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Naupliar Development of *Eucyclops* cf. *serrulatus tropicalis*, *Euc*. cf. *spatulatus*, and *Ectocyclops medius* Kiefer, 1930 (Copepoda: Cyclopidae)

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Supawadee Chullasorn, Wan-Xi Yang, Hans-Uwe Dahms, Pawana Kangtia, Maria Holynska, Wongpiya Anansatitporn, La-Orsri Sanoamuang, and Jiang-Shiou Hwang (2009) Naupliar development of *Eucyclops* cf. *serrulatus tropicalis*, *Euc*. cf. *spatulatus*, and *Ectocyclops medius* Kiefer, 1930 (Copepoda: Cyclopidae). *Zoological Studies* **48**(1): 12-32. All 6 naupliar stages of *Eucyclops* cf. *serrulatus tropicalis* Dussart and Fernando, 1985, *Euc*. cf. *spatulatus* Morton, 1990, and *Ectocyclops medius* Kiefer, 1930 are described from Bangkok, Thailand. Naupliar differences at the genus level were more pronounced than those at the species level in *Eucyclops* and *Ectocyclops* (*Ectocyclops* having a particularly large, round-shaped labrum, and strong spinules on the anterior surface of the coxa, basis, and endopod). Species-specific naupliar characters allow interspecific discrimination (*Euc*. cf. *serrulatus tropicalis* differs from *Euc*. cf. *spatulatus* particularly in its smaller size, in the relative length of the distal antennal exopod segment, and in showing a transverse row of small spinules along the caudal rim). http://zoolstud.sinica.edu.tw/Journals/48.1/12.pdf

Key words: Naupliar development, Larval stages, External morphology.

Cyclopoid copepods develop naupliar larvae as their early postembryonic stages (Dahms 2000, Alekseev 2002). As most free-living Copepoda, the Cyclopoida go through 6 naupliar and 6 copepodid stages (Elgmork and Langeland 1970, Ferrari and Dahms 2007). The naupliar phenotype is quite unlike that of adults, and it is difficult to tell which nauplii belong to which adults, unless the development of isolated females is observed in the laboratory. Naupliar instars have been exposed to different selection pressures, and nauplii therefore have experienced a remarkable adaptive radiation, leading to a diversity of structures, behavioral characteristics, and distribution patterns (Dahms et al. 2007a). Due to their great abundances and variety, nauplii likely also play important ecological roles (Dukina 1956). Life-history studies in the field and investigations of stage-specific phenomena in the laboratory are hampered by a lack of descriptive information and missing keys for identification that are the basis for all work on stage-specific phenomena in the laboratory, heterogeneous assemblages in the field, and behavioral research (Wong et al. 1998, Hwang and

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Strickler 2001, Dahms et al. 2007b, Hwang et al. 2007). Hence, much rearing and descriptive work have to precede any serious attempts to tackle ontogeny-related problems.

In organisms with larval development, both early and late developmental stages show characters of the same genotype. However, in most cases, only the adults have so far been used for reconstructing phylogenetic relationships, although larvae provide a rich source of additional morphological, behavioral, and ecological characters. Qualitative and quantitative structural additions as well as reductions or functional transformations take place during postembryonic ontogeny in the Copepoda. Furthermore, besides structural, meristic, and allometric differences, and the mere number of stages, postembryonic development contributes another type of character: developmental allometry and the sequence of changes during development. Postembryonic instars, both early (i.e., nauplii) and later stages (i.e., copepodids), provide a rich source of additional morphological, behavioral, and ecological characters for evolutionary hypotheses. Therefore, evidence from postembryonic stages may complement those gained from adult characters since an individual exhibits different and significant characters at all phases of its ontogeny which can be used as species-specific character patterns of evolutionary species.

There are several reasons why naupliar characters have thus far been widely neglected in systematic and phylogenetic studies, e.g., difficulties in obtaining detailed information on naupliar characters, nauplii providing fewer characters than later ontogenetic instars and adults, a lack of appropriate comparative data, and conflicting evidence when comparing adult and naupliar character states. In any case, it is more important to find new characters than merely to reinterpret those already known. Phylogenetically valuable apomorphies may be cryptic characters that are often camouflaged by superficial resemblances (Ferrari and Ivanenko 2001). Detailed resolution is a prerequisite for meaningful comparisons. Detailed studies, however, become more difficult as structures become more complicated or smaller. This is particularly true for minute nauplii.

As part of our ongoing studies of copepod life histories and the naupliar development of copepods (Dahms et al. 2007a), we herein describe naupliar stages of *Eucyclops* cf. *serrulatus tropicalis*, *Euc*. cf. *spatulatus*, and *Euc*. *medius*. Compared to other copepod taxa, the naupliar development of cyclopoids is far less studied (Dahms 2004a). Knowledge of naupliar morphology is indispensable for investigations of stage-dependent phenomena (Turki et al. 2002). Besides species discrimination, naupliar morphology can be used as an additional source of characters for elucidating phylogenetic relationships among taxa (Dahms 2004b, Ferrari and Ivanenko 2001).

Eucyclops serrulatus, and *Ect*. medius are widely distributed in limnetic tropical regions (Alekseev 2002). The genera *Eucyclops* Claus, 1893 and *Ectocyclops* Brady, 1904 are among the most important cyclopoids among open-water tropical limnetic zooplankton. Species belonging to *Eucyclops* and *Ectocyclops* inhabit many tropical lakes and reservoirs. Since these species are widely distributed and may become dominant at certain sites and times, descriptions of their developmental instars will be indispensable for several aspects of research, such as ecological studies in the field (Maier 1990) and laboratory (Auvray and Dussart 1966). There are distributional records from northern Thailand (Proongkiat and Sanoamuang 2003). Development within these genera is only known from *Euc. neumanni* (Cicchino 1972) and *Ect. rubescens* (Carvalho 1971). We provide illustrations and describe diagnostic features which will enable valid comparisons of naupliar stages in integrative future analyses.

