion: The nauplii of the Calocalanidae differ considerably from the nauplii of the Paracalanidae and Pseudocalanidae, in that the posterior part of the body tapers towards the caudal spines, and thus has a fusiform aspect. In the setation and other characteristics it is very much like the nauplii of the other two families.

Family PSEUDOCALANIDAE

Clausocalanus furcatus (Brady, 1883)

(Figs. 40-49)

Material: Nauplii I, II and III reared in the Instituto Oceanográfico at Ubatuba, BRAZIL, and at the Caribbean Marine Biological Institute at Piscadera Bay, CURAÇAO. Remaining nauplii taken from fixed plankton samples, collected at Piscadera Bay and off Brazil. Nauplius II was lost after fixation. Probably a stage of short duration, it was not found in other culture dishes.

Habitat: *Clausocalanus furcatus* is usually the most abundant copepod in warm shelf and oceanic tropical and sub-tropical waters off Brazil, off Colombia, Peru and Chile. Off Curaçao, Piscadera Bay, it was found in 83 of the 114 samples taken during summer and winter of 1963 over the shelf and over deep waters. The nauplii were present during the day and, less frequently at night, in waters over the shelf and in offshore waters. The adults and copepodids were not always present during the day.

Movement: *Clausocalanus* nauplii move forwards by turning successive somersaults. The very short posterior region of the body and the absence of balancers does not favour the employment of any other type of locomotion. This movement I consider primitive in relation to the gliding and to the paddle-stroke movements, without rotation around a transversal axis, of the other Calanoida. In the movement by somersaults the body is maintained in a plane vertical to the surface of the sea (Fig. 47, 49).

Nauplius I (Fig. 40): Length 0.11 mm. Colour: pigment spots in the anterior region and rest of the body transparent. Oval or round shape. Labrum, oval, crenulate margin. Caudal armature: 2 spines. Antennule, 0 : 0 : 3. Antenna (Fig. 42): coxopod fused to

basipod, 2; endopod, 2; exopod, 5. Mandible (Fig. 41): coxopod; basipod; endopod, 3; exopod, 4 (3).

Nauplius III (Fig. 43): Length 0.13 mm (Santos) and 0.19 mm (Curaçao). Pear-shaped like the *Paracalanus* and the calanid nauplii; bent like a hook. Labrum, oval; crenulate posterior margin. Caudal armature: 2 ventral serrate spines; 2 terminal serrate spines; 2 sensory setae; lateral margins with minute spines. Antennule, 0 : 3 : 7. Antenna: coxopod, 2 mp; basipod, 1 + 2; endopod, 0 : 3 + 3 term; exopod, 3 : 1 : 1 : 1 : 2. Mandible: coxopod, 1; basipod, 2; endopod, 1 large setose spine + 6; exopod, 1 : 1 : 1 : 2.

Nauplius IV (Fig. 45): Length 0.18 and 0.17 mm (Santos). Pear-shaped, hook-like. Labrum oval. Caudal armature: 4 ventral serrate spines; 2 terminal, serrate spines; 2 sensory setae; 3 lateral spines on each side and many minute spines, in between, on the lateral regions. Antennule, 0 : 3 : 11 (12). Antenna: coxopod, 2 mp; basipod, 1 mp + 2; endopod, 0 : 3 + 4 (3); exopod, 2 : 1 : 1 : 2 (3). Mandible: coxopod, 2-toothed mandible blade + 1; basipod, 5; endopod, 9; exopod, 1 (2) : 1 : 1 : 2. Maxillules, 2 or 3 lobes, 1 : 3 + 3 : 4, or 1 + 5 : 3.

Nauplius V (Fig. 49): Length 0.20, and 0.21 mm (Santos). Pear-shaped, hook-like. Labrum oval. Caudal armature, 4 ventral, serrate spines; 2 terminal, serrate spines; 2 sensory setae; 3 lateral spines on each side, and many minute spines in between on the lateral margins. Antennule, 0 : 3 : 13. Antennae (Fig. 44): coxopod 2 mp; basipod, 1 mp + 2; endopod, 1 : 4 + 4; exopod, 3 : 1 : 1 : 1 : 1 : 2. Mandible: coxopod, 2-toothed mandible-blade (+ 1); basipod, 5; endopod, 3 + 2 + 4; exopod, 1 : 1 : 1 : 2. Maxillule (Fig. 46), 3 (2) : 7 : 4 (5).

Discussion: It is difficult to distinguish between the nauplii of *Paracalanus*, *Clausocalanus*, *Calocalanus* and *Pseudocalanus*. In the shape, behaviour, and size there are minute differences, but the setation and the caudal armature of the four genera are practically alike (see Table 3). The larger calanid nauplii also have setation and shape similar to the Paracalanidae, Calocalanidae and Pseudocalanidae; also the behaviour of all these nauplii is very much the same.

Ctenocalanus vanus Giesbrecht, 1888

(Figs. 50–53, 56)

Material: From fixed samples collected off Santos and off the other parts of the south coast of BRAZIL.

Nauplius III (Fig. 50): Length 0.20 and 0.21 mm, caudal setae included. Body, pear-shaped, bent like a hook, 2-segmented. Labrum, oval. Caudal armature (Fig. 52): 2 long ventral serrate spines; 2 terminal, long, serrate spines; 2 sensory setae; 1 small spine lateral to each of the terminal spines, and a series of minute spines laterally. Antennule (Fig. 53), 0 : 3 : 7. Antenna: coxopod, 2 mp; basipod, 2; endopod, 2 (3) + 3; exopod, 2 : 1 : 1 : 1 : 1 : 1 (2). Mandible: coxopod; basipod, 3 (4); endopod, 4 + 5; exopod, 1 : 1 : 1 : 2.

Nauplius IV (Fig. 51): Length 0.24 mm. Body pear-shaped, bent hook-like, 2-segmented. Labrum oval, margin smooth. Caudal armature: a row of 4 ventral serrate spines; 2 terminal long, serrate spines; 2 sensory setae; 2 serrate spines on the lateral posterior region, on each side; a row of minute spines on the lateral margins. Antennule: 0 : 3 : 11. Antenna: coxopod, 2 mp + 1; basipod, 1 mp + 2; endopod, 2 : 3 + 3; exopod, 2 : 1 : 1 : 1 : 2 (1). Mandible: coxopod, mandibular blade 2-toothed; basipod, 4 (3); endopod, 9 (7); exopod, 1 : 1 : 1 : 2. Maxillule: 2 lobes, 4 : 4.

Nauplius V (Fig. 56): Length 0.25 mm. Body, pear-shaped, bent like a hook, 3-segmented. Labrum, oval. Caudal armature: a row of 4 ventral spines, 2 terminal spines; 2 sensory setae; 3 smaller, lateral spines on each side; several rows of minute spines near to the lateral margins and laterally to the base of the larger spines. Antennule, 0 : 3 : 13 (12). Antenna: coxopod, 2 mp; basipod, 1 mp + 2; endopod, 2 : 3 + 4; exopod, 1 : 1 : 1 : 1 : 1 : 1 (2). Mandible: coxopod, 3-toothed mandible blade; basipod, 4; endopod, 4 + 4 (5); exopod, 1 : 1 : 1 : 2. Maxillule: 3 lobes, 1 : 8 (11) : 5 (6).

Discussion: These nauplii are tentatively ascribed to *Ctenocalanus vanus* as they were the only unknown nauplii of the Pseudocalanidae which appeared frequently in colder (below 17°C) shelf waters or coastal waters where this species is the most numerous.

Clausocalanus arcuicornis "sensu latu" is the other species large enough to produce this nauplius, but it occurs rarely in the coastal and shelf waters off southern Brazil. The sample from which the nauplii were taken contained all the copepodids and adults of *Ctenocalanus vanus*.

GENERAL CONSIDERATIONS ON THE NAUPLII OF CALANIDAE,
EUCALANIDAE, PARACALANIDAE, CALOCALANIDAE
AND PSEUDOCALANIDAE

OBERG (1906) observed a great similarity in the morphology of the nauplii of Calanidae, Paracalanidae and Pseudocalanidae. Based on the morphology of the nauplii, I conclude that the Paracalanidae and Pseudocalanidae are more closely related than are the Paracalanidae and Calocalanidae. It seems to be a general rule for nauplii of Calanoida that the lengthening of their bodies is always accompanied by a lengthening of the caudal spines (see the nauplii of the Pontelliidae, of *Temora*, of *Pseudodiaptomus*). In the Calocalanidae a lengthening of the posterior body region and of the caudal setae is the most characteristic trait, but the nauplius does not lose its symmetry. The nauplii of the Eucalanidae are asymmetrical. If we compare the morphology of the larvae of the Calanidae, Paracalanidae and Eucalanidae (Tables 1, 2 and 3), the Eucalanidae diverge most strongly from the Calanidae.

Besides the morphological likeness there is also a similarity of locomotion in the nauplii of the Calanidae, Paracalanidae, Pseudocalanidae and Calocalanidae. The last mentioned were the only ones observed to move for a longer time without somersaulting. This can be explained by the posterior lengthening of their body with a consequently better balance (the long caudal region acts like a keel). The separation of the Calocalanidae from the Paracalanidae (BERNARD, 1960) is thus justified by the morphology and the physiology of the nauplii.

The nauplii of the Eucalanidae never somersault. They are thus, morphologically and physiologically, very different when compared to the nauplii of the other four families.

Family AETIDEIDAE

Material: Nauplii collected with a closing-net, from the "M. Lomonosov" during the twelfth cruise to the SOUTH ATLANTIC OCEAN from depths between 100 and 300 m and from 300 to 1000 m at 12°44' S–36°36' W, in layers between 300 and 1000 m depth at 14°00' S–35°01' W, from depths between 300 and 500 m at 16°00' S–32°19' W.

Habitat: The layers of water sampled between 200 and 500 or 800 m were from the Subtropical Water mass with salinity 35.00‰–36.00‰ and temperature 10–20°C. Waters from depths between 500 and 1000 m were from the Intermediate Antarctic Water mass, with salinity below 34.55‰ and temperature below 10°C (for nomenclature of water masses see SVERDRUP *et al.* 1954).

Last naupliar stage: Large oval form. Length 0.70, 0.75, and 0.87 mm. Antennule with 12 setae on the last segment. Antenna with 8 or 9 setae on the exopod and 4 setae on the endopod. Mandible with 5 setae on the exopod and 4 on the endopod. Antennal endopod with two segments. Caudal setae broken off.

Discussion: MATTHEWS (1964) reared *Chiridius armatus* (Boeck, 1872) in the laboratory, the nauplius of an aetideid. Nauplii with the globular form of the *Chiridius* nauplii as described by MATTHEWS were found in the "Lomonosov" samples. The first nauplius lacks posterior filaments. The other naupliar stages have 2 caudal filaments. Segmentation of the appendages is badly outlined. The antennae of the first nauplius of these copepods have 5 to 6 plumose setae on the exopod, and this number increases to 6 or 7 in nauplius IV (MATTHEWS, 1964). The endopod has 3 or 4 setae, and is divided into 2 segments. The antennule has three segments, of which the middle segment has 2 or 3 setae at all naupliar stages and successively 3, 4, 9 and 14 setae, in the first, second, third and fourth nauplii respectively. The mandible has 6 or 5 setae on the exopod, 2 or 4 terminal setae on the endopod, and 2 or less lateral setae. A spine can be present on the basipod. MATTHEWS observed a reduction in the number of naupliar stages in *Chiridius*. Probably because of the short season during which the water is warmer, the animal has a shortened development in the depth of the fjords where it thrives. The nauplii lack a mouth and are therefore lecitotrophic.

Several Aetideidae occur in deep waters such as those sampled by the "M. Lomonosov," *Chiridius poppei* Giesbrecht, *Euaetideus acutus* Farran, *E. giesbrechti* Cleve, *Euchirella venusta* Sars, *E. brevis* Sars, *Gaetanus kruppi* Giesbrecht, *G. miles* Giesbrecht, *G. minor* Farran, *Gaidius tenuispinus* (Sars). Rearing experiments should be made to find out to which of these species the nauplii belong.

Family EUCHAETIDAE

(Fig. 60)

Material: Nauplii obtained through rearing in slowly circulating sea water at the Carmabi, from an egg-carrying female *Euchaeta marina*, collected in the outer Piscadera Bay, CURAÇAO, during the day from 30 m. Fixed nauplii collected from the "M. Lomonosov," off BRAZIL.

Habitat: They do not need food and thus can live at great depths in the ocean. The occurrence of Aetideidae, Phaennidae and Euchaetidae in great numbers at depths below 500 m (BJÖRNBERG, 1965b) in Intermediate Antarctic Water can be partly explained by the fact that their nauplii are lecithotrophic, and thus live on the yolk which they carry during their naupliar life.

Movements: The living nauplii of *Euchaeta marina* seemed not to be able to swim. They lay wriggling on their backs at the bottom of the rearing dish. It is probable that the other lecithotrophic nauplii behave in the same way. Twelve hours after placing eggs of *Euchaeta* in waters with temperature above 20°C, I found nauplii in stage V. BERNARD (1965a) obtained first copepodids from the egg after 96 hours at 16.5°C. It seems therefore that this nauplius does not need to swim. Once out of its egg envelopes it will sink slowly in the waters, or will float in them, thanks to its long posterior filaments and to the yolk globule. As it sinks the nauplius probably passes through the different naupliar stages, and metamorphoses before reaching the bottom. *Euchaeta marina* is a characteristic copepod of [the upper layers of oceanic water. Near to the coast its nauplius would probably reach the bottom before metamorphosis, and could be eaten by the benthos.

Light: When kept in the dark for some time, the *Euchaeta marina* nauplius expands the chromatophores distributed in a ring around the terminal posterior area, and the large chromatophore situated dorsally to the yolk globule. A rose coloured ring appears around the posterior region of the nauplius and, less evident, a large X or Y, also rose coloured, shows in the posterior half of the body. Placed under bright light, these chromatophores contract and the nauplius becomes totally transparent (Fig. 60).

Nauplius I: Size 0.30 and 0.34 mm. Shape round, laden with yolk, without mouth, and no caudal armature. Antennule, 0 : 0 :

2 + 1 (short). Antenna: coxopod and basipod fused; endopod, 2; exopod, 5. Mandible: coxopod and basipod fused; endopod, 3; exopod, 3.

Nauplius VI: Size 0.57 mm. Shape oval, laden with yolk, no mouth. Caudal armature: 2 filaments (the left thin, the right thick), 2 short and thick sensory setae, 1 little spine on the right, and 2 on the left. Antennule, 0 : ms + 1 : 7 + 1. Antenna: coxopod; basipod; endopod, 3; exopod, 6. Mandible: coxopod and basipod fused; endopod, 3; exopod, 5. Of the remaining appendages, only maxillipeds well defined, with 1 spine and 1 seta.

Nauplius VI: Size 0.75, 0.70, 0.60 mm. Shape oval, laden with yolk, and no mouth. Caudal armature: 6 filaments. Antennule, 0 : 0 : 7(8). Antenna: coxopod fused to basipod; endopod, 3; exopod, 8. Mandible: coxopod and basipod fused; endopod, 2 or 3; exopod, 4 or 5. Maxillule, maxilla visible or not, maxillipeds and legs I and II outlined.

Nauplius VI: Size 0.90 mm. Shape oval, slightly tapering on the caudal region, no mouth, laden with yolk. Caudal armature: 2 filaments? Antennule, 0 : 0 : 8. Antenna: coxopod fused with basipod; endopod, 3; exopod, 8. Mandible: coxopod and basipod fused, 1; endopod, 1 + 3; exopod, 5. Maxillule, maxilla, maxillipeds, legs I and II, outlined.

Other naupliar stages: All oval shaped, laden with yolk, no mouth.

Nauplius A: 0.37 mm long. Antennule, 0 : 0 : 5. Antenna: endopod, 2; exopod, 6; other segments fused. Mandible: endopod, 3; exopod, 5; other segments fused. Caudal armature, 2?

Nauplius B: 0.45 mm long. Antennule, 0 : 0 : 3. Antenna: endopod, 3; exopod, 5; other segments fused. Mandible: endopod, 3; exopod, 5, and other segments fused. Caudal armature, 2.

Nauplius C: 0.52 mm long. Antennule, 0 : 1 : 3. Antenna: endopod, 3; exopod, 5; other segments fused. Mandible: endopod, 3; exopod, 5; other segments fused. Caudal armature, 2.

Nauplius D: 0.52, 0.54, 0.55, and 0.57 mm long. Antennule, 0 : 0 : 3. Antenna: endopod, 3; exopod, 5; other segments fused. Mandible: endopod, 3; exopod, 5; other segments fused. Caudal armature, 2.

Nauplius E: 0.60 mm long. Antennule, 0 : 0 : 3 + 2ms. Antenna: endopod, 3; exopod, 6, and other segments fused. Mandible: endopod, 3; exopod, 4, and other segments fused. Caudal armature, 2.

Though there is little variation in the setation of these nauplii, they do not belong to the same series, and therefore, species.

The nauplii of *Euchaeta marina* Prest. 1933, which occurred in CURAÇAO and off BRAZIL, have already been described by BERNARD (1965a).

Discussion: The nauplius of *Euchaeta* has kept its embryonic characteristics, according to HANAOKA (1952). The antennae with fused coxopod and basipod, with simple endopod and exopod, do not have masticatory spines because the nauplius does not need them to take food. The mandibles of *Euchaeta marina* show a rudimentary mandibular blade only in the last naupliar stage. NICHOLLS (1934) reared the naupliar stages of *Paraeuchaeta norvegica* (Boeck, 1872). Later BERNARD (1965b) and KOGA (1960a) obtained the nauplii respectively of *Euchaeta marina* and *Paraeuchaeta russelli*. The nauplii of the "M. Lomonosov" collection differ in external morphology from those of *E. marina*, which are 0.30 to 0.56 mm long (BERNARD, 1965a). The nauplii here described were 0.35 to 0.90 mm in length, and probably belong to several different species. As the Phaennidae nauplius, reared by MATTHEWS (1964), also has the general features of an *Euchaeta* nauplius, it is possible that some of these nauplii are Phaennidae instead of Euchaetidae.

Family TEMORIDAE

(Figs. 58, 61-62)

Material: *Temora stylifera* nauplii from water off Ubatuba (BRAZIL) and off CURAÇAO. *T. turbinata* nauplii collected in Piscadera's inner bay (CURAÇAO).

Habitat: *Temora stylifera* nauplii occurred in small numbers and rarely in inshore waters or waters near to the pier in Ubatuba and in Curaçao. They were frequent and abundant in shelf waters off Santos and in coastal waters under the influence of shelf waters like those of São Sebastião (Institute of Marine Biology of the University of São Paulo). *T. turbinata* was very abundant in the Piscadera inner

bay, and very frequent, though less abundant in the Piscadera outer bay. Both waters are of high salinity, more than 36.00‰. In the inner bay the temperature was above 25°C.

Classification: *T. turbinata* nauplii are not as wide anteriorly as those of *T. stylifera*. The posterior terminal spines are asymmetric in *T. turbinata* and almost symmetrical in *T. stylifera* (Fig. 61). In *T. turbinata* the right terminal spine is almost double the size of the left in the caudal armature (Fig. 62).

Discussion: *Temora stylifera* (Dana, 1848) and *Temora turbinata* (Dana, 1852) were present in the samples collected off Brazil and Curaçao respectively. The nauplii of the first were described by GAUDY (1961), those of the second in a work to be published (BJÖRNBERG & SOARES MOREIRA). *Temora* and *Eurytemora* have a nauplius with a round anterior outline which tapers towards the posterior region. They have the form of an inverted drop (Figs. 58, 61–62). The antennules, antennae and mandibles are very much like the appendages of the Calanidae and Paracalanidae. There are more setae in the terminal segment of the antennule and, besides the long setae, there are minute marginal setae. The dorsal shield is practically circular in *Temora stylifera*, and, when alive, rose or orange coloured along the margin. There is a posterior asymmetry and a tendency to a lengthening of the spiny balancers. From stage IV onwards, there are two rows of ventral spines, unlike the Calanidae and the Paracalanidae with only one row. This feature is common to the *Temora* nauplii described up to now. The type of the setae of the posterior region of these larvae indicate that they are related to the nauplii of the Centropagidae, Pontellidae and Pseudodiaptomidae.

Family METRIDIIDAE

(Figs. 67–75)

Material: Fixed nauplii from samples collected during the "M. Lomonosov", XIIth cruise to the South Atlantic, off the northeast coast of BRAZIL.

Habitat: Nauplii IV–VI were present in all the samples of the "M. Lomonosov" except two samples from the surface, taken from 0 to 25 m and from 0 to 100 m.

They are found in layers from 0 to more than 500 m. The nauplii have therefore a wider distribution than the adults. They occurred in Tropical, Subtropical, and Antarctic Intermediate Waters, off the Northeast coast of Brazil.

Nauplius IV (Fig. 70): Length 0.47–0.37 mm. Antennule: 0 : 3 : 9(10). Antenna: coxopod, 2mp + 2; basipod, 1s + 2; endopod, 1s(0) : 3 + 4; exopod, 2(1) : 1 : 1 : 1 : 1 : 1 : 2(1). Mandible: coxopod, with mandibular blade + 1; basipod, 4; endopod, 8(11); a protuberance between endopod and exopod; exopod, 6(5). Maxillule: 2-lobed, 4 : 3. Caudal armature: 2 terminal, ventral spines, 2 latero-dorsal terminal spines, minute setae in a row between the two pairs, 1 lateral spine on each side with minute setae; 4 ventral spines on a protuberance, like an apron, with smaller spines in between; another row of minute setae, anterior to, and lateral, on each side; another row of small lateral setules, on each side, more or less at the same height as the lateral large spines. The labrum is small and oval. The inferior lip is square in outline.

Nauplius V (Fig. 69): Length 0.52–0.45 mm, terminal setae excluded. Antennule (Fig. 71), 0 : 3 : 13(14) + 5 small spines. Antenna (Fig. 67): coxopod, 2mp; basipod, 1s + 2; endopod, 1s + 2 : 3 + 5 term + setules; exopod, 1 + 1 : 1 : 1 : 1 : 1 : 1 : 3. Mandible (Fig. 68): coxopod with mandibular blade, a seta, one larger tooth, and several thin, long teeth (Fig. 75); basipod, 4; endopod, 11; exopod, 2 : 1 : 1 : 2. Maxillule (Fig. 73): 3-lobed, 2 : 9 : 5(6). Caudal armature (Fig. 72): laterally 3 horizontal rows of minute spines, the second and the third with one larger lateral spine; ventrally, 4 very large spines, several small spines in between; terminally, 4 large spines, and small spines between the central pair and the large lateral spines.

Nauplius VI (Fig. 74): Length 0.52 mm. The same morphology as stage V, with added rudiments of the maxillae, laterally to the maxillules, rudiments of the maxillipeds, in the ventral middle region, and rudiments of the first two pairs of legs. There is involution of the caudal armature. None of the examined nauplii VI had terminal spines, which had probably fallen off.

Discussion: Nauplii V of different sizes occur together in the same sample. Adults of smaller size e.g. *Pleuromamma gracilis*, and

of larger size e.g. *P. abdominalis*, also occur in the samples. It is probable that the smaller nauplii belong to the smaller species, and the larger to the larger species.

GIBBONS (1938) identified the nauplius of *Metridia lucens* Boeck. It is characterized by a ventral posterior protuberance to which the ventral spines of the caudal armature are attached at an angle (see OGILVIE, 1953). The very long ventral spines are distant from the terminal spines of the caudal armature (Fig. 72). Two species of *Metridia*, *M. brevicauda* Giesbrecht and *M. princeps* Giesbrecht, occurred in samples of water deeper than 300 m off BRAZIL. The nauplii of *Metridia* species probably are present off Brazil in Intermediate Antarctic Waters, where the genus was most numerous represented.

Pleuromamma also belongs to the Metridiidae. *P. abdominalis* (Lubbock), *P. gracilis* (Claus), *P. borealis* (F. Dahl), *P. xiphias* (Giesbrecht), *P. quadrangulata* (F. Dahl) and *P. piseki* Farran are found in larger numbers in Subtropical (or Central Atlantic) Waters in the region of the Subtropical Convergence, off the south Coast of Brazil and at depths between 100 and 300 m off the east Coast of Brazil. *P. gracilis* and *P. abdominalis* are abundant in samples collected at night in oceanic waters and in depths greater than 50 m. They also live over the continental shelf off Brazil (BJÖRNBERG, 1963). Their nauplii are probably therefore more numerous than the nauplii of *Metridia* in these waters since the adult *Pleuromamma* are more frequent and abundant than *Metridia*. Numerous nauplii were found in the samples collected from the "M. Lomonosov." Several characteristics identify these larvae studied here as *Pleuromamma* nauplii:

- 1) like the *Metridia* nauplius, they have a ventral protuberance with longer spines than those of the caudal armature;
- 2) they occur in samples where there are also numerous young copepodids of *Pleuromamma* and egg-bearing females of the genus;
- 3) *Pleuromamma* are very frequent in the waters where these nauplii are common.

Family CENTROPAGIDAE

Centropages furcatus (Dana, 1852)

(Figs. 76–150)

Material: From living plankton samples collected at the Base Norte, Instituto Oceanográfico (Ubatuba, BRAZIL) in February 1965, and from the pier of the Carma-bi, CURAÇAO. Fixed samples collected off Brazil and Curaçao.

Habitat: Nauplii reared in waters with salinity 36.00‰ or more and temperature 25°C or more in Curaçao; and in waters with more or less 34.00‰ salinity and 20°C or more in Ubatuba. The nauplius lives in coastal, shelf and inshore waters off Brazil (waters of low salinity, near to the coast). In Curaçao it occurred in coastal waters of high salinity. It is circum-tropical and circum-subtropical.

Development: The egg-bearing females and the fertilized females, placed in the rearing dishes, took 13 hours to shed their eggs in the sea water. The spiny eggs (Fig. 81), five of 0.08 and one of 0.10 mm, hatched nauplii, the first hatching $8\frac{1}{2}$ hours after being shed, the last after 31 hours. The first moult occurred 23 hours after the eclosion. Nauplius III changed to stage IV after $24\frac{1}{2}$ hours. The total time taken by the specimens in stage II to reach stage V was $6\frac{1}{2}$ days to $8\frac{1}{2}$ days. The copepodids III and IV took $78\frac{1}{2}$ hours to moult. One copepodid II spent 2 days and 2 hours in this stage. Thus, a great variability was noted in the time of development of each animal.

Movements: The nauplius moves by metachronal paddle-strokes of the antennules, antennae and mandibles. In each appendage each segment moves forwards, also successively, from the proximal to the distal, till the whole limb is stretched out in front of the nauplius. At the beginning of the movement the distal segments are bent backwards while the proximal segments are already at right angles to the body, then rotating forwards. The movement of each pair of appendages is very much like that of the wings during the flapping flight of a bird. The nauplius is also capable of rotating quickly about the longitudinal axis of its body, and of jumping forwards by moving all the appendages almost simultaneously backwards. While grazing the copepodids move slowly. The antennules are maintained rigidly stretched out vertically to the body axis and the antennae and mandibles vibrate, propelling it forwards. The animal is also capable of quick escape movements. It changes the turgidity at the basis of the antennule (see STORCH, 1929). This becomes flaccid and then with the almost simultaneous movement of all the legs backwards, the body is propelled forwards, and the antennules backwards. Thus, they do not slow down the whole movement.

Light: When exposed to light the nauplius becomes practically transparent, due to the total contraction of the chromatophores. In the dark the three posterior chromatophores dilate, and the posterior region is darkened (Fig. 76, 79). The tips of the appendages also become dark red or black.

Colour: The colour of the nauplii has been mentioned above. The copepodids contain red and orange chromatophores in certain parts of the body. The rest of the body is without colour and transparent.

Nauplius I (Figs. 76–77): 6 specimens examined. Length 0.12 to 0.13 mm, average 0.12 mm. Form: oval; reddish; dark; mandibles reaching almost to the posterior region of the body, giving the nauplius a square outline posteriorly. Caudal armature: 2. Labrum, rectangular and oval. Antennule, 0 : 0 : 3. Antenna: coxopod, 2s; basipod; endopod, 2; exopod, 1 : 1 : 1 : 1 (2). Mandible: coxopod; basipod; endopod, 2 or 3 + 1s; exopod, 1 : 1 : 1 : 2.

Nauplius II (Figs. 78–79): 6 specimens examined. Length 0.20 to 0.21 mm; mostly 0.20 mm. Form: oval with anterior part triangular. Caudal armature: 2 sensory setae, 4 rows of minute spines, 2s (lateral). Labrum: more or less rectangular with marginal spines. Antennule, 0 : 0 : 3 or 4. Antenna: coxopod, 1s; basipod, 1s (+ 1); endopod, 4 term + 2(1); exopod, segmented, 1 : 1 : 1 : 2(3). Mandible: coxopod, 1s; basipod, 2s; endopod, 3s + 4; exopod, 1 : 1 : 1 : 2 (Fig. 80).

Nauplius III (Fig. 83): 5 specimens examined. Length, 0.23 to 0.24 mm in Ubatuba, and 0.26 mm in Santos. Oval form, posteriorly pointed. Labrum as in stage II. Anterior region triangular in outline. Caudal armature: 2 sensory setae; 2s + setules, ventrally; 2s + setules, terminally. Antennules, 0 : 0 : 3(4) + 2. Antenna: coxopod, 1s; basipod, 1s + 1; endopod, 4 term + 3; exopod, 1 : 1 : 1 : 1(2) + 1. Mandible: coxopod, 1s; basipod, 1 or 2s; endopod, 3s + 5; exopod, 1 : 1 : 1 : 2(3).

Nauplius IV (Fig. 84): 5 specimens examined. Length 0.26 to 0.31 mm, the large and the smallest sizes collected off Santos. Shape: rectangular with the anterior region a flattened triangle, and a tapering posterior region. Caudal armature: 2 sensory setae, 2s term, 4s (ventral), 2 + 2s (lateral) + ms. Labrum, oval-rectangular, with marginal setae. Inferior labium delimited by spines. Antennule, 0 : 0 : 3 term + 2. Antenna: coxopod, 1s; basipod, 1s + 1(2); endopod, 5 term + 3 (lateral); exopod, segmented, 1 : 1 : 1 : 1 : 2 (+ 2). Mandible (Fig. 85): coxopod, 1s; basipod, 2s; endopod, 3s + 6 (+ 2); exopod, segmented, 1 (+ 1) : 1 : 1 : 1 : 1 : 2. Maxillule: 1 or 2 : 2 or 3.

Nauplius V (Figs. 86, 88): 7 specimens examined. Length 0.31 to 0.35 mm, with a larger number between 0.31 and 0.33 mm. Shape: the same as nauplius IV. Caudal armature: 2 sensory setae, 2 laterals, 4 ventral almost terminal s, 2 term. Labrum: the same as in nauplius IV. Antennule 3 or 4-segmented, 0 : 0 : 3 term + 4. Antenna: coxopod, 1s; basipod, 1s + 1(2); endopod, 4 term + 3; exopod, 1 : 1 : 1 : 1 : 1 : 1 : 1(2). Mandible: coxopod, 1s; basipod, 2s; endopod, 3s + 5 + 1; exopod, 1 : 1 : 1 : 2(3). Maxillule: 1 + 1 : 4(3).

Nauplius VI (Figs. 87, 89): 10 specimens examined. Length 0.33 to 0.38 mm, with a larger number of 0.35 mm. Rectangular longish shape, posteriorly oval. Caudal armature: 2 sensory setae, 2s (lateral) + 4s (ventral), 2s (terminal). Labrum, rectangular-oval, with marginal setules. Inferior labial area, delimited by setules. Antennule, 0 : 0 : 4 term + 7(6). Antenna: coxopod, 1s; basipod, 1s + 2; endopod, 4 term + 4 lateral; segmented exopod, 1 : 1 : 1 : 1 : 1 : 1 : 1 : 1. Mandible: coxopod, 1s + bulge; basipod, 2; endopod, 6 + 3s; exopod, 6 + 1. Maxillule: 3 lobes, 2s : 6(7) : 5(4). Maxilla: 6 lobes. Maxilliped, 2s. Legs I: 2-lobed, 3 : 4. Legs II: 2-lobed, 2 : 3.

Copepodid I (Fig. 109): 4 specimens examined. Length 0.45 to 0.57 mm, the majority 0.56 mm. Four cephalothoracic segments and one not clearly defined. One abdominal segment (Fig. 99). Antennule (Fig. 90): 9 segments. Antenna (Fig. 91): coxopod, basipod (2), endopod (2-segmented, 2 : 3 + 6), exopod (8-segmented, 1 : 1 : 1 : 1 : 1 : 1 : 1 + 3 term). Mandible (Fig. 92): gnathobase, 3 teeth, basipod (2), endopod (2 segments, 4 : 4), exopod (2 segments, 1 : 5). Maxillule (Fig. 93): external lobe I (4), external lobe II (0), exopod (7), internal lobe I (8s), internal lobe II (1), internal lobe III (4); basipod (3), endopod (2 + 2 + 4 term). Maxilla (Fig. 98): coxopod, 2 : 2 + 1; basipod, 2 + 1 : 2 + 1 (+ 1?); endopod, 2 thin : 1 : 2 : 2 or 3. Maxilliped (Fig. 97): coxopod (1 + 2), basipod (2), endopod (1 : 4). Leg I (Fig. 102): coxopod, basipod, endopod (5), exopod (3 + 1 term + 4s). Leg II (Fig. 103): coxopod, basipod, endopod (5), exopod (3 + 1 term + 3s). Leg III (Fig. 107): external lobe (2 + 1s); internal lobe (2).

Copepodid II (Fig. 110): 2 specimens examined. Length 0.62 and 0.69 mm. Five cephalothoracic segments. One abdominal seg-

ment (Fig. 108). Antennule: 15 segments. Antenna (Fig. 94): coxopod, basipod (2), endopod (2 : 5 term + 3 or 5 + 2), exopod (8-segmented, 1 : 1 : 1 : 1 : 1 : 1 : 1 : 3 term + 1). Mandible (Fig. 95): gnathobase (7 teeth), basipod (3 or 2 + 1), endopod (4 : 5), exopod (6 or 5). Maxillule (Fig. 96): external lobe I (6), external lobe II (0), exopod (7), internal lobe I (8s), internal lobe II (1), internal lobe III (4), basipod (3), endopod (2 + 2 + 5 term). Maxilla (Fig. 101): coxopod (2 + 1 : 2 + 1), basipod (2 + 1 : 2 + 1), endopod (2 : 1 : 2 : 2 + 1?). Maxilliped (Fig. 100): coxopod (2 + 2 + 2s), basipod (2 + 2), endopod (1 : 1 : 4). Leg I (Fig. 106): coxopod (1), basipod (0), endopod (8), exopod (1 : 3s + 1 term + 4). Leg II (Fig. 104): coxopod (1), basipod, endopod (1 : 6), exopod (1s : 2s + 1 term + 3 or 4). Leg III (Fig. 105): coxopod, basipod, endopod (5), exopod (3s + 1 term + 3). Leg IV: coxopod and basipod fused, endopod (2s), exopod (2).

Copepodid III (Fig. 111): 9 specimens examined (from Ubatuba and Santos). Length 0.80 to 1.10 mm; usually, 0.87 and 1.00 mm. Five cephalothoracic segments, the last with a lateral spine on each side (Fig. 115). Two abdominal segments. Antennule: 21 segments. Antenna (Fig. 136): coxopod, basipod (2), endopod (2 : 6 term + 5), exopod (1 : 1 : 1 : 1 : 1 : 1 : 1 : 1 + 3 term). Mandible (Fig. 139): gnathobase (7 teeth), basipod (3), endopod (4 : 5 + 1), exopod (6). Maxillule (Fig. 142): external lobe I (7), external lobe II, exopod (7), internal lobe I (9s), internal lobe II (1), internal lobe III (4), basipod (3), endopod (2 + 2 + 5 term). Maxilla (Fig. 146): coxopod (2 + 1 : 2 + 1), basipod (2 + 1 : 2 + 1), endopod (2 : 1 : 2 : 2). Maxilliped (Fig. 148): coxopod (2 : 3 : 2), basipod (3 + 2), endopod (1 : 1 : 2 : 4). Leg I (Fig. 119): coxopod (1), basipod, endopod (1 : 7), exopod (1s + 1 : 3s + 1 term + 4). Leg II (Fig. 120): coxopod (1), basipod, endopod, (1 : 8), exopod (1s + 1 : 3s + 1 term + 5). Leg III (Fig. 122): coxopod (1), basipod, endopod (1 : 5), exopod (1s + 1 : 2s + 1 term + 4). Leg IV (Fig. 121): coxopod, basipod, endopod (6), exopod (3s + 1 term + 3). Leg V (Fig. 114): coxopod and basipod fused, with internal lobe (2s) and external lobe (3s).

Copepodid IV (Fig. 112): 40 specimens examined. Length probable future *males*, 1.10 to 1.13 mm, the majority 1.12 mm. Probable future *females*, 1.18 to 1.20 mm, samples from Ubatuba

and from off Santos. Six cephalothoracic segments, with 2 spines on the last segment, on each side (Fig. 116). Three or four abdominal segments. Antennule: 24 segments. Antenna (Fig. 137): coxopod (1), basipod (2), endopod (2 : 6 term + 6), exopod (1 : 1 : 1 : 1 : 1 : 1 : 1 : 4). Mandible (Fig. 140): gnathobase, 8 teeth; basipod (3 or 4); endopod (4 : 6); exopod (1 : 1 : 1 : 3 or 4). Maxillule (Fig. 144): external lobe I (7), external lobe II, exopod (7), internal lobe I (11), internal lobe II (1), internal lobe III (4), basipod (3), endopod (2 + 2 + 5 term). Maxilla (Fig. 145): coxopod (2 + 1 : 2 + 1), basipod (2 + 1 : 2 + 1), endopod (2 : 1 : 2 : 2 + 1). Maxilliped (Fig. 150): coxopod (2 : 3 : 2), basipod (3 + 2), endopod (2 : 1 : 1 : 2 : 4). Leg I (Fig. 124): coxopod (1), basipod (1), endopod (1 : 8), exopod (1s + 1 : 3s + 1 term + 4). Leg II (Fig. 123): coxopod (1), basipod, endopod (1 : 7), exopod (1s + 1 : 3s + 1 term + 5). Leg III (Fig. 126): coxopod (1), basipod, endopod (1 : 9), exopod (1s + 1 : 3s + 1 term + 5). Leg IV (Fig. 127): coxopod, (1) basipod, endopod (1 : 7), exopod (1 : 3s + 1s term + 5). Leg V (Fig. 125): coxopod, basipod (1s), endopod (5 + 1 plumose), exopod (3s + 1 term + 3).

Copepodid V, *male* (Fig. 118): 7 specimens examined from Ubatuba and off Santos. Length 1.25 to 1.37 mm, the majority 1.37 mm. Six cephalothoracic segments. Four abdominal segments. Antennule 23 segments, the left (Fig. 135) thinner than the right (Fig. 133). Antenna: (Fig. 138): coxopod (1), basipod (2), endopod (2 : 6 term + 6 or 4); exopod (1 : 1 : 1 : 1 : 1 : 1 : 1 : 4). Mandible (Fig. 141): gnathobase (8 teeth), basipod (3), endopod (4 : 7), exopod (1 : 1 : 1 : 3). Maxillule (Fig. 143): external lobe I (7), external lobe II, exopod (9); internal lobe I (11), internal lobe II (1), internal lobe III (4), basipod (3), endopod (4 + 5 term). Maxilla (Fig. 147): coxopod (3 : 3), basipod (3 : 3), endopod (2 : 1 : 2 : 2 : 2). Maxilliped (Fig. 149): coxopod (2 + 3 + 3), basipod (3 + 2), endopod (2 : 2 : 2 : 3 : 3). Leg I (Fig. 128): coxopod (1), basipod, endopod (1 : 2 : 6), exopod (1 + 1s : 1 + 1s : 2s + 1 term + 4). Leg II (Fig. 129): coxopod (1?), basipod, endopod (1 : 2 : 8), exopod (1s + 1 : 1s + 1 : 3s + 5 + 1 term). Leg III (Fig. 131): coxopod (1), basipod, endopod (1 : 2 : 7), exopod (1s + 1 : 1s + 1 : 3s + 1 term + 5). Leg IV: coxopod (1), basipod, endopod (1 : 2 : 7),

exopod (1s + 1 : 1s + 1 : 3s + 1 term + 5). Leg V (Fig. 132): coxopod, basipod (1s), endopod (0 : 6), exopod (1s : 3s + 1s term + 4). – *Female* (Figs. 113, 117, 128–131, 138, 143, 147, 149): 13 spec. examined from Ubatuba and from Cananeia. Length 1.45 to 2.05 mm. It differs from the male in having 3 abdominal segments, the two antennules are alike and have 24 segments each (Fig. 134), the fifth leg (Fig. 130) has coxopod, basipod, endopod (1 : 7), exopod (1s : 3s external + 1s internal + 4 + 1s term).

Discussion: *Centropages* nauplii are known for the North Atlantic species. The developmental stages of *C. hamatus* (Lilljeborg, 1853) were studied by OBERG (1906) and by GURNEY (1931). Those of *C. typicus* Krøyer 1849, by OGILVIE (1953). *C. abdominalis* Sato 1913, from Japan, has larvae identified by KOGA (1960b). The nauplii of *C. krøyeri* Giesbrecht 1892, from the Black Sea, were studied by SAZHINA (1960).

Centropages furcatus is the most common and the most numerous *Centropages* in warm waters such as the coastal and shelf waters off Brazil, and near to Curaçao. Naupliar development in this species took longer than in *C. abdominalis* (KOGA, 1960b).

Nauplius I of *C. hamatus*, *C. typicus*, *C. abdominalis*, *C. krøyeri* and *C. furcatus* have 3 terminal setae on the antennule and 2 posterior furcal setae. *C. hamatus* (Oberg, 1906) and *C. krøyeri* (Sazhina, 1960) have more antennal and mandibular setae than *C. furcatus*. *C. abdominalis* appears to have less mandibular and antennal setae than the other species. *C. krøyeri* can be distinguished easily from all other species since it has a row of ventral setules in the posterior region, at this stage.

Nauplius II: *C. hamatus*, *C. abdominalis*, *C. typicus* have one lateral seta, and *C. krøyeri* has two lateral setae on the antennule, which do not occur in *C. furcatus*. In *C. hamatus* and *C. typicus* there is also a seta more on the antennule. The endopod of the antenna of *C. furcatus* has one seta more than the other nauplii of the genus. The exopod of the antenna of *C. krøyeri* has two setae more than *C. furcatus*. The differences between the species are very small at this stage.

Nauplius III: The species studied at this stage are rather uniform. *C. furcatus* has generally less setae on the appendages, but differs from all other species in having more posterior ventral spines. *C. krøyeri* is characterized by the abundance of ventral posterior setules. *C. hamatus* has only two lateral rows of posterior ventral setules, which are absent in *C. typicus*. The ventral posterior spines of *C. abdominalis* are longer than in *C. typicus*.

Nauplius IV: The caudal armature of *C. furcatus* has 4 ventral spines more than in the other species of *Centropages* already described. The antennules of *C. furcatus* have less terminal setae than in the other *Centropages* nauplii. In *C. krøyeri* there are three rows of ventral setules; in *C. abdominalis*, only one; in *C. hamatus* there are two; in *C. typicus* and in *C. furcatus*, none.

Nauplius V: *C. furcatus*, when compared to other species at this stage, has corresponding differential features mentioned for nauplius IV. *C. hamatus* differs from *C. typicus* in the greater length of the ventral spines, which are still longer in *C. abdominalis*. *C. krøyeri* has a well developed lobe, the maxillule, which is absent in the other species studied.

Nauplius VI: The differential characteristics in the various species are practically the same as in stage V. *C. furcatus* has a group of terminal setae on the distal segment of the antennule, which are longer by 2 or 3 times than the remaining setae of the same segment. This difference in length is not so apparent in the other species. The caudal armature in *C. furcatus* has more spines than in the remaining species. *C. abdominalis* appears to be the species which has less setae in this stage. *C. krøyeri* has many areas with setules on the inferior lip. The setules are more numerous than in *C. hamatus* (cf. fig. 6, pl. II, OBERG, 1906). There are no adequate drawings of *C. typicus* at this stage but, according to OGILVIE (1953), the posterior spines of nauplius VI of *C. typicus* are shorter, when compared with *C. hamatus*. The terminal spines of *C. krøyeri*, all of the same length, appear shorter than those of *C. abdominalis*. In *C. typicus* there is one terminal spine considerably smaller than the other. *C. abdominalis* apparently has long terminal spines, all of equal length. *C. hamatus* differs from *C. abdominalis* in this stage in the number of setules on the inferior lip.

The copepodids of *C. krøyeri* and *C. typicus* were described by GRANDORI (1912). KRISHNASWAMY (1950) described some appendages of a copepodid of *C. tenuiremis* and of the copepodid I of *C. furcatus*. The size of this specimen is similar to the size of Brazilian specimens in the same stage. The antennule of our specimens has one segment more. The mouth appendages are described as being the same as observed in the adult (KRISHNASWAMY, 1950). In Brazilian material a difference in the number of setae of the appendages was noted in copepodid V and in the adult. *C. furcatus* undergoes less changes from copepodid I to adult than the other species studied. The description of the legs of *C. furcatus* by KRISHNASWAMY (1950) corresponds to that of Brazilian specimens. This species differs from *C. krøyeri* and *C. typicus* in having as early as in the copepodid III, two lateral points on the last thoracic segment. From the third copepodid stage onwards, *C. furcatus* has an asymmetrical furca, which does not appear to exist in the species described by GRANDORI (1912). The legs are apparently alike in *C. furcatus*, *C. krøyeri* and *C. typicus*. The other appendages were not discussed (GRANDORI, 1912) and so cannot be compared. Considering the segmentation of the exo- and endopods of the legs, the copepodid of *C. tenuiremis* mentioned by KRISHNASWAMY (1950) is probably the first. The maxilliped of this species has more setae, and the maxilla less than in *C. furcatus*.

The difference between male and female specimens becomes apparent from the copepodid IV stage onwards in *C. krøyeri* (GRANDORI, 1912), but not in *C. furcatus*. Specimens of this species were 1.10 to 1.20 mm long, 18 specimens were 1.12 mm and 9 were 1.20 mm long. This brings us to the conclusion that though morphologically indistinguishable, the males and females may be separated by their size. The smaller is probably the future male, the larger the future female. Copepodid V of *C. furcatus* also has different sizes. In the female to be there are 3 abdominal segments, in the male to be, 4 segments. The fifth legs of the female copepodid V have a pointed protuberance on the lateral margin of segment II of the exopod. This protuberance does not exist in the male. Thus sexual morphological differentiation is retarded in *C. furcatus* when compared to *C. krøyeri* and to *C. typicus*.

The copepodid I of *C. furcatus* can be easily mistaken for the same stage of *Labidocera fluviatilis*; both are approximately the same size and the ventral eye is well developed. The maxillules and legs II are very much alike. *Labidocera* keeps the antennules slightly bent. The antennules are longer in *Centropages* and stretched out in a straight line: there are more setae on the antennae, maxillae, maxillipeds and first legs. The mandibles have a smaller number of setae and the gnathobase has more teeth than in *Labidocera*. The first legs in *Centropages* do not have a terminal spine with a serrate flange. From copepodid II onwards it is very easy to distinguish between *Centropages* and *Labidocera* as the latter species has dorsal cuticular lenses in the cephalic region.

Note: Nauplii of *C. furcatus* were found in samples collected off Santos (Brazil) taken during January–April, June, August and October in salinities between 28.00 and 36.25‰, and in temperatures over 18°C.

Centropages furcatus, *Labidocera fluviatilis*, *Calanopia americana* and *Acartia lilljeborgi* have morphologically similar mouth appendages such as the maxillae, in the copepodid stages and probably feed on microplankton of the same kind. The ecological niches of these four species apparently are not separated. *Calanopia* swims in the plankton at night only; during the day it is buried in the loose mud of the substrate surface. The adult *Acartia* during the day lives over the substrate, without burying itself in it, but the copepodids swim in the surface plankton. *Calanopia* is quicker, and probably selects smaller and quicker food than *Acartia*. *Labidocera* is very slow. Both live in the surface layers, *Labidocera* just below the surface film, and *Centropages* a little further down.

Phylogenetical considerations: HANAOKA (1952a) derived the *Centropages* nauplius from the *Diaptomus* nauplius. He also thinks that the *Epilabidocera* originated from *Centropages*. He classifies the larvae of *Centropages* and of *Epilabidocera* as being of the intermediate type between the planktonic ("pelager") and benthonic ("creeper") nauplii. Both *L. fluviatilis* and *C. furcatus* are entirely planktonic species at all stages of their development and

therefore cannot be considered intermediate, from the ecological point of view. But anatomically the mandibles of these nauplii, with a bilobed masticatory process, are intermediate between the Calanoida with a one-lobed masticatory process, and the Cyclopoida with a bisegmented process. Calanoida are chiefly planktonic and the Cyclopoida are classified by HANAOKA (1952a) as "secondary pelager type," thus as planktonic. From the morphological point of view HANAOKA is right.

Centropages sp.

Material: Fixed sample collected in surface waters in the region of the Subtropical Convergence off BRAZIL.

Nauplius VI (Fig. 82): Length 0.25 mm. Fusiform body. Labrum, pentagonal with many short setules on the margin. Antennule, 0 : 0 : 10. Antenna: coxopod, 1s; basipod, 2s; endopod, 2 : 4; exopod, 5. Mandible: coxopod, with long, pointed mandibular process, 1; basipod, 2s; endopod, bilobed, 6; exopod, 3?. Maxillule: 3-lobed, 3 teeth : 2s : 3s. Maxilla, leaf-like. Maxilliped: pointed lobe, 2s. Leg I: 2 lobes, 3s : 2s + 1s. Leg II: 2 lobes, 2s : 2s. Caudal armature: 2 sensory setae; a long seta (terminal); a larger right thorn, and a smaller left thorn; 4 asymmetrically distributed thorns or very small spines ventrally, pre-terminally; a very small thorn to the left and a larger one to the right of the 4 spines.

Discussion: This nauplius is characterized by its small size and very long antennules. *Centropages furcatus* has larger nauplii. The adult *C. brachiatus* is small, and is found off the south coast of Brazil in waters of Subantarctic origin (with low salinity 34‰ and low temperature, less than 16°C). The sample in which the nauplius occurred was collected from waters with temperature about 20.5°C and salinity 35.7–36.7‰ at the Subtropical Convergence. In the south of this region Subantarctic waters are found with *C. brachiatus*; north of this region *C. furcatus* and the large *C. violaceus* usually occur. As the nauplius under discussion is small, it probably belongs to *C. brachiatus*.

Family PSEUDODIAPTOMIDAE

***Pseudodiaptomus acutus* (F. Dahl, 1894)**

(Figs. 151–249)

Material: Nauplii reared in the Instituto Oceanografico's laboratories at Cananeia and Ubatuba (BRAZIL). Fixed samples from the bay of Santos (Brazil).

Habitat: Collected in coastal waters, frequently brackish. At night adults, copepodids and nauplii are planktonic and can be collected at the surface of inshore and coastal waters. During the day adults and copepodids in the last stages are found near the bottom. The nauplii live in the surface plankton also during the day, and judging from their behaviour in the laboratory, they are both planktonic and benthic, often found creeping over muddy bottoms.

Development: Hatching is about 44 hours after the appearance of the eggs in the egg-sacs. The rearing of the egg-laden female during two successive generations in glass-dishes showed that the species has no first naupliar stage. Nauplius II creeps on the substrate, during eclosion and begins to swim actively as soon as it frees itself of the ovular membranes. This is a very quick process (less than a minute). It took 35 hours from fertilization, observed in a captive female, to the release of eggs. The first nauplius to hatch took 5 days to metamorphose into a copepodid. There was an interval of 8 days between the first and the last eclosion in the same batch of eggs. Nearly all the 17 nauplii of the observed female hatched within two days after the first eclosion. The majority of the larvae passed to the third nauplius stage one day after hatching. However, on the fifth day after the first eclosion, there were still nauplii passing from the second to third nauplius. From the same batch of eggs some specimens were already third copepodids while others were still in the fourth nauplius stage. A first copepodid can take 10 days to reach the adult stage. It remains in each copepodid stage for one to two days. This may be the explanation for the simultaneous occurrence of all the stages of development of one species in the plankton.

Movements: They are varied and suggest the adaptation of the larva also to a benthic life. The antennules and antennae vibrate like insect wings and, when close to the bottom, produce currents which bring food particles to the mouth of the nauplius. The nauplius can also "loop-the-loop" near to the bottom in such a way that, at the highest point of the loop, it is with the ventral side up. When it reaches the substrate the ventral side is down, and the appendages rake the bottom surface; it then starts swimming up again (Fig. 158). The nauplius can also creep over the bottom like harpacticoid nauplii; it can jump forwards and can swim up and down along a sinusoidal path. It does not move by quick successive strokes forwards, like *Acartia* larvae, but by long "glides" between each power stroke of the antennules and antennae. – The copepodids can remain motionless with the head region down and the antennules attached to the substrate by means of the aesthetes or adhesive setae. At the same time the antennae, the mandibular palps and the maxillules vibrate continuously, producing suction currents which move the food particles into the pre-buccal "basket" formed by the other mouth appendages and by the thoracic limbs stretched forwards. Larger particles or unsuitable food are rejected by the almost simultaneous backward motion of all legs, which thus opens the "basket"

(Fig. 181). — Copepodids can also jump forwards by moving all the legs backwards and by laying the antennules against the body during the movement. They always swim with the setae of the first segments of the antennules turned down. The abdomen of the copepodids, while swimming, can remain horizontal or flex up and down.

Food: It feeds on phytoplankton and organic debris from the bottom. In aquaria the specimens are particle feeders.

The female has 17 eggs in the egg-sac.

The colour of the nauplii and of the copepodids is usually dark. The body of the nauplius is black or brown and dark green. The food gives the gut a greenish-yellow colour. The naupliar eye is dark red and the nauplius has a red-brown chromatophore in the posterior region. The antennules are rose coloured and the antennae are yellowish.

Nauplius II (Fig. 151, 155): Length 0.15 and 0.17 mm, caudal setae excluded. It has the shape of a drop, with the anterior region wider and round, and the posterior region tapering. Body not segmented. Labrum covered with minute spines externally. Caudal armature: 1 terminal balancer larger and setose, and the other smaller and smooth, both with minute setae around the insertion point; 2 rows of ventral thin setules before the caudal region. Antennule (Fig. 159), 3-segmented, 1 : 2 : 4 + 12. Antenna (Fig. 163): coxopod with a pointed spatule + 1 hook; basipod, 1 hook + 2; endopod, 3 term + 2 + 4ms; exopod, 5-segmented, 7. Mandible (Fig. 167): coxopod, 1 hook; basipod, 1 (2); endopod, leaflike, 7; exopod, 4-segmented, 5.

Nauplius III (Fig. 152): Length 0.19, 0.21 and 0.22 mm, caudal setae excluded. Shape like nauplius II. Body, 2 segments. Labrum: external hook-like spines in the center, and anteriorly; thin setules on the lateral and posterior margins. Inferior lip ciliated. Caudal armature: 1 strong setose balancer, 1 thin balancer, 2 sensory setae inserted laterally to the balancers; a row of setules around the base of each balancer, 2 rows of ventral setules. Antennule (Fig. 160), 4-segmented, 0 : 1 : 2 + 5ms : 5(6) + 4(5) + 2s. Antenna (Fig. 164): coxopod, 2mp + 1mp; basipod, 1mp + 3 + ms (in a row); endopod, 4 term + 2 + 3 + ms (1 row); exopod, 5-segmented, 6 + 1. Mandible (Fig. 168): coxopod, 1mp; basipod, 3s; endopod, 8s; exopod, 4(5) segmented, 5. Maxillule: a plumose spine.

Nauplius IV (Fig. 153): Length 0.25 mm, caudal setae ex-

cluded. Shape: as in nauplius III. Body segmented. Labrum with central and anterior hooks; marginal, lateral and posterior thin setules. Inferior lip with thin setules. Caudal armature: as in nauplius III. Antennule (Fig. 161), 4-segmented, 0 : 1 : 2 + 5ms : 4 term + 8 + 4 + 3s. Antenna (Fig. 165): coxopod, 2mp + 1mp; basipod, 1mp + 2 + 2; endopod, 3 term + 2 term + 3; exopod, 5-segmented, 8 + 1. Mandible (Fig. 169): coxopod with dented mandibular blade + 1; basipod, 5(4); endopod 6 + 3 + ms; exopod, segmented, 5. Maxillule (Fig. 156): leaf-like, 2 lobed, 6 : 3.

Nauplius V (Fig. 157): Length 2 of 0.27 and 1 specimen of 0.30 mm; longer than nauplius IV. Caudal armature, as in stage IV, but with one more seta on each side. Body with more (3 or 4) segments. Antennule, as in nauplius IV, except the last segment with 10 larger setae, 4 or more thin and smaller setae and 5 spines. Antenna (Fig. 166): coxopod, 2mp + 1; basipod 1mp + 4 + 6ms; endopod, 4 + 4 term + 2 + ms; exopod, segmented, 8(7) + 1. Mandible (Fig. 170): coxopod with mandibular blade + 1; basipod, 3(4)s; endopod, 10; exopod, segmented, 6 + 1. Maxillule: leaf-like, 2 lobes, endopod 6; exopod, 5. Maxilla: 1 plumose spine + 1 thin spine (not always present).

Nauplius VI (Fig. 154): Length 0.30 to 0.33 mm. Labrum and inferior lip as in the stage V. Caudal armature as in the preceding stage, with one pair of terminal spines more. Antennule (Fig. 162) as in nauplius V, but, with 2-4 setae more on the terminal segment. Antenna and mandible like in the stage V. Maxillule: 3 lobes, 7 : 7 : 1 + setules. Maxilla: with a long plumose seta and a crenulated margin. Maxilliped: 1 lobe, 1s + 1. Legs I and II: 2 lobes, 2 : 3.

Copepodid I (Figs. 171-172): Length 0.44 and 0.41 mm. Five cephalothoracic segments and one abdominal segment. Furca: 4 setae. Antennule (Fig. 183): 9 segments. Antenna (Fig. 194): coxopod, 1 + 1; basipod, 2 or 3; endopod, 2 segments, 2 : 3 + 5; exopod, 5 : 1 : 3 term. Mandible (Fig. 200), coxopod with 7-toothed mandibular blade + 3 teeth + 1s; basipod, 4; endopod, internal lobe (3), external lobe (5); exopod, 3 segments, 5. Maxillule (Fig. 208): external lobe I (4), external lobe II (1), exopod (6 + 1), internal lobe I (8 + 2), internal lobe II (3), internal lobe III (2), basipod (2), endopod (1 : 2 : 5). Maxilla (Fig. 238): lobe I (2), lobe II

(3), lobe III (3), lobe IV (3), lobe V (3), endopod (5). Maxilliped (Fig. 243): coxopod, (3 + 2), basipod (2 + 1 + ms), endopod (1 : 4). Leg I (Fig. 213): coxopod, basipod, endopod (8), exopod (3 + 1s term + 3s). Leg II (Fig. 218): coxopod, basipod, endopod (5), exopod (3 + 1s term + 3s). Leg III (Fig. 177): 2 lobes, with 2 protuberances each.

Copepodid II (Figs. 173–174): Length 0.50 to 0.54 mm in 3 specimens. 5 segments in the cephalothorax and 2 abdominal segments, with furca (4 + 1). Antennule (Fig. 184): 14 segments. Antenna (Fig. 196): coxopod (1), basipod (2 + 1), endopod (1 : 8 + ms), exopod (3 : 1 : 1 : 1 : 4). Mandible (Fig. 202): coxopod, mandibular blade (8 teeth + 1); basipod (4), endopod (3 + 5), exopod (1 : 1 : 3). Maxillule: external lobe I (5), external lobe II (1), exopod (6), internal lobe I (10), internal lobe II (3), internal lobe III (2), basipod (2), endopod (1 : 2 : 5). Maxilla (Fig. 239): lobe I to lobe V (3), endopod (5 or 6). Maxilliped (Fig. 245): coxopod (5 + 1s), basipod (2 + 1), endopod (1 triple pointed seta : 1 : 4). Leg I (Fig. 214): coxopod (1 or 0), basipod (1s or 0), endopod (1 : 7), exopod (1s : 2s + 1s term + 4). Leg II (Fig. 219): coxopod (1), basipod (1s), endopod (1 : 7), exopod (1s : 2s + 1s term + 4). Leg III (Fig. 225): coxopod, basipod, endopod (6), exopod (3s + 1s term + 3). Leg IV (Fig. 236): 2 lobes, with two protuberances each.

Copepodid III (Fig. 175): Length 0.58 to 0.68 mm in 10 specimens. Body: 8 segments and furca. Antennule (Fig. 185): 18 or 19 segments. Antenna (Fig. 197): coxopod (1), basipod (2), endopod (2 : 8 or 9), exopod (1 : 1 : 1 : 1 : 2 : 4 term). Mandible (Fig. 203): coxopod, mandibular blade (9 teeth + 1); basipod (4), endopod (3 + 6), exopod (1 : 1 : 4). Maxillule (Fig. 209): external lobe I (6), external lobe II (1), exopod (7 or 8), internal lobe I (9mp + 2), internal lobe II (4), internal lobe III (2), basipod (3), endopod (2 : 2 : 5 + 2). Maxilla (Fig. 240): 5 lobes with 3 setae each and endopod (7). Maxilliped (Fig. 244): coxopod (6), basipod (3), endopod (1 : 1 : 2 : 2 : 3). Leg I: coxopod, basipod, endopod (1 : 7), exopod (1s + 1 : 4 + 2s + 1s term). Leg II (Fig. 220): coxopod, basipod (1s), endopod (1 : 8), exopod (1 + 1s : 5 + 3s + 1s term). Leg III (Fig. 224): coxopod (1), basipod (1s), endopod (1 : 7), exopod (1s : 5 + 2s + 1s term). Leg IV (Fig. 230): coxopod, basipod, endopod (5),

exopod ($3 + 3s + 1s$ term), with the division of the segment indicated.

Copepodid IV, *male* (Fig. 178): Length 0.63 to 0.77 mm in 5 specimens. Body, 9 segments (3 abdominal). Antennule (Fig. 188–189): 21 segments, with the 15th of the right antennule much larger than in the left. Antenna, as in copepodid III, with $11 + 2 + 2$ setae on the terminal segment of the endopod; and a five-segmented exopod, ($1 : 4 : 1 : 1 : 2 + 3$ term). Mandible: coxopod, mandibular blade (9 teeth + r); basipod (4), endopod ($6 + 4$), exopod ($1 : 1 : 1 : 3$). Maxillule (Figs. 210, 211): external lobe I ($7 + r$), external lobe II (1), exopod (9), internal lobe I ($10s + r$), internal lobe II (4), internal lobe III ($3 + r + ms$), basipod ($4 + r$), endopod ($2 : 2 : 2 : 2 : 2$). Maxilla (Fig. 241): Lobe I to V with 3 setae each, endopod ($4 + 3$). Maxilliped (Fig. 246): coxopod (8), basipod ($3 + \text{double seta} + ms$), endopod (1 pectinate seta + 1 simple seta + $ms : 1$ pectinate seta + 1 simple seta : 1 pectinate seta + 1 simple seta : $2 : 4$). Leg I (Fig. 215): coxopod, basipod, endopod ($1 : 7$), exopod ($1 + 1s : 4 + 2s + 1s$ term). Leg II (Fig. 221): coxopod (1), basipod, endopod ($1 : 7$), exopod ($1s + 1 : 5 + 1s$ term + $3s$). Leg III (Fig. 227): coxopod (1), basipod (rs), endopod ($1 : 1 + 7$); exopod ($1 + 1s : 5 + 3s + 1s$ term). Leg IV: coxopod (1), basipod (rs), endopod ($1 : 0 : 7$), exopod ($1s + 1 : 5 + 3s + 1s$ term). Leg V (Fig. 233): the left with endopod and exopod ($3s$ term), the right with exopod only ($3s$ term).

Copepodid IV, *female* (Fig. 179): Length 0.75 to 0.82 mm in 5 specimens. It differs in the body segmentation from the male copepodid because it has the fourth abdominal segment outlined. The antennules, with 21 segments, are similar (Fig. 186). Antenna (Fig. 198), mandible (Fig. 204), maxillule (Fig. 210), and maxilla are similar to those of the male. Maxilliped (Fig. 246): endopod differs from the male endopod in having two setae, one pectinate and one simple on segments I and II (Fig. 247); and on segment III a pectinate seta only. Legs I, II, III (Figs. 215, 221, 226) are similar in male and female specimens. Leg IV (Fig. 228) differs from the male leg IV in not having setae on the coxopod and on the first and second segment of the endopod, not having a small spine on the basipod, and having 6, instead of 7, setae in the last segment of the endopod. The exopod

of leg IV is similar in the male and female. Legs V (Fig. 234) are the same and have 2s, on the terminal segment. Each leg has only one branch, subdivided into 4 segments.

Copepodid V, *male* (Fig. 180): 10 specimens were 0.75 to 0.86 mm long. Body: 6 cephalothoracic segments and 4 abdominal segments + furca. Antennule (Figs. 192–193): 21 segments; from the 10th to the 16th, the segments of the right antennule are much wider than those of the left. Segment 15 is the longest of all. Antenna (Fig. 195): coxopod (1), basipod (2), endopod (2 : 13), exopod (1 : 3 : 3 : 2 + 3). Mandible (Fig. 205): coxopod, mandibular blade (9 teeth + *r*), basipod (4), endopod (4 + 7), exopod (1 : 1 : 1 : 3). Maxillule: external lobe I (7 + *r*), external lobe II (1), exopod (9), internal lobe I (10s + 6), internal lobe II (4), internal lobe III (4), basipod (5), endopod (3 : 5 : 7). Maxilla: lobe I to V with 3 setae each; endopod (5 + *r*). Maxilliped (Fig. 249): coxopod (8), basipod (3 + double seta), endopod (2 pectinate setae : 1 pectinate seta + 1 : 1 pectinate seta + 1 : 3 : 4). Leg I (Fig. 217): coxopod (several ms), basipod (1s), endopod (1 : 1 : 6), exopod (1s + 1 : 1 : 2s + 1s term + 3). Leg II (Fig. 222): coxopod (1?), basipod (1s), endopod (1 : 1 + ms : 7), exopod (1s + 1 + ms : 1s + 1 + ms : 2s + 1s term + 5). Leg III: coxopod (1), basipod (1s), endopod (1 : 2 : 8), exopod (1s + 1 : 1s + 1 : 2s + 1s term + 5). Leg IV (Fig. 229): coxopod (1 + 4ms), basipod (1s), endopod (1 + ms : 2 : 8), exopod (1s + 1 + ms : 1s + 1 + ms : 2s + 1s term : 5). Leg V (Fig. 235): left, with endopod (1s) and exopod (4s); right, without endopod; exopod with large 1s + 3s.

Copepodid V, *female* (Fig. 176): Length 4 specimens 0.99 to 1.03 mm long. Body: 6 cephalothoracic segments, 3 abdominal segments and furca (Fig. 237). Antennule (Fig. 190–191): 22 segments, the left similar to the right. Antenna (Fig. 199), similar to the male antenna, but may have a seta more on the coxopod and on the exopod. Mandible (Fig. 206) and maxillule (Fig. 212) similar to the male appendages. Maxilla (Fig. 242): lobe I to IV (3), lobe V (4), endopod (5 + 3). Maxilliped (Fig. 248) is similar to the male maxilliped, but differs in having numerous marginal setules on the basipod and 3 pectinate setae with two terminal setae on the endopod. Leg I (Fig. 216): coxopod (1 + marginal setules), basipod with fine marginal

setules, endopod with 1 seta more and exopod like in the male. Leg II (Fig. 223): coxopod (1), basipod (1s), endopod (1 : 2 : 8), exopod (1s + 1 : 1s + 1 : 2s + 1s term + 5). Leg III: similar to the male, but with one more spine on the basipod. Leg IV: similar to leg III. Leg V (Fig. 237) left and right legs similar, with one branch and a large terminal spine, a pointed protuberance externally, 2 lateral spines and 1 small terminal spine.

Discussion: JOHNSON (1949) described the post-embryonic development of *Pseudodiaptomus euryhalinus* JOHNSON. UMMERKUTTY (1964) studied the nauplii of *P. aurivilli* Cleve. FABER (1966a) characterized the stages III and IV of the nauplii of *P. coronatus* Williams, considering only the caudal armature. JACOBS (1961) reared *P. coronatus* in the laboratory through four successive generations using *Chlamydomonas* as food. Five nauplii and six copepodids were observed in the total cycle of the species (JOHNSON, 1949; JACOBS, 1961).

Pseudodiaptomus euryhalinus occurs in the East Pacific in the waters of San Diego and Mission bays in California and in the saline waters of the Soledad Creek lagoon. JOHNSON observed the hatching of the nauplius of *P. euryhalinus* at stage II, as in *P. acutus*. The sizes of the naupliar stages are similar to the corresponding *P. acutus* stages. They are also similar in form. There is a larger number of setae, 1 or 2 more, in the antennules, antennae and mandibles of *P. euryhalinus*, and a larger number of spines on the antennules. The labrum of *P. acutus* has large central spines besides numerous minute spines. The large spines do not occur on the labrum of *P. euryhalinus*. On the distal segment of the antennule of *P. euryhalinus* among plumose setae, there is one seta which is shorter and without minute setules. The latter seta does not occur in *P. acutus*. The mandibular blade, in both species, is present, from nauplius IV onwards.

Pseudodiaptomus aurivilli Cleve, from Indian waters, has relatively smaller nauplii which also leave the egg at stage II. The number of long setae of the antennules is larger than in larvae of *P. acutus*, but otherwise there are less setae on the nauplii. UMMERKUTTY (1964) mentions an aesthete on the antennule of the larval

stages IV, V and VI of *P. aurivilli*. It is possible that an aesthete is also present in the antennule of *P. euryhalinus* (the non-plumose seta of the appendage). UMMERKUTTY notes an asymmetry of the antennules in the males of the copepodid stage IV, whilst the 5th pair of legs are almost symmetrical. In *P. acutus*, the asymmetry of the fifth legs can be already observed in the copepodid stage IV.

The Pseudodiaptomidae with their extraordinary specialization of the mouth appendages seem to be an example of secondary adaptation to another habitat amongst the Calanoida. The nauplius of the Pseudodiaptomidae shows some harpacticoid characteristics, such as a tendency to a dorso-ventral depression, shortening of the antennules and positive geotaxis. They do maintain their planktonic character as they do not crawl on the bottom but touch it, and then swim away again. The copepodids remain longer on the substrate. The species is hypoplanktonic.

Family AUGAPTILIDAE

(Figs. 250–252)

Material: From fixed samples collected during the XII Cruise of the "M. Lomonosov" at 01°02' S and 30°02' W, off BRAZIL.

Habitat: Depth of the water layer 300 to 500 m, temperature 12°C, salinity 35.00‰.

Nauplius IV (Fig. 252): Length 0.35 mm. Oval body slightly flattened anteriorly. Oval labrum. Inferior lip with small dispersed spines. Antennules (Fig. 251) with last segment hardly spatulate: 0 : 2 + 1 : 7. Antennae: coxopod with a strong spine, with a tuft of setules + 1s; basipod, 1s; endopod, with 1 setose spine on segment I, and on segment II, 2 strong terminal setae (their tips slightly turned down), 3 thin setae, 2 setules; exopod, segmented with 9 strong setae with coloured tips, finely setose, turned towards the ventral region. The mandible has a coxopod (1), a basipod (1 strong spine + 2 thin spines), an endopod with a crenate outline, on which protuberances 8 setae are inserted, some with brightly coloured points; exopod, with 5 segments, 6 setae, passing in length, the posterior

region of the nauplius. Two long ventral spines represent the maxillules at this stage. The caudal armature has 2 short spines and 2 short sensory setae.

Nauplius V (Fig. 250): Length 0.37 mm. Oval body, slightly flattened anteriorly. Oval labrum, tapering towards the inferior lip. Minute spines on inferior lip. Antennules: 0 : 2 + 1 : 13. Antenna: coxopod, 1 spine with tuft of setules + 1s; basipod, 1 spinose seta; endopod, 1s + 1s : 3 + 4; exopod, 10 segments, 11 setae ending in coloured tips and finely plumose. Mandible: coxopod, 1; basipod, 1 strong plumose spine + 2; endopod, 2 strong plumose spines, situated proximally at right angles to the principal axis of the appendage and turned ventrally, each next to a thin and plumose seta + 4 thin and plumose setae; exopod, 4 segments, 5. Maxillule: 2 lobes (1 : 3 + 1). The seta of the external lobe of the maxillule has 2 spines at the tip. The caudal armature has 2 spines and 2 sensory setae, all short.

Discussion: Several Augaptilidae were found in samples taken in waters off Brazil. *Haloptilus longicornis* (Claus, 1863) was the most frequent and numerous species. It was more numerous among the 10 most numerous species in samples taken off the east coast of Brazil in depths between 100 and 300 m. Copepodids and adult stages were always present in the 6 samples of water from this depth in the "M. Lomonosov" collection. It was not found in waters below 500 m. The Calanoid nauplii first described here are also frequent in the layer between 100 and 300 m. Other copepod larvae are also present in the same samples, but they belong probably to the Metridiidae, the Euchaetidae and Oithonidae.

Haloptilus longicornis, like *Eucalanus elongatus* and *Rhincalanus cornutus*, is a large copepod, very transparent and delicate, with not very compact muscles. Its nauplius, like those of the cited species, must also be large and with thin well separated muscles. The nauplius here described has these characteristics. It also occurs frequently in samples together with copepodids and gravid females of *H. longicornis*. The nauplius described above must be brilliantly coloured when alive because in material fixed four years ago it still had colour in the setae and posterior region. The general shape of the

body and of the antennules is cyclopoid on quick inspection; but the endopods of the mandibles are not subdivided, though strongly crenated. The muscles of the appendages are fan-like, therefore typical of Calanoida. The nauplius which most resembles this one in its general aspect, is the *Eucalanus crassus* nauplius. The antennae are like those of *Pleuromamma*. The mandible, with its crenated endopod and the two long and strong setae, differs a lot from all the other known naupliar mandibles. *Centropages* has a mandible with a bilobed endopod, but the setae of the first lobe are not as long and are spine-like. The depth at which the nauplius here described lives, and the strong setae, curved into hooks which arm its appendages, indicate carnivorous habits. *Centropages* lives in the surface layers and its nauplius is probably phytophagous. If the deep-living nauplius really belongs to *Haloptilus*, its general morphological aspect suggests that the family to which it belongs is related closely to the Eucalanidae and also, more distantly, to the Metridiidae and Centropagidae.

Family CANDACIIDAE

(Figs. 253-266)

Material: Nauplius collected alive at the Caraïbisch Marien-Biologisch Instituut, CURAÇAO, and reared through metamorphosis to the first copepodid stage.

Habitat: In oceanic and shelf waters.

Nauplius VI (Fig. 253): The exuvia of this nauplius was lost soon after the first sketch made. Therefore it is possible that many thin setae were not observed. Before starting to metamorphose the nauplius had a brilliantly orange coloured gut, the rest of the body being transparent. The shape was longish. Length 0.32 mm. Antennule: 0 : 1 : 1 + 3. Antenna: coxopod, basipod, endopod (2), exopod (4) and perhaps more setae which were not seen. Mandible: coxopod, basipod, endopod (2), exopod (3). Maxillule: 2 thin spines, each inserted in the outline of a lobe. Maxilla: crenated protuberance with 3 wide spines, the proximal curved (Fig. 254). The maxilliped was not observed; it is so small in copepodid I, that in nauplius

VI it is probably only slightly outlined, if at all. The 2 first pairs of legs are visible. Each leg has two lobes with two or three pointed protuberances (Fig. 255). The caudal armature (Fig. 259) has two long plumose sensory setae; 1 pair of short ventral spines, situated almost terminally; 1 pair of spines inserted laterally at the base of the sensory setae and 1 more pair of short lateral spines.

Copepodid I (Fig. 262): Length 0.50 mm. Rounded body, short abdomen (3.5 times smaller than the cephalothorax). Antennule: short, reaching the second thoracic segment. The body has twice the largest width in the length. Antennule: 11 segments, setae as in Fig. 260. Antenna (Fig. 266): coxopod, basipod, endopod (2 + 3 + 1s), exopod (5 + 1s). Mandible (Fig. 261): coxopod with mandibular blade (2 teeth), basipod, endopod (2 + 3), segmented exopod (6). Maxillule (Fig. 258): internal lobe I (1s + 2); internal lobe II (2); endopod (3); exopod, a protuberance. Maxilla (Fig. 263): coxopod (1 + 2), basipod (2 + 1 hook), endopod (2 hooks + 1). Maxilliped (Fig. 264): coxopod (4s), basipod (2s), endopod (2s + 2). Leg I (Fig. 256): coxopod, basipod, endopod (2 + 3 term + 1), exopod (3s + 1s term + 2). Leg II (Fig. 257): coxopod, basipod, endopod (1 : 3), exopod (3s + 1s term + 3).

Discussion: *Candacia* nauplii were first described by BERNARD (1965a) for *C. armata* of the Mediterranean. The time of development from nauplius I to copepodid I at 16.5°C, in waters enriched by vitamins and growth substances, was 6 days (BERNARD, 1965a). The nauplius of the Candaciidae is lecithotrophic and lacks a mouth. The *Candacia* collected with greatest frequency in Curaçao is *C. pachydactyla*. It is therefore possible that the nauplius described here belongs to this species. Compared to the nauplius of *C. armata* (BERNARD, 1965a) it seems to have less setae, and to have a retarded development of the maxillule. This is larger in the nauplius VI of the Mediterranean species. The spines of the caudal armature of *C. armata* are longer than those of the nauplius here described. The brown colour of the nauplius of *C. armata*, when alive, differs completely from the orange-red of the Curaçao larva.

Family PONTELLIDAE

Labidocera fluviatilis F. Dahl, 1894

(Figs. 267–270, 172–273, 275–277)

Material: Nauplii and copepodids reared in the laboratory of the Base Norte of the Instituto Oceanográfico in Ubatuba from nauplii II. Also fixed plankton samples collected off Ubatuba, off Cananéia, and from the Plankton Sample Collection of the Instituto Oceanográfico of the University of São Paulo, BRAZIL.

Development: In Ubatuba, during summer (Feb. 2 to Feb. 19, 1965), with water temperature varying between 18° and 28°C, the nauplii in the rearing dishes moulted after a period of time which varied from 12 hours to 2½ days after the previous moult. The copepodids started moulting 2 or 2½ days after the metamorphosis. From the 6th to the 11th of February (1965) 14 nauplii II had changed into copepodids. Brought to São Paulo, one copepodid II took 6 days to moult into a copepodid III, receiving neither food nor fresh sea water in the rearing dish. I calculate 48 days for the total development of the nauplius I to the adult in Ubatuba waters. Gravid females were not collected and thus the nauplius I is unknown for this species. SAZHINA (1967) describes the egg of *Labidocera brunescens* as being round, and without spines, laid directly into the sea.

Movement: The first copepodids of *Labidocera* and *Centropages* are very much alike but are easily distinguishable by their different way of moving. *Labidocera* keeps the antennules nearly always half curved instead of quite outstretched as *Centropages*. It also moves slowly, but not with a perfect gliding movement as *Centropages*. The antennae and the mandibles vibrate metachronally, and the feet remain turned towards the front of the animal (Fig. 326). It moves with the body inclined 45° to the surface of the sea. By lowering or raising its abdomen the copepodid controls its downward or upward swimming. It leaps forwards, like all other calanoids, with the almost simultaneous movement backwards of all the legs and by laying the antennules against the body. The nauplii swim with paddle-strokes of the appendages, which result in successive forward impulses. The antennules and antennae curve downwards every time they are lowered, and they also flex when moved forwards, and only stretch out at the end of the motion. The movement of the appendages of the nauplii is similar to the flapping of the wings of a bird.

Light: *Labidocera* remains on the surface of the sea or of the water of the aquarium, during the day, generally swimming with the back partially or totally turned towards light which comes chiefly from above. It has transversal phototaxis (JANDER, 1965). Its nauplius is also positively phototactic, remaining on the lighted side of the aquarium.

Food: The nauplius lives on small green cells of the plankton. The copepodids also eat phytoplankton.

Nauplius II (Figs. 267, 269): Length of 3 specimens 0.22 to

0.27 mm, including the caudal seta, and the eye protuberance. Body, undivided. Labrum, oval, with fine marginal setae. Area of the lower lip outlined by a row of small setae. 3 pairs of limbs. Caudal armature: 1b (long and spiny), 1b (short) + 4s (short). Antennule: 3 segments, 1 : 1 : 3 or 4 term + 3 (dorsal, marginal) + 4 (ventral and marginal). Antenna: coxopod, 2s (setose); basipod, 1s (setose) + \mathbf{x} ; endopod, 3 term + 4ms (almost terminal) + 1 (lateral, with setule); exopod, 6 segments, 1 : 1 : 1 : 1 : 1 : 2. Mandible (Fig. 273): coxopod, 1; basipod, 3; endopod, 2 lobes, 3 : 5; exopod, 4 segments, 1 : 1 : 1 : 2.

Nauplius III (Fig. 268): Length 0.30 and 0.28 mm, including the caudal seta. Body undivided. Labrum with marginal setules. Caudal armature: 2 sensory setae, 1b (spinose, long and on the left), 1b (short, and to the right); 8ms (subterminal); 2s (short, ventral, subterminal). Antennule: 3 segments, 1 : 1 : 4 term + 2 + \mathbf{x} . Antenna (Fig. 272): coxopod, 2s (setose) + 2; basipod, 1s + \mathbf{x} ; endopod, 4 term + ms (subterminal) + 1 (with lateral setule); exopod, 1 : 1 : 1 : 1 : 1 : 3. Mandible (Fig. 275): coxopod, 1; basipod, 4; endopod, 2 lobes, 3 (spinose) : 5; exopod, 1 : 1 : 1 : 2(3).

Nauplius IV (Fig. 270): Length of 6 specimens 0.32–0.43 mm. Body divided into two segments, 3 pairs of limbs, and the fourth outlined. Labrum like in nauplius III. Caudal armature, 2 sensory setae + 1b (long, on the left) + 1b (short, terminal) + 2s (ventral) + 1s + 8ms (subterminal). Antennule (Fig. 277): 0 : 1 : 1 : 6 (long) + 3 or 4 (short). Antenna: coxopod, 2s; basipod, 1s + 1 (short) + 5ms; endopod, 2 segments 1 : 1 (short) + 1 (long) + 5ms + 3 term + 1 term (short); exopod, \mathbf{x} + 1 : 1 : 1 : 1 : 2. Mandible (Fig. 276): coxopod, mandibular blade + 4 teeth; basipod, 4 (setose) + 1 + 1; endopod, 3 (setose) + 4 + \mathbf{x} ; exopod, 5. Maxillule: 3 (long) + \mathbf{x} .

Nauplius V (Fig. 280): Length 0.42, 0.44 and 0.50 mm. Body with one division, 3 pairs of limbs and outlined maxillule. Antennule (Fig. 278): 0 : 1 : 1 : 4 term + 2(3) + 2 (long) + 4 (short). Antenna (Fig. 282): coxopod, 2s; basipod, 1s + 2; endopod, 1 : 4 term + 1 (branched) + 8ms + 2; exopod, 7 segments, 9(8). Mandible (Fig. 279): coxopod, mandibular blade, 4 teeth; basipod, 4 setose; endopod, 3 (setose) + 5 or 6 (long); exopod, 6 segments, 7. Maxil-

lule: 6 setae on a lobe. Labrum and caudal armature like in stage IV.

Nauplius VI (Fig. 283): Length 0.44 to 0.62 mm, but most of the 9 specimens measured a little over 0.50 mm. Five body segments outlined. Labrum as in stage IV. Lower lip area with minute little spines. Three functioning appendages and 5 more outlined. Antennule (Fig. 281): 0 : 0 : 1 : 1 + ms : 6ms + 4 term + 1 (long) + 4, (short) + 3 (long) + 2 (short). Antenna (Fig. 285): coxopod, 2s; basipod, 1s (long) + 2 + 3ms; endopod, 1 : 2 + 1 (branched) + 4 term + ms; exopod, 7 segments, 8. Mandible (Fig. 287): coxopod, mandibular blade, 4 teeth; basipod, 3 (setose) + 1; endopod, 2 lobes, 4 : 6 (long); exopod, segmented, 6. Maxillule: 5 lobes, 0 : 0 : 0 : 3 : 5. Maxilla: 2 lobes, anterior lobe (2), posterior lobe (5). Maxillipeds: outlined, 2 lobes on the ventral median region. Leg I: endopod, 3; exopod, 2 + 3s. Leg II: endopod, 2; exopod, 2. Caudal armature (Fig. 284): 2 sensory setae, 1b (long), 2s term (short) + ms + 2s (short, ventro-lateral) + 2ms (lateral) + 2s (dorsal).

Copepodid I (Fig. 289): 7 specimens, 0.58 to 0.67 mm long with 4 specimens longer than 0.60 mm. Five cephalothoracic segments; one abdominal segment. Antennule: 9 segments. Antenna (Fig. 296): coxopod (1), basipod (2), endopod (2 : 10), exopod (2 : 2 : 4 + 1). Mandible (Fig. 300): gnathobase, 1 tooth (large) + 3 teeth + 1; basipod, 4; endopod, 6 + 2; exopod, 6 segments, 6. Maxillule (Fig. 304): external lobe I (4), external lobe II (0), exopod (6), internal lobe I (8), internal lobe II (3), internal lobe III (2), basipod (1), segmented endopod (6). Maxilla (Fig. 311): coxopod, 2 lobes, 4 : 2; basipod, 2 lobes, 2 : 2; endopod, segmented, 4. Maxilliped (Fig. 307): coxopod, basipod (1 : 2 : 1), endopod (1 : 1 : 2). Leg I (Fig. 327): coxopod, basipod, endopod (5), exopod (3 + 4s + 1s term). Leg II (Fig. 331): coxopod basipod, endopod (5), exopod (3 + 4s + 1s term).

Copepodid II (Fig. 290–291): 16 specimens, 0.70 to 0.90 mm long, the greatest number with 0.77 mm, and the largest specimens, obtained in Cananea. Body with 5 cephalothoracic segments + 1 not completely separated, and 2 abdominal segments. Antennule (Fig. 295): 11 or 13 segments. Antenna (Fig. 297): coxopod (1), basipod (1), endopod (2 : 10 or 11), exopod (0 : 4 : 4). Mandible (Fig. 301, 303): gnathobase, 2 teeth (large) + 3 teeth + 1; basipod,

4; endopod, 4 + 6; exopod, 5 segments, 6. Maxillule (Fig. 305): external lobe I (6), external lobe II (0), exopod (7), internal lobe I (8), internal lobe II (3 + ι), internal lobe III (4 or 3), basipod + endopod (8). Maxilla (Fig. 312): coxopod (2 + 2 : 2), basipod (2 : 1), segmented endopod (1 : 4 or 5). Maxilliped (Fig. 308): lobe I (1), lobe II (2), lobe III (1), endopod (1s + 1 : 1 : 3). Leg I (Fig. 328): coxopod, basipod (1), endopod (8), exopod (1s : 5 + 3s + 1s term). Leg II (Fig. 332): coxopod (1), basipod, endopod (8), exopod (1s : 5 + 2s + 1s term). Leg III (Fig. 335): coxopod, basipod, endopod (6), exopod (3 + 3s + 1s term). Leg IV (Fig. 339): 2 lobes outlined, with 2 setae each.

Copepodid III (Fig. 292–293): 18 specimens, 1.01 to 1.08 mm long (usually 1.05 mm) with the wider part of the body 0.31 to 0.25 mm wide; and 1.05 to 1.21 mm, when the wider part of the body measures 0.35 mm. Thus, animals both with a wide and narrow body are present at this stage. Body: 4 or 5 cephalothoracic segments, 2 abdominal segments. Antennule (Fig. 294): 18 to 20 segments. Antenna (Fig. 298): coxopod (1), basipod (1?), endopod (2 + 2 : 8 + 4 + ι); exopod (0 : 1 + 3 : 2 : 2 : 2). Mandible (Fig. 302): gnathobase (2 teeth + 3 teeth + ι), basipod (4), endopod (4 : 5 + ι), exopod segmented (5 + ι). Maxillule (Fig. 306): external lobe I (7), external lobe II (1), exopod (8), internal lobe I (8), internal lobe II (4), internal lobe III (4 or 3), basipod + endopod (11). Maxilla (Fig. 310): coxopod (3 + ι + 2 : 2), basipod (2 : 2), endopod (1 : 2 : 2). Maxilliped (Fig. 309): lobe I (2), lobe II (2), lobe III (1 + 1s), endopod (1 or 2 : 2 : 1 : 2). Leg I (Fig. 329): coxopod (1), basipod, endopod (8), exopod (2 : 3s + 4 + 1s term). Leg II (Fig. 333): coxopod (1), basipod, endopod (9), exopod (1 + 1s : 5 + 1s term + 3s). Leg III (Fig. 336): coxopod (1), basipod, endopod (8 or 7), exopod (1s : 5 or 4 + 1s term + 2s). Leg IV (Fig. 338): coxopod (1), basipod, endopod (6), exopod (3 + 1s term + 3s). Leg V: 3 outlined lobes which in the wide form (Fig. 341) have a lobe ending in two points and in the narrow form (Fig. 340), are rounded.

Copepodid IV, *male*: Length 1.27 to 1.38 mm (5 specimens). *Female*: Length 1.38 to 1.56 mm (6 specimens). The male body is narrow, the female wide. Abdomen (Figs. 346, 347): 3 segments. Antennule (Fig. 313): 23 segments. Antenna (Fig. 316): coxopod (1),

basipod (1), endopod ($2 + 2 : 7 + 4$), exopod ($0 : 3 : 2 : 1 : 3$). Mandible (Fig. 319): gnathobase (6 teeth + 1), basipod (4), endopod ($4 + 5 + 1$), exopod, segmented (5). Maxillule (Fig. 318): external lobe I (9), external lobe II (1?), exopod (9), internal lobe I (12), internal lobe II (3 or 4), internal lobe III (3 or 4) basipod (3), endopod ($4 : 5$ or 3 term). Maxilla (Fig. 322): coxopod ($4 : 2 : 2$), basipod ($2 : 2$), endopod ($1 + 2 : 1 : 1 : 4$). Maxilliped (Fig. 324): lobe I (2), lobe II ($2 + 1$), lobe III ($1 + 2ms$), endopod ($2 : 2 : 1 : 3$). Leg I (Fig. 330): coxopod (1), basipod, endopod (8), exopod ($1s : 3s + 1s$ term + 5). Leg II (Fig. 334): coxopod (1), basipod, endopod ($8 + 1$), exopod ($1s : 5 + 3s + 1s$ term). Leg III (Fig. 337): coxopod (1), basipod, endopod (8), exopod ($1s : 3s + 1s$ term + 5). Leg IV: coxopod (1), basipod, endopod (8), exopod ($3s + 1s$ term + 5). Male leg V (Figs. 343, 347): coxopod, basipod (1s), endopod smaller than exopod: the left (3s), smaller than the right ($3s + 1s$). Female leg V (Fig. 346) as the male, but, both left and right legs of the same size (3s).

Copepodid V: Length of *male* 1.75 mm; of *females* 1.80, 1.95, 1.90 and 2.00 mm. The male (Fig. 345) has 3(4) segments in the abdomen, the female 3 (Fig. 349). Male antennules: left (Fig. 314) with 23 or 24 segments, and right (Fig. 315) with 21 or 22 segments (in adult with 16). Female antennule has 24 segments. Antenna (Fig. 317): coxopod (1), basipod (1?), endopod ($1 + 2 + 2 : 7 + 1 + 6$) as in adult, exopod ($0 : 3 : 1 : 1 : 1 : 1 : 1 : 1$). Mandible (Fig. 320) as in adult: gnathobase (8 teeth + 1), basipod (4), endopod ($4 + 6 + 1$), exopod (5 segments, 6). Maxillule (Fig. 323): external lobe I (10 or 11), external lobe II (1), exopod (10), as in male and female adults; internal lobe I ($8 + 4$), which in the adult female has 16; internal lobe II (3); internal lobe III (4); basipod ($3 + 4$), as in adult; endopod ($1 : 1 : 3$) and in adult, $2 : 2 : 5$. Maxilla (Fig. 321): coxopod ($6 + 4 + 1 : 2$), basipod ($1 : 2 : 1 : 1$), endopod ($5 + 1$). In the adult the maxilla has a larger number of setose setae on the endopod ($6 + 2$). Maxilliped (Fig. 325): lobe I ($1 + 1$), lobe II ($2 + 1$), lobe III ($1 + 2$), endopod ($2 : 2 : 1 : 1 + 3$). In the adult it is similar. Leg I: coxopod (1), basipod, endopod ($3 : 6$), exopod ($1 + 1s : 1 + 1s : 5 + 1s$ term + 2s). Leg II: coxopod (1), basipod, endopod ($3 : 8$), exopod ($1 + 1s : 1 + 1s : 5 + 1s$

term + 3s). Leg III like leg II. Leg IV: coxopod (1), basipod, endopod (3 : 7), exopod (1s + 1 : 1s + 1 : 5 + 1s term + 3s). Legs V: in the male, one shorter than the other, without endopod, 4s. The longest leg V has a large protuberance on the last segment. In the female, both legs V are similar and have endopod and exopod. The exopod is bifurcated at the distal margin.

Discussion: FLEMINGER (1965, p. 127) refers to *Labidocera fluviatilis* F. Dahl as a synonym of *L. darwinii* Lubbock, the first *Labidocera* described of the genus and collected off Argentina below the 38° S. Later FLEMINGER & TAN (1966) and FLEMINGER (1967) noticed the strong endemism in *Labidocera* and cited *L. fluviatilis* as a species separate from *L. darwinii*. This was followed here. The comparison between *L. darwinii* and *L. fluviatilis*, from the places where they were originally found, will prove whether or not they are different species.

Developmental stages similar to those of *Labidocera fluviatilis* and *L. acutifrons* were studied in the following species: *Epilabidocera amphitrites* McMurrich (by JOHNSON, 1934b), *Labidocera jollae* Esterly and *L. trispinosa* Esterly (by JOHNSON, 1935), *L. bengalensis* Krishnaswamy (by UMMERKUTTY, 1964), and *L. brunescens* Czernavsky (by SAZHINA, 1967). The sizes of the several naupliar stages of *L. fluviatilis* are almost the same as those of *L. jollae*, larger than those of *L. trispinosa* and *L. brunescens*, and smaller than those of *E. amphitrites*. They are also a little smaller than those of *L. bengalensis*. *L. brunescens* has a maxillular spine in the exuvia of the naupliar stage III. In the American species there is only the outline of a lobule visible below the chitin in stage III. The species have a similar caudal armature, and alternately short and long setae on the distal segment of the antennule, with the exception of *L. brunescens*. *L. bengalensis* is the species in which the nauplii differ most from the others. The nauplii are longer, almost like those of *Pontellopsis* (UMMERKUTTY, 1964). The spines in the labrum are larger than in other species and the spine on the basipod of the antenna as well as the balancers in the caudal armature are very long.

Of the various species studied *L. bengalensis* grows most in length as is evident from the comparison between the lengths of the first

and last naupliar stages. In *L. fluviatilis* the growth of the nauplii is small and in 18 days they metamorphose. In this species the difference between the size of the nauplius IV and V is so small that, to distinguish one stage from the other, it is necessary to examine the distribution of the setae very carefully. *L. fluviatilis* grows most during the copepodid stages. These develop rather slowly in consequence, taking 30 days to reach maturity after the metamorphosis.

Considering only the larval stages it seems that *Labidocera* belongs to a phylogenetically more ancient stock than *Pontellopsis* and *Pontella*. The acicular character of the nauplii is probably a specialization. *L. bengalensis*, the only *Labidocera* known until now to have a long nauplius, is probably intermediate between the less differentiated *Labidocera* and the specialized *Pontellopsis*. *L. acutifrons* is widely dispersed in the warm oceanic waters and has the least differentiated caudal armature of the various pontellid nauplii studied. Usually the animal with the widest distribution is the least differentiated. The endemic species are more specialized, and probably derived. There are still very few species of *Labidocera* with known nauplii. More should be studied to elucidate the species relationships within the genus.

***Labidocera acutifrons* (Dana, 1849)**

(Figs. 271–274)

Material: Nauplii, probably belonging to this species, collected at the Caraïbisch Marien-Biologisch Instituut, CURAÇAO.

Habitat: In oceanic waters off Brazil, and off Curaçao in coastal waters with high salinity (more than 36.00‰).

Nauplii: They differ little from *L. fluviatilis*. The colour was blue and yellow when alive, whereas *L. fluviatilis* was rose coloured.

The smaller nauplius, 0.18 mm long, is in stage III (Fig. 271). It has 3 long setae and two short ones on the distal segment of the antennule. *L. fluviatilis* has a different setation and is larger at this stage. The endopod of the antenna has 3 lateral setae (in *L. fluviatilis* there is only one). The mandible is similar in both species. The

caudal armature of *L. acutifrons* in the third naupliar stage has two short and subequal balancers besides two spines, which are lateral instead of ventral as in *L. fluviatilis*.

The larger nauplius of *L. acutifrons*, 0.40 mm long, is in stage IV (Fig. 274). It has about the same length as nauplius IV of *L. fluviatilis*. There are more setae on the antennule (Fig. 288) and on the antenna than in *L. fluviatilis*. The mandible is smaller in *L. acutifrons*. The setae of the caudal armature have more or less half the length of the setae of the same stage of *L. fluviatilis*. Compared to this species, *L. acutifrons* has considerably reduced balancers and the labrum is enlarged posteriorly instead of narrowed.

The growth of *L. acutifrons* is very considerable from stage III to IV since at stage III, the nauplius is about half the size of the same stage in *L. fluviatilis*. At stage IV it reaches the length of the nauplius IV of *L. fluviatilis*.

Pontellopsis brevis (Giesbrecht, 1889)

(Figs. 364, 366, 368–371, 382–392)

Material: 6 nauplii reared to the stage of copepodid I collected from 22 to 27 August 1963, off the Carmabi, CURAÇAO; nauplii, stages II–VI, collected off Santos, BRAZIL, in shelf waters (1962–1964); 6 nauplii collected off the coast of Brazil from 17°16' S and 27°43' S in tropical waters; 110 nauplii collected in coastal water between 23°35' S and 25°7' S off Brazil; 1 nauplius collected off Curaçao in coastal waters; 1 nauplius collected in coastal water off Brazil at 01°22' N; 34 nauplii collected in surface shelf water off the South Coast of Brazil.

Habitat: The temperature of the water in which the larvae were collected varied from 15.3°C–28.4°C, more frequently from 21°–27°C; the salinity was generally above 34‰. All the nauplii were collected during the day, usually in the upper 35 m layer. The nauplii occurred during all the months of the year except in November and in December, probably through want of enough sampling at this time of the year. – From the data mentioned above the nauplii live preferably in surface waters, with salinity about 34.00‰ or more and temperature above 19°C. The species reproduces the whole year round. The adult lives in shelf waters (BJÖRNBERG, 1963), but the nauplius seems to prefer coastal water.

Movement: The nauplius moves by vibrating its three pairs of limbs, in the same way as in *Labidocera*, by successive impulses forwards (Figs. 391, 392). The nauplius can also clean the setae of the appendages and caudal armature, by flexing the body and using one of the pairs of limbs or the caudal spines as a brush.

Food: The colour of the gut, generally green, is an indication of phytophagous habits. Tintinnid lorica were observed in several larvae.

Colour: Near to the coast, in the south of Brazil, where the water has a low salinity, the nauplius is pale orange. In waters of higher salinity (36.00‰ or more), off Curaçao, the nauplii are blue and green coloured after the first stage which, owing to the yolk still present in the nauplius, is orange.

Nauplius II (Figs. 383, 389): Length of 2 specimens 0.47 and 0.49 mm, including the caudal spines. Shape: needle-like, wider anteriorly and tapering posteriorly. Caudal armature: a ring of short spines around the insertion base of the two balancers (Fig. 387), which are spinose. One balancer is more or less twice the length of the other. Another specimen had a row of minute spines anteriorly to the caudal armature. Labrum: long, pointed in the posterior margin, which is armed with very fine setae. Antennule, 1 : 0 or 2 + 1 : 4. Antenna: coxopod (1s + 1), basipod (1s + 1 or 2), endopod (2 or 1 + 3 term), exopod (5 segments, 6 or 5) (Fig. 384). Mandible: coxopod (0 or 1), basipod (2 or 3), endopod (2 lobes, 3 : 4), exopod (5 segments, 5) (Fig. 385).

Nauplius III (Fig. 388): Length of 5 specimens 0.84 to 1.00 mm, including the balancers. Acicular shape. Caudal armature: ventral minute setae irregularly distributed; a row of pre-caudal, dorsal setules; 2 ventral pre-terminal spines; a long, spiny and terminal balancer, to the left; and a short, also terminal, balancer to the right, both surrounded by setules at the base; 2 dorsal spines. Labrum long, widened posteriorly, and pointed. Antennule (Fig. 390): 3 segments, the first segment with three segments outlined, 1 : 1 : 4 + 2 + 5ms or 7ms. Antenna: coxopod (2s), basipod (1s + 2s + 1); endopod (2 : 4 term + 3 + 1 or 2), exopod (5 segments, 7). Mandible: coxopod (1), basipod (2 + 1), endopod (4 + 4 + 1) or (3 + 4), exopod (segmented, 5 or 6). Maxillules: 2 very small ventral spines, seen with difficulty.

Nauplius IV (Fig. 386): Length of 6 specimens 0.85 to 1.15 mm (generally more than 1.00 mm long). Acicular shape. Caudal armature: 3 rows (1 dorsal) of short setae, and many setules latero-ventrally dispersed; 2 pre-terminal ventral spines; 1 balancer, short and to the right, and 1 long and spiny balancer to the left; 4 short spines at the insertion of the balancers. Labrum, tapering anteriorly, posteriorly widened and with a pointed process. Antennule (Fig. 371), 0 or 1 : 1 + 1 + 5ms : 6 + 6 + ms. Antenna: coxopod (2s), basi-

pod (1s + 2 + ms), endopod (1 : 3 term + 2 + 2ms or 4ms), exopod (5 or 6 segments, 7 or 8). Mandible: coxopod (1?), basipod (3), endopod (4 + 4 or 5), exopod (5 segments, 5). Maxillule: 2 lobes with 2 setae on the endopod and 3 on the exopod.

Nauplius V (Fig. 364): Length of 9 specimens including the balancers 1.26 to 1.45 mm. Acicular shape. Caudal armature: 7 rows of setules (Fig. 369), the third formed by 3 ventral series of setules; 4 ventral, pre-terminal spines, with setules at the insertion region; 2 terminal spines and 2 balancers, with setules at the base of insertion. The right balancer is very short; the left one is longer than the half length of the body. Antennule, 0 or 1 : 2 + 1 + 4ms: 1 or 3ms + 5 (short) + 3 (long) + 4 (terminal setose). Antenna: coxopod (2s), basipod (2s + 2), endopod (1 : 4 term + 3 + m), exopod (Fig. 369), 5 segments, 7 + 2 (short). Mandible: coxopod (1 or 2), basipod (2), endopod (9 or 8), exopod (5 segments, 5). Maxillule: 3 lobes (1 : 2 : 5). Maxilla: outlined lobe.

Nauplius VI (Fig. 366): Length, including balancers, in 12 specimens 1.34 to 1.70 mm. Acicular shape. Caudal armature as in stage V. Labrum, similar in stage V. Antennule (Fig. 368): 0 or 1 : 1 + 3s + 1 (long) : 7 (short) + 7 (long, lateral) + 4 (terminal). Antenna: coxopod (2s + 1), basipod (1s + 1), endopod (1 : 5 long + 6 short + 2ms), exopod (7 segments, 8). Mandible: coxopod (1 + mandibular widening), basipod (3), endopod (4 + 6), exopod (5 segments, 5). Maxillule: 3 lobes + basipod, outlined (0 : 2 : 7). Maxilla: 1 lobe with serrated margin. Maxilliped: 1 lobe, with terminal point. Leg I: 2 lobes, endopod (2s), exopod (2s + 2s). Leg II: 2 lobes, endopod (2s), exopod (3s). Two more pairs of posterior appendages are outlined ventrally.

OTHER PONTELLID LARVAE

(Figs. 350–363, 365, 367, 373–381, 393–401)

Material: Larvae from the plankton collected off CURAÇAO, and in the samples of the "M. Lomonosov" collection, BRAZIL.

Nauplius II from Curaçao (Fig. 350): Length 0.63 mm, larger than the *Pontellopsis brevis* stage. Shape of the body as in *P. brevis*. Labrum rounded. Antennule with spines (absent in *P. brevis*) on segment II and III. Antenna: one spine less on

the basipod, one spine and two setae more on the endopod. Mandible: 2 spines more on the basipod, 2 setae less on the endopod; and one more on the exopod, when compared with *P. brevis* in the same stage.

Nauplius III (Fig. 351) of sample M-736 ("M. Lomonosov"): Length of 3 specimens 0.62, 0.67 and 0.72 mm. Smaller than in *P. brevis*. Rounded labrum. Antennule: more minute spines on the last segment and 3 minute, marginal spines (absent in *P. brevis*) on the second segment. Antenna: less setae and spines on the coxopod, basipod, and endopod. Mandible: as in *P. brevis*. The caudal armature is also similar in both species, but the ventral spines are inserted more posteriorly.

Nauplius IV (Fig. 355) of the sample M-736 ("M. Lomonosov"): Length 0.73 mm, balancer included. Labrum without point, but less rounded than in III. Antennule with a series of minute spines on the margin of segment II, and no spines on segment III. Thus it differs from the nauplii with rounded labrum from Curaçao and from *P. brevis*. It has fewer spines on the ventral region and on the antenna, than the Curaçao larva.

Nauplius IV (Fig. 352) of sample M-735 ("M. Lomonosov"): Length 1.62 mm (balancer included). The largest nauplius of the Pontellidae in stage IV known at present. Labrum rounded, body covered by more spines than in *P. brevis*. Antennule with minute spines on segment II and on the last segment. The other appendages have the same setation more or less as *P. brevis*.

Nauplius IV from Curaçao (Fig. 373): Length 0.77 mm, smaller than in *P. brevis*. Rounded labrum without pointed process. Antennule with less setae than in *P. brevis*. Antenna with more setae (7 or 8) on the endopod and (9) on the exopod. Mandible with one seta more on the exopod and on the basipod. Less spines on the caudal armature than in *P. brevis*. Minute spines or setules on the ventral region of the body absent, possibly lost.

Nauplius V from Curaçao (Fig. 377): Length 1.07 mm, smaller than in *P. brevis*. Labrum rounded. Antennules armed with setae, without spines. Setation more or less as in *P. brevis*: less setae on the exopod and on the endopod of the antenna and more setae on the mandible. It does not have the ventral band of minute spines which is present in the *P. brevis* nauplius. The maxillules are composed of two lobes, with 2 setae on the inner lobe and 4 setae on the outer lobe. *P. brevis* has a maxillule with 3 lobes in this stage, and the outline of the maxilla.

Nauplius VI from Curaçao (Fig. 375): Length 1.33 mm, smaller than in *P. brevis*. Rounded labrum, without point. Antennule (Fig. 378): 0 : 1 + 1 + 5 or more ms: 4 ms (marginal) + 4 ms (distal) + 8 (short, marginal) + 3 (median) + 2 (long marginal) + 3 term. Antenna, mandible and caudal armature similar to the appendages of *P. brevis*. The maxillules are more developed than in *P. brevis*, but the outline of legs III is not visible.

Copepodid I of *Pontellopsis* (Figs. 365, 367): It was obtained in Curaçao from a pontellid nauplius. It is similar to the description of the same stage of *P. mediterranea* as published by Claus (1893, p. 20–22), and similar also to the copepodid I of *P. brevis* found in Brazilian waters. Figures 393 to 401 are drawings of the various appendages. Antennule: 9 segments. Antenna: coxopod, 1; basipod, 1; endopod, 8; exopod, 7. Mandible: coxopod, with mandibular blade (4 teeth); basipod; endopod, 2 : 4; exopod, 5. Maxillule: internal lobe I, 6s; internal lobe II, 2s; internal lobe III, 2s; basipod; endopod, 6; external lobe I, 1s; external lobe II, 1s; exopod, 6. Maxilla: lobe I, 3; lobe II, 2; lobe III, 2; lobe IV, 3; lobe V, 2; endopod, 1 : 1 : 3. Maxilliped: basipod, 1; lobe I, 3; lobe II, 2; endopod, 2 segments, 1. Leg I: coxopod;

basipod; endopod, 5; exopod, 4 + 4s. Leg II: coxopod; basipod; endopod, 6; exopod, 3 + 1s term + 3s. Leg III, outlined.

Discussion: *Pontellopsis brevis* is the only species in the genus which is frequent off the South of Brazil; it occurs in shelf waters, in coastal and in oceanic waters (BJÖRNBERG, 1963). *Labidocera fluviatilis* occurs only in inshore and coastal waters, and its larva is quite different. *L. acutifrons* also has a different nauplius and occurs only in oceanic waters.

Off Santos, Ubatuba and Cananeia (Brazil) only one *Pontellopsis* nauplius occurred, the one with the pointed labrum. Its stages II to VI, and copepodids I, II, III of *P. brevis* were always found together. Thus, the nauplius was also identified as *P. brevis*.

The pontellid larvae of the samples collected from the "M. Lomonosov" off the North of Brazil in 1962 belong to two different species, and also differ from the *P. brevis* nauplii. One series of nauplii, found in surface waters from 0 to 25 m depth, were small compared to the corresponding stages of *P. brevis*. They were nauplii III and IV, and differed from *P. brevis* mostly in the spines present in the antennules and the rounded labrum. Another pontellid nauplius in stage IV was caught in a closing net from deeper layers (25–50 m depth) at the same collecting station. The distribution of spines on the antennule of this nauplius differs from that on the smaller nauplii collected in the upper 25 m, and on the corresponding stages of *P. brevis*. It has a larger number of spines in the posterior part of the body.

The species of Pontellidae found off the North and East coasts of Brazil are *Pontellopsis perspicax* (Dana, 1849) and *Pontellina plumata* (Dana, 1849), according to GAUDY (1963) and BJÖRNBERG (1963). LEGARÉ (1961) collected *P. plumata* and *P. brevis* off Venezuela, not very far from Curaçao. *P. plumata* is a little smaller than *P. brevis*, and could thus have nauplii like those found in Curaçao or in the "M. Lomonosov" collection, with a rounded labrum. *P. perspicax*, much larger, being almost 3 mm long, could have a nauplius such as the giant stage IV of the "M. Lomonosov" collection.

The other pontellid nauplii known are those of *Pontella mediterranea* (Claus) and *Pontellopsis occidentalis* Esterly. The first were described by CLAUS (1893) and by SAZHINA (1967), and those of *P. occidentalis* by JOHNSON (1965). *P. mediterranea* differs from all others here mentioned in the large mandibular blade present in nauplius VI, absent in *Pontellopsis*. It also has a triangular anterior region when observed dorsally. In the other nauplii described the anterior region is rounded. The nauplii of *P. occidentalis* are very much like those of *P. brevis* in the setation and shape of the body. They differ because they are shorter, and the terminal spines in the caudal region are longer than in *P. brevis*. This species also has two very short internal spines which correspond to two aesthetes in *P. occidentalis*. If there are also aesthetes in *P. brevis*, they are exceptionally small. The larvae of Pontellidae here described, except those of *L. fluviatilis*, either do not have a mandibular blade or have instead a protuberance on the coxopod of the mandible of nauplius VI. The copepodid I of *P. brevis* is very much like the copepodid I obtained in Curaçao. Its size varies between 0.84 and 0.92 mm. It is therefore longer than the Curaçao copepodid of 0.80 mm. The colour of the *P. brevis* copepodid is dark blue with red stripes across. The copepodid II measures 0.98 to 1.15 mm.

HANAOKA (1952a) showed the relationship of the Centropagidae to the Pontellidae, based on the distribution of setae and on the shape of the endopod of the mandible.

The species studied by JOHNSON (1965), SAZHINA (1967), UMMERKUTTY (1964) and myself corroborate the ideas of HANAOKA. In the nauplius of *Centropages furcatus* there is no mandibular blade. The Centropagidae also seem to tend towards the formation of the mandibular blade during the metamorphosis as observed in the Pontellidae nauplii. Several tintinnid lorica were found in the gut of nauplii of *P. brevis*. As the lorica is always open at the distal end, the larva need not crush it to digest the contents. Mandibular blades are not necessary if tintinnids are the principal food of the nauplius.

The only larvae large enough to be mistaken for the *Pontellopsis* nauplii are those of *Rhincalanus* and *Eucalanus elongatus*, but these are much wider and the terminal setae are very small compared to the balancers of *Pontellopsis*. Differences in the setation also permit the separation of the Pontellidae from the Eucalanidae. When alive, the nauplii of *Pontellopsis* can be readily distinguished from those of *Rhincalanus* and *Eucalanus* by their blue and yellow colour.

Family ACARTIIDAE

Acartia lilljeborgi Giesbrecht, 1892

(Figs. 402–410, 428–430, 433, 435, 437–438, 444–480, 485–487, 489–513)

Material: Nauplii collected at the Base Norte and Base Sul of the Instituto Oceanográfico, Univ. of São Paulo, reared in the laboratory. Fixed samples collected at the Base Norte, laboratory at São Sebastião, at Caraguatatuba, and at Santos (BRAZIL) and also from the Plankton Sample Collection of the Instituto Oceanográfico.

Habitat: Surface waters, with salinity from 28.00‰–34.00‰, temperatures from 17°–28°C more or less, in the coastal region, off the South of Brazil.

Development: *Acartia lilljeborgi* nauplii took one to two days to moult. The majority moulted after 28 or 36 hours, and some moulted 12 hours after the last ecdysis. Thus development from the first naupliar stage to copepodid I, takes about 7 to 9 days in laboratory conditions, with abundant food and in temperatures not lower than 20°C.

Movements: (Fig. 416) The nauplius moves by means of little successive strokes, vibrating the antennules and the mandibles. It follows a circular direction, a spiral downwards, a zig-zag (up or down), or moves in directions resulting from the combination of the others mentioned. It can turn on its longitudinal axis like a screw-driver. The copepodid movement is of the gliding type, slowly forwards while grazing, or a zig-zag forwards by successive strokes, one stroke a little to the left, the next a little to the right, as has already been observed for other *Acartia* (CONOVER, 1956). – The antennules are usually well stretched out (Fig. 419).

The adults are showing a strong vertical migration, but the copepodids and nauplii do not migrate so markedly (BJÖRNBERG & WILBUR, 1968). In the absence of light *Acartia lilljeborgi* does not migrate.

Colour: Nauplii and copepodids are transparent, the gut frequently green or light yellow, indicating a phytophagous habit. This was also observed in other *Acartia* (CONOVER, 1956). In living plankton kept in the laboratory, the copepodids and adults also eat small nauplii of other species. – The nauplii have three chromatophores (black when distended) around the anus, and the naupliar eye is black or dark red. Nauplii kept in the dark have two coloured points, one anteriorly and one posteriorly, besides the naupliar red eye.

Nauplius I (Fig. 402): Length of 4 specimens 0.12 mm. Oval shaped. Caudal armature, 2 setae, short and thin. Labrum, oval shaped. Antennule, 0 : 1 : 3. Antenna: coxopod, 1s; basipod, 1; endopod, 1 or 2 + 2; exopod, segmented, 5. Mandible: coxopod, 1; basipod, 2 (setose) + 1; endopod, 4 (setose); exopod, 3 segments, 4.

Nauplius II (Fig. 403): Length of 18 specimens from 0.13 to 0.15 mm. Oval shaped, anteriorly flattened. Caudal armature with two rows of thin setules and 2 terminal sensory setae (one ventral and one dorsal). Oval labrum, finely setose at the margin. Labium setose. Antennule, 0 : 2 : 4. Antenna: coxopod, 1mp; basipod, 1mp + 1 setose; endopod, 3; exopod, 1 : 1 : 1 : 2. Mandible: coxopod, 1 setose; basipod, 2 setose; endopod, 4 with setules; exopod, segmented, 5.

Nauplius III (Fig. 404): Length of 16 specimens from 0.15 to 0.18 mm, with the greater number 0.16 mm long. Oval shaped, anteriorly flattened. Caudal armature: 2 rows of setules, 1 ventral and 1 terminal spine with lateral, serrate flanges (Fig. 408), 2 sensory setae (dorsal and ventral). Labrum: oval and finely setose at the margin. Antennule (Fig. 429), 0 : 2 : 6. Antenna (Fig. 444): coxopod, 1mp; basipod, 1mp + 1 setose; endopod, 4 + 2 + 1ms; exopod, 5 segments, 5. Mandible (Fig. 437): coxopod, 1s; basipod, 2 spiny setae; endopod, 3s + 5 or 6; exopod, segmented, 5. Maxillule (Fig. 406): outlined – 1 short + setose seta.

Nauplius IV (Fig. 405): Length of 22 specimens from 0.18 to 0.24 mm, with a greater number 0.18 and 0.20 mm long. Oval form, flattened anteriorly. Caudal armature: 2 rows of lateral setules, 4s with lateral flanges (Fig. 408) and 2 sensory setae. Labrum, oval and finely setose on the posterior margin. Antennule (Fig. 430), 0 : 2 : 7. Antenna (Fig. 446): coxopod, 1mp; basipod, 1mp + 1; endopod, 4 + 2 + 1s; exopod, 5 segments, 7. Mandible (Fig. 438): coxopod,

1mp; basipod, 2s; endopod, 3 + 6; exopod, 5 segments, 5 + 1. Maxillule: 1 lobe, 2s + 1s + 1s anteriorly.

Nauplius V (Fig. 410): Lengths of 12 specimens between 0.22 and 0.25 mm, with the greater number 0.24 mm long. Oval shape, flattened anteriorly. Caudal armature: 3 lateral rows of setules, 4s, 2 sensory setae. Oval labrum, posteriorly setose. Antennule (Fig. 433), 0 : 2 : 8. Antenna (Fig. 445): coxopod, 1mp; basipod, 1mp + 1; endopod, 4 + 2 + 1s; exopod, 5 segments, 5 + 2. Mandible: coxopod, 1; basipod, 2s; endopod, 3 + 6; exopod, 5 segments, 5 + 2. Maxillule: 1 lobe, 3s + 1 lateral s + 1 anterior s. Maxilla: a protuberance.

Nauplius VI (Fig. 409): Length of 10 specimens between 0.23 and 0.30 mm, with the greater number between 0.24 and 0.27 mm. Oval shape, flattened anteriorly and posteriorly elongated, but maintaining a rounded outline. The nauplius is not so transparent at this stage. It has 5 well delimited segments. Caudal armature: 2 rows of setules in regression, 4s (very long), 2 sensory setae + 2s beside the large ventral spines. Labrum oval and laterally setose. Antennule, 0 : 2 : 8 + 1. Antenna: coxopod, 1mp in regression; basipod, 1mp in regression and 1; endopod, 6(7); exopod, 6 segments, 6(8). Mandible: coxopod, 1 + mandibular blade; basipod, 2s; endopod, 3s + 6 + 1; exopod, 5 segments, 6. Maxillule: 2 lobes, 3s : 2. Maxilla: 1 lobe, lateral to the maxillule. Maxilliped: 1 lobe, anterior and internal to the maxillule. Leg I: lobe I, 2s; lobe II, 2s + 1. Leg II: internal lobe, 2s; external lobe, 2s + 2s.

Copepodid I: Length 0.45 mm. Five-segmented cephalothorax; one-segmented abdomen (Fig. 447). Furcal setae 3 + 1. Antennule (Fig. 448), 8 segments. Antenna (Fig. 450): coxopod (1), basipod (2), endopod, 2 : 4; exopod, 3 : 3. Mandible (Fig. 449): coxopod; gnathopod, 6 teeth; basipod, 1; endopod (2 + 4); exopod, 1 : 1 : 3 + 1. Maxillule (Fig. 455): external lobe I (4), external lobe II, exopod (2), internal lobe I (7, setose); internal lobe II (3); internal lobe III (1), basipod with marginal microsetae; endopod, 5. Maxilla (Fig. 453): lobe I (2 + 1); lobe II (1); lobe III (1 + 1); lobe IV (1 + 1); lobe V (1); endopod (1 + 1 + 3). Maxilliped (Fig. 454): coxopod, lobe I (1), lobe II (2), lobe III (1); basipod; endopod (3, serrate). Leg I (Fig. 451): coxopod; basipod, endopod (2 + 4); exopod (0 : 3 + 1s

term + 3). Leg II (Fig. 452): coxopod; basipod; endopod; (5) exopod (2s + 1s term + 1 serrae seta + 3).

Copepodid II (Fig. 456): Length of 5 specimens 0.52 mm (2 specimens), 0.55 (2 specimens), 0.57 mm. Five cephalothoracic segments, one abdominal segment (and one, abdominal, outlined). Furcal setae: 3 + 1. Antennule (Fig. 457): 12 segments. Antenna: coxopod (1); basipod (5); endopod (8); exopod (7) (Fig. 458). Mandible (Fig. 459): coxopod, gnathopod (5 teeth + 1); basipod (1); endopod (2 : 4); exopod (1 : 5). Maxillule (Fig. 460): external lobe I (6 + 1); external lobe II (1); exopod (2); internal lobe I (7 or 8); internal lobe II (3); internal lobe III (1); basipod (microsetae on the margin); endopod (5). Maxilla (Fig. 464): lobe I (2 + 1); lobe II (1 + 1); lobe III (2 + 1); lobe IV (2); lobe V (1); endopod (4 + 1 + 1?). Maxilliped (Fig. 465): coxopod, lobe I (2), lobe II (2), lobe III (1); basipod with setose margin; endopod, 4s. Leg I (Fig. 463): coxopod; basipod; endopod (5); exopod (2 segments, 1s : 7). Leg II (Fig. 461): coxopod, basipod, endopod, (7), exopod (1s : 2s + 1 serrate terminal seta + 5). Leg III (Fig. 462): coxopod (1s); basipod (1s); endopod (5); exopod, 1s term (serrate) + 2s + 3.

Copepodid III (Fig. 494): Length of 15 specimens 0.62 to 0.75 mm (the greater number of 0.63 mm), furcal setae excluded. Five cephalothoracic segments, 2 abdominal segments (Fig. 498). Three furcal setae + 3. Antennule (Fig. 493): 19 segments. Antenna (Fig. 503): coxopod (1), basipod (5), endopod (11), exopod (7 + 1). Mandible: gnathopod (6 teeth + 1) (Fig. 507), basipod (1), endopod (2 + 4), exopod (1 : 1 : 3 + 1) (Fig. 506). Maxillule (Fig. 511): external lobe I (8), external lobe II (1), exopod (2), internal lobe I (8 or 7), internal lobe II (3), internal lobe III (1), basipod (minute setae), endopod (5). Maxilla (Fig. 466): lobe I (2 + 1), lobe II (1 + 1), lobe III (2), lobe IV (2), lobe V (1), endopod (4 + 1 + 1). Maxilliped (Fig. 469): coxopod (2 : 2 : 1), basipod (minute setae + 1 serrate spine), endopod (3 serrate spines : 1 serrate spine). Leg I (Fig. 472): coxopod, basipod, endopod (1 : 5 + 2ms), exopod (1s + 1s : 8 or 7 + 1s). Leg II (Fig. 475): coxopod (1s), basipod, endopod (6 or 7), exopod (1s : 5 + 2s + 1 term). Leg III (Fig. 479): coxopod (1s), basipod, endopod (7), exopod (1s : 4 + 1s + 1 term). Leg IV (Fig. 476): coxopod, basipod (1), endopod (5), exopod (3 + 2s + 1 term).

Copepodid IV, *male* (Fig. 495): Length 0.85, 0.86 and 0.88 mm. Two abdominal segments; 5 furcal setae. Antennule (Fig. 492): 19 segments. Antenna (Fig. 504): coxopod (1), basipod (6), endopod (12 + minute setae), exopod (3 + 5). Mandible (Fig. 509, 510): gnathobase (6 or 7 teeth), basipod (1), endopod (5 + 2), exopod (5 + x). Maxillule (Fig. 512): external lobe I (9 or 10), external lobe II (1), exopod (2), internal lobe I (9), internal lobe II (3), internal lobe III (1), basipod (minute setules), endopod (4). Maxilla (Fig. 467): lobe I (3 + x), lobe II (1 + 2), lobe III (2), lobe IV (2), lobe V (1 + x), endopod (4 + 2). Maxilliped (Fig. 470): lobe I (2), lobe II (2), lobe III (1), basipod (setules + 1), endopod (3 : 1 + x). Leg I (Fig. 474): coxopod, basipod, endopod (1 : 3 + 3), exopod (2 : 8 or 7 + 1s). Leg II: coxopod, basipod (1 + 1s), endopod (7), exopod (1s : 5 + 2s + 1 term). Leg III (Fig. 477): coxopod, basipod (1 + 1s), endopod (7), exopod (1s : 5 + 2s + 1 term). Leg IV: coxopod, basipod (1 + x), endopod (7), exopod (1s : 5 + 2s + 1 term). Leg V (Fig. 485): coxopod and basipod fused bearing one seta; left and right legs with 2 segments, the distal segment is twice the length of the proximal, and each has one terminal seta. The terminal seta of the right is twice the length of the left terminal seta.

Copepodid IV, *female* (Fig. 499): Length of 13 specimens 0.87 to 0.90 mm, mostly 0.89 mm or more. It has the same features as the male in this stage except legs V (Fig. 480) with the distal segments narrower than the proximal, and no terminal seta.

Copepodid V, *male*, (Fig. 497): Length 1.00, 1.10 (2 specimens) and 1.12 mm. Abdomen four-segmented. Six furcal setae, one very thin (Fig. 501). Antennule (Fig. 490, 491): 21 and 22 segments. Antenna (Fig. 505): coxopod (1), basipod (8), endopod (12 or 11 + minute setae), exopod (8). Mandible (Fig. 508): gnathopod (7 teeth), basipod (1 + setose margin), endopod (7 + 2), exopod (6). Maxillule (Fig. 513): similar to the appendage of copepodid IV, but with 2 setae more on the endopod. Maxilla (Fig. 468): lobe I (4), lobe II (x or 2 + 1), lobe III (1 or 1 + x), lobe IV (2 + x or 2), lobe V (2 + x), endopod (4 + 1). Maxilliped (Fig. 471): lobe I (2), lobe II (2), lobe III (1), basipod (1 + minute setae), endopod (1 : 1 : 1 : 1 + x). Leg I (Fig. 473): coxopod, basipod, endopod (1 : 3 + 3), exopod (0 : 2 : 5 + 2). Leg II, III (Fig. 478) and leg IV alike, with a 3-

segmented exopod. Legs V (Fig. 487): left ramus with 2 spines, right ramus with 3s.

Copepodid IV, *female* (Fig. 496): It differs from the male copepodid in size: 1.13 to 1.14 mm. The abdomen has 3 segments (Fig. 502). The legs V are symmetrical (Fig. 486): the basipod with a long seta, and the exopod, with a spine-like protuberance. The legs II, III, and IV have the same number of setae as the male's: coxopod, basipod (1s + 1), endopod (2 : 5), exopod (1s : 1s + 1 : 5 + 1 + 1 term).

***Acartia danae* Giesbrecht, 1889**

(Figs. 420–426, 431–432, 434, 436, 439–443, 481–484, 488)

Material: Living and fixed nauplii from samples collected from the pier and from a boat, at the Carmabi, CURAÇAO. Fixed nauplii from the plankton collection of the Instituto Oceanográfico, BRAZIL. *A. danae* was not reared in the laboratory.

Habitat: Nauplii of *A. danae* were collected in large numbers in salinity 36.00‰ or more, and temperatures around 25°C or more off Curaçao.

Nauplius II (Fig. 420): Length 0.14 mm. With the characteristics of nauplius II of *Acartia lilljeborgi*, but differing in having a strongly setose labrum, the endopod of the antenna (Fig. 440) with 1 seta more, the endopod of the mandible (Fig. 436) with 4 extra setae and exopod of the same with indistinct segmentation and 4 + 2 setae.

Nauplius III (Figs. 421, 424): Length of 2 specimens 0.17 mm and 0.16 mm. The features are the same as those of nauplius III of *A. lilljeborgi*, with the exception of the following: labrum with strong setae, exopod of the antenna with 6 + 1 setae, endopod of the mandible with 4 setose setae + 6 thin setose setae and mandibular exopod with indistinct segments and 6 setae.

Nauplius IV (Figs. 422, 425): Lengths of 3 specimens 0.17, 0.19, and 0.20 mm. With the same features as nauplius IV of *A. lilljeborgi* except the strongly setose labrum, the exopod of the antenna with 6 + 1 setae, the coxopod of the mandible with 1 hook + 1 spine, the maxillary lobe with only 2 spines + 1 spine.

Nauplius V (Fig. 423): Length of 20 specimens between 0.19 and 0.24 mm, with the greater number 0.21 mm long. The same features as the nauplius of *A. lilljeborgi* except the antennule with 7 thin setae in the last segment (Fig. 432), the coxopod of the mandible with a protuberance, the different outline of the mandibular blade, the endopod of the mandible with 8 setae and the 4-segmented exopod, with 6 setae. Maxillary lobe as in *A. lilljeborgi*, with 2 spines + 1 very small spine (not easily visible) + 1 spine anteriorly + 1 spine towards the mid-ventral region.

Nauplius VI (Fig. 426): Length of 38 specimens 0.20 to 0.29 mm, with the greater number 0.25 mm long. Features the same as in nauplius VI of *A. lilljeborgi* with the following exceptions: segment III of the antennule (Fig. 434) has 9 setae, and 1 spine; the endopod of the antenna (Fig. 443) has 7 setae + 2 spines; the mandibular blade of the coxopod of the mandible (Fig. 439) is outlined, but not as clearly as in *A. lilljeborgi*; the endopod of the mandible has 10 setae; the maxillule has 7 or 8 setae on the external lobe and 5 spines (minute) on the internal lobe; the maxillary lobe has 5 setae; the maxilliped is outlined; the internal lobe of the leg II has 2 spines + 1 small spine.

Copepodid I: Length of 3 specimens 0.33 and 0.35 mm. Body segmentation, and antennule as in copepodid I of *A. lilljeborgi*. Antenna: basipod (3); remaining setation and segmentation as in copepodid I of *A. lilljeborgi*. Mandible: as *A. lilljeborgi*, except the endopod with 2 + 6. Maxillule: external lobe I (4); external lobe II (1); exopod (2); internal lobe I (6); internal lobe II (3); and remaining morphology as in *A. lilljeborgi*. Maxilla: lobe I (2 + 1); lobe II (1); lobe III (1 + 1); lobe IV (2 + 1); lobe V (1); endopod (1 + 3). Maxilliped: as *A. lilljeborgi*. Leg I: coxopod, basipod, endopod (4), exopod (1s term + 3 + 4s). Leg II: coxopod, basipod, endopod (4); exopod (2s + 1s term + 1 term + 3).

Copepodid II: Length of 10 specimens 0.50 (3 specimens), 0.505 (6 specimens) and 0.51 mm. Division of the body and setation of the furca as in *A. lilljeborgi*. Antennule: 10 or 12 segments. Antenna: coxopod (1); basipod (4); endopod (8 + 1); exopod (8). Mandible: as in *A. lilljeborgi*, except the exopod with 4 term + 2s + 1 (long). Maxillule: as in *A. lilljeborgi*, except the external lobe I with 6, and

the internal lobe I with 6s. Maxilla: lobe I ($2 + 1$), lobe II (1), lobe III (2), lobe IV ($1 + 1$), lobe V (1); endopod ($4 + 1 + 1$). Maxilliped as in *A. lilljeborgi*. Leg I: coxopod, basipod; endopod, (0 : 4); exopod, 1s (long) : 3s (long) + 4 + 1 term. Leg II: coxopod, basipod, endopod (6), exopod (3s + 1 term + 5). Leg III: coxopod, basipod (1), endopod (5), exopod (1s term + 3 + 2s + 1s term). Leg IV: 2s.

Copepodid III: Length of 8 specimens 0.62 to 0.63 mm (the majority 0.63 mm). It differs from *A. lilljeborgi* at this stage in having 6 furcal setae, 13 (?) segments in the antennules, endopod of the antenna with 12 setae, internal lobe I of the maxilla with 7, and lobes IV and V with 2 setae, maxilliped with 5 setose setae on the endopod, leg I with 6 + 3s on segment II of the exopod, leg III with $4 + 2s + 1$ on the exopod (distal segment).

Copepodid IV, *male* 0.75 mm (2 specimens); *female* 0.76 mm long (4 specimens). It fits the descriptions of the copepodid IV of *A. lilljeborgi*, except in the following details: 18 segments in the antennule, 11 or 12 setae on the endopod of the antenna, 10 setae on the external lobe I of the maxillule, 8 setae on the internal lobe I of the same and 6 or 5 setae on the endopod of the maxillule. There are $2 + 1$ on lobe I of the maxilla; on lobes IV and III there are 2 setae; on lobe V, $1 + 1$; on the endopod of the maxillule, $4 + 5f$. The maxilliped has 1 setose, long and terminal seta, which is short in *A. lilljeborgi*. The left leg V in *A. danae* (Fig. 484) has 2 minute lateral spines and a terminal spine. In the *female* (Fig. 481) the distal segment has approximately half the size of the proximal segment on the rami of the legs V.

Copepodid V, *male*: Length 0.99 and 1.00 mm. Abdomen 3-segmented as in the female copepodid. The gnathopod has 8 teeth instead of 7 as in *A. lilljeborgi*. The maxilla has 1 seta less on lobes III and IV and 1 seta more on lobe V, when compared with *A. lilljeborgi*'s. The endopod of leg I has 6 terminal setae, the exopod has $6 + 3s$. The leg II has coxopod, basipod ($1s + 1$), endopod (3 : 6), exopod ($1s + 1 : 1s + 1 : 5 + 2s$ term + 1 term). The same setation is observed on leg III and IV, the endopod of which differs from *A. lilljeborgi* in having 2 : 7. The 2 spines of the left leg V of *A. danae* (Fig. 488) are also larger than in *A. lilljeborgi*. The other features of *A. danae* and *A. lilljeborgi* are alike in this stage. *Female*:

Length 1.05 mm (2 specimens). The ovocytes are visible in the immature female. It is morphologically similar to the male of the species in stage V excepting the greater length and the symmetrical legs V. The legs V of *A. lilljeborgi* in this stage are as *A. danae*.

***Acartia negligens* Dana, 1849**

(Figs. 411–415, 417–418, 427)

Material: From samples collected off the South of BRAZIL. The sample from which we obtained the nauplii of *Acartia negligens* drawn in the text, was collected at 30°17' S and 43°59' W and donated by the Brazilian Navy, Department of Hydrography and Navigation, to the Instituto Oceanográfico.

Nauplius II (Fig. 411): Length 0.13 mm. It differs from *Acartia lilljeborgi* and *A. danae* in the same stage, in having thicker first plumose seta on the basipod of the mandible. Setules of the caudal armature like those of *A. clausi* (see OGILVIE, 1953).

Nauplius III (Figs. 415, 418): Length 0.15 and 0.16 mm. It differs from the described nauplii because the first plumose seta of the basipod of the mandible is thicker than the others. The row of setules of the caudal armature is finer, and the setules are shorter and more numerous than in the other two *Acartia* species described.

Nauplius IV of *A. negligens* (Figs. 412, 413, 414, 417): Length 0.17 mm. It differs from *A. danae* and *A. lilljeborgi* in the same stage because of the shorter length of the caudal spines, and because of the third row of ventro-lateral setules, which is smaller and more regularly disposed.

Nauplius VI (Fig. 427): Length 0.24 mm. It has less developed maxillules, maxillae and maxillipeds, fewer caudal spines and smaller setules on the caudal rows than *A. lilljeborgi*.

DISCUSSION OF THE ACARTIA NAUPLII

Nauplii of *Acartia* were studied by OBERG (1906), HANAOKA (1952), GURNEY (1931), and characterized by OGILVIE (1953), CONO-

VER (1956), SAZHINA (1960) and FABER (1966a and b). The species studied were *A. bifilosa*, *A. longiremis*, *A. tonsa* and *A. clausi*. CONOVER's comprehensive work (1956) on the biology of *Acartia* furnished anatomical details of the several naupliar and copepodid stages of *A. tonsa* and *A. clausi*, the horizontal and vertical annual distribution of the different stages in the plankton of Long Island Sound during 1952-54; the physiology of each stage of development in laboratory conditions and in the field. Conover tried to rear the two species in the laboratory, but was not successful although he kept several copepods alive for several weeks. ZILLIOUX & WILSON (1966) reared *A. tonsa* in glass dishes during 25 successive generations, feeding them on algae.

Both *A. lilljeborgi* and *A. danae* are difficult to keep alive for a long time under laboratory conditions. The nauplii die easily, but the copepodids and adults remained alive and in good condition for one or two days in temperatures which varied from 18° to 25°C. I reared nauplii of *A. lilljeborgi* through 5 to 6 successive moults, up to the metamorphosis into copepodid I in February 1965. I did not try to rear *A. danae* and *A. negligens*. The *A. danae* larvae were taken directly from the plankton in Curaçao as this species was the only *Acartia* present in those waters at the time, and therefore the *Acartia* nauplii could belong only to this species.

The nauplii of *A. tonsa* and *A. clausi*, chiefly in the last stages, are about the size of the *A. lilljeborgi* nauplii. The first nauplii are smaller than in *A. lilljeborgi*. The development of *A. lilljeborgi* in Ubatuba and in Cananeia is much more rapid than that of *A. tonsa* and *A. clausi* in the Northern Hemisphere, where they produce only 4 generations per year (CONOVER, 1956). In Cananeia and in Ubatuba (Brazil), nauplii and copepodids of *A. lilljeborgi* at all stages of development are found in the plankton during the whole year. In the Caribbean *A. danae* nauplii and copepodids are also found all the year round. In 180 plankton samples taken 3 or 4 times a day and 2 or 3 times at night, during successive days in January, February, March, April, July and August 1963, *A. danae* was always present in larval stages in Curaçao waters. During the other months of the same year no plankton was sampled and thus, it was impossible to establish the number of generations per year. As the species repro-

duce quickly it is necessary to collect plankton daily during a whole year so as to obtain information on the subject. This animal is one of the dominant copepods in the coastal and mangrove waters of high salinity in Curaçao.

The nauplius I of *A. lilljeborgi* can be distinguished from *A. bifilosa* and *A. longiremis* (OBERG, 1906) by the absence of a thin, short seta on the first segment of the antennule. The first nauplius of *A. clausi* (CONOVER, 1956) is smaller and has one more terminal ventral seta on the last segment of the antennule. The first nauplius of *A. tonsa* is smaller and the two caudal setae are longer in the fixed animal, and turned outwards, when compared to the same stage in *A. lilljeborgi*. This species in the second naupliar stage differs from *A. bifilosa* and *A. longiremis*, as drawn by OBERG (1906), in having only one series of caudal setules. It differs from *A. tonsa* (CONOVER, 1956) in being larger, having 2 setae on the second segment of the antennule (*A. tonsa* has only one) and having the row of ventral setules situated anteriorly in the caudal region not interrupted. The nauplius II of *A. clausi* (CONOVER, 1956) is smaller and the posterior series of ventral setules is uninterrupted. In *A. lilljeborgi* it is interrupted. Nauplius III of *A. lilljeborgi* differs from the same stage of *A. bifilosa* and *A. longiremis* in having one seta less on the terminal segment of the antennule; from nauplius III of *A. clausi* and *A. tonsa* in having one seta more on the same segment. The nauplius IV of *A. lilljeborgi* differs from the corresponding *A. bifilosa*, *A. longiremis*, and from *A. clausi* in having a row of caudal terminal and maxillary setae which are shorter. It differs from *A. tonsa* in having a small spine-like seta above the maxillule. This is not subdivided into two lobes as in *A. tonsa* and in *A. clausi*; it has only one lobe as in *A. bifilosa*. The nauplius V of *A. lilljeborgi* can be distinguished from *A. bifilosa*, *A. longiremis*, *A. clausi* and *A. tonsa*, by its shorter labrum and caudal setae, and by its maxillary lobe which is not subdivided. *A. danae* differs from *A. lilljeborgi* in naupliar stage V in having the marginal setules of the labrum distributed in two rows (one row in *A. lilljeborgi*), and in having one spine less on the maxillule. Generally they are both very much alike, but can be distinguished by the habitat, *A. lilljeborgi* living in waters with low salinity (below 34.00‰), and *A. danae* living in waters with high salinity (above 35.00‰). In *A.*

danae the caudal setules are a little smaller and more regularly distributed, and of a smaller size generally than *A. lilljeborgi*. The nauplius VI of *A. lilljeborgi* differs from *A. bifilosa* and *A. longiremis* in having a larger number of setae on the terminal segment of the antennule and from *A. tonsa* and *A. clausi*, in having a smaller number of the same setae. In nauplius VI of *A. danae* the gnathobase is not as developed as in *A. lilljeborgi*. The maxillules, maxillae and maxillipeds are apparently more developed in the nauplius VI of *A. danae*. The number of setae on the various lobes is also larger.

Off the South of Brazil in subtropical waters of the surface, with salinity higher than 35.00‰ and temperature around 18°C, *A. danae* is partially replaced by *A. negligens*. In these waters some *Acartia* nauplii show different characteristics from those belonging to *A. danae*, though indistinguishable in size. One plumose seta of the basipod of the mandible is twice as thick as the other; in *A. danae* they are of the same thickness. The spines or minute setules of the caudal armature distributed in rows are very small and very regularly disposed, whilst in *A. danae* they are larger, and in *A. lilljeborgi* larger still, especially in the three last naupliar stages. This characteristic also distinguishes *A. negligens* from the other species of which the nauplii were described by OBERG (1906), CONOVER (1956) and SAZHINA (1960).

In *A. lilljeborgi*, in the female and male copepodid V, the spines on the last thoracic segment and on the abdominal segments are distributed similarly to those of the adult *A. tonsa*. This species occurs in colder coastal waters of subantarctic origin (BJÖRNBERG, 1963) and is characteristic of coastal waters in North America (CONOVER, 1956; BOWMAN, 1961). *A. lilljeborgi* replaces *A. tonsa* in the warmer coastal waters off Brazil and in the Caribbean (LEGARÉ, 1961; ZOPPI, 1961; GONZÁLEZ & BOWMAN, 1965), in waters where the temperatures are rarely below 18°C.

Acartia floridana must have evolved from *A. tonsa* in the brackish mangrove waters in Florida (DAVIS & WILLIAMS, 1950). The similarity between the copepodid V of *A. lilljeborgi* and the adult *A. tonsa* suggests that the latter speciated from the former in waters of lower salinity and temperature, by a phenomenon similar to neoteny. The nauplii of the species of the Northern Hemisphere, *A. clausi*, *A.*

bifilosa, *A. longiremis*, *A. tonsa*, have longer spines on the caudal region and seem to be closely related. *A. danae* with its small spines and *A. negligens* with still smaller spines in the caudal region of the nauplius, seem to show another trend within the genus. Within the group *A. longiremis* and *A. clausi* show another trend towards the loss of the rostrum in the copepodids. *A. lilljeborgi* also belongs to this group as it may or may not have the rostrum (see BOWMAN, 1965). *A. lilljeborgi*, *A. clausi*, *A. longiremis* and *A. bifilosa* do not have a spiny inner ramus of the fifth pair of feet in the female. *A. lilljeborgi* in the adult stage has two lateral spines at the posterior margin of the last thoracic segment, in common with *A. danae* and *A. negligens*, in which the lateral spines are gradually smaller.

Considering the many new species found recently in the plankton of regions which have been well studied recently, copepods seem to be able to speciate rather quickly. This is observed mostly in coastal areas, where there are more barriers separating populations, which favours the phenomenon. *Acartia* lives in coastal waters. In the various trends mentioned above among the species from the West Atlantic, the name of *A. lilljeborgi* recurs frequently. Based on this I propose the tentative species-relation-tree in which from *A. lilljeborgi* one branch leads to *A. clausi* and to *A. longiremis*, exemplifying the trend to the loss of rostral filaments and towards the lengthening of the caudal spines of the nauplius. The other branch gives rise to *A. danae* and to *A. negligens*, representing the trend towards the lengthening of the exopod filament of the fifth legs in the female, towards the diminution of the spines in the caudal armature of the nauplius and reduction of the lateral spines on the posterior margin of the last thoracic segment in the adult female. *A. tonsa* may also have originated from *A. lilljeborgi*, by neoteny.

The nauplii of *Acartia* can be mistaken in the living plankton for nauplii of *Oithona*, especially in the first stages, when their size is very reduced. It is then easy to distinguish them from *Oithona* nauplii by their movements. *Acartia* moves following a zig-zag course, like *Oithona*, but it can also circle round and round or spiral up and down, movements which *Oithona* cannot make. The first nauplius of *Acartia* is also very similar to the first nauplius of *Centropages* and of

Paracalanus. In Brazilian waters, in inshore and bay plankton, it differs from *Centropages* in being dark, and from *Paracalanus*, in being smaller.

HARPACTICOIDA

Family ECTINOSOMIDAE

Microsetella rosea (Dana, 1952)

(Figs. 514-547)

Material: Nauplius I was reared from eggs of females separated from the plankton in CURAÇAO. The nauplii II, III, IV and VI were taken from fixed samples, collected off Curaçao and Santos, BRAZIL.

Habitat: In coastal waters of Curaçao; in coastal waters and principally in shelf waters off the South of Brazil, and in other tropical waters.

Movement: The nauplius moves by small successive little strokes. This movement by a series of little jumps or jerks is characteristic of nauplii with short antennules and appendages, used as propulsion organs, such as *Microsetella* and *Euterpina*.

Colour: Rose-coloured nauplii and copepodids.

Nauplius I (Figs. 514-515): 3 specimens examined. Length 0.11 mm (in a sample taken off Santos), and 0.12 m (reared in Curaçao). Oval shaped, pointed posteriorly and flattened dorso-ventrally. Caudal armature: 2 long, setose, pre-terminal spines, setae dispersed in the ventral and marginal posterior region, 2 short sensory setae (?). Labrum with the anterior setose margin in the shape of a half-circle, and the posterior margin, almost straight, also setose. Antennule, 1 : 1 + 2 : 2 or 3 + setules. Antenna: coxopod and basipod fused, 1 large spine + 2s; endopod, 2 long setae + numerous setules; exopod, segmented, 4 + 1s. Mandible: coxopod; basipod, 1; endopod, 4; exopod, segmented, 4 setae (3 long ones) setose. Four chromatophores are in the posterior region of the nauplius.

Nauplius II (Fig. 517): Length of 1 specimen 0.14 mm. Oval shaped, with a posterior point; flattened dorso-ventrally. Caudal armature: 2 setose posterior spines, 1 series of pre-terminal ventral

setules, interrupted in the median region, setules at the base of the posterior spines. Labrum semi-circular with a straight posterior setose margin, and dispersed setae in the anterior marginal region. Antennule, as in nauplius I. Antenna: coxopod; basipod, 1 large and setose spine + 3s; endopod, 2 + 1 + ms; exopod, 4 segments, 1 + 4 (Fig. 516). Mandible: coxopod; basipod, 1 long seta; endopod, 3 or 4 term; exopod, segmented, 3.

Nauplius III (Fig. 518): Length (specimens from Santos) 4 of 0.14 mm and 1 of 0.14 mm. Shape of the body as in nauplius II, but without a posterior pointed process. Caudal armature: 2 large spines; 2 smaller spines, sensory seta (seen in the nauplius in lateral view); 2 very small, ventral and terminal spines; 2 rows of ventral setules, the second of which with 2 pre-terminal, ventral, median spines; setules at the base of the posterior spines. Antennule: as in nauplius II. Antenna (Fig. 524): coxopod, basipod (1 geniculate setose spine + 2 thin, long spines + 1); endopod, 2 long setae + 3 marginal setules; exopod, 4 segments, 5. Mandible (Fig. 525): coxopod; basipod, 1; endopod, 5 or 4 + setules; exopod, 3 segments, 3 + 2. Maxillule: 1 lobe, 1 seta. Labrum with setules on the posterior margin and two tufts of setules anteriorly.

Nauplius IV (Fig. 519): Length of 11 specimens (from Santos) 0.15 mm (4 specimens) and 0.16 mm (7 specimens). Shape as in nauplius III. Caudal armature: 3 pairs of terminal spines, sensory seta, setules on the base of the spines, 2 rows of setules + 1 pair of ventral setae. Labrum as in the other stages described, with two tufts of setules on the anterior margin. Antennule (Fig. 520), 1 : 1 setose seta + setules: 4 + setules. Antenna (Fig. 526): coxopod, basipod (1 large spine setose at the tip, with a median setule + 2 posterior setae + setules); endopod, 3 + setules; exopod, 4 segments, 4. Mandible (Fig. 527): coxopod, 1; basipod, 3 + setules; endopod, 5; exopod, 3 segments, 2 : 1 : 2. Maxillule: 1 + 1 setule (Fig. 521).

Nauplius VI (Fig. 528): Length of 14 specimens 0.15 to 0.19 mm. Shape as in nauplius IV. Caudal armature: 3 pairs of terminal spines, setules at the base of the spines + 4 rows of ventral setules, interrupted in the median region, sensory seta. Labrum with numerous marginal setules, all around (Figs. 528 and 522). Antennule,

1 : 2 setose + setules : 3 term + 1 lateral seta. Antenna: coxopod; basipod, 1 large spine with setules at the tip + 2 thin setae + minute, anterior, marginal spines; endopod, 3 + setules; exopod, 4 + 1 + setules. Mandible (Fig. 523): coxopod, 1s; basipod, 3 + setules (+ 1 long seta); endopod, 5 + 1 setose seta + setules; exopod, 3 segments, 1 : 1 : 1 : 1. Maxillule: 1 long seta + 3 setules. Maxilla: 1 row of setules. Maxilliped: 1 pair of spines. Leg I: 2 lobes with 2s on each side. Leg II: 2 lobes with 3s on each side.

Copepodid I, from the metamorphosis of a nauplius, 0.22 mm length (caudal setae excluded), with 2 pairs of legs and 1 pair of legs outlined, 5 body segments and legs with only one segment in the endopods and exopods. The specimens obtained from the fixed plankton were of the following lengths: 2 of 0.24 mm, 1 of 0.23 mm (Figs. 529, 532).

Copepodids II (Fig. 533), were taken from fixed plankton, 0.24 mm to 0.29 mm long (the majority, 0.27 mm), caudal setae excluded. Six-segmented body, a third pair of legs, with one segment in the exopod and in the endopod (Fig. 535). The other legs have two segments in the endopods and exopods (Fig. 534). The fourth pair of legs is outlined (Fig. 537).

The remaining copepodids correspond to 4 different forms: 1) probably copepodid III, 0.27 to 0.30 mm long, from Santos, and 0.31 mm long from Curaçao (Fig. 536), with 4 pairs of legs, the fifth pair present, 2 segments on the exopods and endopods of the first to the third pair of legs, and one segment in the endopods and exopods of the fourth pair, the fifth pair of legs only outlined; 2) probably female copepodid IV (Fig. 538), 0.47 mm long, from Curaçao, with fifth legs (Fig. 544) much more developed than the corresponding legs in the male; 3) male copepodids V (Fig. 539), 0.31 and 0.32 mm long, 4 pairs of legs and a fifth pair less developed than in the copepodid of Fig. 540, 8 body segments, 3 segments in the exopods and endopods of the legs I to IV; 4) copepodid V female, 0.39 to 0.51 mm long, 4 pairs of legs with 3 segments in the exopods and endopods, 8 body segments, a fifth pair of legs (Fig. 543), more developed than in the preceding copepodid.

A great variation in the length of the adult males and of the females was noted. Females varied from small forms of 0.38 to 0.44

mm to long and elegant forms of 0.63 mm. In these, the setae of the fifth legs were longer and the basipod smaller than in the small form, in which the setae were shorter and the basipod larger. Could this be another, giant, fifth copepodid of the female; or does the adult *Microsetella* have two different female forms? Figures 541 and 542 represent the different forms. Different forms of fifth legs were also found in the males (Figs. 545 to 547). Dimorphism of the adult male was found in *Euterpina acutifrons*, by HAQ (1965b), and it may occur also in other harpacticoid species of the plankton.

Discussion: OGILVIE (in LOVEGROVE, 1956) identified and described the nauplii of *Microsetella norvegica*, the biology of which was studied by FISH (1955) in the Gulf of Maine. Photographs of the nauplii were published in his work, but the details of the setation were not quite clear. OGILVIE made drawings of the caudal armature chiefly, and of the antennules, without going into the details of the remaining morphology of the nauplius.

The larval stages of *Microsetella rosea* differ from those of *M. norvegica* in the following characteristics: in nauplius I the larger number of fine setae in the caudal armature and ventral region; large setae in the caudal armature, which are relatively smaller than in *M. norvegica*. This was to be expected because in many copepods the longer the abdomen, and the caudal armature in the copepodid, the smaller the naupliar caudal armature and vice-versa. The adult of *M. rosea* has longer furcal setae relative to *M. norvegica*, and therefore has naupliar caudal setae relatively smaller. It is a species that presents very interesting problems during its development, and in the adult stage.

Other harpacticoid larvae which occur in the surface plankton belong to the Miracidae (*Miracia efferata* Dana, *Oculosetella gracilis* Dana and *Macrosetella gracilis*), to the Tachydiidae (*Euterpina acutifrons* Dana), and to *Longipedia*. The Miracidae are Harpacticoida which live in the plankton but have retained some of their benthic habits. CALEF & GRICE (1966) proved that there is an association between *M. gracilis* and the blue-green alga *Trichodesmium thiebauti*. This association, in this case with *Oscillatoria* (*Trichodesmium*) *erythraea*, was first demonstrated by KRISHNASWAMY (1949, also noted

in his 1951 paper). This is the substrate onto which the nauplii (Fig. 556) and young copepodids hang by means of special hooks of the mandibles and antennae (Figs. 557–558) developed in the larval stages. The body of the nauplius is not so flattened as in *Microsetella*, there is not a great development of the muscles since the nauplii move very little while hanging onto the algal filament. Their colour is bright orange, and they can be distinguished easily from *Microsetella* nauplii by the large hooks on their appendages (see also BJÖRNBERG, 1965; TOKIOKA & BIERI, 1966).

The naupliar stages of *Euterpina*, the most cosmopolitan hypoplanktonic copepod of coastal waters, were described by TESCH (1915), HAQ (1965b) and BERNARD (1963). They are always present in samples taken near the coast and in inshore waters from Curaçao to the Argentine (see RAMÍREZ, 1966). HAQ (1965b) studied the feeding of its hypoplanktonic nauplii which live on the bottom debris, but the nauplii also seem to be able to feed while in the plankton. *Euterpina* can be distinguished from *Microsetella* by its rounded appearance in ventral view (Figs. 551–552), by a small labrum, a large masticatory process on the antennae and a very complicated musculature, criss-crossing in all directions – it is a typical harpacticoid larva. The colour is dark. The *Euterpina* larva turns on its long axis, with the back or the venter up, and then down again, a movement which is not executed as frequently by *Microsetella* nauplii.

CYCLOPOIDA

Family OITHONIDAE

Oithona oculata Farran, 1913

(Fig. 555)

Material: Nauplii reared in the laboratory from the egg to the first naupliar stage, in the Carmabi at CURAÇAO, and in the Base Norte, Instituto Oceanográfico, at Ubatuba, BRAZIL.

Habitat: Copepodids and adults are frequent at night in the surface plankton of coastal waters.

Nauplius I (Fig. 555): Length 0.10 mm (1 specimen). Oval body and naupliar eye very conspicuous in a dark circular area. Caudal armature: 2 thin posterior ventral setae, almost terminal. A little above, internally, there are 2 dark chromatophores. Rose coloured pigment is concentrated near the region where the stomodaeum opens into the stomach (in the living animal). Labrum, almost pentagonal. Antennule: 0 : 1 : 3 + 1. Antenna: coxopod + basipod (fused), 1s + 1; endopod, 2 + 2 or 3; exopod, segmented, 6 + 1. Mandible: coxopod, basipod, 1 + 2; endopod, 2 segments, 3 : 3 + 1; exopod, 3 segments, 4.

Discussion: The nauplius is very much like the corresponding stage of *Oithona nana* and *O. simplex*. When alive it is soon recognized by the different colouration. When fixed it is distinguishable by its larger size and by some details in the distribution of setae, form of the labrum and number of spines.

***Oithona simplex* Farran, 1913**

(Figs. 559–566)

Material: The nauplii I were reared from the egg at the Carmabi, CURAÇAO. Advanced larval stages, from fixed plankton samples collected off Curaçao, and off Santos, BRAZIL.

Habitat: *Oithona simplex* is numerous and common in coastal and shelf waters, and it may occur in oceanic waters off Brazil and Curaçao, but is rarely taken by the commonly used plankton nets owing to its small size.

The eggs, small and opaque (3 or 4 in each egg-sac), took 24 hours to get large and transparent, when they hatched.

Colour: Nauplius I orange or rose anteriorly and at tips of appendages; labrum orange; eye dark red, and gut green in transmitted light.

Nauplius I: Length 0.07 mm (1 specimen). Body oval, labrum round or triangular (Figs. 559–560). Caudal armature: 2 ventral filaments, almost terminal. Antennule: segments not clearly separated, 0 : 1 + 3. Antenna: coxopod, 2s; basipod, 2 short setae; endopod, 1s + 3; exopod, segmented, 5. Mandible: coxopod, basi-

pod, 2; endopod, 2 segments, 2 plumose setae: 3; exopod, 3 segments, 4.

Nauplius III (Fig. 562): Length 0.10 mm. Oval-shaped, labrum almost square. Caudal armature: 2 filaments. Antennule, 0 : 1 : 4. Antenna: coxopod, 2s; basipod, 1 or 2 short setae; endopod, 1 short seta + 3; exopod, 5 segments, 5. Mandible: coxopod; basipod, 2 or 1; endopod, 2 segments, 3 : 4; exopod, 4 segments, 4. Maxillule: a strong, flanged, serrate spine, with a row of minute setules laterally and internally.

Nauplius IV (Fig. 563): Length 0.11 mm. Oval shaped, labrum almost square; body two-segmented. Caudal armature: 2 larger filaments, sensory setae, between which 2 flanged small serrated spines, and lateral to the filaments two more smaller spines. Antennule, 0 : 2 : 3. Antenna: coxopod, 2s; basipod, ?; endopod 1 + 3; exopod, with the setae almost in a tuft, inserted in the last segments, 5 segments, 5. Mandible: coxopod, 1; basipod, 1?; endopod, 3 : 3 or 4; exopod, segmented, 4. Maxillule as in nauplius IV.

Nauplius V (Fig. 564): Length 0.12 mm. Body with the same shape, divided into two segments. Labrum shaped as in stage IV. Caudal armature approximately as in nauplius IV. Antennule, 0 : 2 : 3. Antenna: coxopod, 2s; basipod, ?; endopod, 1 + 2 or 3; exopod, 6. Mandible: coxopod, ?; basipod, 1; endopod, 2 segments, 3 : 3; exopod, segmented, 4. Maxillule: two-segmented lobe with 5 distal, foleate spines + 1. Two tufts of setules on the inner margin of the inner lobe.

Nauplius VI (Figs. 561, 565–566): Length 0.14 mm. Body, labrum, caudal armature, as stage V. Antennule, 4 segments, 0 : 2 : 2 : 8. Antenna: coxopod, 2s; basipod, ?; endopod, 1 + 3; exopod, 5-segmented, 8 + 1. Mandible: coxopod, ?; basipod, 2; endopod, 3 plumose setae: 4; exopod, segmented, 4. Maxillule: coxopod, lobe with 5 foleate spines + 1 seta.

Discussion: *Oithona simplex* is easily recognized in the advanced larval stages by its serrate, flanged, caudal spines and by two large strong serrate ventral spines or by the hand-shaped maxillule. The maxillules of stage V and VI are different from all other maxillules of the known naupliar stages of the *Oithona* and *Oithonina*. They also diverge from the larval maxillules of the Oncaeidae and

Corycaeidae, which are very much like the *Oithona* maxillules. More nauplii of other Oithonidae should be studied, in order to decide whether or not this species should remain in the family, and in the genus *Oithona*.

***Oithona ovalis* Herbst, 1955**

(Figs. 567–580)

Material: Reared from the egg at the Base Norte and Base Sul of the Instituto Oceanográfico to the stage of nauplius II. The remaining stages from fixed or living plankton samples collected at the same Bases and off Santos, BRAZIL.

Habitat: In inshore brackish waters in the South of Brazil, where it dominates over all other copepod nauplii in number.

Movement: Typical of the Cyclopoida, zig-zag, by little forward strokes. About the feeding movements see STORCH (1928).

Colour: Dark, with a longitudinal black bar antero-posteriorly in the middle of the body. The remaining parts are transparent.

Nauplius I (Fig. 567): Length 0.09 and 0.08 mm. Oval shaped. Caudal armature: 2 fine setae. Antennule, 0 : 0 : 1 : 3. Antenna: coxopod, 1; basipod, 1; endopod, 2 or 3 + 1; exopod, 6. Mandible: coxopod, basipod, endopod (2s : 2 + 2), exopod (4).

Nauplius II (Fig. 568–570): Length, one specimen 0.10, and two 0.11 mm long. Shape: oval. Labrum: oval, almost circular, with 2 tufts of setules anteriorly and 2 posterior tufts. Caudal armature: 2 thin posterior setae, 2 thin ventral setae (= maxillules). The labium area is delimited by two ventral and lateral rows of setules. Antennules, 0 : 0 : 2 : 3 + tuft of setules (Fig. 570). Antenna: coxopod, 1 large spine + 1 seta; basipod, 2; endopod, 2 + 2 or 3; exopod, pre-terminally segmented (Fig. 569), 1 : 3 : 3. Mandible: coxopod (Fig. 573), basipod, 1; endopod, 3 : 3 + 1; exopod, 4 segments, 4.

Nauplius III (Fig. 571, 574–575): Length 0.12 and 0.11 mm. Shape: oval. Labrum rounded anteriorly and crenate posteriorly, with setose margin and 4 longer setules. Caudal armature: 2 pairs of lateral and terminal thin setae, 2 short terminal spines, between the

two pairs of setae. Labium limited by two rows of setules. Antennule, 0 : 1 : 2 : 3 + 3 term. Antenna: coxopod, 2s; basipod, 2; endopod, 2 + 2 term, exopod, 1 : 3 : 3. Mandible: coxopod, lobe I (1), lobe II (1); basipod, 2; endopod, 3 : 3; exopod, 4 segments, 0 : 1 : 1 : 2. Maxillule: a flanged, serrate spine ventral and pre-caudal.

Nauplius IV (Fig. 572): Length 0.12 and 0.13 mm. Shape oval. Labrum, rounded anteriorly, with 2 lateral tufts of setules; crenate posteriorly, with another 2 tufts of setules laterally to 2 thin and short spines. Caudal armature: 2 pairs of thin, terminal, lateral setae, with a tuft of setules at the insertion base, and between the two pairs, 2 terminal, ventral spines. Inferior labium as in the stage III. Antennule, 0 : 1 : (x) + x : 4 term + 5 or 6 setules. The seta (x) is especially long. Antenna: coxopod, 2; basipod, 2; endopod, 2 term + 2; exopod, 5 segments, 7. Mandible: coxopod, lobe I (1), lobe II (1); basipod, 2; endopod, 3 : 4; exopod, 4 segments, 0 : 1 : 1 : 2. Maxillule: 2 lobes with spines on the proximal articulation, lobe I (2s, short, lateral + 1 long seta), lobe II (2s, short, distal + 1 very long seta).

Nauplius V (Fig. 577): Length 0.11 to 0.14 mm. One specimen in this stage was 0.19 mm long. Body shape, caudal armature, and labium as in nauplius IV. Labrum, with more setules than in nauplius IV. Antennule, 0 : 1 : x + 1, (long and thick): 7 + 2 + 4 term. Antenna: coxopod, 2s; basipod, 2; endopod, 2 term + 2; exopod, 6 segments, 7. Mandible: coxopod, lobe I (1), lobe II (1); basipod, 2; endopod, 3 : 4; exopod, 5 segments, 1 : 1 : 1 : 1 : 1. Maxillule: basipod, 1 + 2; endopod, 4 + 1 long term; exopod, 2 + 1 term.

Nauplius VI (Figs. 576, 578–580): Two forms were found in this stage, one long and one short: 0.15 mm to 0.18 mm and 0.14 mm. The short form may be the nauplius VI, just after moulting, and the long form may represent the same stage just before metamorphosis. In both stages the body and the labrum are as in nauplius IV, but the caudal region is flattened in the short form and very distended and tapering in the long form. The two larger terminal spines of the caudal armature are longer and stronger and two very fine setae may appear between them. The 2 pairs of lateral thin setae are still present. Antennule, 0 : 1 : x + long and strong seta: 5 or 4 term + 4 to 8 lateral setae. Antenna: coxopod, 2s + 1 or 2; basipod, 2 or 1;

endopod, 2 term + 2 (lateral); exopod, segmentation only distally and a longer segment at the end, 1 : 1 : 1 : 1 : 3. Mandible: as in the stage V. Maxillule: basipod, 2 + 1s; endopod, 2 + 3 term; exopod, 2 + 1 (long). On the ventral region there are also the outlines of the succeeding four pairs of appendages.

Discussion: *Oithona ovalis* Herbst, characteristic of brackish bay waters and Brazilian mangrove regions, has been mistaken in an earlier work (BJÖRNBERG, 1963) for *Oithona minuta* T. Scott. GONZÁLEZ & BOWMAN (1965) consider it a synonym of *Oithona hebes* Giesbrecht, 1891. There is really a great similarity between the adults, but the endopod of the mandible of the adult *O. ovalis* always has 4 setae instead of 5, as in *O. hebes*. In Curaçao, neither occurs. They are apparently replaced by *Oithona nana* Giesbrecht, which prefers more saline waters. The nauplius of *O. nana* is very much like the *O. ovalis* nauplius. In the first, the labrum (see HAQ, 1965a; and Fig. 548) has a more strongly lobulated posterior margin than in *O. ovalis*, and the two spinules on the lobules are longer and stronger. In *O. ovalis* the posterior margin of the labrum is only slightly crenate, and the marginal spinules or setules are very thin. In the caudal armature of *O. nana* there are apparently setules (Fig. 548), in a Curaçao specimen, or spines, in the specimen described by HAQ, on each side of the long lateral setae. The terminal spines of the posterior region are small in *O. nana* and strong in *O. ovalis*. This is a feature also noted in *O. similis* (OBERG, 1906), but this species differs from *O. ovalis* in the diverse ornamentation of the labrum. The nauplii of *O. minuta* (SAZHINA, 1960) are smaller than those of *O. ovalis* and *O. nana*. The easiest difference to observe between *O. minuta* and *O. ovalis* is in the caudal armature. In the first nauplius of both it has the same aspect. In the second it has two long ventral setae less, when compared with *O. ovalis*. The third nauplius of *O. minuta* lacks the two short spine-like setae between the two pairs of long terminal, caudal thin setae. *O. minuta* in naupliar stage IV has only one lobe in the maxillule (two lobes in *O. ovalis*) and less setae, only two instead of the several setae which are present in the other species. Nauplii V and VI in *O. ovalis* have more spines on the maxillules than *O. minuta* in the same stages. The caudal armatures of

this species and of *O. nana* are apparently the same. In the last naupliar stages they differ in the size and in the smaller ornamentation of the maxillule.

Judging from the naupliar features there is a very close relationship between the species *O. similis*, *O. nana*, *O. ovalis* and *O. minuta*. The nauplii of *O. plumifera*, and *O. helgolandica* are closely related but differ from the *O. similis*-*O. ovalis* group.

***Oithona (Oithonina) nana* Giesbrecht, 1892**

(Figs. 548, 553)

Habitat: Frequent and abundant in CURAÇAO waters of outer and inner bays, with temperature above 25°C and salinity above 36‰.

Remarks: The development of *Oithona nana*, was described by MURPHY (1923) and in more detail by HAQ (1965a). The nauplii I, 0.08 mm long, are easily obtained from egg-carrying females reared in micro-aquaria. The eggs are black in transmitted light. One or two days after being in the rearing dishes the nauplii leave the eggs. The females carried 2 to 8 eggs each, in Curaçao. As the eggs matured they became clear and translucent. Their colour changed to red. The recently hatched nauplius was transparent with black stains and a yellow-brown bar mid-longitudinally. This bar corresponds to the gut. The second pair of appendages and the eye were red in transmitted light. Figures 548 and 553 give an idea of the naupliar morphology.

***Oithona plumifera* Baird, 1843**

(Fig. 554)

Habitat: It is a very euryhaline species, and may be found in water with salinity above 30‰, but, in large numbers only in waters with more than 34‰. It lives in a wide range of temperatures also. Because of its large size and transparency, it is the easiest nauplius to identify. *Oithona plumifera* is the most frequent nauplius found in tropical and shelf waters off CURAÇAO and BRAZIL.

Remarks: The developmental stages of this species, described by GIBBONS & OGILVIE (1933), are easily obtained: the first stages

from egg-carrying females, reared in the laboratory, and the remaining from the plankton of shelf and oceanic waters off Brazil, or from coastal waters of high salinity off Curaçao. They are large and transparent nauplii, flattened dorso-ventrally, and almost rectangular in outline, when seen in ventral view (Fig. 554).

Family ONCAEIDAE

Oncaea media Giesbrecht, and *Oncaea venusta* Philippi

(Figs. 581–626)

Material: First two naupliar stages obtained by rearing eggs from females of *Oncaea media* and *O. venusta*, and the advanced stages, from fixed samples collected in shelf waters off Santos (BRAZIL) and from coastal water off CURAÇAO.

Movements: The velocity of locomotion in *O. media* was measured in aquaria as the animal swam actively to the surface. It varied between 0.57 to 0.75 cm/s. The sinking is usually passive, benign 0.12 to 0.22 cm/s.

Oncaea migrate when placed in glass cylinders with sea water in the laboratory. In the morning under direct sunlight they accumulate at the surface. At about 12 : 00 they migrate down and at 16 : 30 h they are dispersed. It should be interesting to make controlled experiments and to verify the causes of this phenomenon.

Colour: The nauplii are yellow to orange and the copepodids may be of the same colour. They may be red stained if they belong to *O. venusta* or lilac to violet coloured in the *O. media* species.

Oncaea media and *O. venusta* shall be described together as it was impossible to separate the nauplii one from the other in the fixed plankton samples. Both species occur in the waters where the samples were taken, and both have similar nauplii. The number of samples in which the nauplii occurred were not enough to separate them by their size distribution curves. Nauplii I and II were reared from the eggs of each species.

Nauplius I of *Oncaea media* (Figs. 581–582). Length 0.05 to 0.06 mm. Oval body, slightly flattened dorso-ventrally. Caudal armature: 2 long and thin setae. Labrum, rounded. Antennule, 1 : 1 : 3 or 4. Antenna: coxopod, 1 + 1; basipod, 2 spiny setae; endopod, 2 or 3 term, exopod, 1 : 1 : 1 : 1 : 3 term. Mandible: coxopod,

1 or 2; basipod, 2; endopod with 2 lobes, internal (2 spines) and external (4 setae); exopod, 1 : 1 : 1. Nauplius I of *O. venusta* (Fig. 584). Length, 0.09 mm. Body as in *O. media*, but with more setae.

Nauplius II of *O. media* (Figs. 585–586): 0.08 mm long. Oval body. Caudal armature: 2 long setae. Antennule: 1 : 1 : 3 (?). Antenna: coxopod, 1s; basipod, 1s + 1; endopod, 1 or 2 + 3 or 2; exopod, 4 segments, 7 or 8. Mandible: coxopod, 1; basipod, 1 or 2; endopod, 3 : 4; exopod, 3. Nauplius II of *O. venusta* (Fig. 587): Oval shaped, with a labrum posteriorly armed with marginal setules. Antennule: 1 : 1 : 4. Antenna: coxopod, 1s + 1; basipod, 2; endopod, 2 + 3; exopod, 4 segments, 6 or 7. Mandible: coxopod, 1; basipod, 2; endopod, 2 segments, 3 : 4; exopod, 4 segments, 5. Caudal armature: 2 terminal filaments + 2s ventrally (= maxillules).

Nauplius III (Fig. 589): Length 0.9 mm. Oval body, elongated. Caudal armature: 2 pairs of long posterior setae. Labrum: as in nauplius II. Antennule, 1 : 1 : 3 term. Antenna: coxopod, 1s + 1; basipod, 1s + 1; endopod, 2 : 3; exopod, 5 segments, 5. Mandible (Fig. 590): coxopod, 1; basipod, 1; endopod, 3 : 4; exopod, 4 segments, 4. Maxillules: 2 ventral spines.

Nauplius IV (Fig. 592): Length 0.10 mm. Oval, elongated body, with one division outlined. Caudal armature: 2 pairs of long posterior setae. Antennule, 1 : 2 : 3. Antenna: coxopod, 1s (large) + 1; basipod, 1 (long) + 2 or 1; endopod, 3 (long) + 1 (long) + 1 (lateral); exopod, 5-segmented (one segment long, terminal) 6. Mandible: coxopod, 1; basipod, 2; endopod, 3 : 4; exopod, 4 segments, 4. Maxillules: 2 lobes, each with a ventral spine.

Nauplius V (Fig. 593): Length 0.15 and 0.13 mm. Long oval body, slightly flattened posteriorly. Caudal armature: 2 pairs of long posterior setae. Antennule, 1 : 2 : 5. Antenna: coxopod, 1s (large) + 1; basipod, 2 + 1 or 0; endopod, 2 lateral, short setae, 1 long terminal, 3 terminal setae; exopod, 5 segments, 8 or 6. Mandible: coxopod, 1; basipod, 2; endopod, 3 : 4; exopod, 4 segments, 4. Maxillule: 1 digitiform lobe with 2 term (1 long internal seta and 1 short external seta).

Nauplius VI (Figs. 588, 591, 594–595): Length 0.15 to 0.18 mm. Oval or rectangular elongated body. Antennule: 1 : 2 : 6 or 7. Antenna: coxopod, 0 : 1s (long) + 1; basipod, 1 (long) + 1; endopod,

4 or 3 term + 3 or 2 (lateral); exopod, 6 segments, 8 (1 term, very long). Mandible: coxopod, 1 large s; basipod, 2; endopod, 3 : 4 or 5; exopod, 5 segments, 6 or 5. Maxillule: basipod fused to coxopod, 1 long external seta; endopod, 1 large and 1 small spine; exopod, 1 very long and 1 very short terminal seta. Maxilla, maxilliped and legs outlined.

Copepodid II: The youngest copepodid found in the plankton (Fig. 596): Length 0.22 to 0.37 mm, the majority between 0.28 and 0.30 mm. Two-segmented abdomen and four or five-segmented cephalothorax. Antennule, 7 segments, with the fourth segment larger (Fig. 603). Antenna: 0 : 0 : 3s + 4 (Fig. 607). Maxillule: endopod, 1 + 2mp (setose); palpus, 4 (Fig. 611). Maxilla: coxopod + basipod; endopod, 2 setose spines (Fig. 614). Maxilliped (Fig. 610): coxopod; basipod, 2; endopod, 1 hook (plumose). Leg I (Fig. 622): coxopod, basipod (1); endopod (1 : 5 + 1s term); exopod (1s : 4s + 4). Leg II (Fig. 618): coxopod, basipod, endopod, 1 : 3 + 2 + 1s term; exopod, 1s : 2s + 1s term + 4. Leg III (Fig. 621): coxopod, basipod; endopod, 2 long setose setae + 1s term (long) + 1s; exopod, 1s : 2s + 1s term + 3. Leg IV: 1 lobe, 2s (Fig. 613).

Copepodid III: Length 0.25 to 0.45 mm, with many specimens about 0.35 mm long. The cephalothorax is five-segmented (Fig. 597) and the abdomen (Fig. 599) is three-segmented. Antennule: 7 segments. There are few differences in the other head appendages relative to copepodid II. The exopods and the endopods of the legs are 2-segmented (Figs. 617, 619, 620), except in legs IV (Fig. 623). Besides the figures mentioned, figures 606 and 616 are drawings of the setation on the appendages of the copepodid.

Copepodid IV (Fig. 598): Length 0.28 to 0.70 mm, mostly between 0.37 and 0.50 mm. Cephalothorax, five-segmented; abdomen with four segments. There are two types of abdomen: one with segment II shorter and segment IV longer, and the other with segment II longer relative to the first type (compare Fig. 598 with Fig. 600). In this stage leg IV also has both rami composed of two segments (Fig. 625). Leg I is as in the copepodid III. Legs II and III are like legs II of the copepodid III (Fig. 624).

Copepodid V: In the *female* copepodid the abdomen has 4 segments (Fig. 601) and the length of the specimens is from 0.39 to

0.84 mm. The *male* copepodid has 5 abdominal segments (Fig. 602), with the first as long as the third, the second equal to the sum of all the others, the fourth equal to half the length of the third. The lengths of this copepodid are 0.50 to 0.70 mm. In this stage of development all the legs have rami with 3 segments, except legs V, represented by three setae in the female and 2 setae in the male. Fig. 626 is an illustration of the setation on leg IV of this copepodid.

Discussion: Species of the Oncaeidae are among the most numerous in coastal, shelf and oceanic waters off Brazil, and dominate in numbers over the coastal water copepods off Curaçao. *O. mediterranea* is the only species of *Oncaea* with identified nauplii (HANAOKA, 1952b). The nauplii of *O. mediterranea* (HANAOKA, 1952b) are relatively larger than those of *O. media* and *O. venusta* obtained in CURAÇAO. In nauplius III of Curaçao the maxillules are represented by 2 ventral spines. In *O. mediterranea* they are two filaments or long setae. The antennule of our species has more setae than in *O. mediterranea*. Nauplius IV of *O. mediterranea* is a little larger than in *O. media* and the caudal armature is very similar or identical to that of *Oithona*'s. As the nauplii of the genera *Oithona* and *Oncaea* are very similar, it is easy to mistake one for the other. In stage IV and V *O. mediterranea* is larger and has fewer setae on the antennules than *O. media*. The maxillule is more developed in the nauplii from Japan. In *O. mediterranea*, it is segmented in the last naupliar stage, whilst in *O. media* it is not. This species has more setae on the mandible and antennae than *O. mediterranea*. *Oithona* nauplii can be distinguished from those of *Oncaea* by their shorter antennules and antennae.

Several species of *Oncaea* occur off BRAZIL and CURAÇAO in warm surface waters: *O. venusta* Philippi, 1843; *O. media* Giesbrecht, 1891; *O. subtilis* Giesbrecht, 1892; *O. curta* Sars, 1916. The two first species, because of their size and number, can colour the plankton red-orange if *O. venusta* dominates, and lilac-carmine red, if *O. media* is the most numerous. *O. subtilis* and *O. curta* can appear in large numbers once in a while but, as they are smaller, and their colour is yellowish they are less conspicuous. *O. venusta* lives in oceanic

waters and *O. media* in shelf waters off Brazil, but may also appear in coastal waters of high salinity. Here and in Curaçao they may dominate other copepods in number. Other species live in deeper and colder waters off Brazil and Curaçao. *O. conifera* may appear in colder surface waters. It is therefore very difficult to identify nauplii and copepodids off Brazil and Curaçao if they belong to *Oncaea*. While alive, it was possible to distinguish *O. media* copepodids from others by their usual lilac-colour. Copepodids V of *Oncaea* could be divided in length groups of 0.50, 0.70, to 0.75 and 0.80 mm. These different lengths probably correspond to different species.

Oncaea media carries 12 to 30 eggs in each egg-sac. The same female can be fertilized several times. By rearing *O. media* and *O. venusta*, I obtained nauplius I and II of each species in Curaçao, but from the second stage onwards all the rearing experiments failed. In order to obtain the copepodid I of *Oncaea*, I collected nauplii VI apparently belonging to the same series as nauplii I and II. The nauplii were reared through metamorphosis, but on examining the copepodid I, it had the characteristics of a young *Sapphirella*; this genus is considered by some to be the copepodid of *Hemicyclops* (see VERVOORT & RAMÍREZ, 1966; and OWRE & FOYO, 1967). The copepodids identified with certainty as belonging to *Oncaea* were those from stage II onwards. It is possible that the last naupliar stages and the first copepodid are temporarily parasitic, or they pass so rapidly from one phase to the other that the first copepodid remains inside the naupliar exuvia till it reaches stage II. The samples from which the copepodids of *Oncaea* were taken, also contained first copepodids of *Sapphirella*. If the *Oncaea* had planktonic, free copepodids I, these would also be caught as they would probably be as small as the copepodids of *Sapphirella*. More sampling with finer nets, or success in the rearing of *Oncaea* will solve the problem.

Family CORYCAEIDAE

Because of their numbers and frequency, they are water mass indicators. HANAOKA (1952) identified a nauplius of *Corycaeus*. I reared *Farranula* (*Corycella*) *gracilis*, *Corycaeus speciosus*, *Corycaeus giesbrechti* and *Corycaeus amazonicus* up to nauplius I for all species and up to nauplius II for the two last species. The remaining nauplii were not obtained. In waters of high salinity and high temperature *F. gracilis* occurred abundantly in all copepodid stages together with very numerous cyclopoid nauplii. When the nauplii were brought into the laboratory, young stages of *Farranula* appeared, but it

was never possible to establish with certainty if one produced the other. It is possible that some of the older nauplii from the other Corycaeidae live in the depth or are parasitic as no nauplii were found in the surface plankton in numbers which might correspond to the number of copepodids.

Farranula (Corycella) gracilis (Dana, 1853)

(Figs. 627–631, 633)

Material: Nauplius I reared in the laboratory from the egg, and the remaining nauplii collected in CURAÇAO waters off the Caraïbisch Marien-Biologisch Instituut. From fixed samples taken off the North of BRAZIL.

Habitat: Extremely abundant in Curaçao waters and in warm oceanic waters elsewhere, which contain egg-laden females of the species, the whole series of copepodids, along with the series nauplius III–IV described below.

Distribution: KLEVENHUSEN (1933) showed that *Farranula gracilis* is a species of warm water (more than 25°C), which prefers surface layers, although it was also taken by closing nets from depths between 1000 and 800 m. Its occurrence in these samples can be explained by the phenomenon of contamination (see GRICE & HULSEMAN, 1965) already observed for small species of Calanoida. *F. gracilis* lives in great abundance (64.5% of the Corycaeidae total for the South Atlantic, according to KLEVENHUSEN) in oceanic waters, but it may invade shelf waters (BJÖRNBERG, 1963) and can be found in coastal waters also. Its nauplii occur chiefly in warm oceanic waters. In the Caribbean (CERVIGÓN, 1964) it is likewise the most frequent and numerous species of the family. It was found in Piscadera Bay waters almost every day during Winter and Summer of 1963. It did not occur in the inshore waters of the Piscadera inner bay (Curaçao).

Colour: Nauplius I is slightly blue, with red chromatophores in the caudal and medio-dorsal region. The naupliar eye is red.

Nauplius I: Length 0.08 mm. Labrum and body, oval shaped and elongated (Fig. 633). Antennule, 0 : 1 : 2 (?). Antenna: coxopod, 1s + 1; basipod, 2; endopod, 2 + 1; exopod, 4 segments, 6. Mandible: coxopod; basipod, 1; endopod, 2 segments, 1 : 3; exopod, 3 segments, 4. Caudal armature: 2 long setae.

Nauplius III (Fig. 627): Length 0.15 mm. Antennule: 0 : 1 : 5. Antenna: coxopod, 1s + 1; basipod, 1s + 1; endopod, 2 + 3; exopod, 5 segments, 7. Mandible: coxopod, 1; basipod, 2; endopod, 2 segments, 1 thick ramified seta + 2 setose setae + 1 : 4; exopod, 4, segments, 4. Maxillules: 2 lateral spines. Caudal armature: 2 strong

ventral spines, 2 strong caudal spines, 2 pairs of thin (sensory?) setae on each side.

Nauplius IV (Fig. 628): Length 0.16 mm. Labrum with marginal setules. Caudal armature: 2 short curved ventro-lateral spines, and between them and near to them, 2 strong ventral spines; 2 thin (sensory?) setae on each side; 2 strong dorsal spines. The body is elongate and oval shaped, more rounded anteriorly and posteriorly; with four visible segments. Antennule: 1 : 1 + 1 : 4. Antenna: coxopod, 1s; basipod, 1s + 1; endopod, 2 + 3; exopod, 5 segments, 6 or 7. Mandible: coxopod, 1; basipod, 2; endopod, 1 thick ramified seta + 3 : 4; exopod, 4 segments, 4. Maxillule: 2 lobes, 3 : 2.

Nauplius V (Fig. 630): Length 0.20 mm. Antennule: 1 : 1 : 2 : 6. Antenna: coxopod, 1s; basipod, 1s + 1; endopod, 2 + 3; exopod, 6 segments, 8. Mandible: coxopod, 1; basipod, 1 + 1 (strong and pectinate); endopod, 2 segments, 1 strong, ramified + 3 : 5; exopod, 4 segments, 4. Maxillule: coxopod + basipod, 1; endopod, 3; exopod, 3. Labrum with marginal setules. Labium limited by two rows of setules, more or less parallel. Just above the maxillules there is a row of more conspicuous setules on each side. Caudal armature (Fig. 629): 2 small ventral spines a little below the maxillules; 2 larger spines a little further below, and separate from each other, 2 strong posterior ventral spines, 2 small curved spines, lateral to the strong spines; 2 very thin spines between the two pairs of curved spines; 2 strong posterior dorsal spines. The body has the same shape as in the preceding stage, but it is more inflated posteriorly, with 5 visible segments.

***Farranula (Corycella) rostrata* (Claus, 1863)**

(Fig. 632)

Material: It is a typical species of the region of the Subtropical Convergence, distributed from 20° to 40° S (KLEVENHUSEN, 1933). Its nauplius was therefore expected in that region. It ought to be a little different from the nauplii attributed to *F. gracilis*. A nauplius was found in a sample collected at 33°02' S. in subtropical surface water off South BRAZIL, with the characteristics expected (Fig. 632).

The nauplius of *Farranula rostrata* found differs from the nauplius attributed to *F. gracilis* in stage V, in having less setae on the an-

tennule and antenna, and less spines on the caudal armature. This has 2 pairs of spines or short ventral setae, one pair of short straight spines laterally on each side, between which are 2 stronger ventral spines, which are less chitinized than in the *F. gracilis* nauplii. There are also 2 pairs of long and thin setae in the caudal armature. The 2 strong dorsal caudal spines, present in the preceding nauplius are absent in this specimen.

***Corycaeus (Onychocorycaeus) giesbrechti* F. Dahl, 1894**

(Figs. 635, 638, 639–641)

Material: Reared to nauplius II in the laboratory of the Instituto Oceanográfico, at Ubatuba, BRAZIL, from the egg.

Distribution: KLEVENHUSEN (1933) considers this species to be coastal and belonging to the surface plankton. Its nauplii are probably not easily captured as they are very small. It occurs in the Caribbean (CERVIGÓN, 1964; LEGARÉ, 1961), in CURAÇAO, and off Brazil, abundantly. The nauplii have a labrum and a light green and rose coloured gut.

Nauplius I (Fig. 635): Length 0.10 mm. Antennule (Fig. 640): 2 : 2 : 3 + 2. Antenna (Fig. 641): coxopod, 1s + 1; basipod, 1 (long) + 1; endopod, 2 : 3; exopod, longer than endopod, nearly three times its length, 4 segments, 6. Mandible (Fig. 639): coxopod, 1; basipod, 2; endopod, 2 segments, 2 + 1 : 3 + 1; exopod, 3 segments, 4. Shape of the body: elongate and oval. Labrum, oval. Caudal armature: 2 long filaments.

Nauplius II (Fig. 638): Length 0.12 mm. Antennule, 2 : 1 : 4. Antenna: coxopod, 2s, basipod, 1 (setose) + 1; endopod, 3 : 3; exopod, 5 segments, 6. Mandible: coxopod, 1; basipod, 2 (setose) + 1; endopod, 2 segments, 1 ramified + 3 : 4 (plumose); exopod, 3 segments, 1 (long) : 1 : 2. The body is oval and elongate, with an oval elongate labrum, setose in the median region of the posterior margin. Caudal armature: 2 pairs of long lateral filaments + 1 pair of short and fine setae between the two pairs.

***Corycaeus (Ditrichocorycaeus) amazonicus* F. Dahl, 1894**

(Figs. 636–637, 642)

Material: Nauplius I and II reared from the egg in the laboratory of the Inst. Oceanográfico at Ubatuba, BRAZIL.

Distribution: *Corycaeus amazonicus* has been found from Caribbean to Argentine waters off Mar del Plata (KLEVENHUSEN, 1933; CERVIGÓN, 1964; GONZÁLEZ & BOWMAN, 1965; RAMÍREZ, 1966). Egg-laden females were collected for rearing purposes in Ubatuba, in coastal waters, but, under influence of cold waters. The eggs, as in *C. giesbrechti*, are green. The nauplii are rose coloured anteriorly and the gut is green posteriorly. The nauplii are more strongly pigmented than in *C. giesbrechti*.

Nauplius I (Fig. 637): Length 0.08 mm. Antennule, 1 : 0 : 4. Antenna: coxopod, 2s; basipod, 1 + 1; endopod, 1 : 2; exopod, 1 : 1 : 1 : 3. Mandible (Fig. 636): coxopod, basipod, 2; endopod, 2 segments, 1 : 4; exopod, 3 segments, 1 : 1 : 2. Body: oval, elongate. Labrum, rounded. Caudal armature: 2 filaments.

Nauplius II (Fig. 642): Length 0.11 mm. Antennule, 1 : 0 : 4. Antenna: coxopod, 1s + 1; basipod, 1 + 1; endopod, 2 + 3; exopod, twice longer than the endopod, 4 segments, 5. Mandible: coxopod; basipod, 1 (long) + 1; endopod, 2 segments, 2 : 3 or 4; exopod, 4 segments, 5. Body: oval, elongate, with labrum ornamented by dispersed setules on the posterior margin. Caudal armature: 2 pairs of ventral filaments.

***Corycaeus (Corycaeus) speciosus* Dana 1849**

(Figs. 643–645)

Material (Fig. 644): Nauplius I obtained from the eggs of a female in CURAÇAO.

Nauplius I: Body elongate and oval, 0.12 mm long; labrum rounded. Antennule, 0 : 1 : 3. Antenna (Fig. 645): coxopod, 1; basipod, 1 (+ 1); endopod, 1 : 2; exopod, twice as long as the endopod, 1 : 1 : 3. Mandible (Fig. 643): coxopod, 1; basipod, 2 + setules; endopod, 2 : 3; exopod, 3 segments, 1 : 1 : 2. Colour: it contains globules of orange colour (yolk?) in the posterior region, red stains over the body. Posteriorly it is greenish.

CONCLUSIONS ON THE EVOLUTION OF COPEPODS

The data presented in this work fall into two main categories: morphological and behavioural. The data on the distribution of nauplii are not numerous enough to permit generalizations, but from the evolutionary point of view it is possible to compare the morphology of the nauplii, and thus to summarize and draw conclusions from the data observed. On the other hand, "species-specific behaviour is in part the product of evolutionary process" and, therefore, subject to the same generalizations as the comparative morphology of the developmental stages (HINDE & TINBERGEN, 1966).

Ancestral forms are either undifferentiated and simple or have features which are repeated, developed or reduced in the various derived forms (SANDERS, 1963). Asymmetry is considered to be derived from symmetrical characteristics in the Bilateria to which the copepods belong. Concerning the evolution of copepods a further problem, observed in insects, has to be considered: "how far larvae and adults can, each in their own habitats, follow quite independent evolutionary pathways" (SNEATH, 1964). Therefore should the evolution of the larvae be established independently of the adults; and if so, what is the morphology of the ancestral copepod nauplius? Nearly all the first orthonauplii have, when alive, an oval or rounded shape. It is probably the most primitive form, because the first orthonauplius is the least differentiated larval form in the life cycle of free-living copepods.

The antennules, though nearest to the syncerebrum, which is known as one of the important organizers in embryology, do not achieve full development in many species till the final moult of the fifth copepodid (HOLTFRETER, 1951). The next appendages nearest to the nervous system are the antennae and the mandibles; these undergo less changes during the naupliar life and copepodid stages. Both are biramous. In the first orthonauplii, they are usually indistinctly segmented into a protopod, with a coxopod and a basipod, an outer segmented branch, the exopod, and an inner unsegmented branch, the endopod. The setae on these segments and branches are

predominately of the simple type, i.e. thin and spine-like or plumose. The appendages, as just described, are here considered to be of the most primitive or fundamental type among the copepods.

The main activities of the nauplii are locomotion and nutrition. To move and eat they use their muscles and their appendages. Therefore, any study on the evolution of copepod larvae must take into account the complexity of the muscle system and the specialization of the appendages of the body. The symmetry of the body, its compressed or depressed shape, its length, can also affect the locomotory capacity of the nauplius. Based on these features nauplii can be separated into three fundamental groups already characterized by DIETRICH (1915): I – the Cyclopoida (here included GIESBRECHT's Podoplea, except the Harpacticoida); II – the Harpacticoida; and III – the Calanoida.

I) In the Cyclopoida the nauplii have the most primitive body shape (Figs. 548 to 645). Their appendages are usually armed with simple setae and their caudal armature is symmetrical, composed of setae and spines. Their muscles have the simplest distribution observed (Fig. 570; Fig. 554). The Oncaeidae, the orthonauplii of the Corycaeidae, the Notodelphyidae, the Ergasilidae have the same features.

If the arthropod appendages of the fossil Arthropleuridae (VANDEL, 1949) are considered as primitive, the segmented endopod is the ancestral type. The cyclopoid nauplii are then more primitive than both the calanoid nauplii and most of the Harpacticoida since they have a bimerous endopod (i.e. with 2 segments) on the mandible, whereas the same endopod is unimerous in the other two groups. The swimming of the cyclopoid nauplii is also very simple, by "paddle-strokes" of the antennae and mandibles. They are incapable of any other motion, owing to their simple muscle system. On the other hand, the simplicity of their morphology can be the result of the loss of highly specialized characteristics, but, in free-living individuals such generalized regression is unlikely.

HEBERER (1932) finds that adult Cyclopoida are near to the ancestral form because they have a symmetrical genital apparatus.

GAULD (1966) considers the movement and the feeding of adult *Oithona* simple.

Thus, it seems that in addition to the cyclopoid nauplius approximating to the ancestral form, some of the adult Cyclopoida are also near to the ancestral form.

Let us now consider the evolution within the group. Only the free-living forms will be taken into consideration, because the parasites and commensals are highly specialized, and therefore undoubtedly derived. Among the Oithonidae there appear to be two groups, one including *Oithona similis*, *O. nana*, *O. ovalis* and *O. minuta*, the other including *O. plumifera* and *O. helgolandica*. *Oithona minuta* is probably the most primitive. It is the simplest form in the first group of known nauplii of Oithonidae, by virtue of its unspecialized caudal armature and the simplicity of the setae on the limbs. *O. nana* is the next simplest. It may have evolved *O. ovalis* in brackish water and *O. plumifera* in oceanic water; *O. ovalis* has a slightly different caudal armature, and *O. plumifera* could be the result of an evolutionary trend towards the lengthening of the naupliar body.

O. simplex does not fit into either group. With its flanged, serrate spines, it is the cyclopoid nauplius nearest to the calanoid nauplius; the most differentiated one known amongst the Oithonidae.

From the Oithonidae nauplius there is an evolutionary trend to the elongate nauplius with simple, but long caudal filaments of the Oncaeidae. Another trend gave origin to the complicated caudal armatures of the Corycaidae. The fresh water Cyclopoida must have branched off also from the Oithonidae. One evolutionary line led from *Cyclops leuckarti* to *C. strenuus*, *Macrocyclops fuscus*, *Eucyclops serrulatus* and *E. speratus*. *Eucyclops* is the most developed of all with a scythe-like spine on the mandibular endopod (HANAOKA, 1944). Other cyclopoid nauplii of fresh water copepods, such as *Speocyclops* spp. (LESCHER-MOUTOUÉ, 1966), *Macrocyclops albidus* (MANFREDI, 1925), *Cyclops vicinus* (AUVRAY & DUSSART, 1967) are less specialized than the *Eucyclops* nauplii.

The most complex cyclopoid nauplius described so far is that of *Thespesiopsyllus paradoxus*, found in the stomach of ophiuroids, where it leads a parasitic life (BRESCIANI & LÜTZEN, 1966). The

copepodid and adult stages of this monstrolloid are free-living. The nauplius has one segment of the endopod transformed into a hook and the other bearing a hook-like formation. The antennae, with a gnathit and an arthrit, are very far from the fundamental type. The maxillules, uncommonly large, with several rows of minute spines, and modified setae, are the most evolved of the appendages. All these features are undoubtedly adaptations to the parasitic life.

II) In the Harpacticoida there is also a symmetrical nauplius with simple setation in the Longipediidae and Canuellidae. It is similar to the *Acartia* (Calanoida) nauplius. It has a segmented endopod on the mandible. The caudal region in *Longipedia* is armed with a long median spine, not present in *Sunaristes* (Canuellidae) (see LANG, 1948). The musculature of these nauplii has not been examined. All the other nauplii of the harpacticoids have masticatory, cutting processes, hooks and other very specialized features on both antennae and mandibles, or on one pair of these appendages. These are adaptations to their life on the substratum. Their muscular system is complex and they can therefore execute complex movements.

LANG (1948) is also of the opinion that the adult *Longipedia* and the Canuellidae are primitive, and that their nauplii are simple when compared with the nauplii of other Harpacticoida. The next most primitive nauplius described is that of *Cerviniopsis* (LANG, 1948). Here, the coxopod of the antenna has developed a strong masticatory process, characteristic of the harpacticoid nauplii, but the mandibles retain the simple arrangement observed in the fundamental form. It has only one segment on the mandibular endopod, and is therefore a derived form. The more complicated forms appear through *Phyllognathopus*, which, besides the masticatory process, has a more evolved mandibular endopod with five spines (see LANG, 1948). In these derived forms the antenna has a strong spine (prehensile according to LANG) on the endopod, besides the feature already mentioned. The mandibles have strongly built spines on the endopod. They may fuse (e.g. *Zaus*) or not (*Canthocamptus*), assuming a blade-like or a scissor-like form, respectively. LANG (1948) gives importance to the prehensile spine on the endopod of the an-

tenna, and divides the "Chirognathe" harpacticoids into two groups according to the presence or absence of this feature. The Ectinosomidae belong to those which lack such a feature, and the Tachidiidae belong to those which have the prehensile spine on the endopod of the antenna. *Microsetella*, the planktonic ectinosomid, has a nauplius which, in many ways, resembles the *Phyllognathopus* larva. Both animals are secondary adaptations, the first to planktonic life, the second to a terrestrial habitat. *Euterpina acutifrons* is a hypoplanktonic tachidiid, living near the bottom. Its nauplius, perhaps also through secondary adaptation, has no prehensile spine on the endopod of the antennae, even the masticatory process of this appendage has suffered a complete regression, and a gnathopod develops on the mandible in the sixth naupliar stage. The endopod only assists in pushing the food towards the mouth (see HAQ, 1965b).

The Miracidae are the most evolved of the planktonic harpacticoids. Their nauplii suffer a reduction of the exopod of the antenna which is partial in *Miracia* and total in *Macrosetella*. The prehensile spine and the endopod are well developed. The spine develops into a large hook (Fig. 558). The mandible (Fig. 557) is also considerably modified. The exopod is reduced to a seta. The endopod is armed with two strong hooks and setae. The caudal armature is considerably reduced and the shape of the body is elongate.

Because of the many different habitats in which the Harpacticoida live, the adaptations of their nauplii are varied and interesting (see GURNEY, 1932). The psammophilous nauplius of *Stenhelia palustris* is shortened on the antero-posterior axis, it has an endite on the antenna, its endopod has no prehensile spine and the mandible is considerably dilated, with a very large exopod armed with spiny process and spine (BRESCIANI, 1960). It moves along a helicoidal path specially adapted to its life in the interstices of sand.

Most of the developmental cycles of the harpacticoids should be re-investigated so as to determine whether there are cycles containing five naupliar stages only. The cycles re-investigated, such as those of *Euterpina acutifrons*, revealed the presence of six stages. In many copepods it is difficult to distinguish between the fourth and the fifth naupliar stage (see for *Euterpina*, HAQ, 1965a).

III) The *Calanoida* are possibly the most difficult group to analyse from the evolutionary aspect. Two current opinions exist: one considers the *Calanidae* as the most primitive (GIESBRECHT, 1892); the other considers the *Centropagidae* as the nearest to the ancestral form (GURNEY, 1931). HANAOKA (1952) is of the opinion that the calanid nauplius has less evolved characteristics. Several facts favour this assumption. 1) There are no morphological specializations in the appendages of these nauplii. 2) They are more symmetrical than many of the other calanoids. 3) They have no balancers, their movement being therefore a continuous somersaulting, which involves a great loss of energy relative to the small advance made. 4) The adults are less dimorphic and have the fifth pair of legs more symmetrical than is usual in other copepods.

DAHL (1956) considers filter-feeding as primitive, and finds that the *Calanidae* have arrangements of the appendages and the central nervous system closely approaching the general plan found ontogenetically. HEBERER (1932) after studying the male genital apparatus also considers the calanids as near to the ancestral type. Against this assumption several points should be considered: 1) their caudal armature is specialized, with the large leaf-like spines, resulting from the fusion of several setae; they have no balancers, which are otherwise present in the majority of the planktonic nauplii; 2) their movement is too complex to be considered primitive, as it results from the activity of a very complex set of muscles; 3) the somersaulting provides a quick means of deceiving an enemy and, thus, of escaping from it. It can therefore be an adaptation to successful life in the plankton. 4) The calanid adults, though considered morphologically simple, are specialized filter-feeders (GAULD, 1966). They can feed only when swimming or suspended. According to general opinion the ancestral form should be undifferentiated such that it was adaptable to different environments. Calanids are restricted to a planktonic life and to filter-feeding. Any change in conditions leading to a temporary life near the substratum is fatal to these animals. Within the *Calanoida* it is certain that the *Calanidae*, the *Paracalanidae* and the *Calocalanidae* form a closely related group (cf. Tables 1 and 3). Perhaps only the *Calocalanidae*, with their elongated naupliar body and the very large spines of the caudal

armature, should be separated as a family. The Calanidae probably gave origin to the Paracalanidae and to the Pseudocalanidae. The Calocalanidae are closely related to the genus *Paracalanus*, from which they may have been derived by elongation of the body and lengthening of the caudal spines in the nauplius. The nauplii of the Metridiidae also possibly originated from the Calanidae; their caudal armature leaves no doubt about their relationship. The Calanidae larvae are the most primitive within the group because they have a larger number of setae on the antenna and on the mandible in the nauplius, in addition to primitive features of the adult, e.g. a larger number of segments in the body.

Three other calanoid nauplii appear to have retained several primitive features: the Diaptomidae (and Pseudodiaptomidae), the Centropagidae and the Acartiidae. The *Acartia* nauplii have a primitive oval shape, very small leaf-like spines in the caudal region, and are among the most symmetrical nauplii of the Calanoida. Their appendages are not specialized and they are armed usually only with simple plumose setae. The adults are less specialized than the Centropagidae, they are more symmetrical; they are omnivorous, particle-feeders (cf. MULLIN, 1966). Many of their species have become adapted to brackish water and to water of high salinity. The Cyclopoida, through a naupliar form like that of *Oithona simplex*, may have given origin to the *Acartia* nauplii through a complication in the muscle system, and disappearance of one of the endopod segments. The nauplii nearest to *Acartia* are the Diaptomidae and Pseudodiaptomidae. They still maintain the cyclopoid type of maxillule in the third naupliar stage, and the caudal armature is composed of rows of setules as in *Acartia*; but two of the terminal spines are considerably longer and the asymmetry of the nauplius is increased relatively to *Acartia*. The antennules are short as in *Acartia* but have many more setae and spines. Adaptation to brackish and fresh water habitats, known among the Acartiidae and Cyclopoida, is also observed in the Diaptomidae and Pseudodiaptomidae. Some of the most symmetrical naupliar forms of the two families are found among the Diaptomidae, but the forked, caudal seta is a specialization. The Pseudodiaptomidae are specialized in their adult and

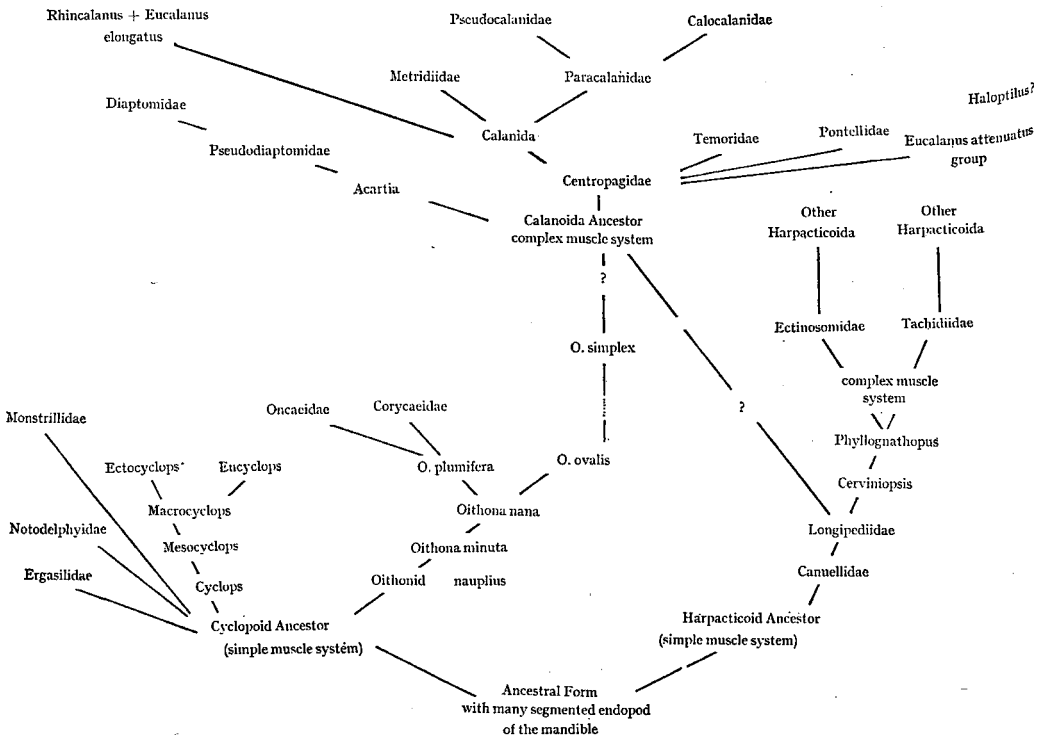
copepodid forms, but might have been derived from a simpler ancestor. They could have either evolved from the Acartiidae, or have been derived from the Centropagidae by regression of the caudal spines and complication of the antennule morphology.

In the naupliar Centropagidae and Eucalanidae, except *Rhincalanus* and *Eucalanus elongatus*, there is considerable asymmetry of the caudal region. The antennules are as in *Acartia*, provided with setae only in the second and third segment. In *Centropages* the two lobes of the endopod reveal the relation to the Cyclopoid nauplii (see HANAOKA, 1952a). In the Eucalanidae the endopod is not bilobed, and *Eucalanus attenuatus* and its group are closely related to the *Centropages* nauplii. The asymmetry of the caudal armature, the lengthening of the nauplius and the loss of lobes in the mandibular endopod are accentuated in the Eucalanidae. The way of swimming of the eucalanid nauplius can also be derived more easily from the centropagid behaviour. In *Eucalanus elongatus* and in *Rhincalanus* the lengthening of the naupliar body is still more accentuated, but there has been either regression of the caudal setae and a strong evolution of the caudal spines, which are very small in the *E. attenuatus* group, or *E. elongatus* is not related to the other Eucalanidae. The adult form can be explained as a convergence, not homologous with the other *Eucalanus*, and then the *Rhincalanus* and *E. elongatus* can be related directly to the Calanid-Paracalanid group, from which it is derived easily by lengthening of the body and (in *Rhincalanus*) by fusion of the coxopod spines. Nauplii such as those attributed to *Haloetilus* can be derived from the *E. crassus* nauplius.

Centropagidae and Pontellidae are closely related. *C. furcatus* has no mandibular blade. *Pontellopsis* also has none. *Labidocera* nauplii have longer spines and shorter sensory setae in the caudal armature when compared with *Centropages*. The mandible is very much like the *Centropages* mandible. Locomotion is identical. In *Pontellopsis* the caudal spines are very long (balancers) and the body has also lengthened considerably. The mandibular endopod loses the bilobed aspect. Temoridae are related to Centropagidae. The lengthening of the caudal spines (balancers) and the redistribution of the lateral spines on the caudal armature of *Centropages* would lead to the morphological aspect of *Temora*.

The centropagid nauplius can give origin to the calanid larva through the lengthening of the caudal spines and regression of the sensory setae. Here the tendency towards the lobe formation in the mandibular endopod is lost. The maxillules appear late in the fourth naupliar stages, and then as foliate bilobed structures armed with spines and setae. In *Centropages*, *Eucalanus* and in the Pontellidae they appear in nauplius IV as one or several filaments or setae inserted in a slight swelling on the ventral area of the nauplius.

In view of the fact that most nauplii of the Calanoida are asymmetrical and that no calanoid nauplius with segmented mandibular endopod has been reported up to now, I consider the Calanoida to be the most evolved of the three groups. They can be derived from the Harpacticoida, through the Longipediidae, and from the Cyclopoida, through such nauplii as of *Oithona simplex*.



FAMILY TREE FOR NAUPLII OF COPEPODA

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TABLE 1 (continued).

APPENDAGES NAUPLIAR STAGES				SPECIES	
	II	III	IV	V	VI
En	—	—	—	—	2:3(4)+5+1ms
	2+3term	1:3+3term	2:3+4t+5ms	2:4+5+ms	3:4+5+ms
	1m+1m+3term	3t	1:3+4	3:3+5	2:3+5
	2+3term	2:3+4	2:3+4	2:4+5	4:2+3
	4	3+4	2:3+4	2:3+4	2:3+5
	1:1+3term	1:3+4	2:3+4	2:3+5	2:4+4
Ex	—	—	—	—	12
	6	9	9	11	11
	6	9	10	10	11
	7	9	10	11	12
	6	8	9	11	12
	7	8	9	10	12
MANDIBLE	—	—	—	—	blade 3teeth+1
	1	1	blade 2teeth+1	blade 2teeth+1	blade 3teeth+ms+1
	1m	1	blade 3teeth+1	blade 4teeth	blade 7teeth+1
	1	1	blade 2teeth+1	blade 2teeth+1	blade 2teeth+1
	1	1s+1	blade 2teeth+1	blade 2teeth+1	blade 3teeth+1
	1	1	blade 2teeth+1	blade 2teeth+1	blade 2teeth+1
B2	—	—	—	—	4(3)
	2	3	3	5+1m	6
	2m	4	4+bulge	5+bulge	3+2+bulge
	2	3	4	4+1	1+5
	2	3	4	6	6
	2	3	4+1	4+1	5+1
En	—	—	—	—	2+2+2+3
	3+2+3	4+2+3	4+1:2+2+2	2L=2+2+1:2+2+2	2L=2+2+2:2+2+2

TABLE 1 (continued).

APPENDAGES NAUPLIAR STAGES				SPECIES	
II	III	IV	V	VI	
2ms+3	4+2+4+ms	3+2+2+4	5+2+4	5+2+4	<i>C. ton.</i>
3:2+3	3:2+4	4+1:2+4	3+2:2+4	3+2:2+4	<i>C. fin.</i>
2+2+3	5:4	5:6	2:3+4	2L=2+2+2:2+2+2	<i>U. vul.</i>
3+2+3	3+6	4+6	4+2+4	4+6	<i>C. hel.</i>
—	—	—	—	6	<i>N. min.</i>
4S=5	4S=5	4S=5	5S=6	5S=6	<i>C. car.</i>
4S=5	4S=5	4S=6	4S=6	4S=6	<i>C. ton.</i>
4S=5	4S=6	4S=6	4S=6	4S=6	<i>C. fin.</i>
4S=5	4S=6	4S=6	4S=6	4S=6	<i>U. vul.</i>
4S=5	4S=6	4S=6	4S=6	5S=6	<i>C. hel.</i>
MAXILLULE					
		—	—	1:1:2:8(7):5:1	<i>N. min.</i>
		2L=4:3	4L=1:1:7:5	6L=4s:3:4:8:7:1	<i>C. car.</i>
	1 lobe=1	2L=5:3	4L=2:2:2:2+4:5	8L=7s:3:2:8:7:1	<i>C. ton.</i>
	outline	2L=4:4	3L=2:8:5	8L=8:3:4:2:2:2+4:7:1	<i>C. fin.</i>
		2L=4:4	3L=2:8:5	5L=2:2:4:7:0	<i>U. vul.</i>
		2L=5:3	4L=2:2:8:5	4L=3:4:8:6	<i>C. hel.</i>
MAXILLA					
		—	—	5L=1:2:1:2:2	<i>N. min.</i>
				6L=2:2:3:1:3:2	<i>C. car.</i>
				6L=2:2:2:3:1+4	<i>C. ton.</i>
				6L=3:3:3:2:1+5	<i>C. fin.</i>
				6L=2:2:2:3:1+5	<i>U. vul.</i>
			1L=2	7L=2:2:2:3:2:3	<i>C. hel.</i>
MAXILLIPED					
				2	<i>N. min.</i>
				1L=1	<i>C. car.</i>
				1L=2	<i>C. ton.</i>
				2S=0:2	<i>C. fin.</i>

TABLE 1 (continued).

APPENDAGES NAUPLIAR STAGES				SPECIES	
II	III	IV	V	VI	
LEG I					
				2S=0:1	<i>U. vul.</i>
				1L=2	<i>C. hel.</i>
				2L=2:2+1s	<i>N. min.</i>
				2L=2:2+1	<i>C. car.</i>
				2L=4:3	<i>C. ton.</i>
				2L=2:2+1	<i>C. fin.</i>
				2L=2:2	<i>U. vul.</i>
				2L=4+1:3	<i>C. hel.</i>
LEG II					
				2L=2:1+1s	<i>N. min.</i>
				2L=2:2	<i>C. car.</i>
				2L=3:2	<i>C. ton.</i>
				2L=2:1	<i>C. fin.</i>
				2L=2:2	<i>U. vul.</i>
				2L=3:2	<i>C. hel.</i>
Spines and					
'feelers' of	—	—	—	4v+6l+2t+2F+ms	<i>N. min.</i>
CAUDAL	2	2F+2v+2t+ms	4v+4l+2t+2F+ms	4v+6l+2t+2F+ms	<i>C. car.</i>
	2	2F+2v+2t+ms	4v+4l+2t+2F+ms	4v+6l+2t+2F+ms	<i>C. ton.</i>
ARMATURE	2	2F+2v+2t+ms	4v+4l+2t+2F+ms	4v+6l+2t+2F+ms	<i>C. fin.</i>
	2	2F+2v+2t+ms	4v+4l+2t+2F+ms	4v+6l+2t+2F+ms	<i>U. vul.</i>
	2	2F+2v+2t+ms	4v+4l+2t+2F+ms	4v+6l+2t+2F+ms	<i>C. hel.</i>

The data on *C. tonsus* were taken from CAMPBELL (1934), those on *C. finmarchicus* from LEBOUR (1918), those on *U. vulgaris* from BJÖRNBERG (1966), and those on *C. helgolandicus* from SAZHINA (1961). The caudal armature in nauplius IV has 2 lateral larger spines or hooks on each side, and one or more very small spines laterally (ms). These are included in the description of the caudal armature together with the larger hooks, by some authors (MARSHALL & ORR, 1955), but were not included here.

TABLE 2

LENGTH, SETATION AND SEGMENTATION OF THE KNOWN NAUPLII OF THE EUCALANIDAE

Symbols used: F = sensory setae (feelers); B = balancers; l = lateral; v = ventral; ms = minute spine; term = terminal; numbers in brackets indicate variation; colon (:) separates setae belonging to different segments or lobes; + separates different tufts or types of setae or spines; *(asterisk) = extremely small spines visible in the exuviae; — = existing feature, not yet studied
R. cor. = *Rhincalanus cornutus*, *R. nas.* = *Rhincalanus nasutus*, *R. gig.* = *Rhincalanus gigas*, *E. elo.* = *Eucalanus elongatus*, *E. pil.* = *Eucalanus pileatus*, *E. cra.* = *Eucalanus crassus*, *E. att.* = *Eucalanus attenuatus*

	NAUPLIAR STAGES						SPECIES
	I	II	III	IV	V	VI	
Length in micra	—	450-470	770 (Curaçao)	1000-1075	1200	1330-1450	<i>R. cor.</i>
	—	—	650-700	820-890	1000	1160	<i>R. nas.</i>
	—	—	860	1180	1520	1800	<i>R. gig.</i>
	214-260	270-420	430-720	620-880	745-1092	920-1230	<i>E. elo.</i>
	245	295-300	350-390	410-425	525	600-680	<i>E. pil.</i>
	—	—	500-550	600-680	770-811	980-1000	<i>E. cra.</i>
	—	—	—	—	780	945	<i>E. att.</i>
ANTENNULE	—	—	0:1+2s:6+1s	0:2+8s:7+1s	1:1+4s:11+ms	0:1+2+4s:14	<i>R. cor.</i>
	—	1:1+5ms:4+ms	1:1+2s:6+1s	—	1:1:11	1:1:14	<i>R. nas.</i>
	0:1:3	1:2:4	1:2:7	1:2:11	1:2:14+ms	1:2:17+ms	<i>E. elo.</i>
	0:1:3	0:2:5	0:2:7	0:2:10	0:2:12	0:2:16(15)	<i>E. pil.</i>
	—	—	0:2:7	0:2:9	0:2:11	0:1:2:14(16)	<i>E. cra.</i>
	—	—	—	—	0:2:10+1	0:2:14+5ms+ms	<i>E. att.</i>
ANTENNA	—	1mp+ms+1	1mp+ms+1	1mp+ms+1	1mp+ms+1	1mp+ms+1	<i>R. cor.</i>
coxopod	—	1mp+ms+1	—	—	—	1s+1	<i>R. nas.</i>
	1s	1s	2s+1	2s+1	2s+1	2s+1	<i>E. elo.</i>
	bulge	1s+1	2s+1	2s+1	2s+1	2s+1	<i>E. pil.</i>

TABLE 2 (continued).

	NAUPLIAR STAGES					SPECIES	
	I	II	III	IV	V	VI	
basipod	—	—	2s	2s	2s	2s	<i>E. cra.</i>
	—	—	—	—	2s	2s	<i>E. att.</i>
	—	1	1	1+1	2	1+1s+2	<i>R. cor.</i>
	—	—	—	—	2	2	<i>R. nas.</i>
	—	1	2	2	2	2	<i>E. elo.</i>
	—	1	2	2	2	2	<i>E. pil.</i>
	—	—	2	2	2	2	<i>E. cra.</i>
	—	—	—	—	2	2	<i>E. att.</i>
	—	—	1+3	2+4	2+3	2+4	<i>R. cor.</i>
	—	1+3	—	—	—	—	<i>R. nas.</i>
endopod	1+2	1:1+3	1:2+4	1:2+4	2:3+5	2:3+5	<i>E. elo.</i>
	2	2+3	1+1(long):3+4	1+1(long):3+4	1+1(long):3+5(4)	2+1(long):4+5	<i>E. pil.</i>
	—	—	1(long):3+4	1(long):3+4	1+1(long):4(5)+5	1+1(long):4+5	<i>E. cra.</i>
	—	—	—	—	1+1(long):3+5+1	1+1(long):3+5	<i>E. att.</i>
	—	—	5	5	7+1	10(11)	<i>R. cor.</i>
	—	7	—	—	—	—	<i>R. nas.</i>
	6	7	9	10	10	11(12)	<i>E. elo.</i>
	6	6	9	10	10	11	<i>E. pil.</i>
	—	—	9	9	10	10	<i>E. cra.</i>
	—	—	—	—	9	9	<i>E. att.</i>
MANDIBLE	—	—	1	blade 2teeth+1 + bulge	blade 2teeth+1	blade 3teeth+2	<i>R. cor.</i>
coxopod	—	1	—	—	—	—	<i>R. nas.</i>
	1+1	1	1	blade 3teeth+2	blade 4teeth+2	blade 5teeth+2	<i>E. elo.</i>
	—	1	1+ bulge	blade 3teeth+1	blade 3teeth+2	blade 4teeth+2	<i>E. pil.</i>
	—	—	1	blade 3teeth+2	blade 5teeth+2	blade 5teeth+2	<i>E. cra.</i>
	—	—	—	—	blade 4teeth	blade 4teeth+2	<i>E. att.</i>
	—	—	—	—	—	—	

TABLE 2 (continued).

NAUPLIAR STAGES						SPECIES
I	II	III	IV	V	VI	
basipod	—	3	3	3(4)	5(3)	<i>R. cor.</i>
	1+1	—	—	—	—	<i>R. nas.</i>
1	2	2	2	2	2	<i>E. elo.</i>
—	1	3(4)	4	6(4,3)	6(4)	<i>E. pil.</i>
—	—	3	4	5	5	<i>E. cra.</i>
—	—	—	—	5	5	<i>E. att.</i>
endopod	—	6	6	3+4	7(8)	<i>R. cor.</i>
—	1+5	—	—	—	—	<i>R. nas.</i>
2+3	3+5	4+6	4+6	4+6	4+6	<i>E. elo.</i>
2+1s	6	4+7	2+9	2+6+3	11	<i>E. pil.</i>
—	—	4+6	4+6	4+6	4+6	<i>E. cra.</i>
—	—	—	—	2+2+5	4+5	<i>E. att.</i>
exopod	—	5	5	5(6)+1	5	<i>R. cor.</i>
—	5	—	—	—	—	<i>R. nas.</i>
5	5	6	6	6	6	<i>E. elo.</i>
4	5	6	6(8)	5(8)	5(8)	<i>E. pil.</i>
—	—	6	8(7)	7	7	<i>E. cra.</i>
—	—	—	—	5(6)	5	<i>E. att.</i>
MAXILLULE	—	—	1 lobe=1s+1s	1 lobe=2s+3	—	<i>R. cor.</i>
	—	—	—	—	—	<i>R. nas.</i>
	outlined	1 lobe=2:2	1 lobe=3:1:1:3:3	5 lobes=5:3:4:8:4	5 lobes=5:3:4:8:4	<i>E. elo.</i>
	—	2 lobes=3:2	2 lobes=2+7:4	2 lobes=2+9:4(5)	2 lobes=2+9:4(5)	<i>E. pil.</i>
	—	2 lobes=2:2	3 segments=0:4:4	3 segments=5:2+5:4	3 segments=5:2+5:4	<i>E. cra.</i>
	—	—	2 lobes=1:4(5):3	3 lobes=bulge:7:5	3 lobes=bulge:7:5	<i>E. att.</i>
MAXILLA	—	1s	1s	1s	4(5) lobes or bulge:7	<i>R. cor.</i>
	—	1 lobe; 4 bulges	1 lobe; 4 bulges	1 lobe; 4 bulges	4(5) lobes=5	<i>E. elo.</i>

TABLE 2 (continued).

NAUPLIAR STAGES					SPECIES	
I	II	III	IV	V	VI	
MAXILLIPED						
				—	5 lobes	<i>E. pil.</i>
				—	5 lobes = 2:1:1:2:1	<i>E. cra.</i>
				—	5 lobes = 3:1:1:1:4	<i>E. att.</i>
					1 lobe = 2s	<i>R. cor.</i>
					2 segments = 2 term	<i>E. elo.</i>
					2 segments = 3	<i>E. pil.</i>
					1 lobe = 2	<i>E. cra.</i>
					2 segments = 2	<i>E. att.</i>
LEG 1						
					2 lobes = 3s:3s	<i>R. cor.</i>
					2 lobes = 3s:3s	<i>E. elo.</i>
					2 lobes = 2s:3s	<i>E. pil.</i>
					2 lobes = 4s:2s	<i>E. cra.</i>
					2 lobes = 3s:4s	<i>E. att.</i>
LEG 2						
					2 lobes = 3s:3s	<i>R. cor.</i>
					—	<i>R. nas.</i>
					2 lobes = 3s:3s	<i>E. elo.</i>
					2 lobes = 2s:3s	<i>E. pil.</i>
					2 lobes = 2s:2s	<i>E. cra.</i>
					2 lobes = 3s:4s	<i>E. att.</i>
CAUDAL ARMATURE						
—	—	2F+2+2sl+ms	2F+2B+2+4sl+msv	2F+2B+6sl+ms	2F+2B+6sl+ms	<i>R. cor.</i>
—	2F+msl+msv	2F+2+2msl	2F+2B+2+4sl+msv	—	—	<i>R. nas.</i>
2s	2s	2F+2sv+2	2F+2sv+2sv+4sl	2F+2B+2sv+2sv+6sl	2F+2B+2sv+2sv+6sl+msv	<i>E. elo.</i>
1(0)s	2s	2F+2sv+2	2F+2+4sv	2F+2+4sv	2F+2B+4sv	<i>E. pil.</i>
		2F+2sv+2	2F+2+4sv	2F+2+4sv+1sv	2F+2+2+4sv+2sv	<i>E. cra.</i>
				2F+1+2+3sv	2F+2+2+4sv+	<i>E. att.</i>
					2sv*+ms+ms	

TABLE 3

SIZE OF NAUPLII AND DISTRIBUTION OF SETAE ON APPENDAGES
OF THE PARACALANIDAE, PSEUDOCALANIDAE AND CALOCALANIDAE

Symbols used: s = spine; S = segment; L = lobe; l = lateral, v = ventral; ms = minute spine; t = terminal; pr = protuberance; F = sensory seta (feeler); numbers in brackets indicate variation; colon (:) separates setae belonging to different segments or lobes; the sign + separates different tufts or types of setae or spines; B1 = coxopod; B2 = basipod; En = endopod; Ex = exopod.

P. cra. = *Paracalanus crassirostris*, *P. par.* = *Paracalanus parvus*, *C. fur.* = *Clausocalanus furcatus*, *C. sty./pavo* = *Calocalanus styliremis*/
P. acu. = *Paracalanus aculeatus*, *C. van.* = *Ctenocalanus vanus*, *Pseud.* = *Pseudocalanus*

	NAUPLIAR STAGES				SPECIES		
	I	II	III	IV			
Length in micra	60-80	90	119-130	140-170	180-185	180-205-210	<i>P. cra.</i>
	90	105	160-150	205-210	240-250	250	<i>P. par.</i>
	99-110	—	130-190	170-210	205-255	—	<i>C. fur.</i>
	—	—	—	170-190	202-215	215-225	<i>C. sty./pavo</i>
	—	—	—	215-200	220	—	<i>P. acu.</i>
	—	—	200-215	245	255	—	<i>C. van.</i>
	176	187	260	330	380	440	<i>Pseud.</i>
ANTENNULE	0:0:3	0:3:4	0:3:7	0:3:11	0:3:13	0:3:13	<i>P. cra.</i>
	0:3:3	1:2:4	1:2:7	1:2:11	1:2:13	1:2:13	<i>P. par.</i>
	0:0:3	—	0:3:7	0:3:10	0:3:13	—	<i>C. fur.</i>
	—	—	—	0:3:11	0:3:13(14)(15)	0:3:13(14)	<i>C. sty./pavo</i>
	—	—	—	0:3:11	0:3:14	—	<i>P. acu.</i>
	—	—	0:3:7	0:3:11	0:3:13	—	<i>C. van.</i>
	1:2:3	1:2:4	1:2:7	1:2:10	1:2:13	1:2:15	<i>Pseud.</i>
ANTENNA B1:B2	1s:1s	1s:1	1s:1	1s:1	2s+1:2	2s+1:2	<i>P. cra.</i>
	—	—	—	2s:2	—	—	<i>P. par.</i>
	2s	—	2s:1+2	2s:1s+2	2s:1s+2	—	<i>C. fur.</i>
	—	—	—	2s:2+1s	2s:2	2s:2	<i>C. sty./pavo</i>

TABLE 3 (continued).

NAUPLIAR STAGES				SPECIES	
I	II	III	IV	V	VI
—	—	—	2s:2	2s:2	—
—	—	2s:2	2s:1s+2	2s:1s+2	—
—	1s+1:1	2s:2	2s:1+2	2s:1+2	2s+1:1+2
En	2	0:1+3	1+3	2:3+3	2:3+4
—	—	—	2:2+3	—	—
2s+1	—	0:3+3	0:3+3	1:4+4	—
—	—	—	2:3+4	2:4+4	2:4+4
—	—	—	2:2+3	—	—
—	—	2+3	2:3+3	2:3+4	—
—	1:1+3	2:3+3	2:3+4	2:4+5	2:5+6
Ex	5	3S=5	6S=9	5S=9	5S=9
—	—	—	—	—	—
4	—	5S=5+1+2	5S=8	6S=9	—
—	—	—	5S=8	6S=9	6S=9
—	—	—	6S=10	6S=10	—
—	—	6S=7	6S=7(8)	6S=7(6)	—
4S=7	5S=9	6S=10	6S=10	7S=9	7S=10
MANDIBLE	0:1s	1:1	1:3	Blade, 3teeth:4	Blade, 2teeth:4
B1:B2	—	—	—	—	—
0:0	—	pr. 1:2	Blade, 2teeth:5	Blade, 2teeth+1:5	—
—	—	—	Blade, 2teeth:4	Blade, 2teeth+1:4(3)	Blade, 2teeth+1:4
—	—	—	Blade, 2teeth:4	Blade, 2teeth:4	—
—	—	3(4)	Blade, 2teeth:4	Blade, 3teeth:4	—
—	pr:2	pr:3	Blade, 2teeth:3	Blade, 3teeth:3	Blade, 4teeth:4
En	2	4	9	10	10
—	—	—	—	—	—
2+1s	—	7	8	9	—

*P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.**C. sty./pavo**P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.**C. sty./pavo**P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.**C. sty./pavo**P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.*

TABLE 3 (continued)

NAUPLIAR STAGES				SPECIES	
I	II	III	IV	V	VI
—	—	—	8	9(10)	9
—	—	—	8	9	—
—	—	9	9	9	—
—	7	5+6	10	9	10
Ex	2(6)	5	3S=5	4S=5	4S=5
—	—	—	—	—	—
4	—	4S=5	4S=5	4S=5	—
—	—	—	4S=4	4S=5	4S=5
—	—	—	4S=5	4S=5	—
—	—	4S=5	4S=5	4S=5	—
—	4S=5	4S=5	4S=5	4S=5	4S=6
MAXILLULE					
—	—	—	2L=3:5	3L=2:8:5	3L=pr:5(6):6
—	—	—	2L=3(4):6(7)	3L=2:7:4(5)	—
—	—	—	2L=3:3	3L=2:7:5	—
—	—	—	—	3L=1:6:5	5L(4L)=3:1:1:1+3:5
—	—	—	2L=4:4	3L=1:8:5	—
—	—	—	2L=4:2	3L=2:8:6	—
—	—	—	—	—	4L+2S=3:3:2:5:7:1
CAUDAL	2	2	6sl+ms+4sv+2st+	6sl+2st+4sv+ms+	6sl+2st+4sv+ms+
ARMATURE	2	2	2F	2F	2F
—	—	—	4sl+ms+4sv+2st+	6sl+2st+4sv+ms+	6sl+2st+4sv+ms+
—	—	—	2F	2F	2F
—	—	—	6sl+ms+4sv+2st+	6sl+2st+4sv+ms+	6sl+2st+4sv+ms+
—	—	—	2F	2F	2F
—	—	—	6/4sl+4sv+ms+	6/4sl+4sv+2st+	6/4sl+4sv+2st+
—	—	—	2st+2F	ms+2F	ms+2F

*C. sty./pavo**P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.**C. sty./pavo**P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.**C. sty./pavo**P. acu.**C. van.**Pseud.**P. cra.**P. par.**C. fur.**C. sty./pavo*

TABLE 3 (continued).

	NAUPLIAR STAGES				SPECIES		
	I	II	III	IV	V	VI	
CAUDAL ARMATURE	—	—	—	6sl + ms + 4sv + 2st + 2F	6sl + 2st + 4sv + ms + 2F	—	<i>P. acu.</i>
	—	—	2sv + 2st + 2F + ms	4sl + 4sv + 2st + 2F + ms	6sl + 4sv + 2st + 2F + ms	—	<i>C. van.</i>
	2s	2s + ms	2sv + 2st + 2F + ms	4sl + 4sv + 2st + 2F + ms	6sl + 4sv + 2st + 2F + ms	6sl + 4sv + 2st + 2F + ms	<i>Pseud.</i>

The data on *Pseudocalanus minutus* and on *P. parvus* were taken from OBERG (1906) and OGILVIE (1953). *C. styliremis* and *C. pavo* have the same distribution of setae on the appendages, differing only in the caudal armature, which has 6 small lateral spines in *C. styliremis*, and only 4 small lateral spines in *C. pavo*. In stage IV of *Paracalanus*, the first lateral spine is very fine and inconspicuous. The setation on the antennule's first and second segments is 1:2, according to some authors (OBERG, 1906), and 0:3 according to others.

EXPLANATIONS OF FIGURES

Symbols used: A_1 = antennule; A_2 = antenna; b = basipod; c = coxopod; e = spine; en = endopod; et = terminal spine; ex = exopod; L = labrum; La = labium or inferior lip; L I = lobe I; L II = lobe II; M = mandible; M_1 = maxillule; M_2 = maxilla; M_3 = maxilliped; m = minute spine; P_1 = first leg; P_2 = second leg; se = sensory seta (feeler).

Fig. 1–9. *Calanoides carinatus* (from Santos). – 1: Nauplius II, 0.23 mm long, ventro-lateral view. – 2: Antennule of nauplius IV. – 3: Nauplius III, 0.32 mm long, ventral view. – 4: Antenna of nauplius V. – 5: Nauplius IV, 0.42 mm long, ventral view. – 6: Nauplius V, 0.45 mm long, ventro-lateral view. – 7: Nauplius VI, 0.54 mm long, ventro-lateral view. – 8: Caudal armature of nauplius V, profile. – 9: Detail of the mandibular blade of nauplius VI. [Scales 0.1 mm]

Fig. 10–15. *Eucalanus crassus* (from Santos). – 10: Nauplius III, 0.55 mm, ventral view. – 11: Antennule of nauplius III. – 12: Antenna of nauplius III. – 13: Nauplius V, 0.77 mm, ventral view. – 14: Nauplius VI, 1.00 mm, ventral view with the mandible and the maxillule partially removed on the right side, so as to permit a good view of the maxilla. – 15: Mandible of nauplius III.

Fig. 16. *Eucalanus pileatus*. Schematic representation of the movements of the appendages of nauplius VI while grazing. The antennae and the mandibles vibrate, and a gliding motion results. The sensory setae sometimes change their position. The antennules remain outstretched. [Scales = 0.1 mm]

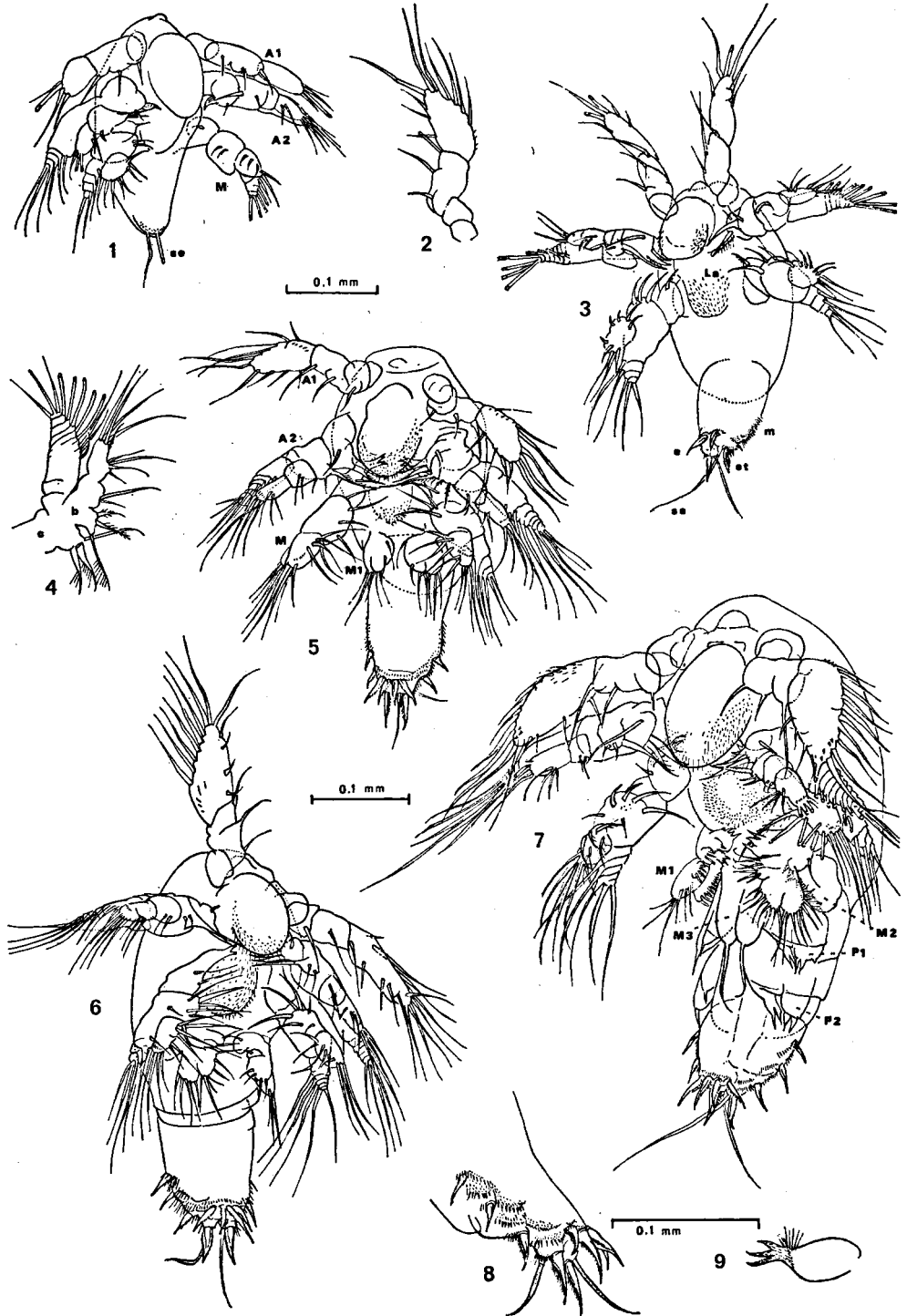
Fig. 17–18. *Eucalanus attenuatus*. – 17: Posterior ventral region of nauplius VI (from Curaçao); one of the sensory setae cut off. – 18: Nauplius V, 0.79 mm (off Chile), ventral view.

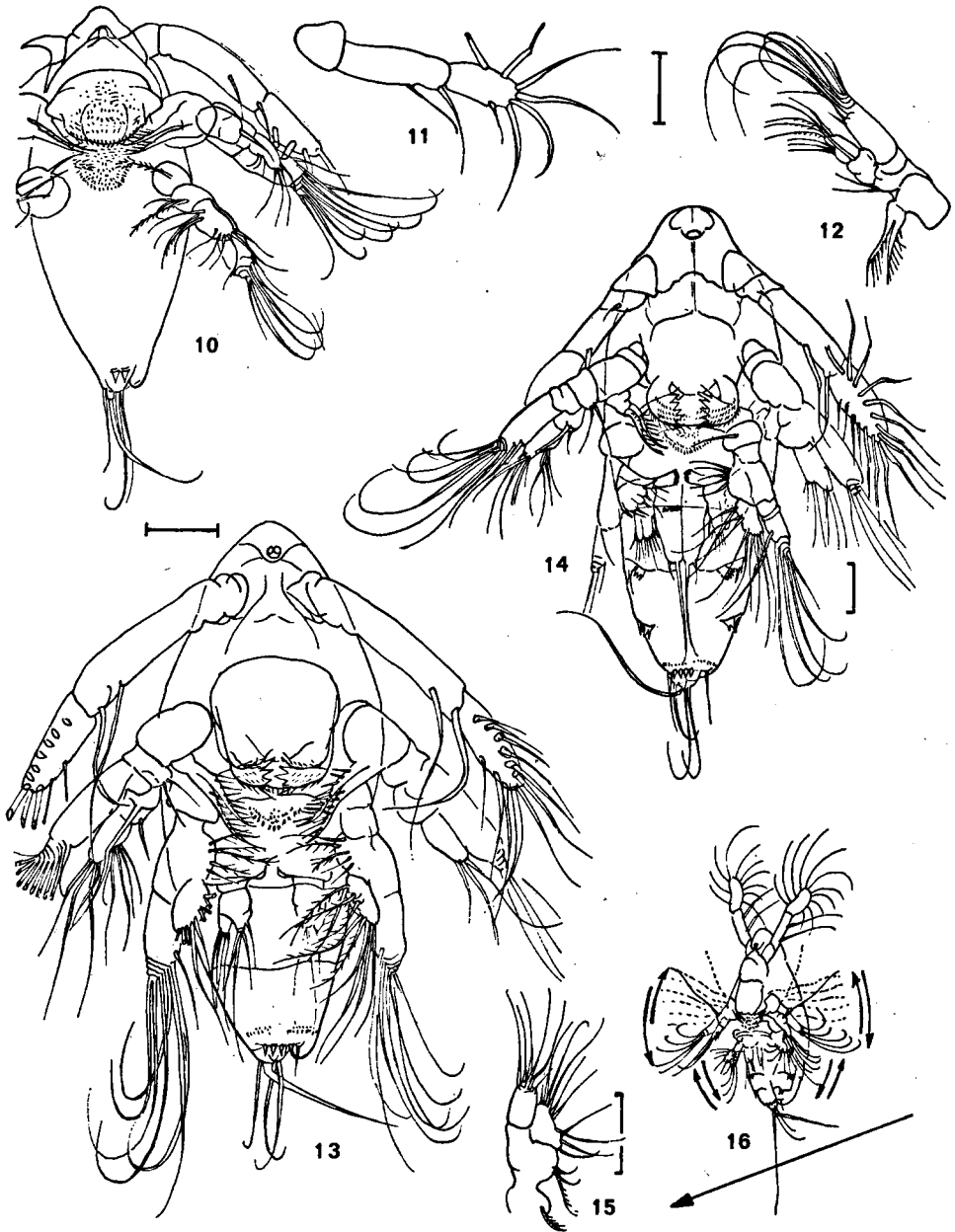
Fig. 19–20. *Eucalanus crassus*. – 19: Posterior region of nauplius V, profile, showing position of the setae of the caudal armature during locomotion. – 20: Nauplius IV, 0.65 mm (off Santos), ventral view. [Scales = 0.1 mm]

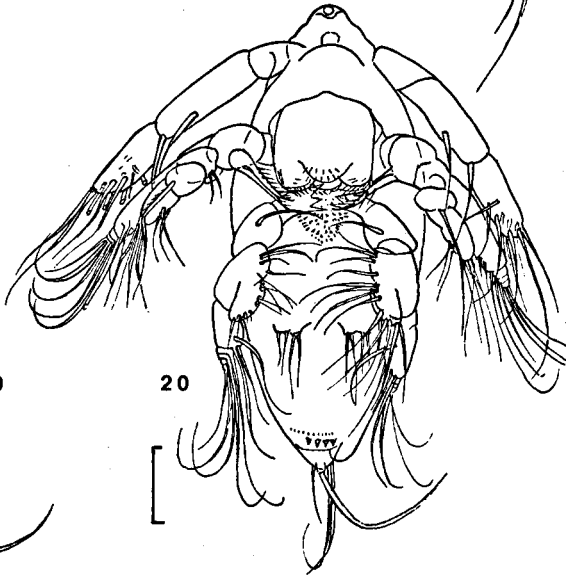
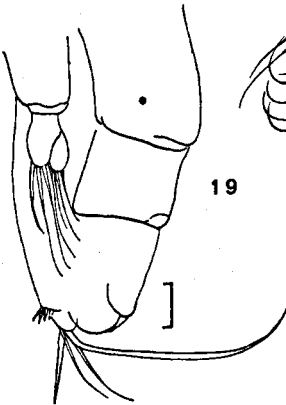
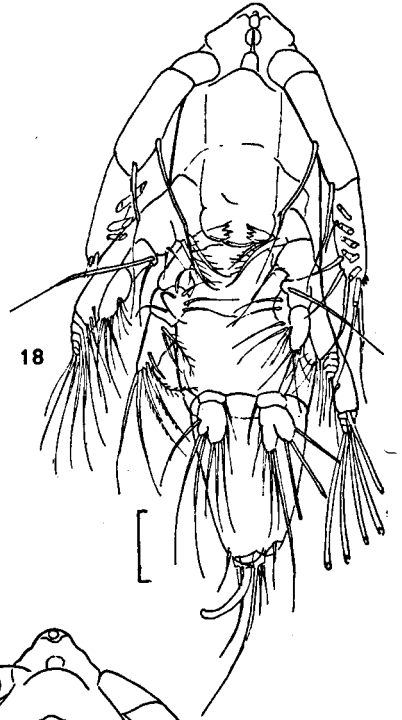
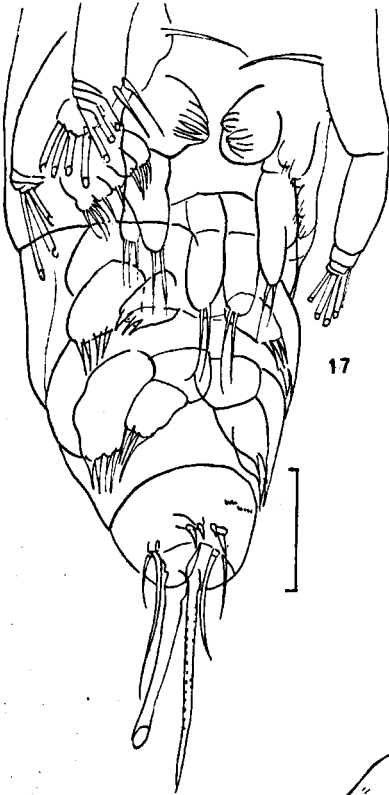
Fig. 21–32. *Paracalanus crassirostris*. – 21: Nauplius I, 0.07 mm (Ubatuba), ventral view. – 22: Maxillule of nauplius VI. – 23: Nauplius II, 0.09 mm (Ubatuba), ventro-lateral view. – 24: Nauplius III, 0.12 mm (Ubatuba), ventro-lateral view. – 25: Caudal armature of nauplius IV, ventral view. – 26: Antennule of nauplius IV. – 27: Caudal armature of nauplius V, ventro-lateral view. – 28: Nauplius V, 0.18 mm (Curaçao), profile. – 29: Nauplius VI, 0.20 mm (Ubatuba), ventral view; right mandible not represented. – 30: Maxillule from nauplius V. – 31: Mandible of nauplius V. – 32: Mandible from nauplius VI. [Scales = 0.1 mm]

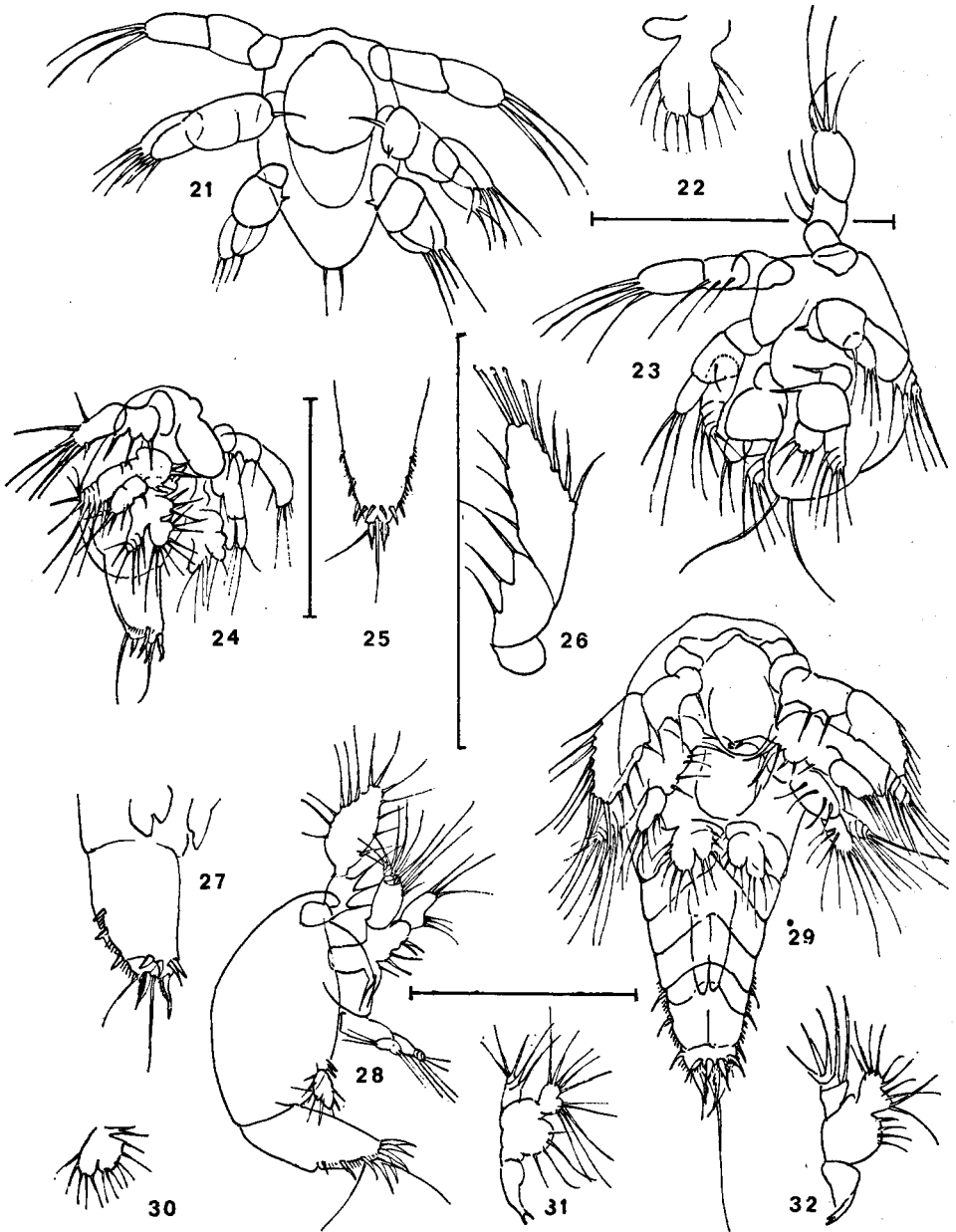
Fig. 33–34, 36–37. *Calocalanus pavo* (from Curaçao). – 33: Nauplius V, 0.21 mm, ventral view. – 34: Detail of the maxillule and maxilla of the nauplius of Fig. 37, ventral. – 36: Nauplius IV, 0.17 mm, ventro-lateral view. – 37: Nauplius VI, 0.22 mm, beginning metamorphosis, ventro-lateral view.

Fig. 35, 38–39. *Calocalanus styliremis* (from Ubatuba). – 35: Mandibular palp of nauplius IV. – 38: Caudal armature of nauplius VI, 0.21 mm long, profile. – 39: Caudal armature of nauplius VI, 0.16 mm long, ventro-lateral view. [Scales = 0.1 mm]









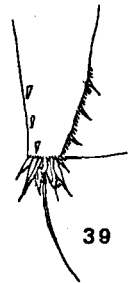
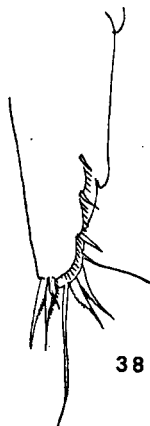
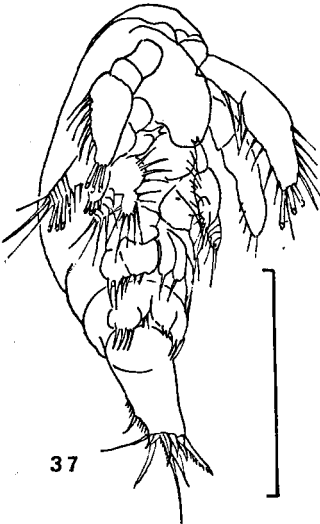
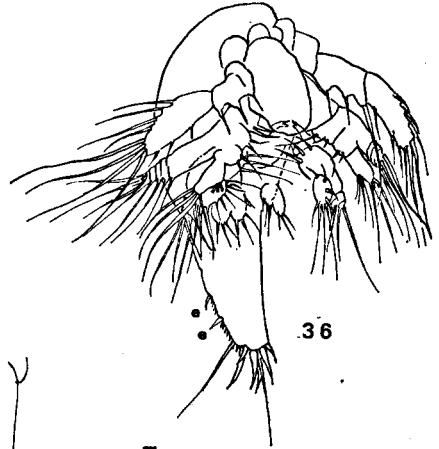
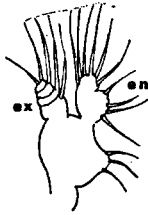
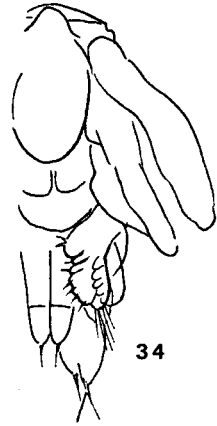
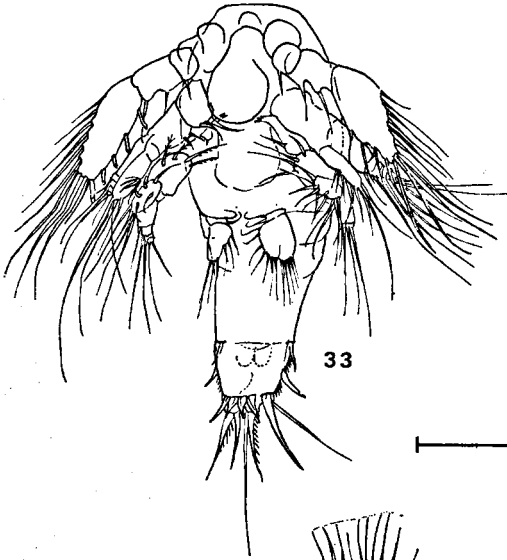


Fig. 40–49. *Clausocalanus furcatus*. – 40: Nauplius I, 0.11 mm incl. caudal setae (Curaçao), ventral view. – 41: Mandible of nauplius I. – 42: Antenna of nauplius I. – 43: Nauplius III, 0.13 mm (Santos), ventro-lateral view. – 44: Antenna of nauplius V. – 45: Nauplius IV, 0.21 mm (Santos), ventral view. – 46: Maxillule of nauplius V. – 47: Schematic representation of nauplius III, the setae indicating the direction of the naupliar movement as it turns a somersault. – 48: Schematic representation of the naupliar locomotion during somersaulting. – 49: Nauplius V, 0.25 mm (Ubatuba). [Scales = 0.1 mm]

Fig. 50–53, 56. *Ctenocalanus vanus* (from Santos). – 50: Nauplius III, 0.21 mm incl. caudal setae, lateral view. – 51: Nauplius IV, 0.24 mm incl. caudal setae, ventral view. – 52: Caudal armature of nauplius III. – 53: Antennule of nauplius III. – 56: Nauplius V, 0.25 mm, latero-ventral view.

Fig. 54–55, 57. *Paracalanus aculeatus* (from Santos). – 54: Mandible of nauplius IV. – 55: Caudal armature of nauplius IV, profile. – 57: Nauplius V, 0.22 mm, ventral view. [Scales = 0.1 mm]

Fig. 58, 62. *Temora turbinata* (from Curaçao). – 58: Nauplius IV, 0.26 mm, profile, schematic. – 62: Nauplius VI?, 0.24 mm, latero-ventral view.

Fig. 59. *Rhincalanus cornutus* (from Curaçao). Nauplius IV, 0.77 mm, ventral view.

Fig. 60. *Euchaeta marina* (from Curaçao). Nauplius VI, 0.52 mm, ventral view.

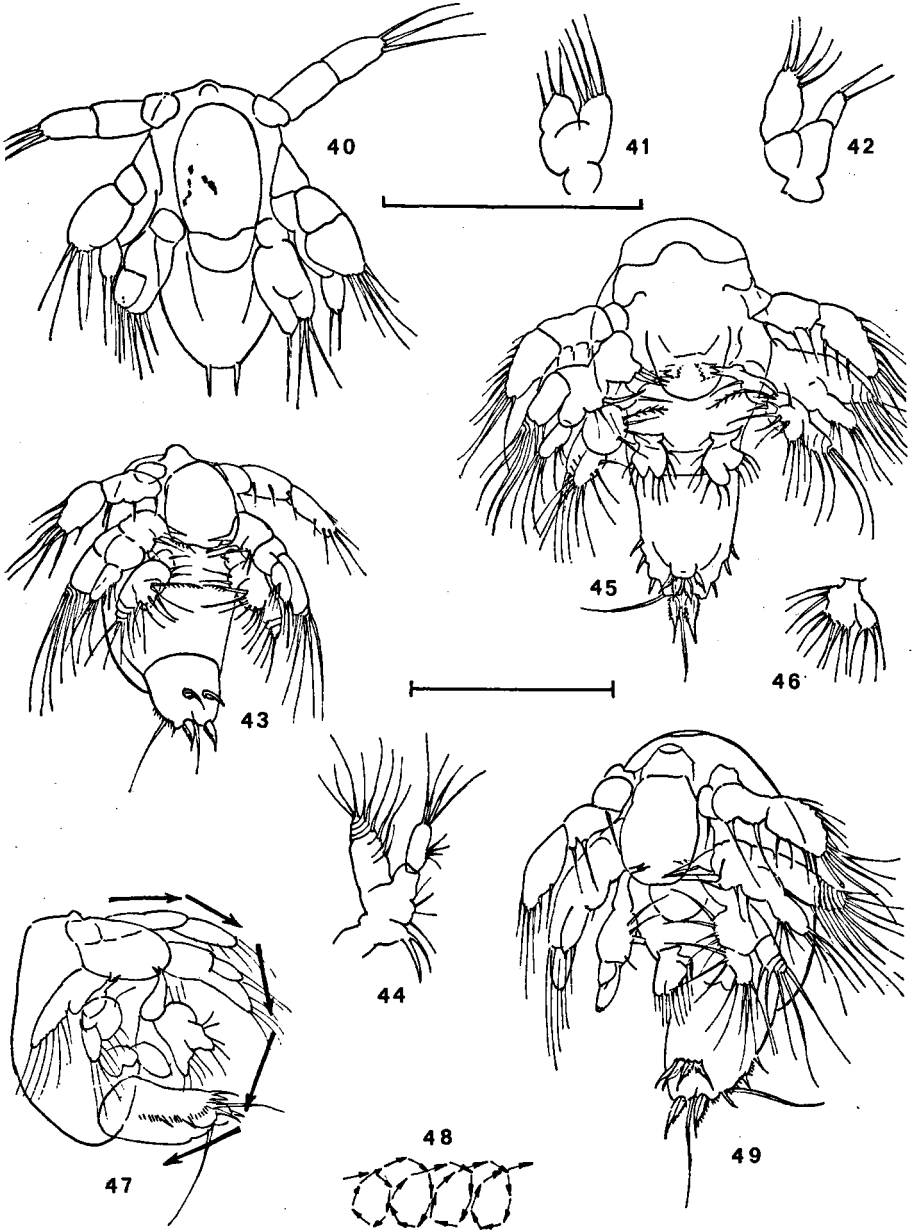
Fig. 61. *Temora stylifera* (from Curaçao). Nauplius V, 0.23 mm, ventral view.

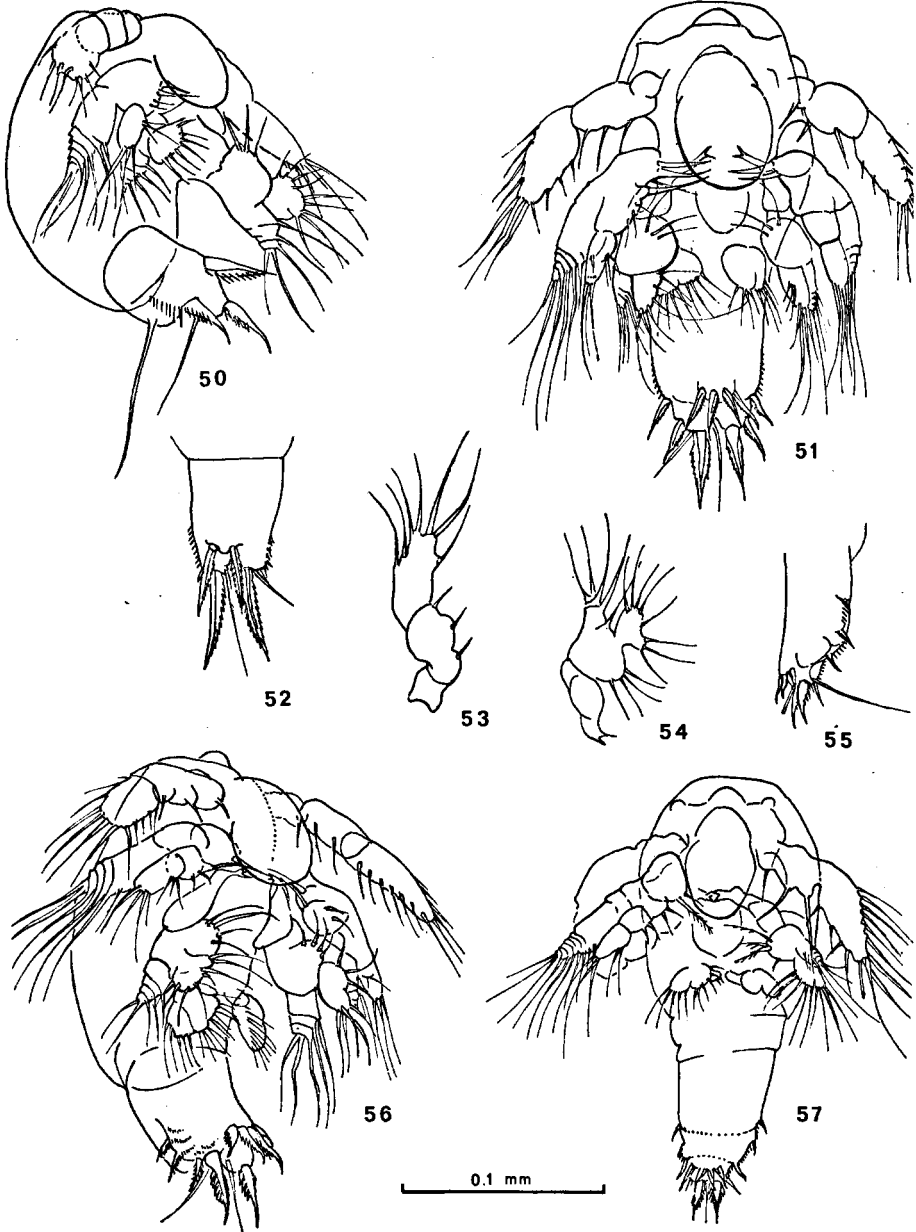
Fig. 63–66. *Nannocalanus minor* (off Chile). – 63: Antennule of nauplius VI. – 64: Antenna of nauplius VI. – 65: Mandible of nauplius VI. – 66: Posterior region of nauplius VI, latero-ventral view, showing maxillule, maxilla, maxillipeds, legs and caudal armature. [Scales = 0.1 mm]

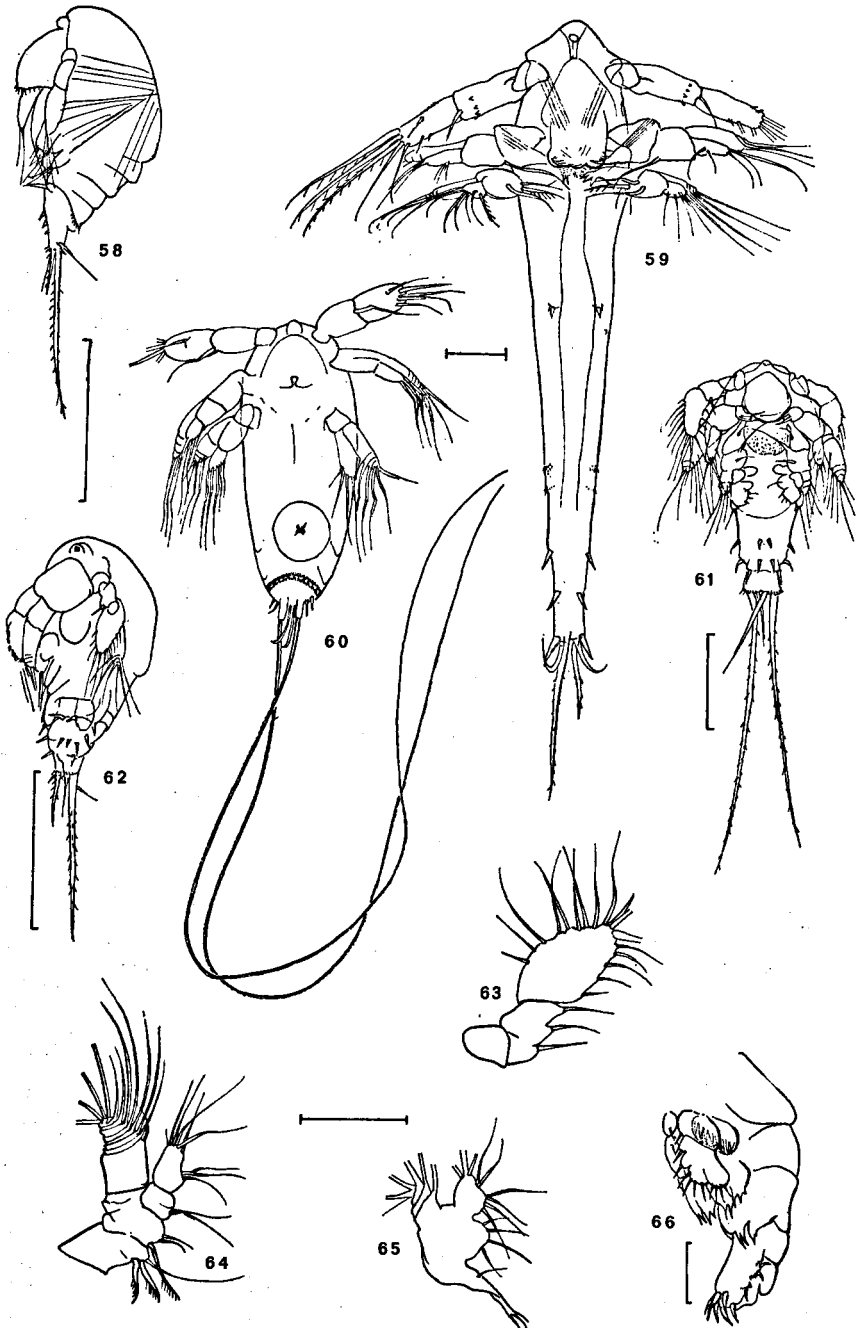
Fig. 67–75. *Pleuromamma* sp. ("Lomonosov" coll.). – 67: Antenna of nauplius V. – 68: Mandible of nauplius V. – 69: Nauplius V, 0.53 mm, ventral view. – 70: Nauplius IV, 0.47 mm, ventral. – 71: Antennule of nauplius V. – 72: Nauplius V, profile, detail of the maxillule and caudal armature. – 73: Maxillule of nauplius V. – 74: Nauplius VI, 0.51 mm. – 75: Mandible blade of nauplius V. [Scales = 0.1 mm]

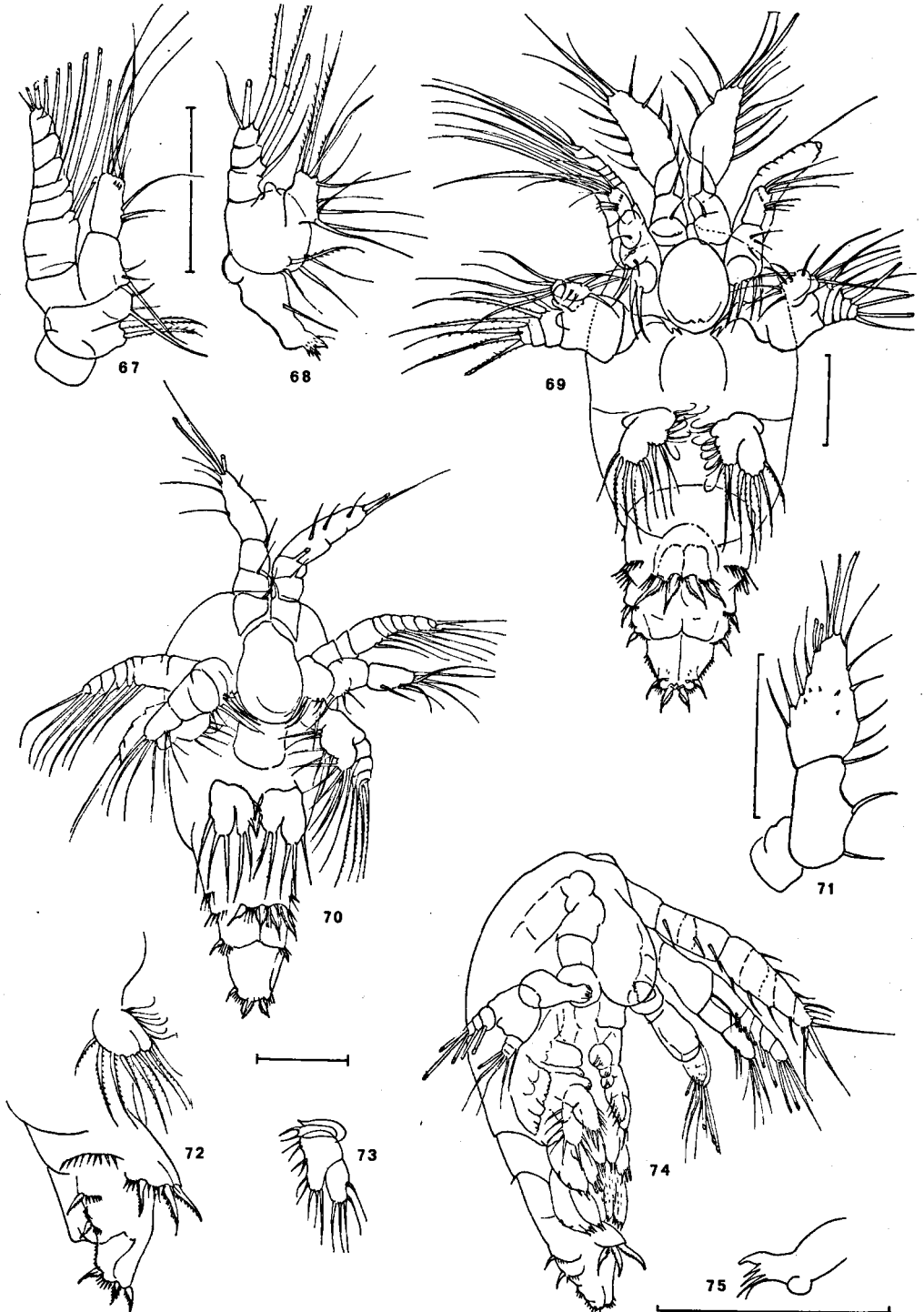
Fig. 76–81. *Centropages furcatus* (from Ubatuba). – 76: Nauplius I, 0.12 mm, obtained by rearing, just after leaving the ovular envelopes, ventral view; the colour indicated by stippling. – 77: Nauplius I, 0.12 mm, latero-ventral view, from a preserved plankton sample. – 78: Nauplius II, 0.21 mm, ventral view. – 79: Nauplius II, 0.20 mm, latero-ventral view, with chromatophores expanded. – 80: Nauplius II, mandible. – 81: Egg, 0.12 mm, from egg-carrying female.

Fig. 82. *Centropages* sp. (from the Subtropical Convergence region). Nauplius VI, 0.25 mm. [Scales = 0.1 mm]









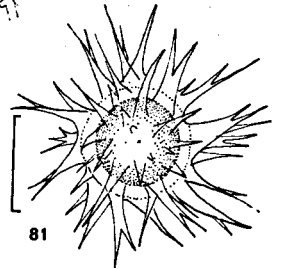
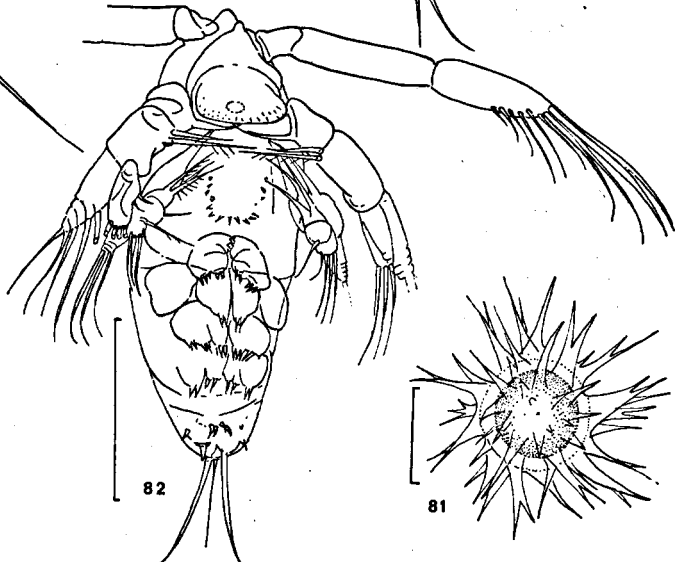
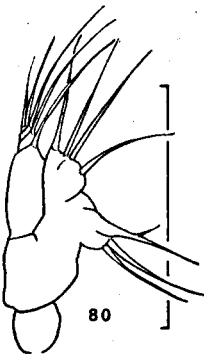
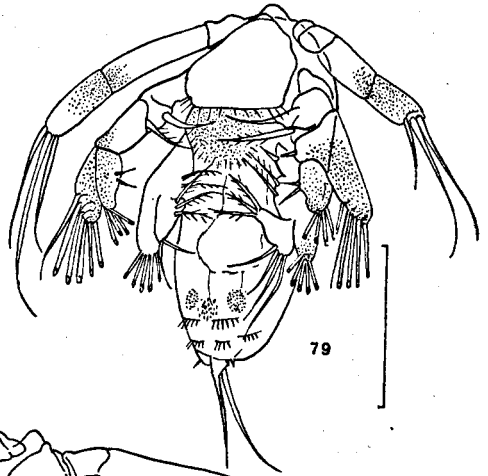
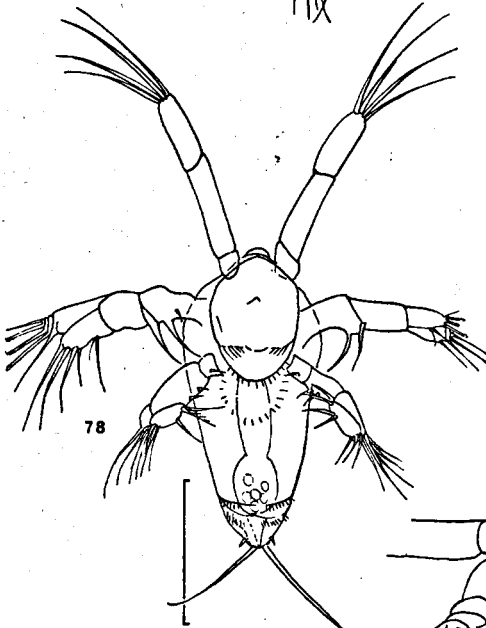
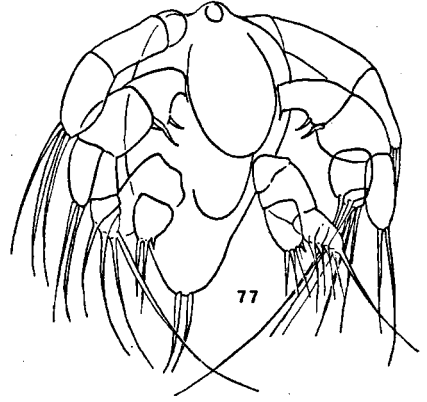
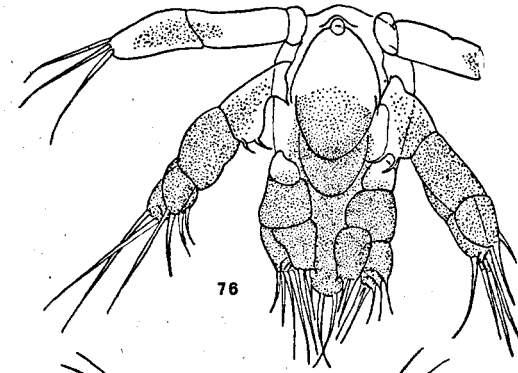


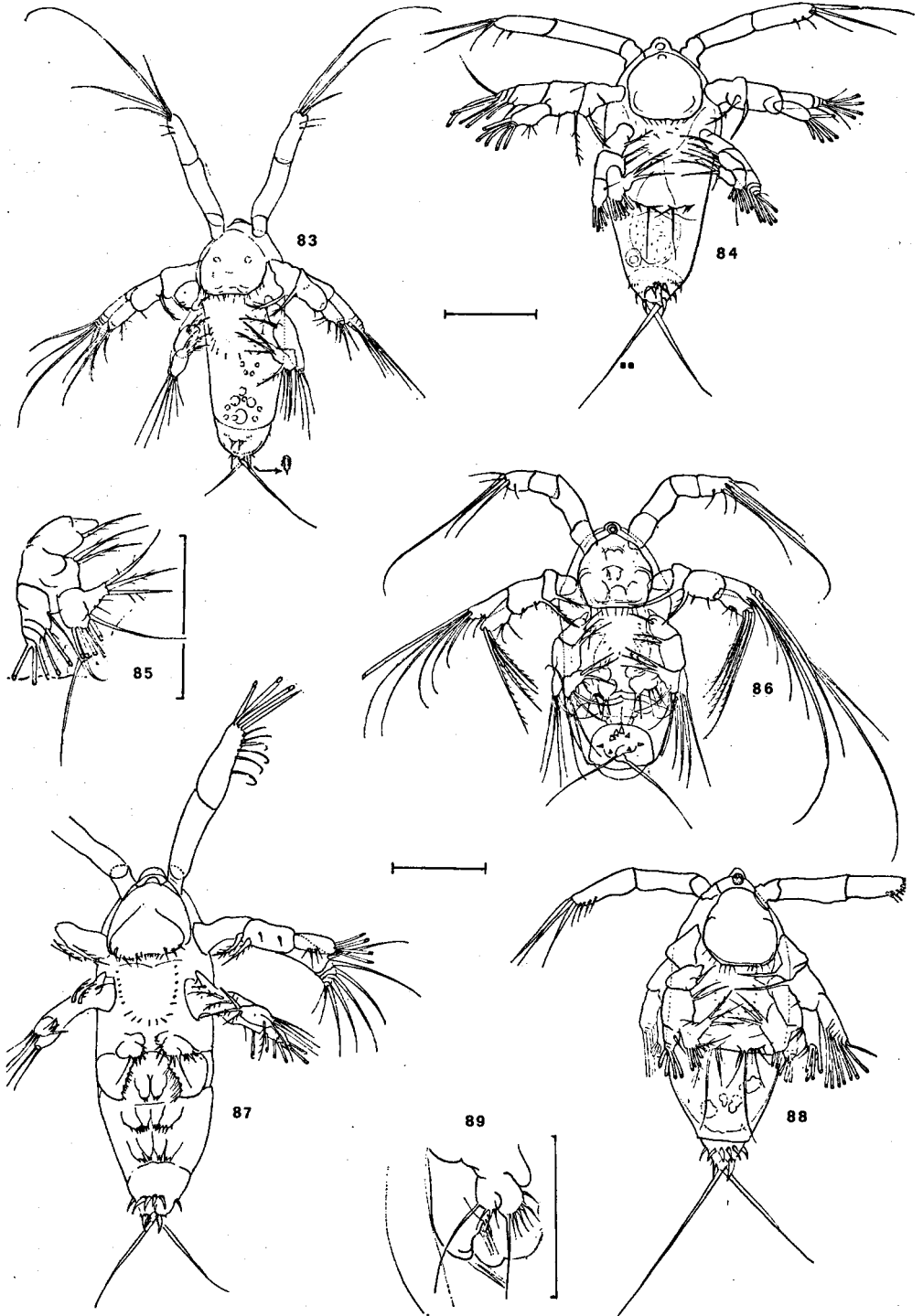
Fig. 83–89. *Centropages furcatus*. – 83: Nauplius III, 0.26 mm (off Santos), ventral view and detail of caudal spine. – 84: Nauplius IV, 0.26 mm (off Santos), ventral view. – 85: Mandible and outline of the maxilla of nauplius IV. – 86: Nauplius V, 0.32 mm (Ubatuba), with caudal region bent forwards, ventral view. – 87: Nauplius VI, 0.37 mm (off Santos), ventral view. – 88: Nauplius V, 0.33 mm (Ubatuba). – 89: Maxillule and maxilla of nauplius VI. [Scales = 0.1 mm]

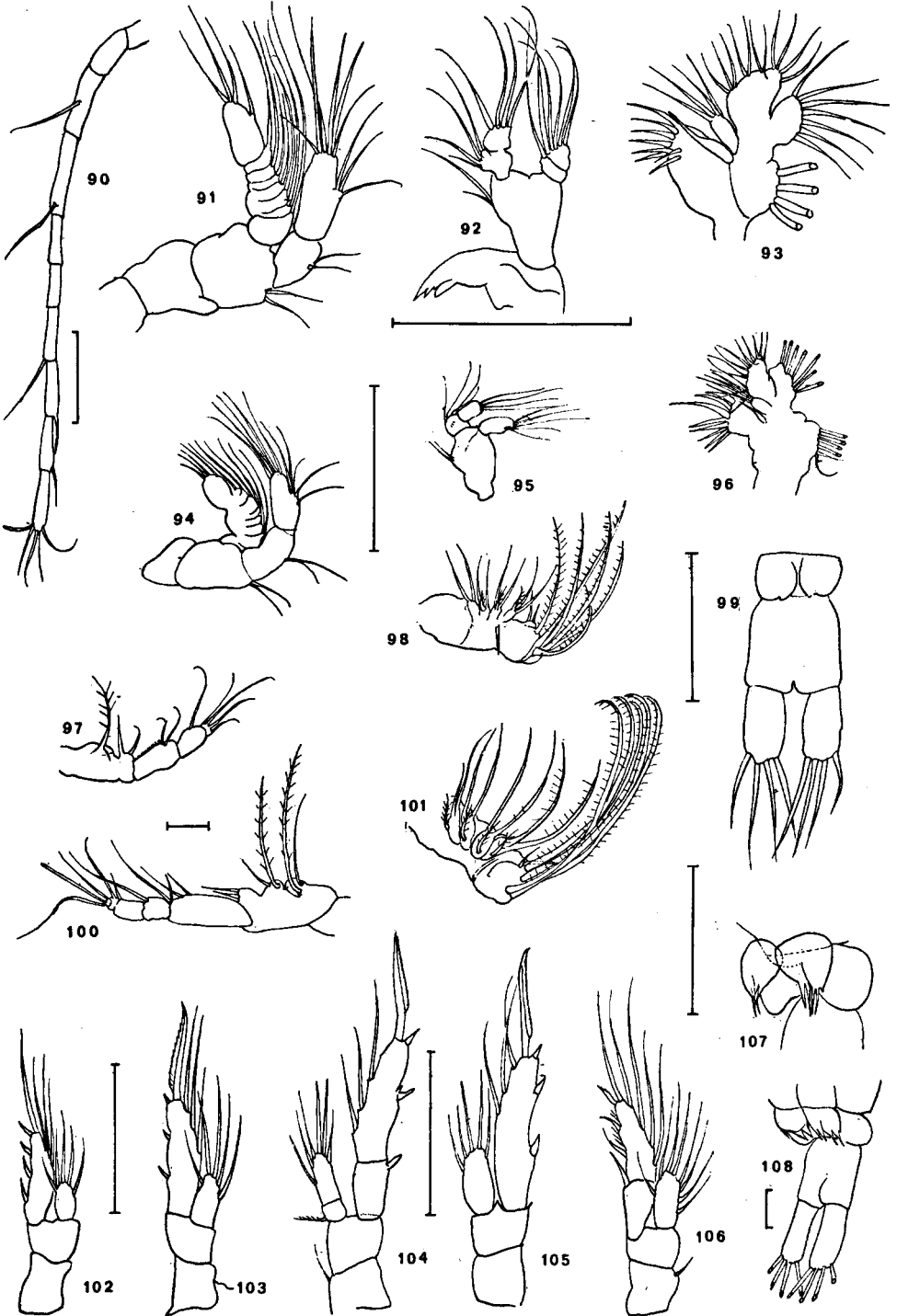
Fig. 90–108. *Centropages furcatus*. – 90: Antennule of copepodid I. – 91: Antenna of copepodid I. – 92: Mandible of copepodid I. – 93: Maxillule of copepodid I. – 94: Antenna of copepodid II. – 95: Mandible of copepodid II. – 96: Maxillule of copepodid II. – 97: Maxilliped of copepodid I. – 98: Maxilla of copepodid I. – 99: Abdomen and last thoracic segment of copepodid I. – 100: Maxilliped of copepodid II. – 101: Maxilla of copepodid II. – 102: Leg I of copepodid I. – 103: Leg II of copepodid I. – 104: Leg II of copepodid II. – 105: Leg III of copepodid II. – 106: Leg I of copepodid II. – 107: Legs III on last thoracic segment of copepodid I. – 108: Abdomen, last thoracic segment and legs IV of copepodid II. [Scales = 0.1 mm]

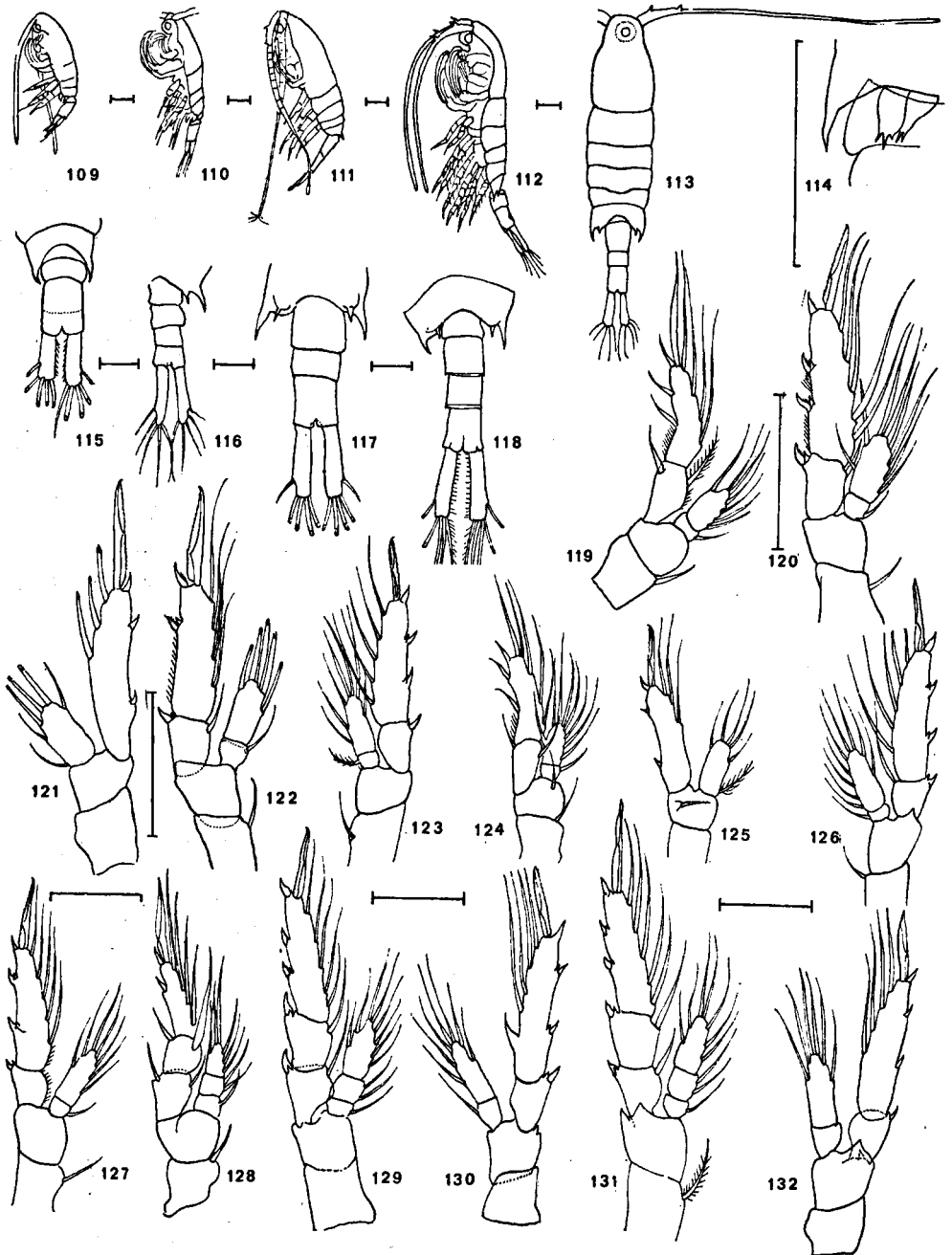
Fig. 109–132. *Centropages furcatus* (from Ubatuba). – 109: Copepodid I, 0.56 mm, profile. – 110: Copepodid II, 0.70 mm, profile. – 111: Copepodid III, 1.07 mm, profile. – 112: Copepodid IV, male, 1.15 mm, profile. – 113: Copepodid V, female, 1.40 mm, dorsal, right antennule not represented. – 114: Leg V of copepodid III, on last thoracic segment, partially covering the first abdominal segment. – 115: Abdomen and last thoracic segment of copepodid III. – 116: Abdomen and last thoracic segment of copepodid IV. – 117: Abdomen and last thoracic segment of copepodid V, female. – 118: Abdomen and last thoracic segment of copepodid V, male. – 119: Leg I of copepodid III. – 120: Leg II of copepodid III. – 121: Leg IV of copepodid III. – 122: Leg III of copepodid III. – 123: Leg II of copepodid IV. – 124: Leg I of copepodid IV. – 125: Leg V of copepodid IV. – 126: Leg III of copepodid IV. – 127: Leg IV of copepodid IV. – 128: Leg I of copepodid V. – 129: Leg II of copepodid V. – 130: Leg V of copepodid V, female. – 131: Leg III of copepodid V, female. – 132: Leg V of copepodid V, male. [Scales = 0.1 mm]

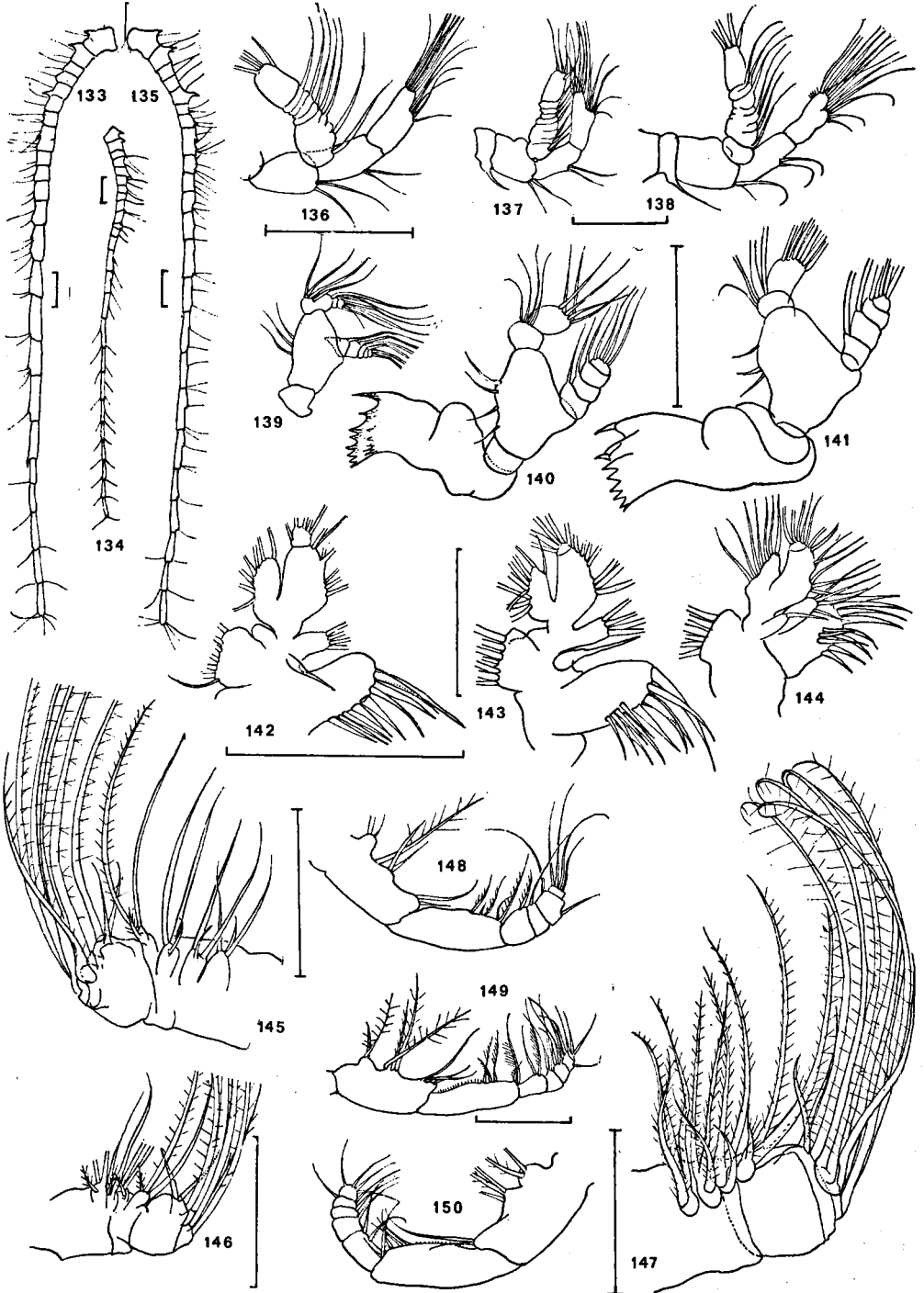
Fig. 133–150. *Centropages furcatus* (from Ubatuba). – 133: Right antennule of male copepodid V. – 134: Antennule of female copepodid V. – 135: Left antennule of male copepodid V. – 136: Antenna of copepodid III. – 137: Antenna of copepodid IV. – 138: Antenna of female copepodid V. – 139: Mandible palp of copepodid III. – 140: Mandible of copepodid IV. – 141: Mandible of male copepodid V. – 142: Maxillule of copepodid III. – 143: Maxillule of female copepodid V. – 144: Maxillule of copepodid IV. – 145: Maxilla of copepodid IV. – 146: Maxilla of copepodid III. – 147: Maxilla of female copepodid V. – 148: Maxilliped of copepodid III. – 149: Maxilliped of female copepodid V. – 150: Maxilliped of copepodid IV. [Scales = 0.1 mm]

Fig. 151–158. *Pseudodiaptomus acutus* (from Ubatuba). – 151: Nauplius II, exuvia, 0.19 mm, dorsal view. – 152: Nauplius III, 0.22 mm, ventral view. – 153: Nauplius IV, 0.25 mm, profile. – 154: Nauplius VI, 0.30 mm, latero-ventral view. – 155: Nauplius II, 0.19 mm, profile. – 156: Left maxillule of nauplius IV. – 157: Nauplius V, 0.25 mm, ventral view of exuvia. – 158: Schematic representation of the movement of the nauplius over the substratum, touching it and then swimming up again. The arrows indicate the successive forward strokes of the nauplius. [Scales = 0.1 mm]









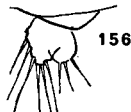
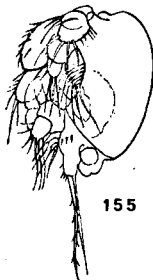
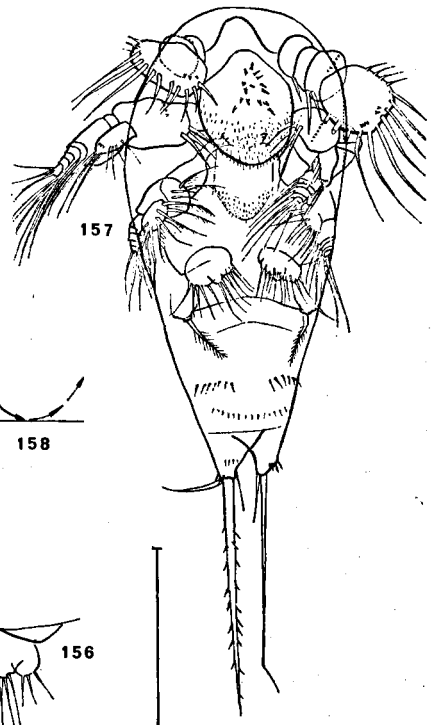
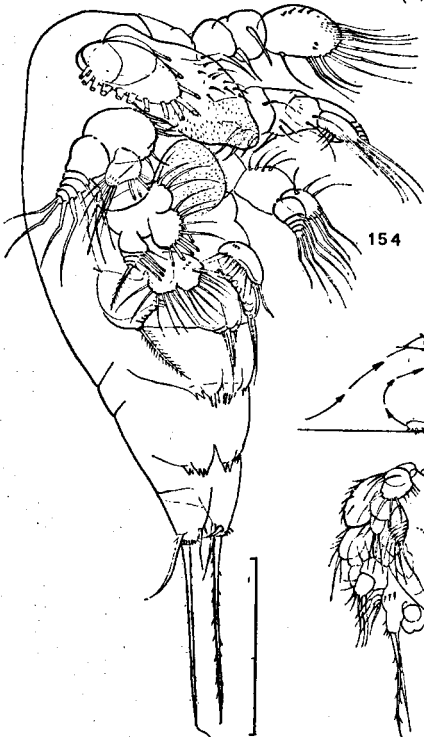
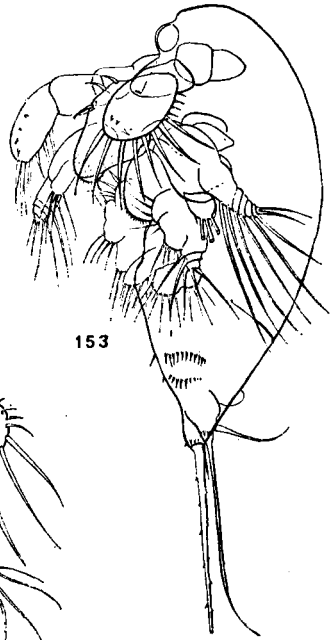
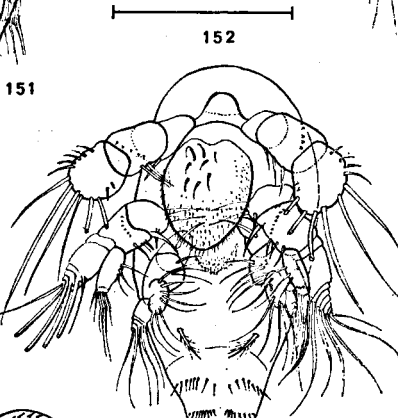
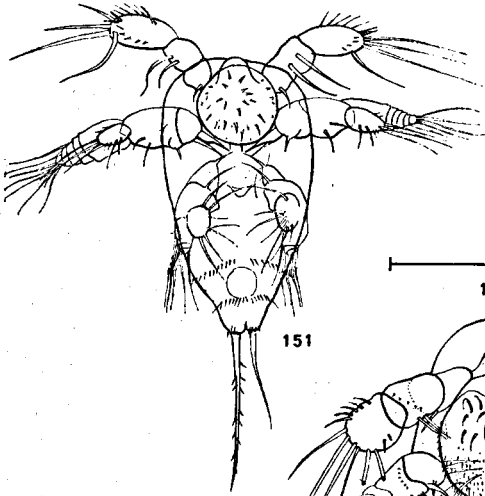
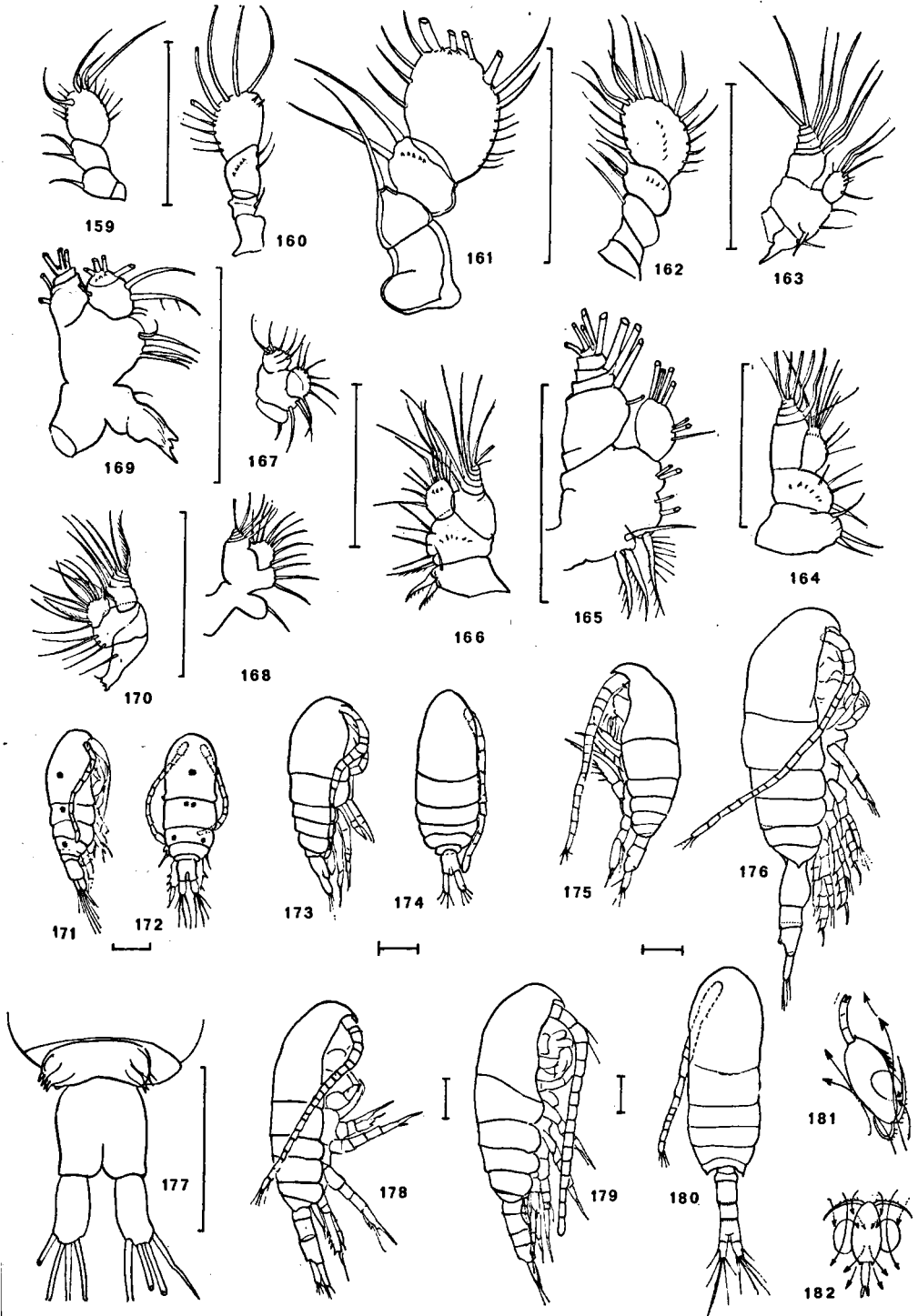
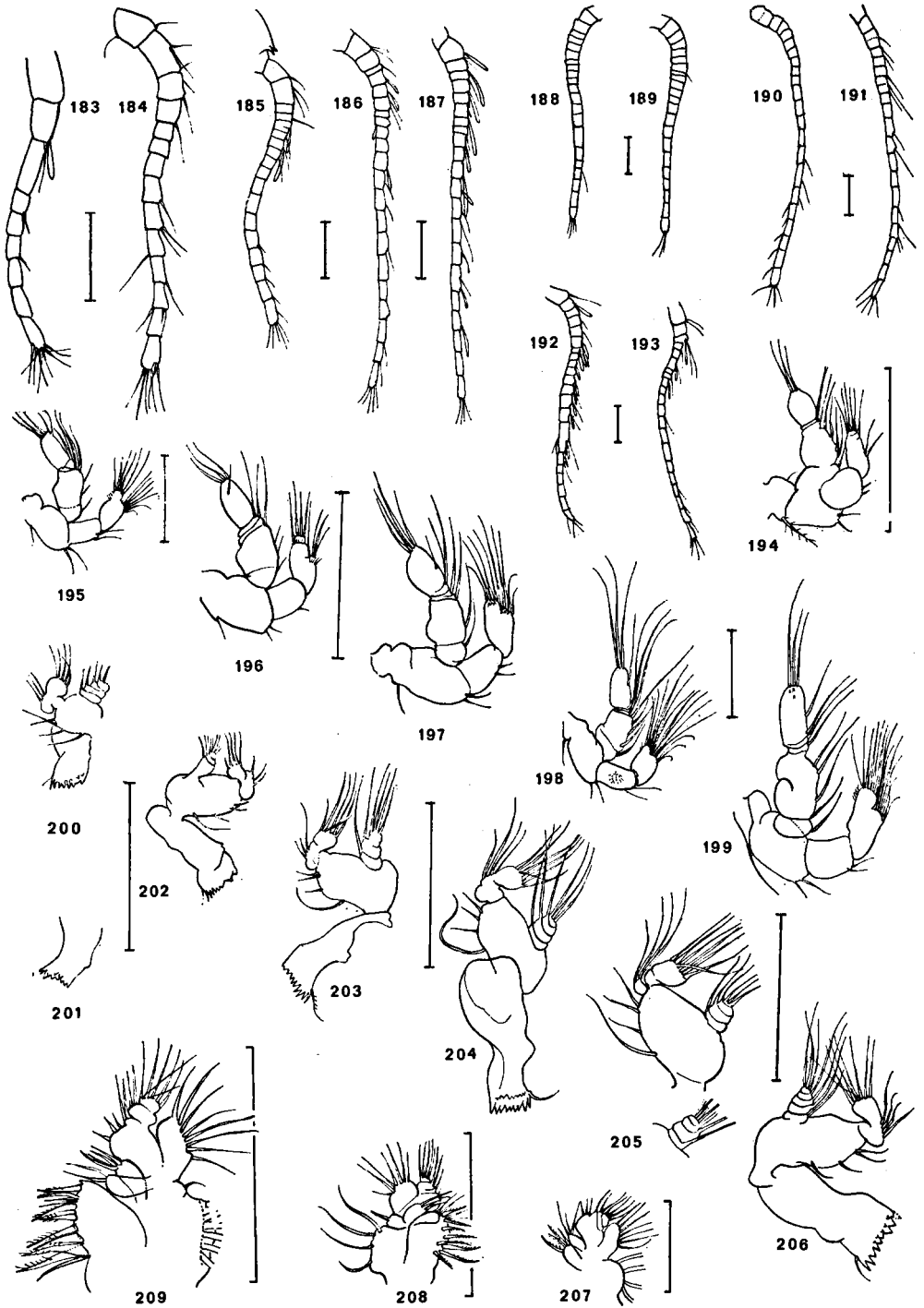


Fig. 159–182. *Pseudodiaptomus acutus* (from Ubatuba). – 159: Antennule of nauplius II. – 160: Antennule of nauplius III. – 161: Antennule of nauplius IV. – 162: Antennule of nauplius VI. – 163: Antenna of nauplius II. – 164: Antenna of nauplius III. – 165: Antenna of nauplius IV. – 166: Antenna of nauplius V. – 167: Mandible of nauplius II. – 168: Mandible of nauplius III. – 169: Mandible of nauplius IV. – 170: Mandible of nauplius V. – 171: Copepodid I, 0.44 mm, profile. – 172: Copepodid I, 0.44 mm, dorsal view. – 173: Copepodid II, 0.54 mm, profile. – 174: Copepodid II, 0.54 mm, dorsal view. – 175: Copepodid III, 0.62 mm, profile. – 176: Female copepodid V, 0.99 mm, profile. – 177: Abdomen and last thoracic segment of copepodid I, legs III outlined, ventral view. – 178: Male copepodid IV, 0.77 mm, profile. – 179: Female copepodid IV, 0.81 mm, profile. – 180: Male copepodid V, 0.78 mm, dorsal view. – 181: Trophic currents produced when the copepodid adheres to the substrate with the antennular aesthetes (schematic representation). – 182: Trophic currents produced when in suspension (schematic representation). [Scales = 0.1 mm]

Fig. 183–209. *Pseudodiaptomus acutus* (from Ubatuba). – 183: Antennule of copepodid I. – 184: Antennule of copepodid II. – 185: Antennule of copepodid III. – 186: Antennule of female copepodid IV. – 187: Right antennule of female copepodid V. – 188: Right antennule of male copepodid IV. – 189: Left antennule of male copepodid IV. – 190: Left antennule of female copepodid V. – 191: Right antennule of female copepodid V. – 192: Right antennule of male copepodid V. – 193: Left antennule of male copepodid V. – 194: Antenna of copepodid I. – 195: Antenna of male copepodid V. – 196: Antenna of copepodid II. – 197: Antenna of copepodid III. – 198: Antenna of female copepodid IV. – 199: Antenna of female copepodid V. – 200: Mandible of copepodid I. – 201: Mandibular blade of copepodid I. – 202: Mandible of copepodid II. – 203: Mandible of copepodid III. – 204: Mandible of female copepodid IV. – 205: Mandibular palp of male copepodid V, and exopod of the mandible of male copepodid IV. – 206: Mandible of female copepod V. – 207: Maxillule of copepodid I, detail. – 208: Maxillule of copepodid I. – 209: Maxillule of copepodid III. [Scale = 0.1 mm]

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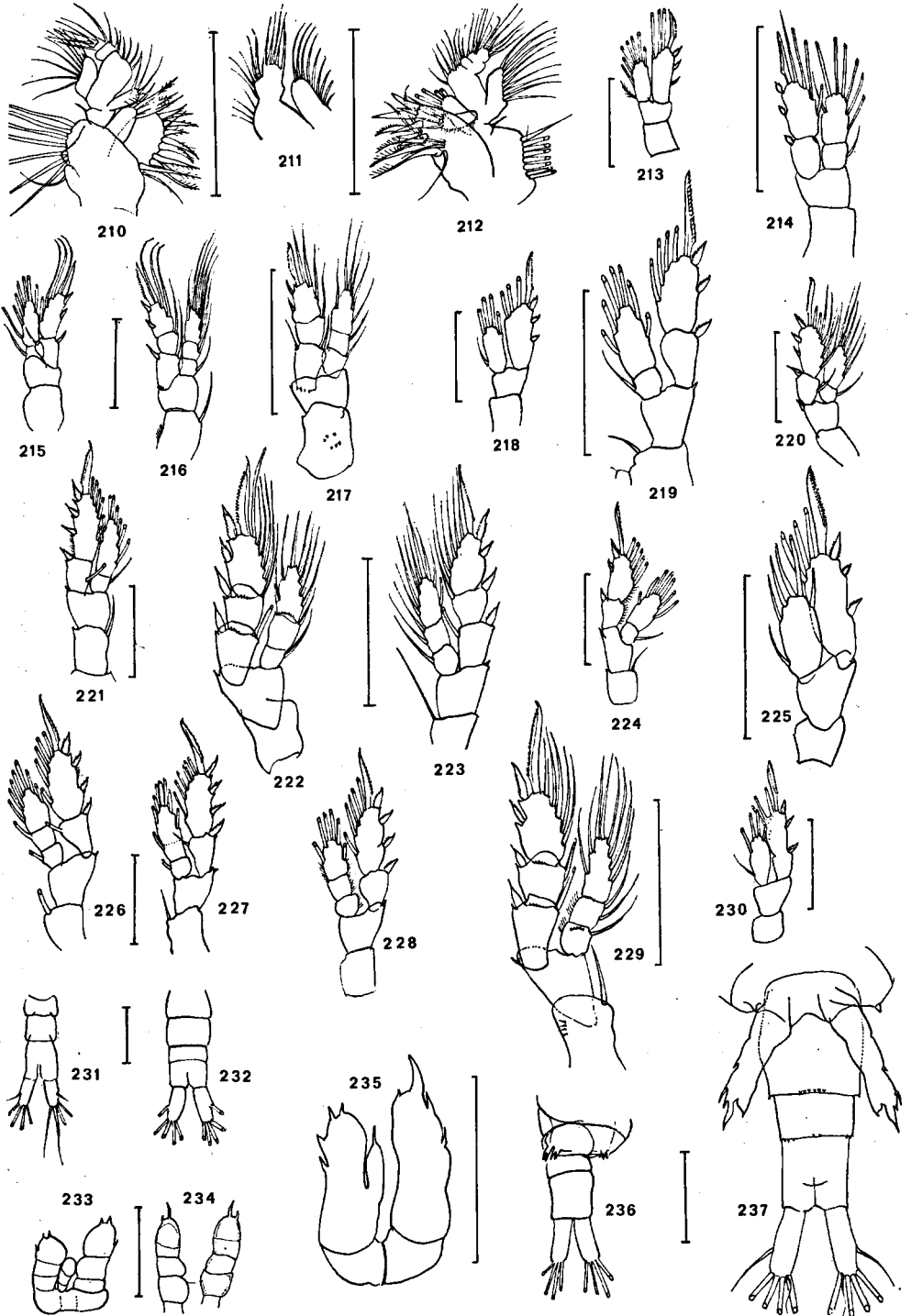


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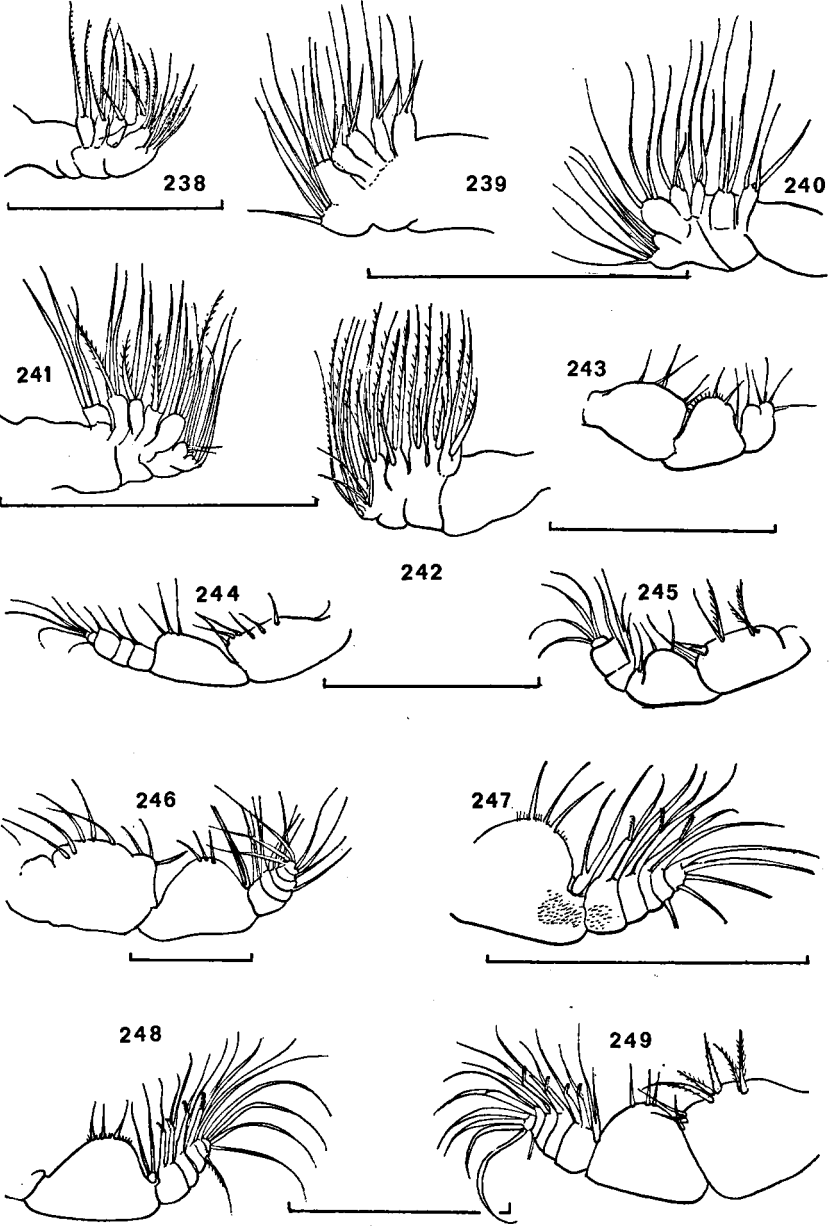
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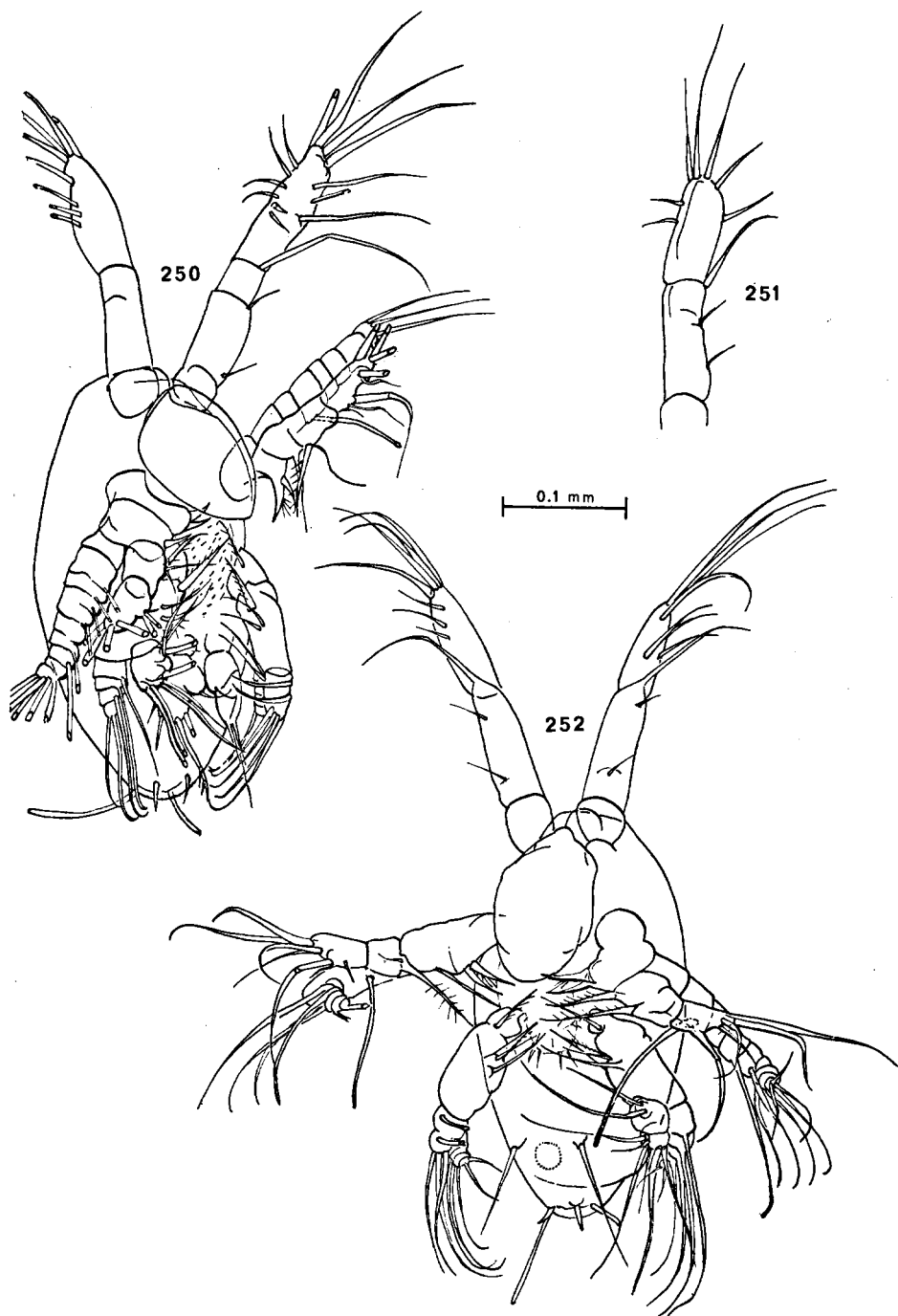
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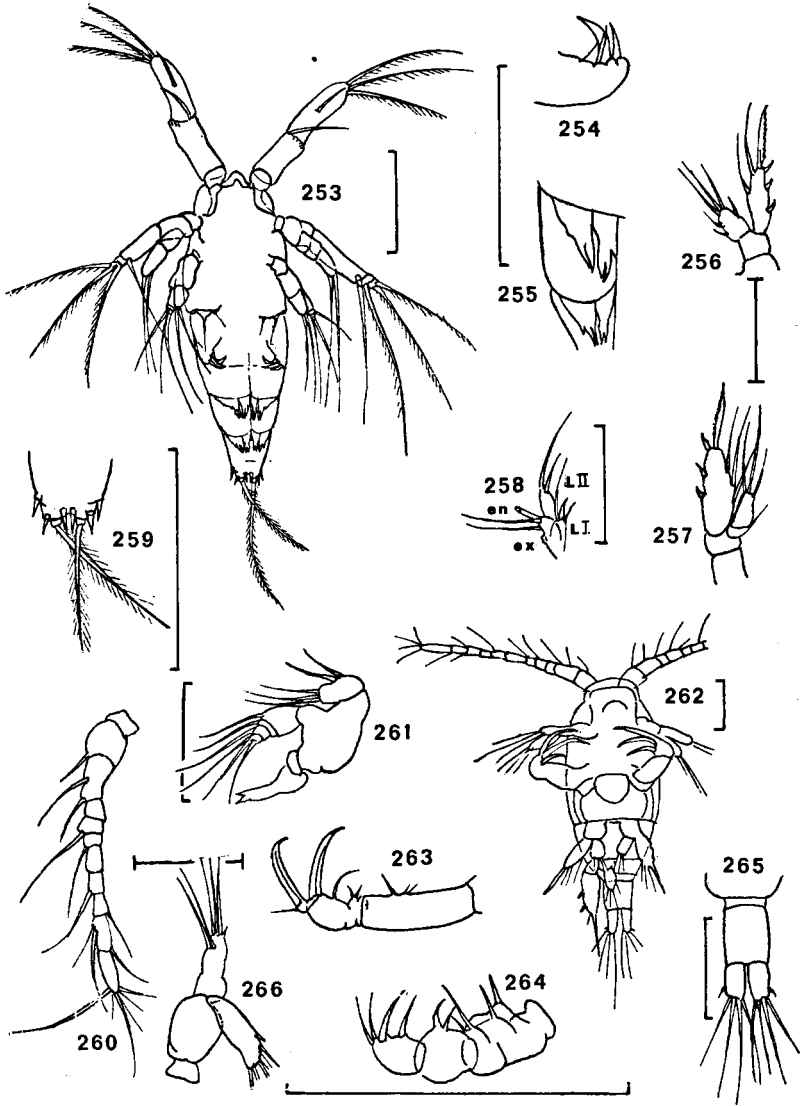
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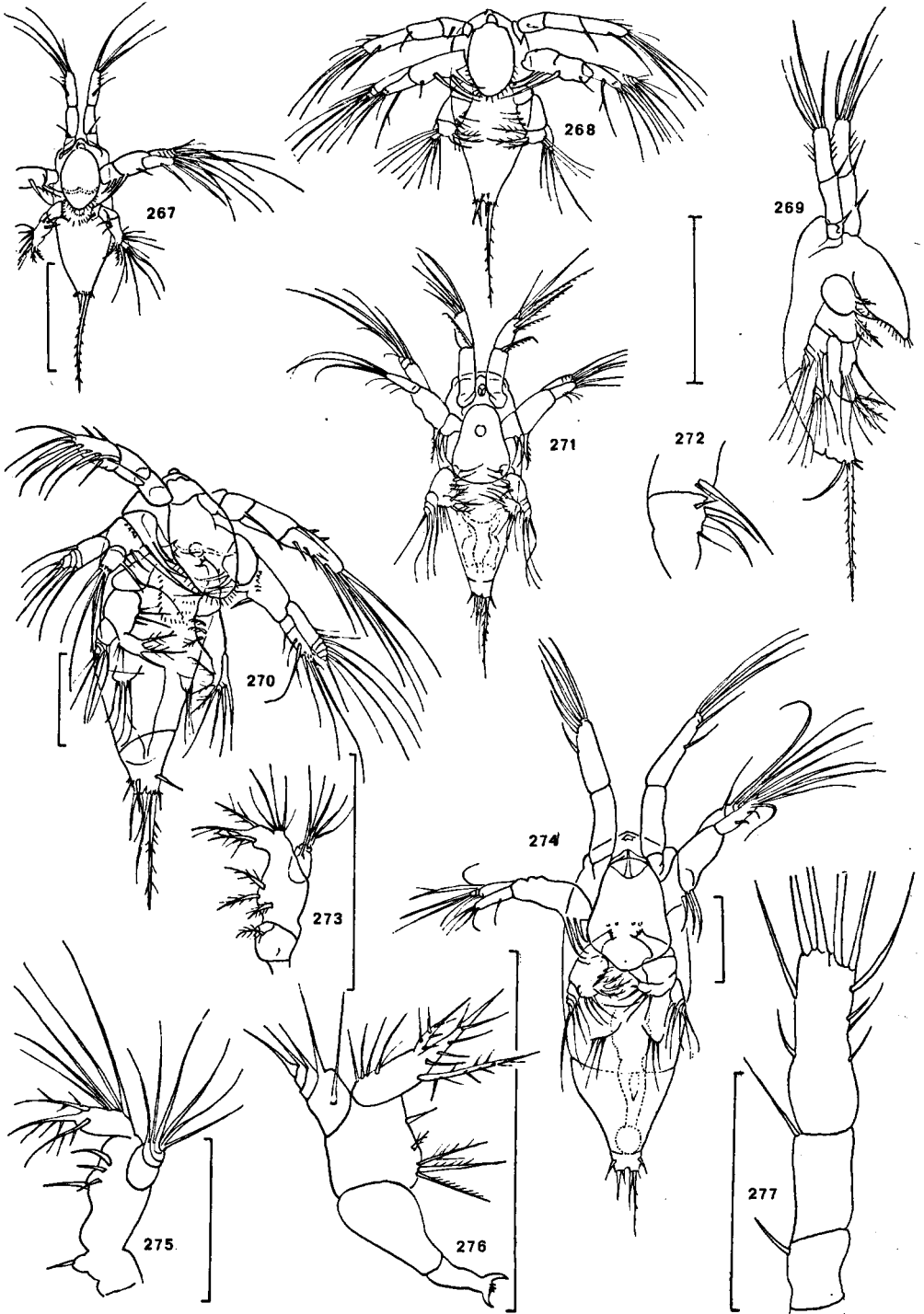
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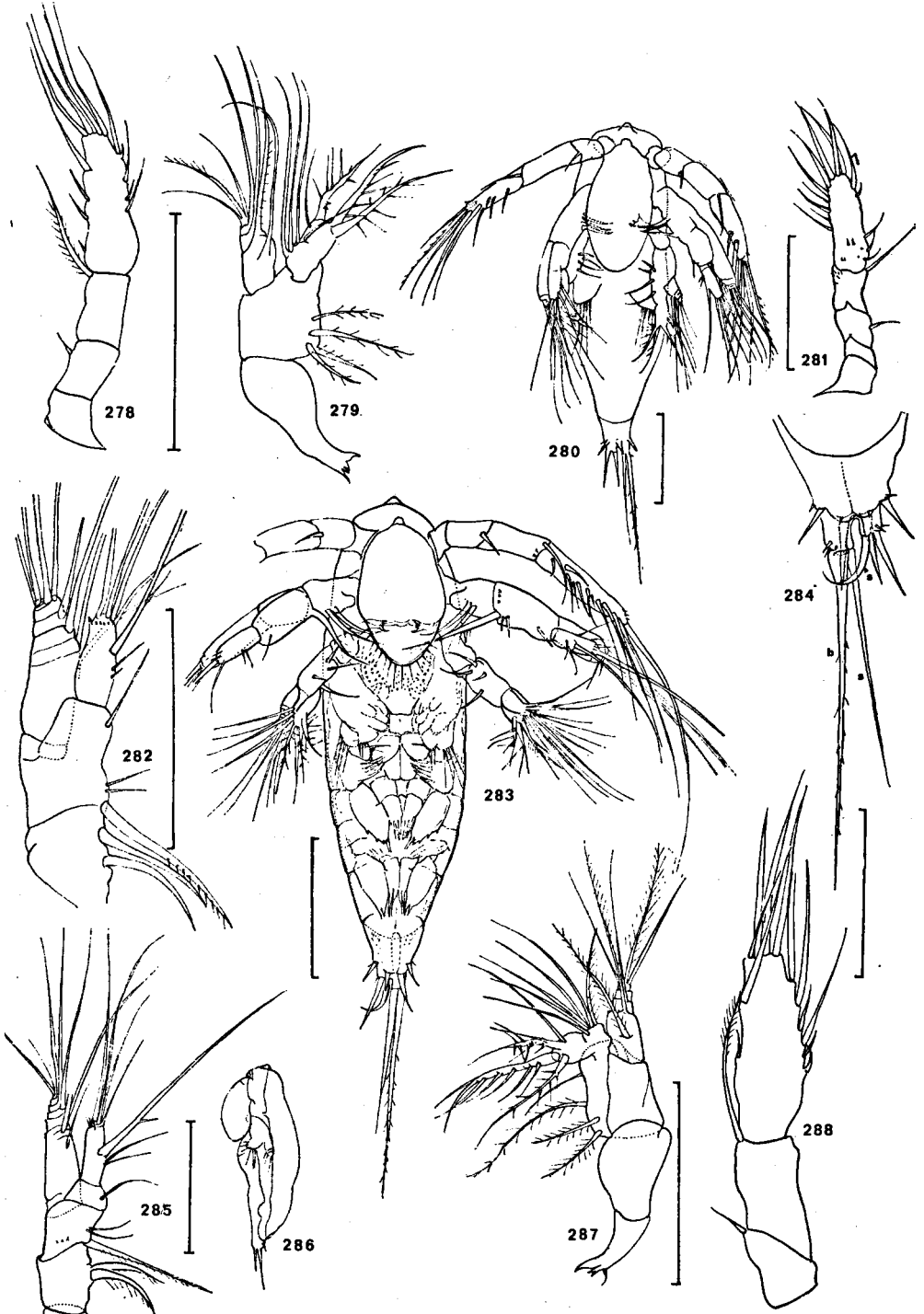
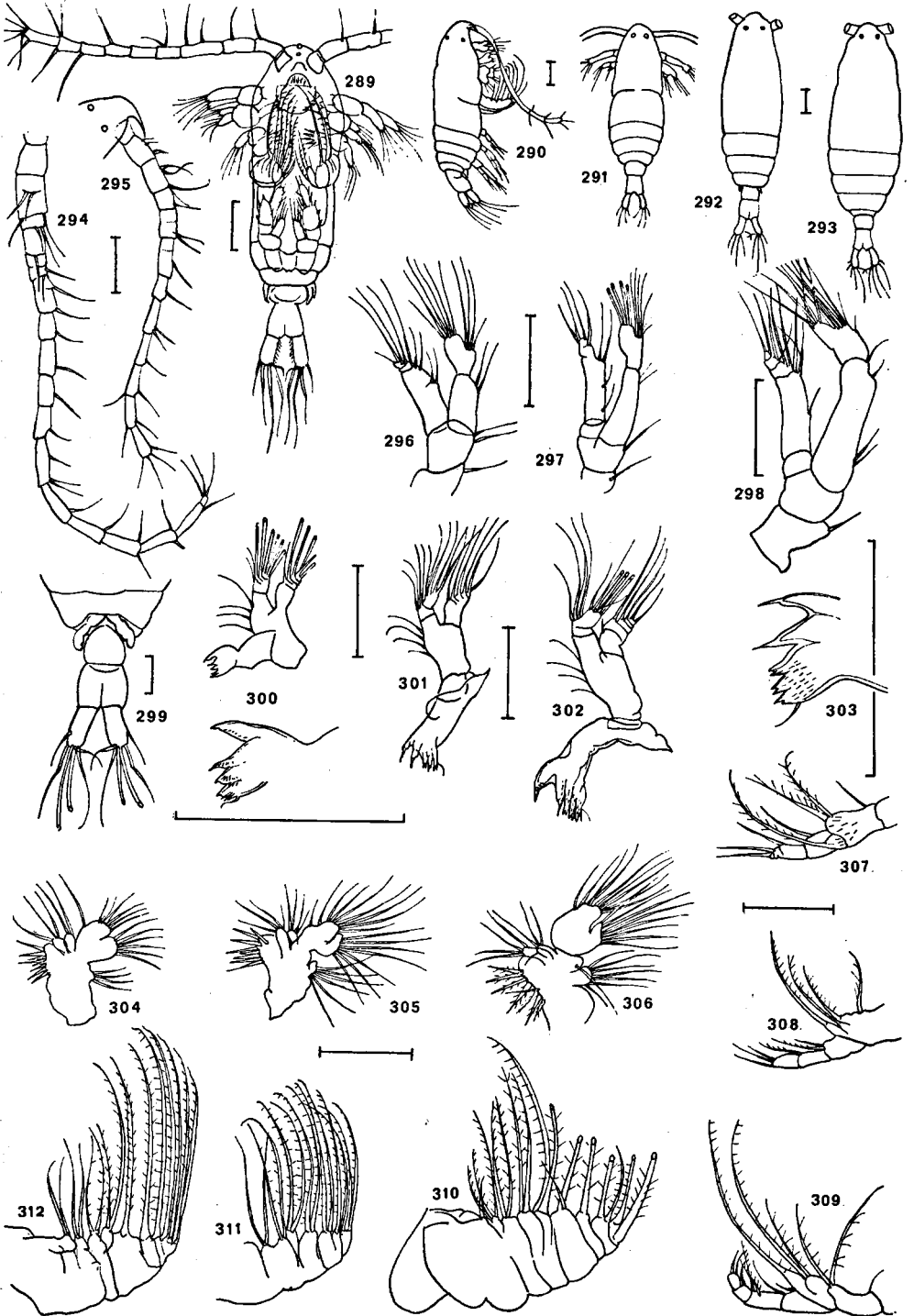
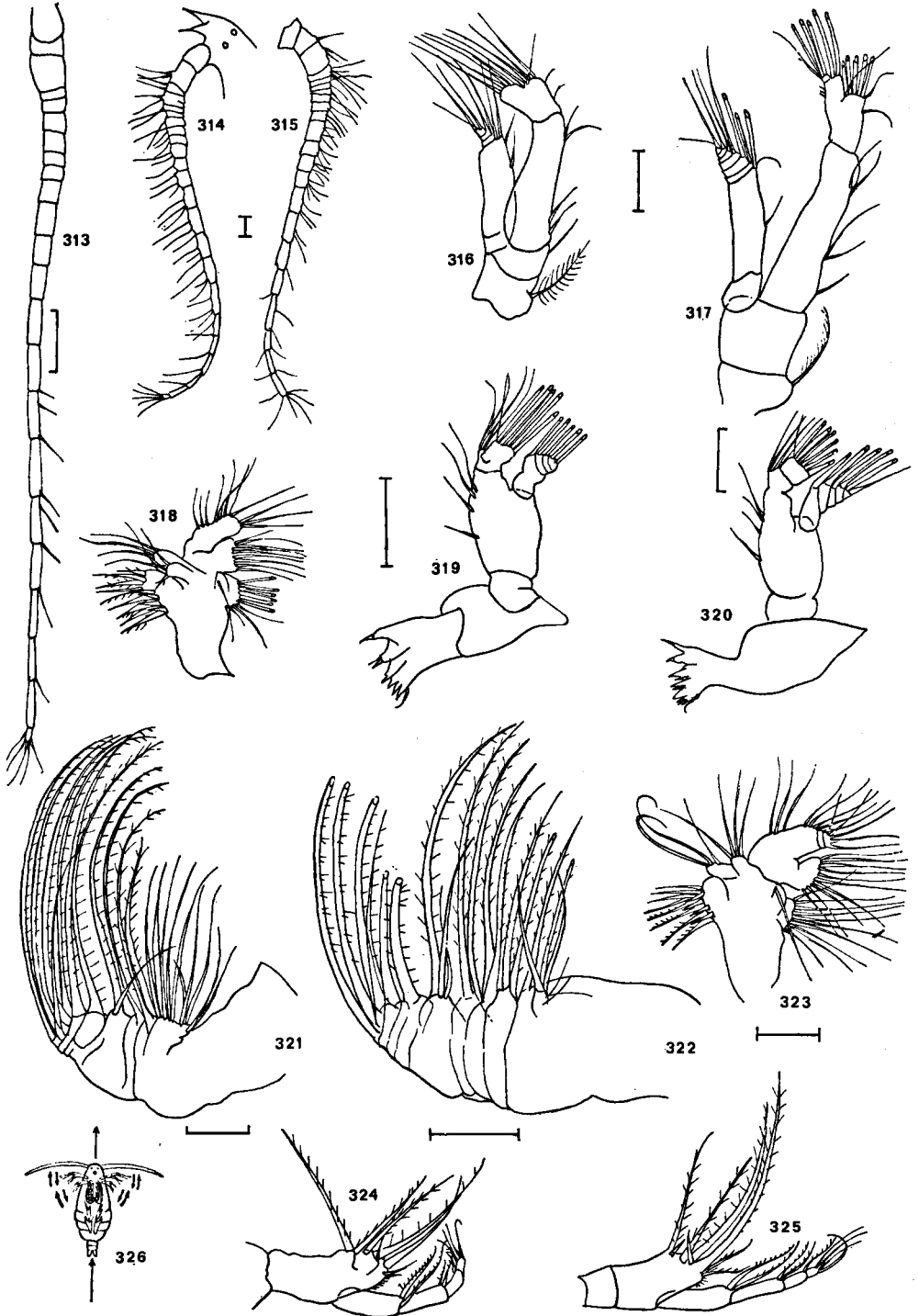


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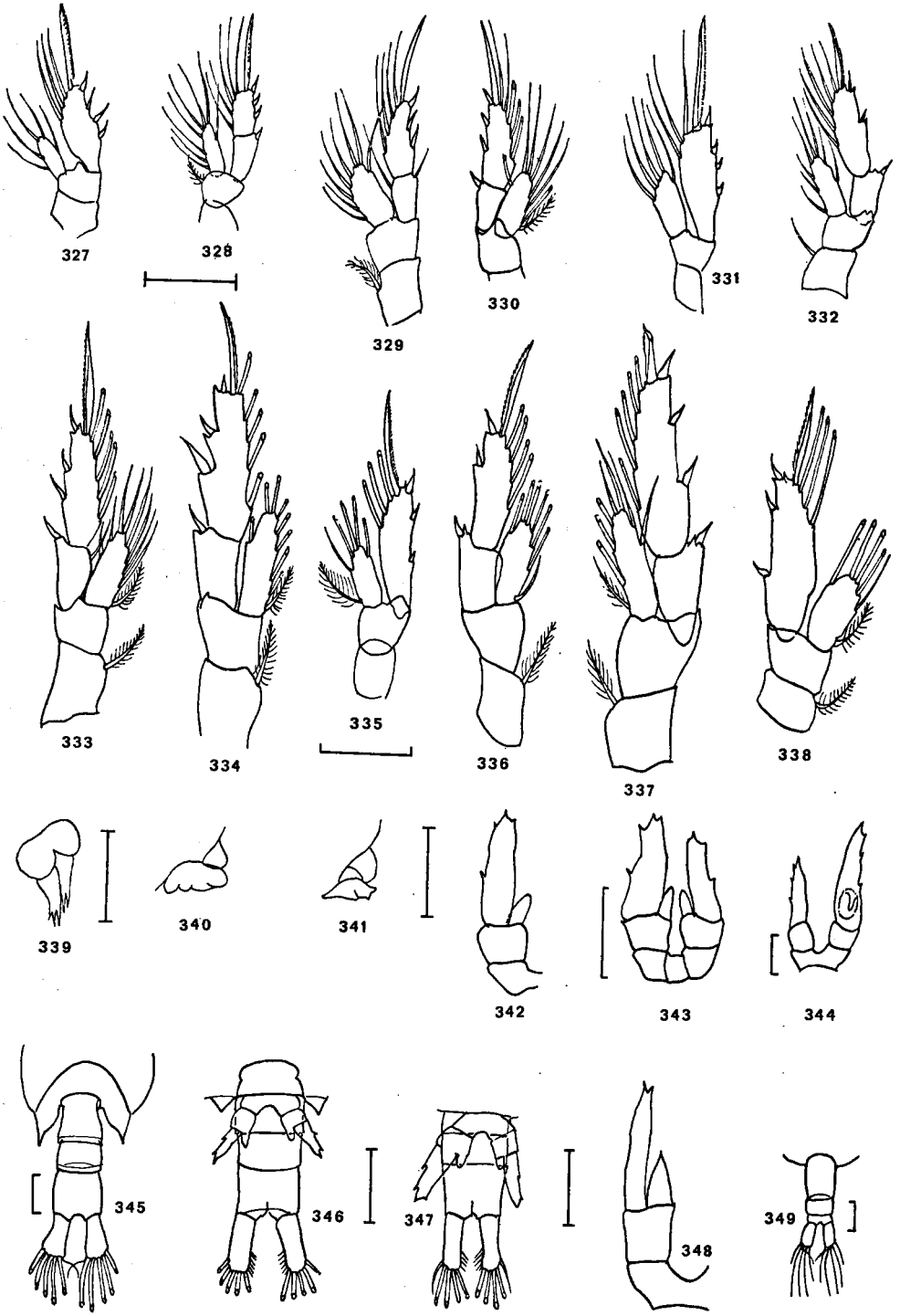


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Fig. 372. *Pontellid* (from sample M-736). Caudal armature of nauplius III (see Fig. 351). [Scales = 0.1 mm]

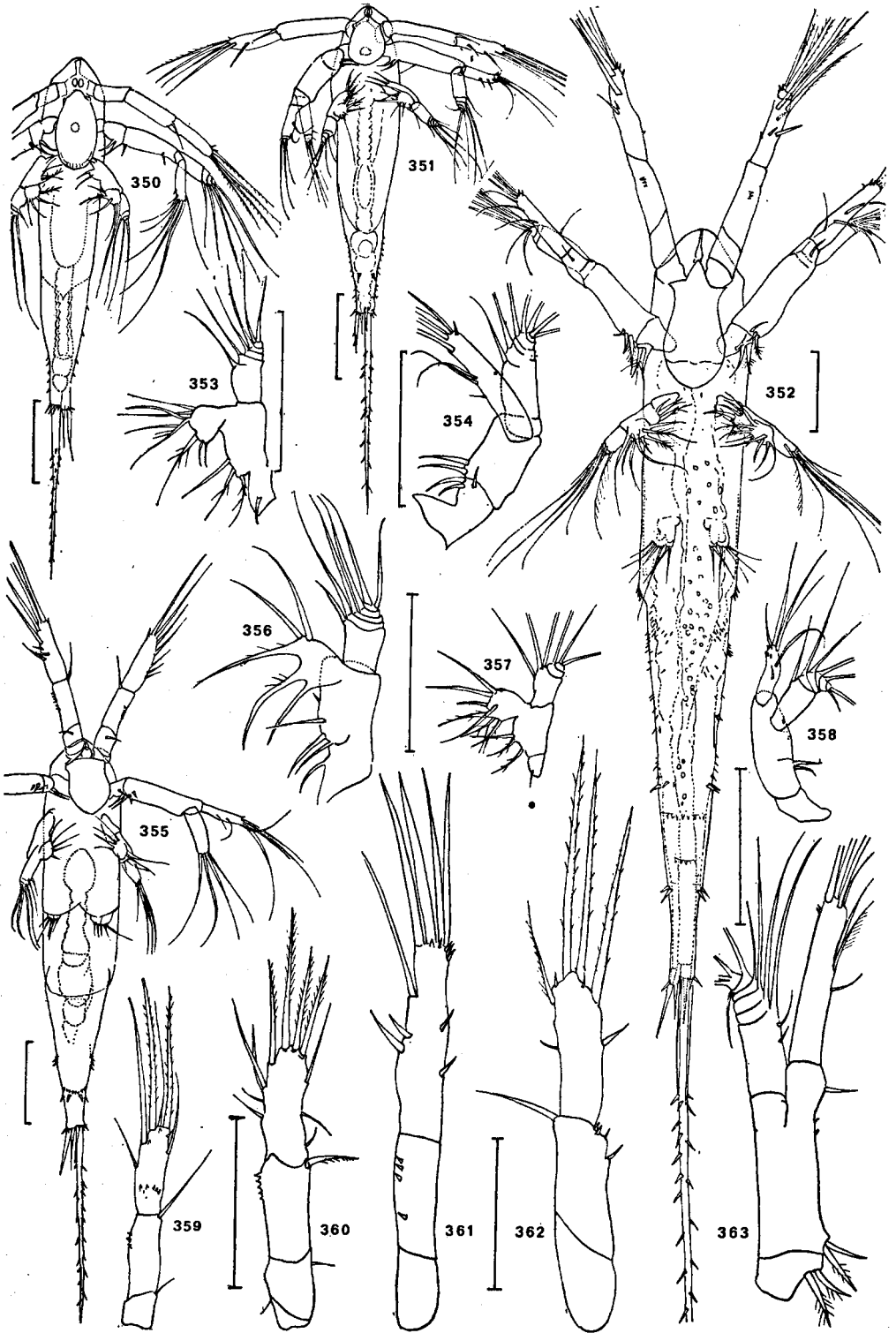
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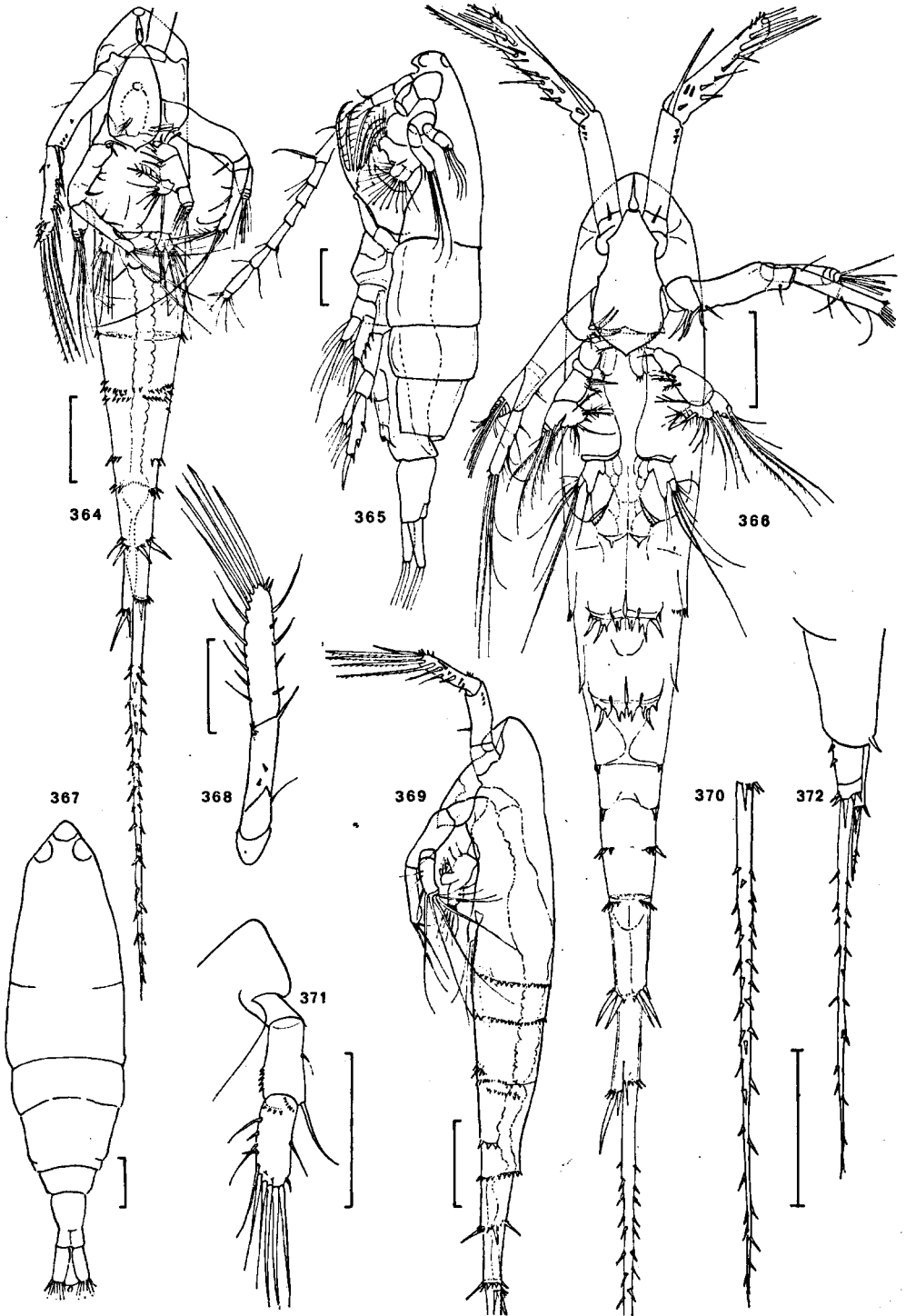
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Fig. 375, 378, 380. *Pontellid nauplius VI*. – 375: Nauplius VI, 1.33 mm, ventral. – 378: Antennule of nauplius VI. – 380: Antenna of nauplius VI.

Fig. 379. *Pontellid nauplius IV* (from Curaçao). Schematic representation of nauplius IV, 0.70 mm, profile.

Fig. 381. *Pontellid* (M. Lomonosow coll., sample M-736). Schematic representation of nauplius III. [Scales = 0.1 mm]





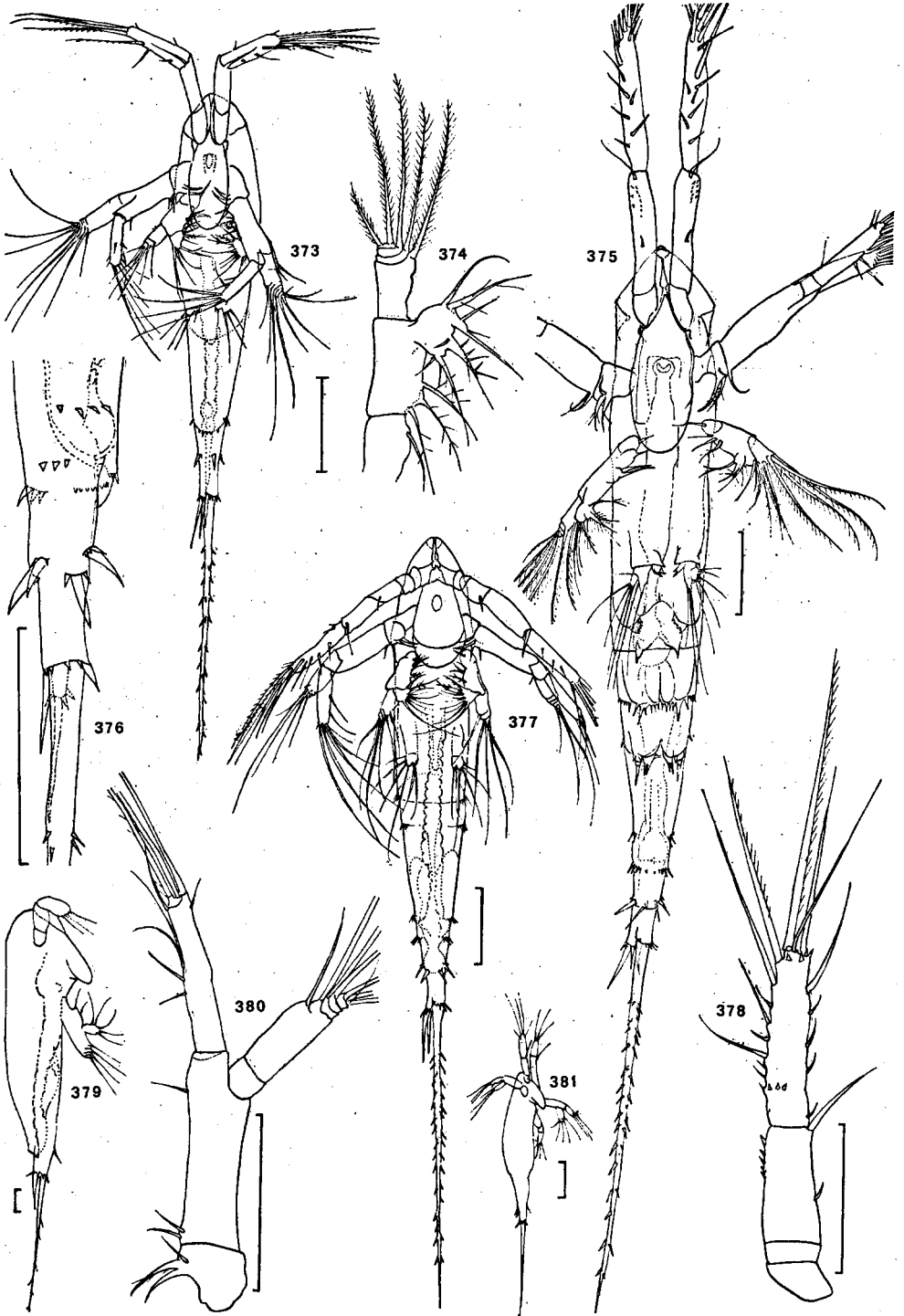


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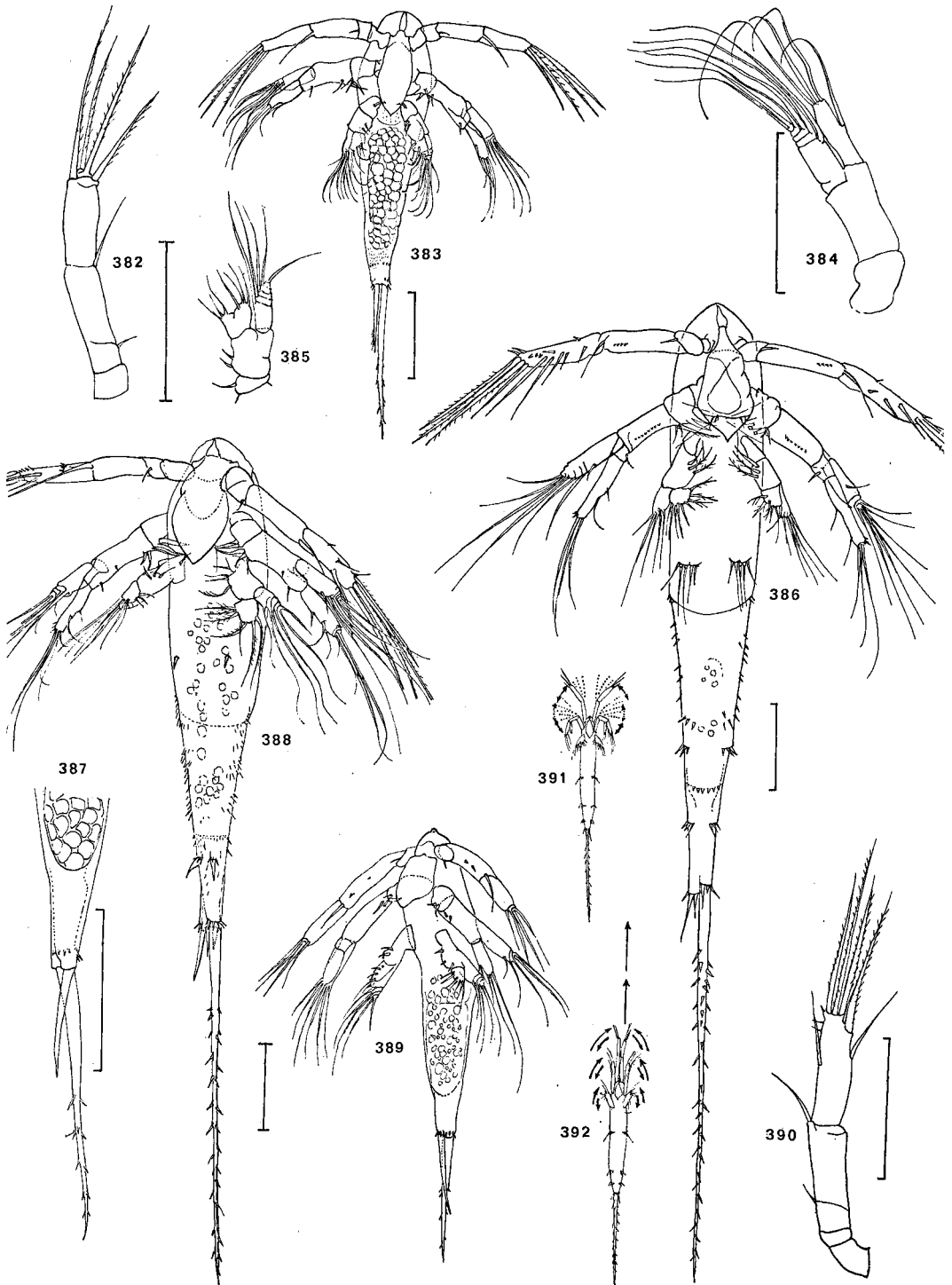
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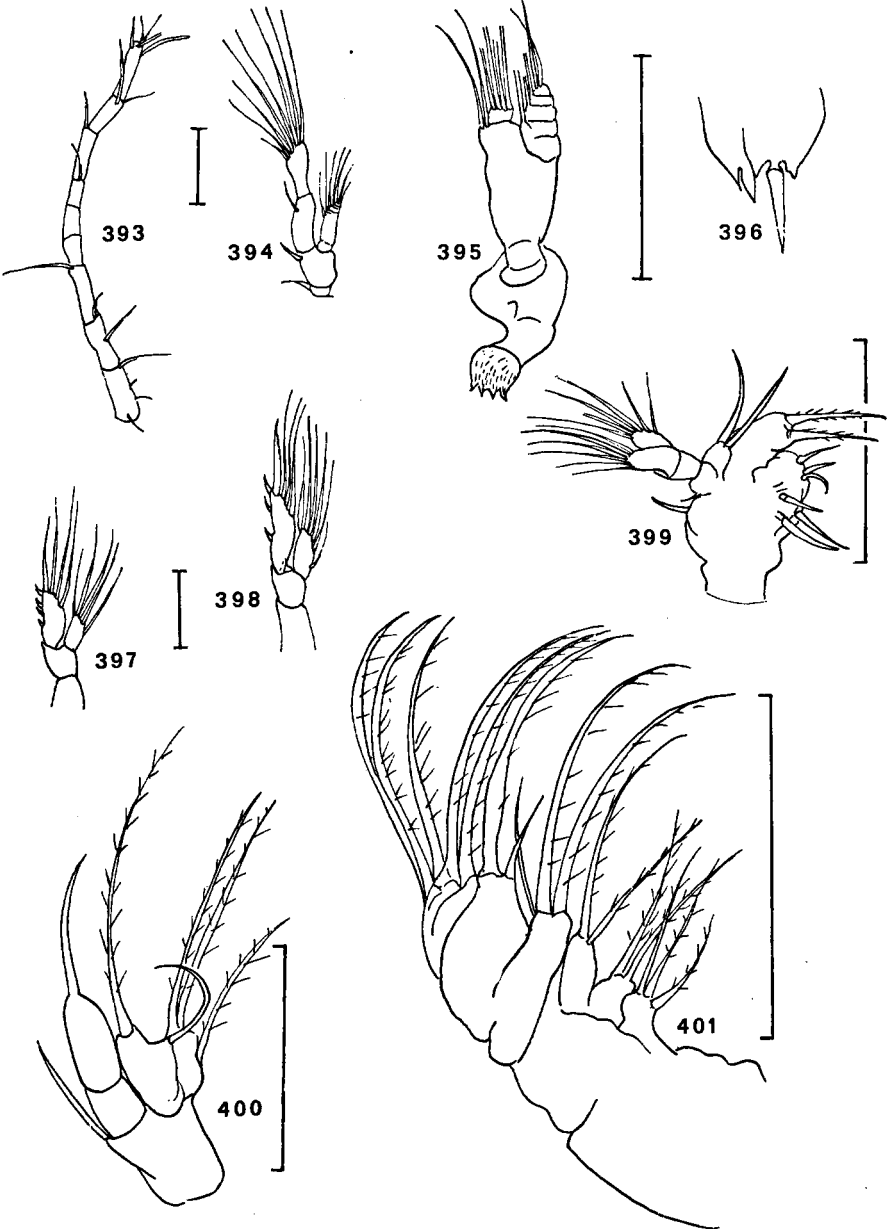
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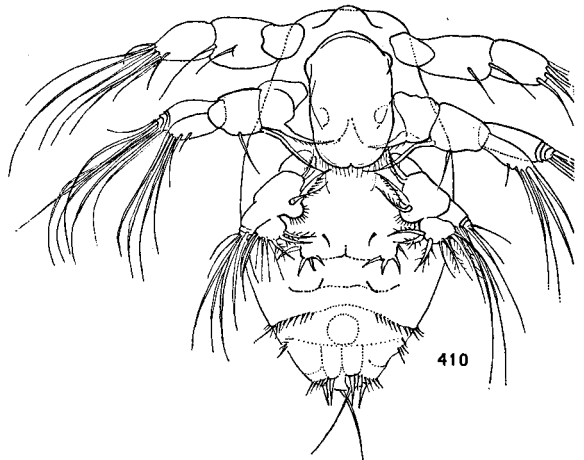
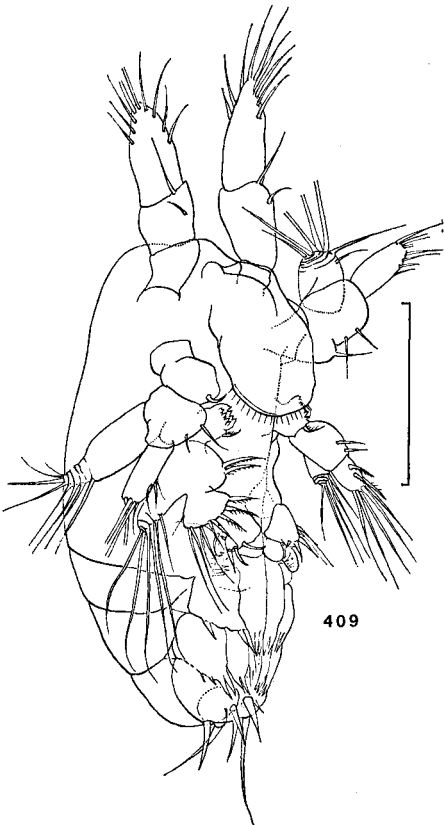
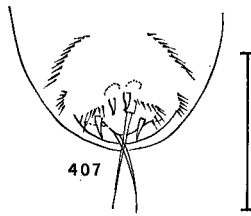
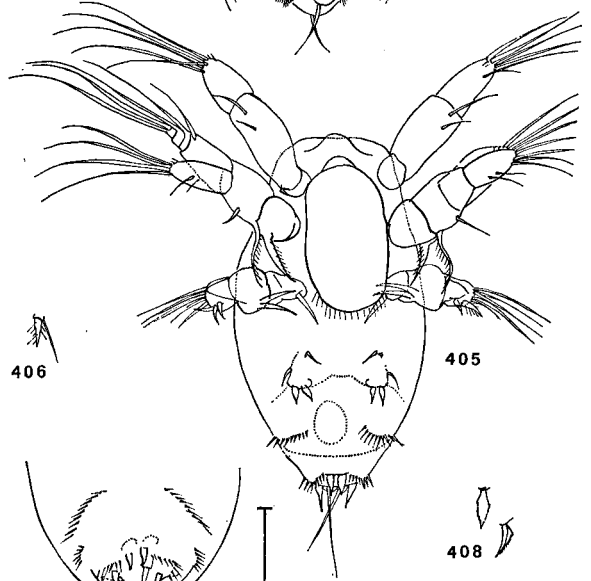
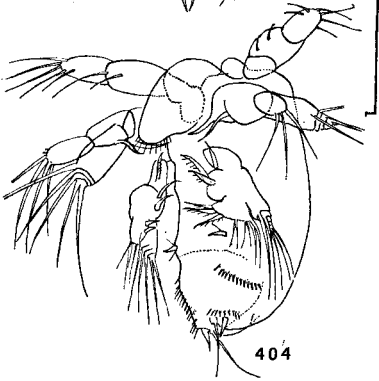
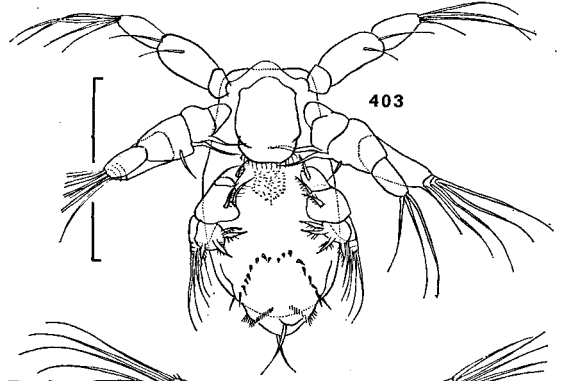
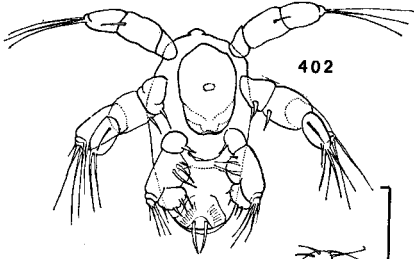
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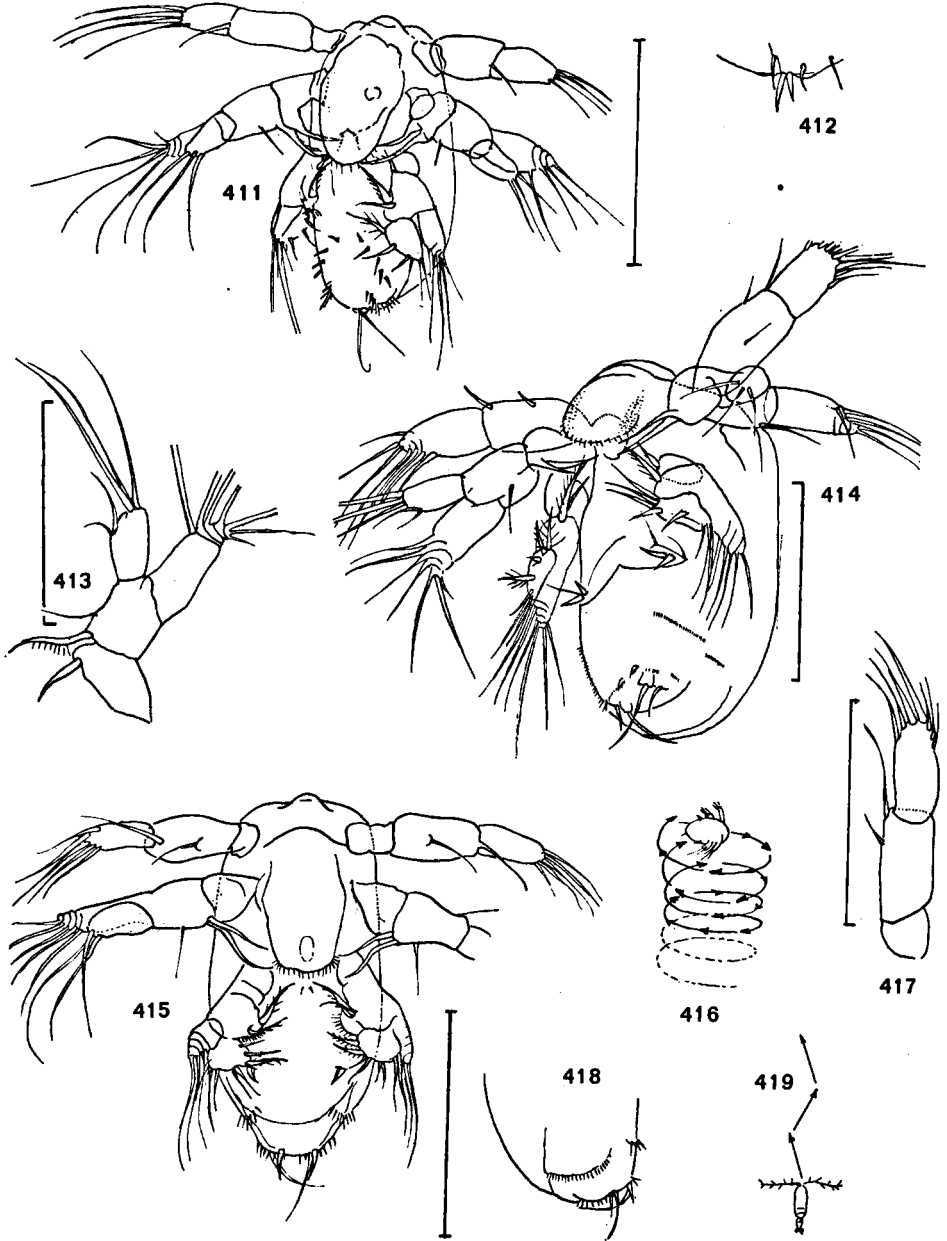
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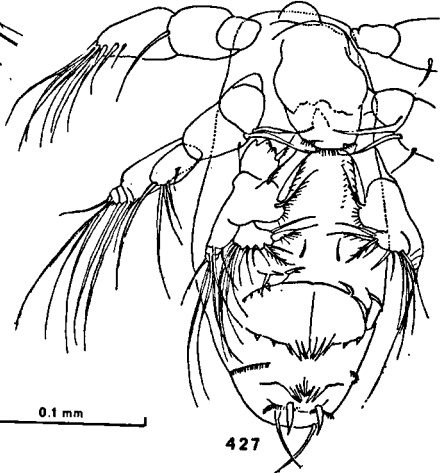
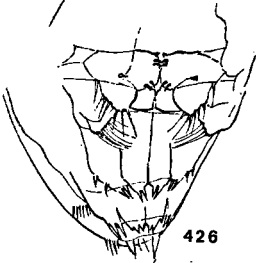
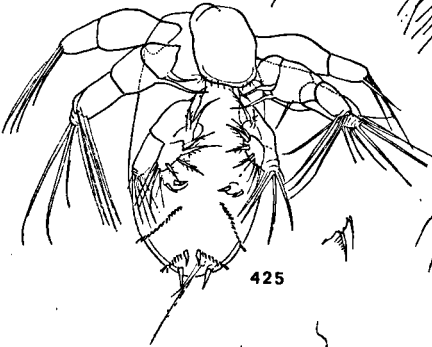
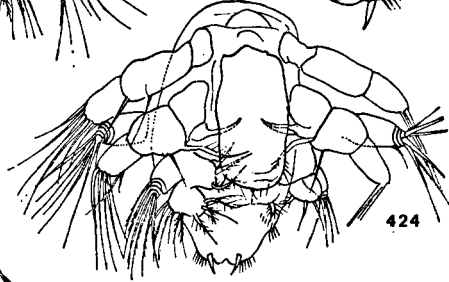
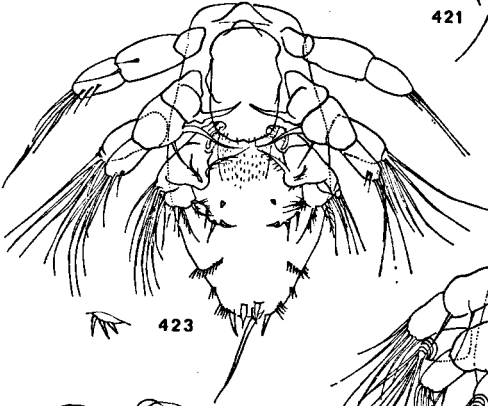
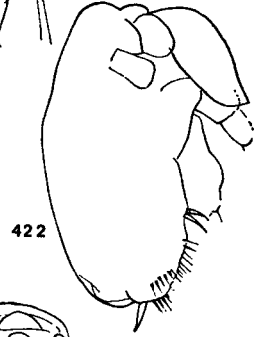
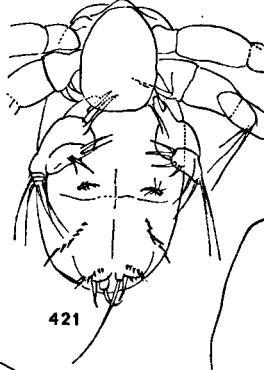
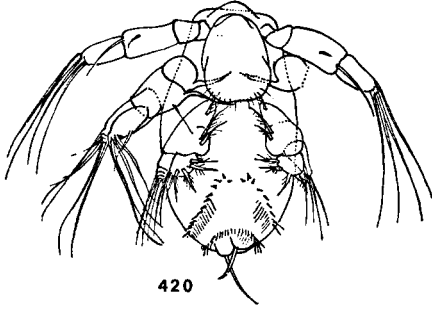
Fig. 427. *Acartia negligens* (from Brazilian waters). Nauplius VI, 0.24 mm, ventral view. [Scales = 0.1 mm]











0.1 mm

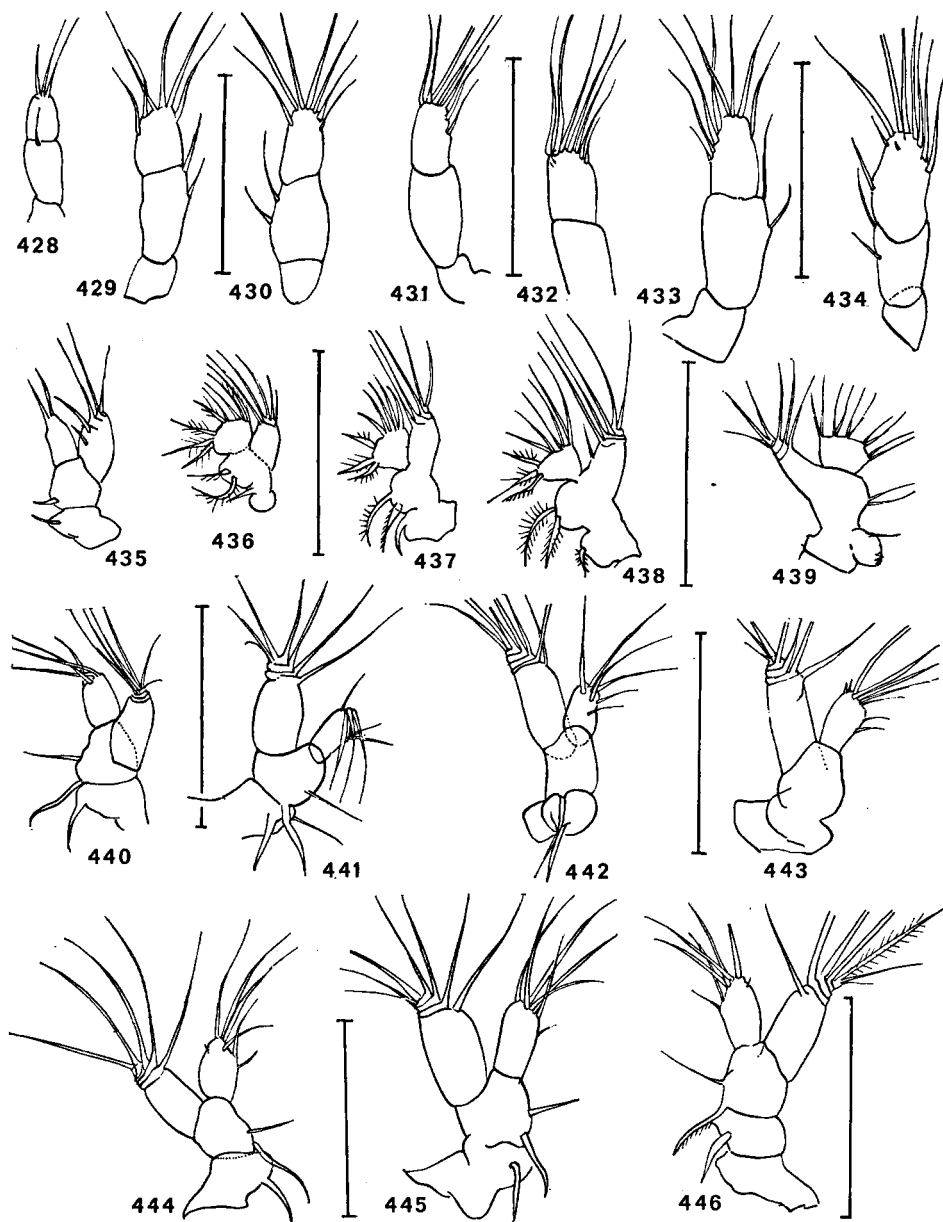
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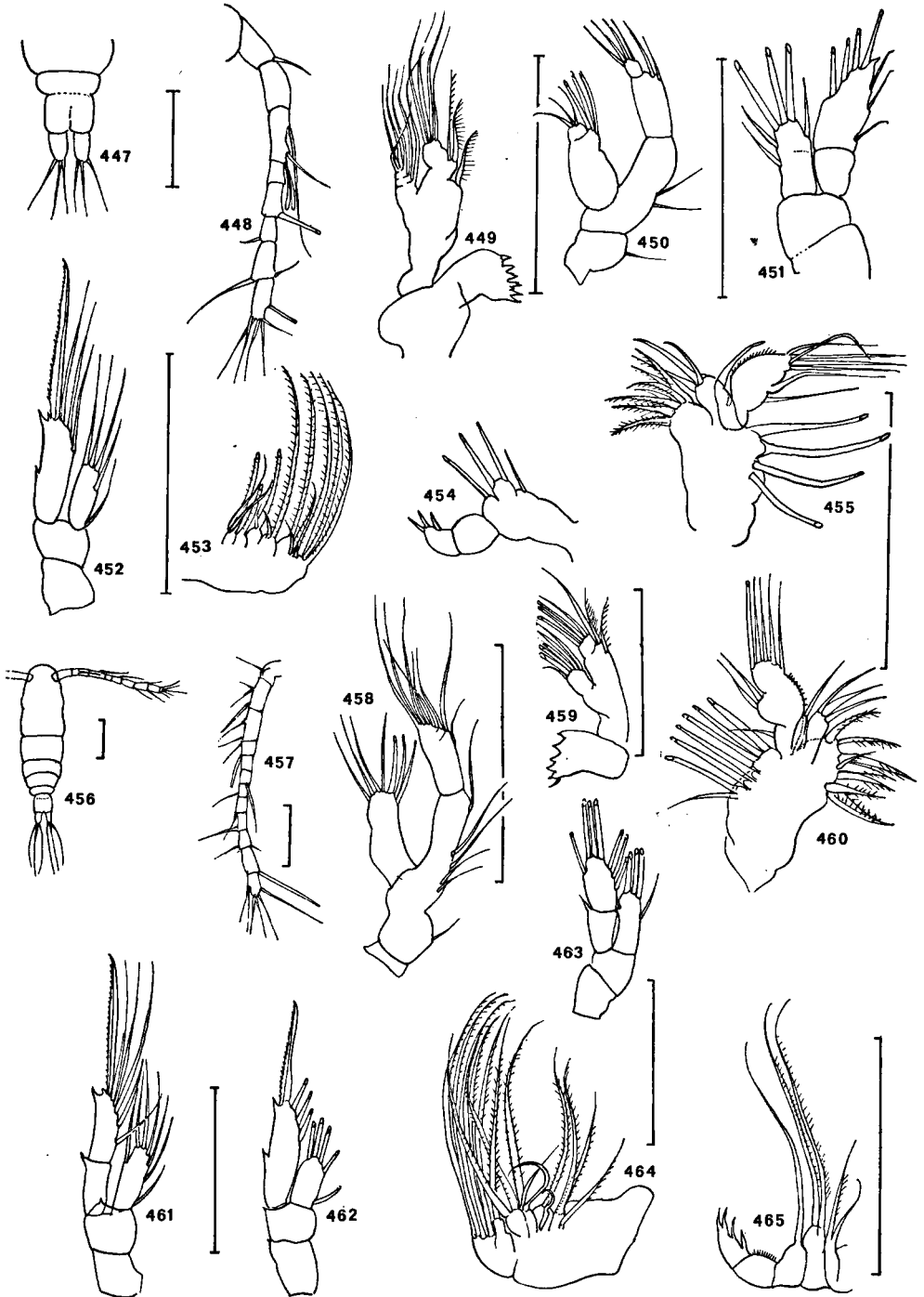
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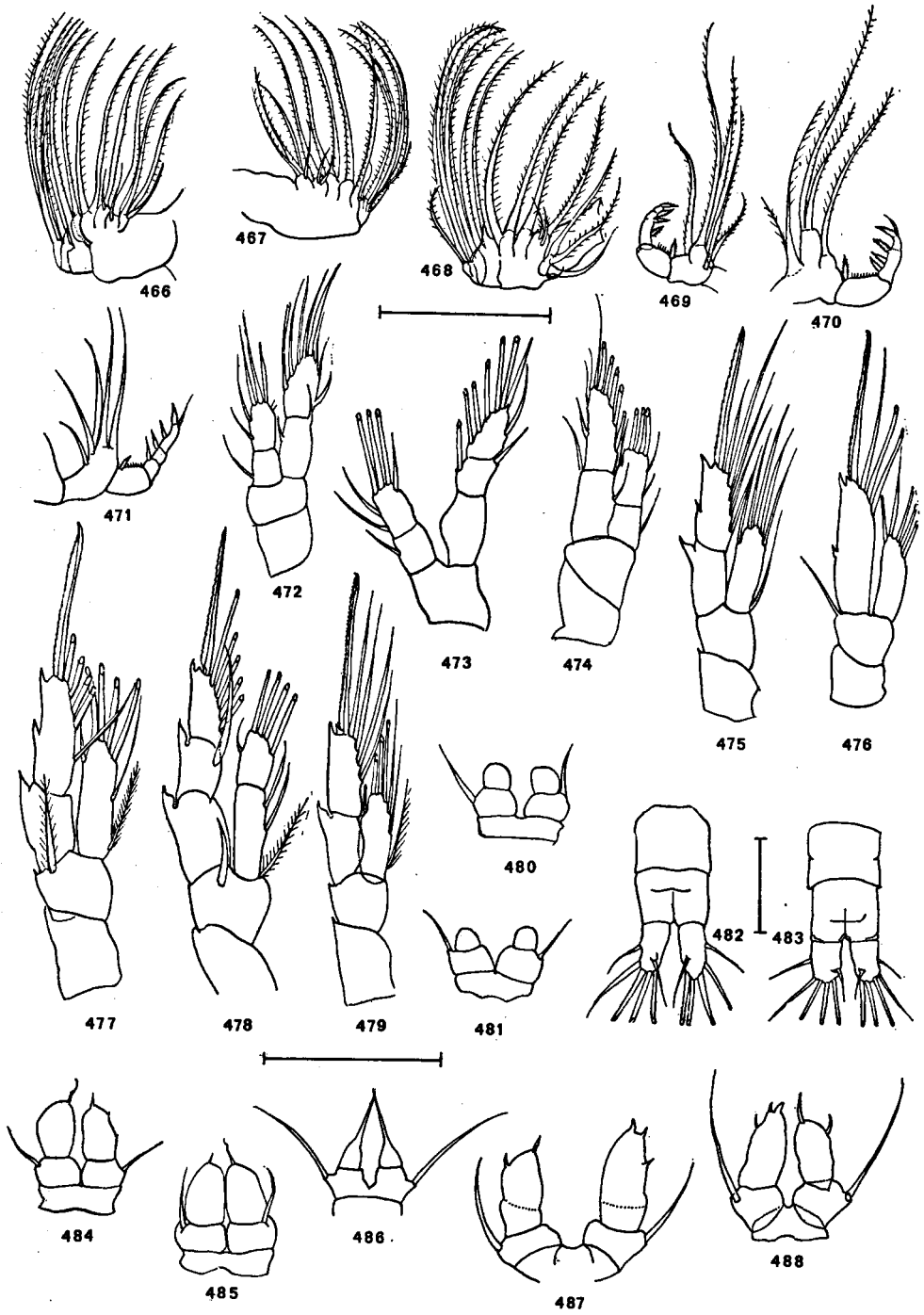
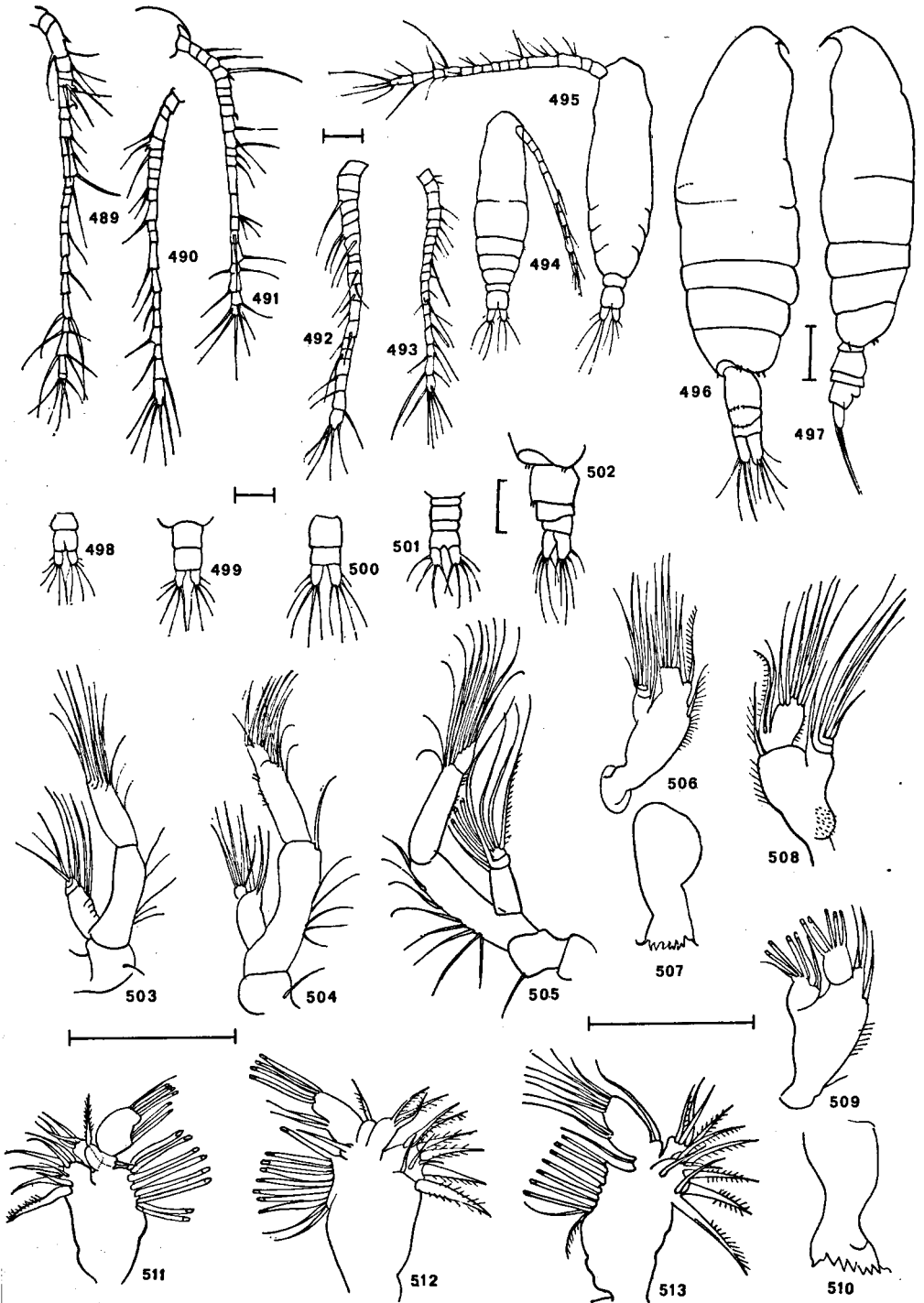
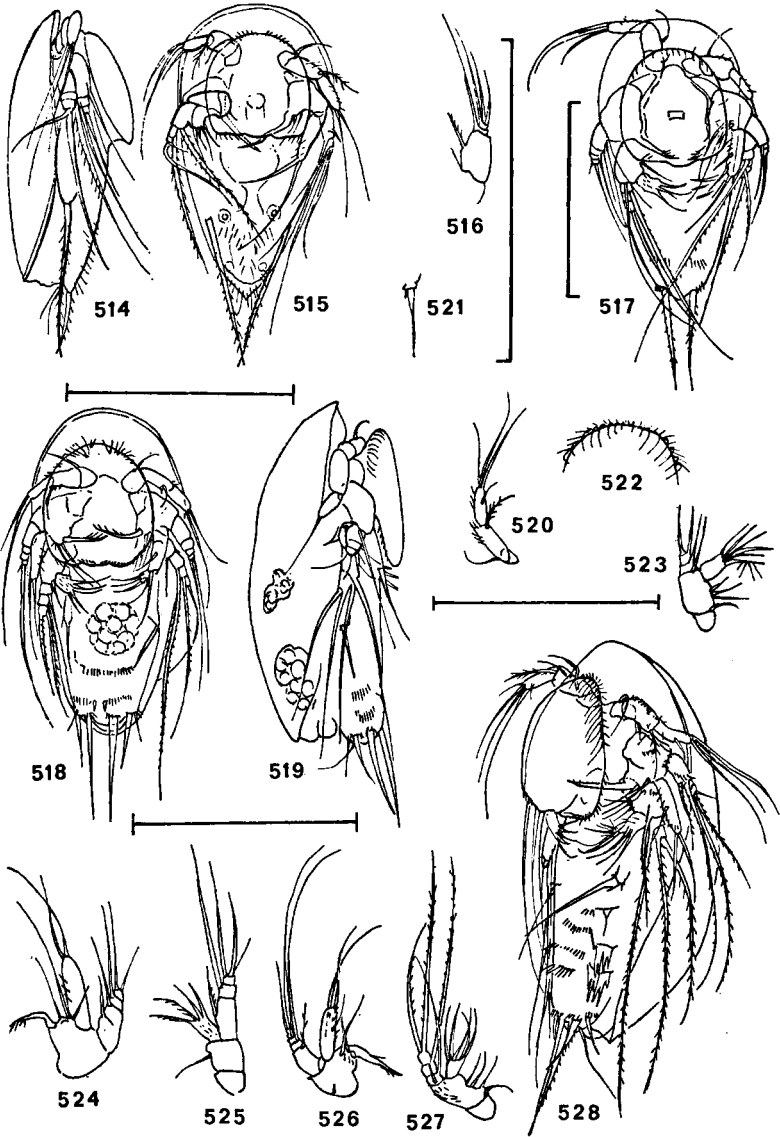


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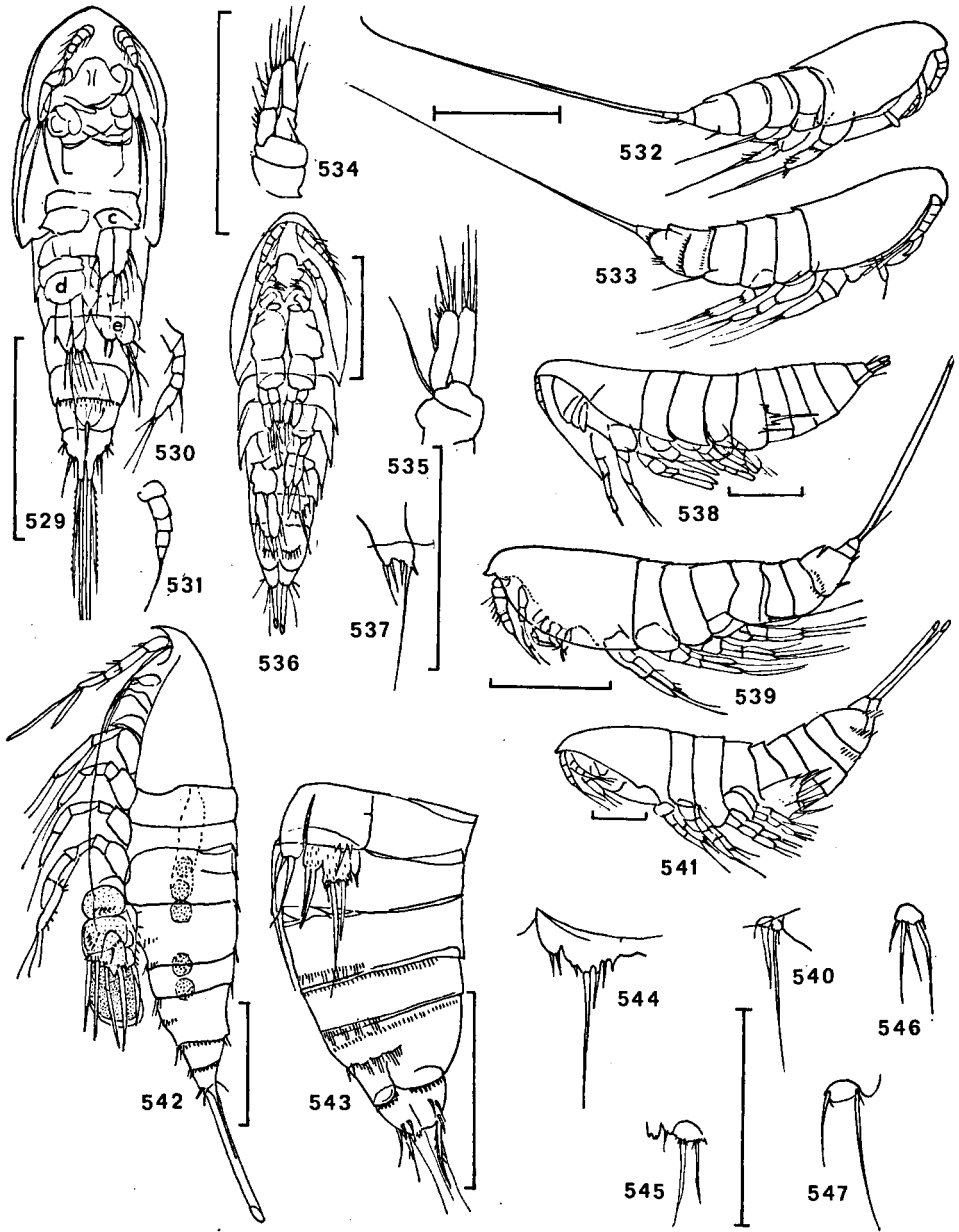


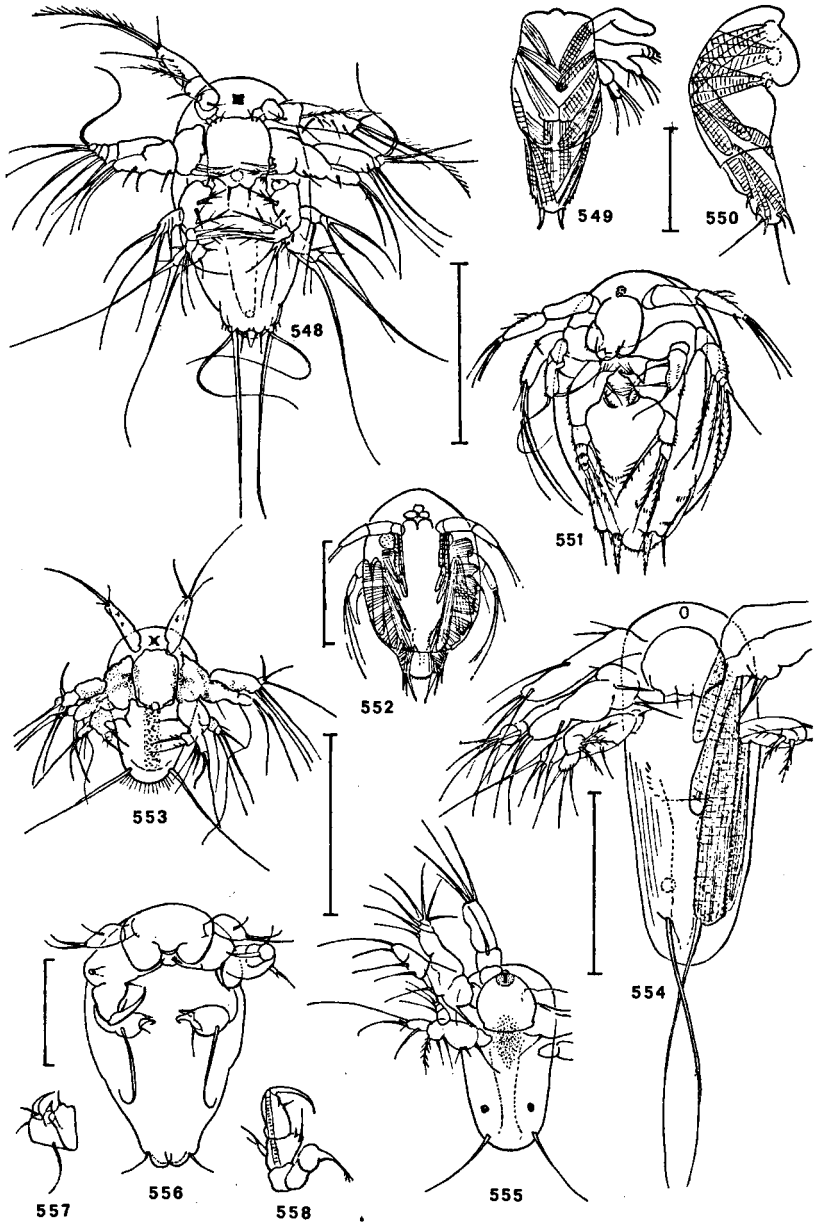
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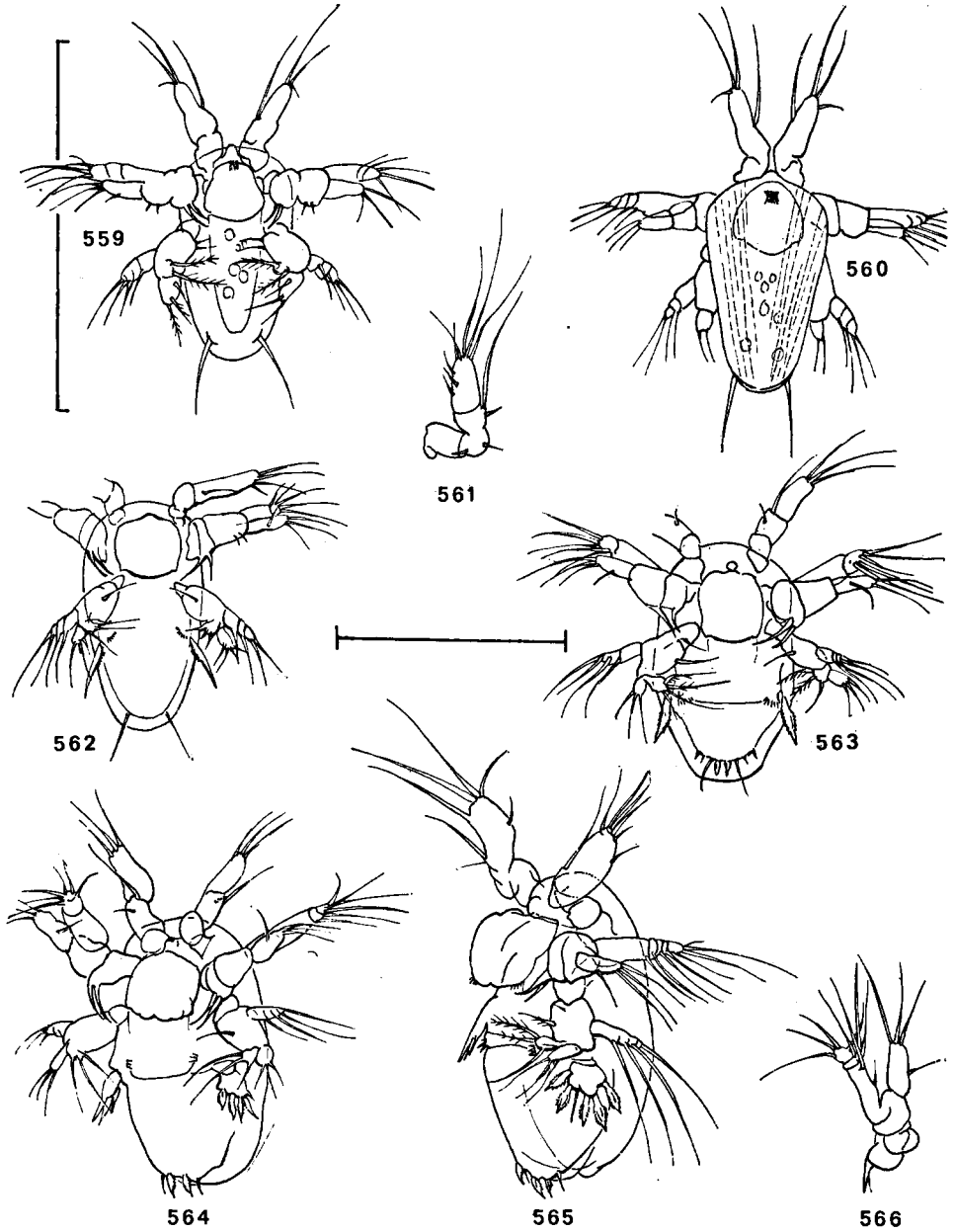
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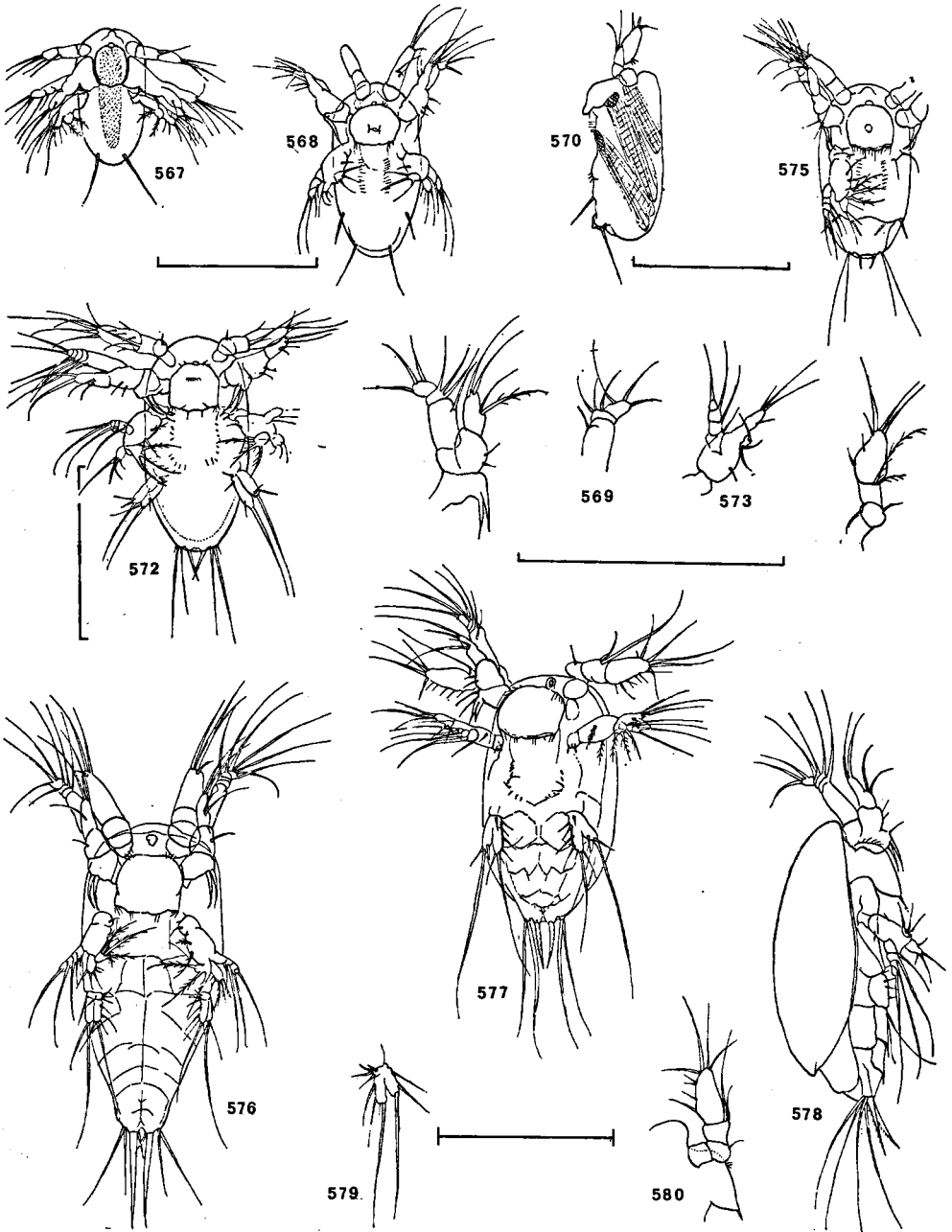
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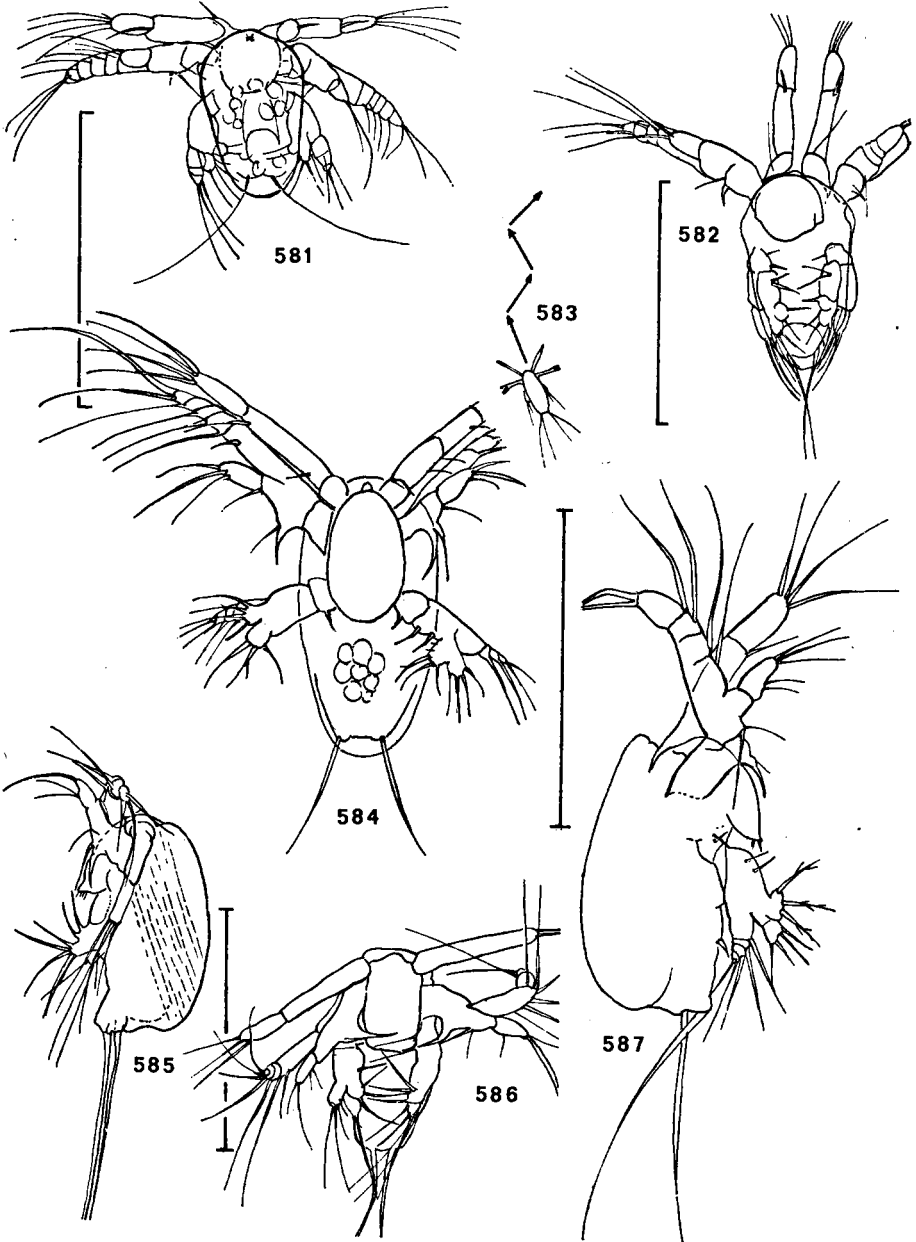
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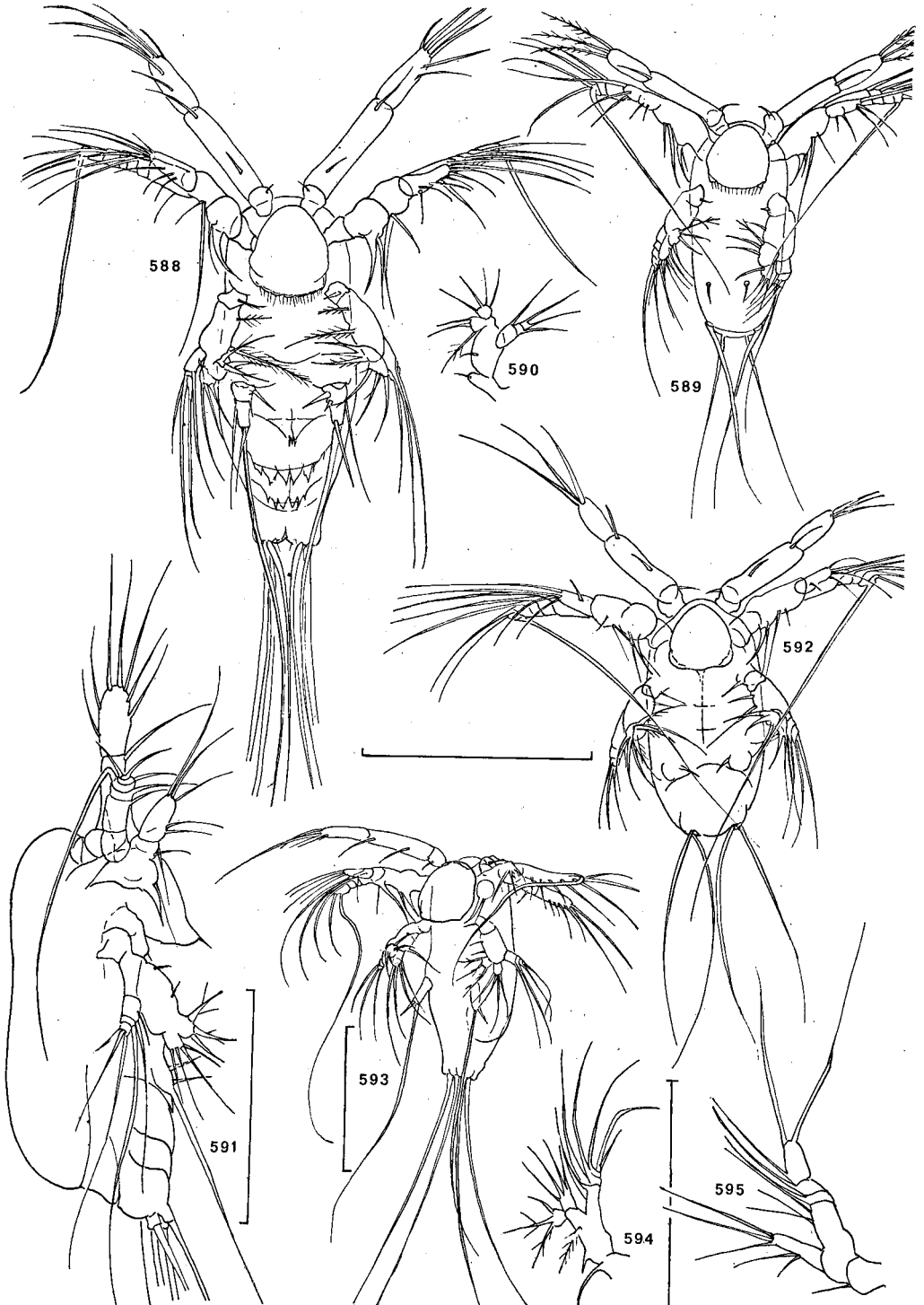


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Fig. 634. Schematic representation of the movement of a corycaeid; arrows indicating direction and impulses. [Scales = 0.1 mm]

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Fig. 643–645. *Corycaeus speciosus* (from Curaçao). – 643: Mandible of nauplius I. – 644: Nauplius I, 0.12 mm, ventral view. – 645: Antenna of nauplius I. [Scales = 0.1 mm]