The present study provides a thorough description of nauplii belonging to the cyclopoid species *Euc*. cf. *serrulatus tropicalis* Dussart and Fernando, 1985; *Euc*. cf. *spatulatus* Morton, 1990; and *Ect. medius* Kiefer, 1930.

MATERIALS AND METHODS

Collection data

Adults of *Euc*. cf. *serrulatus tropicalis*, *Euc*. cf. *spatulatus*, and *Ect. medius* were collected from rooted sediments of the water lettuce, Pistia stratiotes L., in freshwater ponds at Ramkhamhaeng Univ., Bangkok, Thailand on 22 June 2006 by S. Chullasorn, P. Kangtia, and W. Anansatitporn. The species were identified according to Dussart and Defaye (2006).

Ovigerous females which provided the developmental stages were subsequently decanted over a screen with a 50 μm mesh size and rinsed into smaller bowls for transport to the laboratory. The developmental stages used in this study represent the offspring of exclusively single-female cultures.

Nauplii were reared from individual females to ensure reliable species identification. Ovigerous females were transferred to individual Petri dishes containing pond water. Females were kept at 25°C as a rule at a light-dark cycle of 12:12 h. About 50 % of the water was renewed each week. When the nauplii emerged, some of them were isolated in watch glasses, and the exuviae of subsequent molts were collected to substantiate stage numbers and to study microscopic details. They were fed dried formulated ornamental fish food (see Dahms et al. 2007a b). A few drops of a food suspension was added every day, which settled as a fine, semitransparent coating over the entire bottom of the glass. No attempt was made to exclude small protozoan contaminants or to prevent algal growth.

Preparations

Nauplii at various stages were fixed in 5 % buffered formalin and embedded in glycerol. This clarifies nonexuvial material within a few weeks and provides information on hidden posterior structures when observed by phase-contrast microscopy. Unfortunately, the natural color of the nauplii and the color and shape of the red naupliar eye are lost quite soon, so the naupliar eye was not illustrated. Nauplii were mounted whole, and broken glass-fibers were added to prevent them from being compressed and to facilitate rolling to allow inspection from all sides. Body measurements are given from the frontal portion of the naupliar shield to the caudalmost protrusion of the hind-body (length), and the widest lateral tips of the naupliar shield (width). Otherwise, 2-5 specimens per stage were used for the investigation of stage-specific variability. Species were identified with the aid of Dussart and Fernando (1985), Fryer (1955), Morton (1990), and Alekseev (2002).

Descriptive terminology

The following terms are defined according to their use in the following text. The 1st to 6th naupliar stages are respectively abbreviated as N I, II, III, IV, V, and VI. Nauplii of *Euc. serrulatus*, *Euc. spatulatus*, and *Ect. medius*, as do those of other cyclopoids, have at least 3 pairs of appendages: the 1st and 2nd antennae, and the mandibles. The body is usually covered by a smooth naupliar shield in the earlier stages, whereas the hind body protrudes from it in later stages. At the posterior end of the body, there is at least 1 caudal seta on either side of the anal area. The labrum originates as a lobular flap near the frontal margin of the body, between the bases of the 1st antennae, and extends posteriorly across the ventral surface of the body. The metasomal ventral body wall is a tongue-like structure arising at the base of the antennal protopod. The 1st antenna is uniramous. The naupliar 2nd antenna noticeably differs from that of the adult (and copepodids) in having a coxal masticatory process (= gnathobase). The 2nd antenna further consists of a coxa, basis, endopod, and exopod. The mandible is composed of the same elements except the precoxa. The endopod consists of an inner process and usually a lateral field of setae arising on the outer lateral margin. The postmandibular appendages (1st and 2nd maxilla, maxilliped, and legs 1 and 2) may develop successively from N II onwards. The singular form is used for all appendages. Large outgrowths are called setae or spines. A typical seta is generally a flexible, finely attenuate element which is bare or has a double row of fine hair-like outgrowths. In the latter case, it is called pinnate, or if the fine spinules are more irregular, it is called spinulose. A typical spine is generally short, relatively inflexible, and usually bears a double row of tiny spinules. Very small flexible elements originating from the endocuticle are referred to as setules. Aesthetascs (aesthetes sensu Gurney 1931) are presumed to be sensory elements of the 1st antennae with sclerotized bases and are more transparent than normal setae with blunt or rounded ends. The complements of setae, setules, spines, and aesthetascs are called elements of a particular structure and are collectively called the armature. In addition to setae, setules, and spines, the body segments or appendages present a variety of ornamenting cuticular projections. Spinules can be very fine hair-like cuticular extensions of setae and spines, the labrum, and ventral body wall, or small, pointed, conical processes. Denticles are minute triangular outgrowths. Spinules and denticles are referred to as ornamentation.

Description

Individuals of all 6 naupliar stages are pelagic and swim freely. Cyclopoid nauplii in general are circular to oval in shape, becoming more elongate in the course of development. The naupliar dorsal shield covers the entire body in the 1st stage (Figs. 1, 6, 11). At N III and later stages, the hind body gradually protrudes caudally from the naupliar shield. In later stages, lateral margins of the ventral body wall are completely fused to the caudal portion of the body. Externally, there is a 4th appendage (= 1st maxilla) present from N II onwards. At N VI, the precursors of legs 1 and 2 are clearly visible as medial, armed lobes,

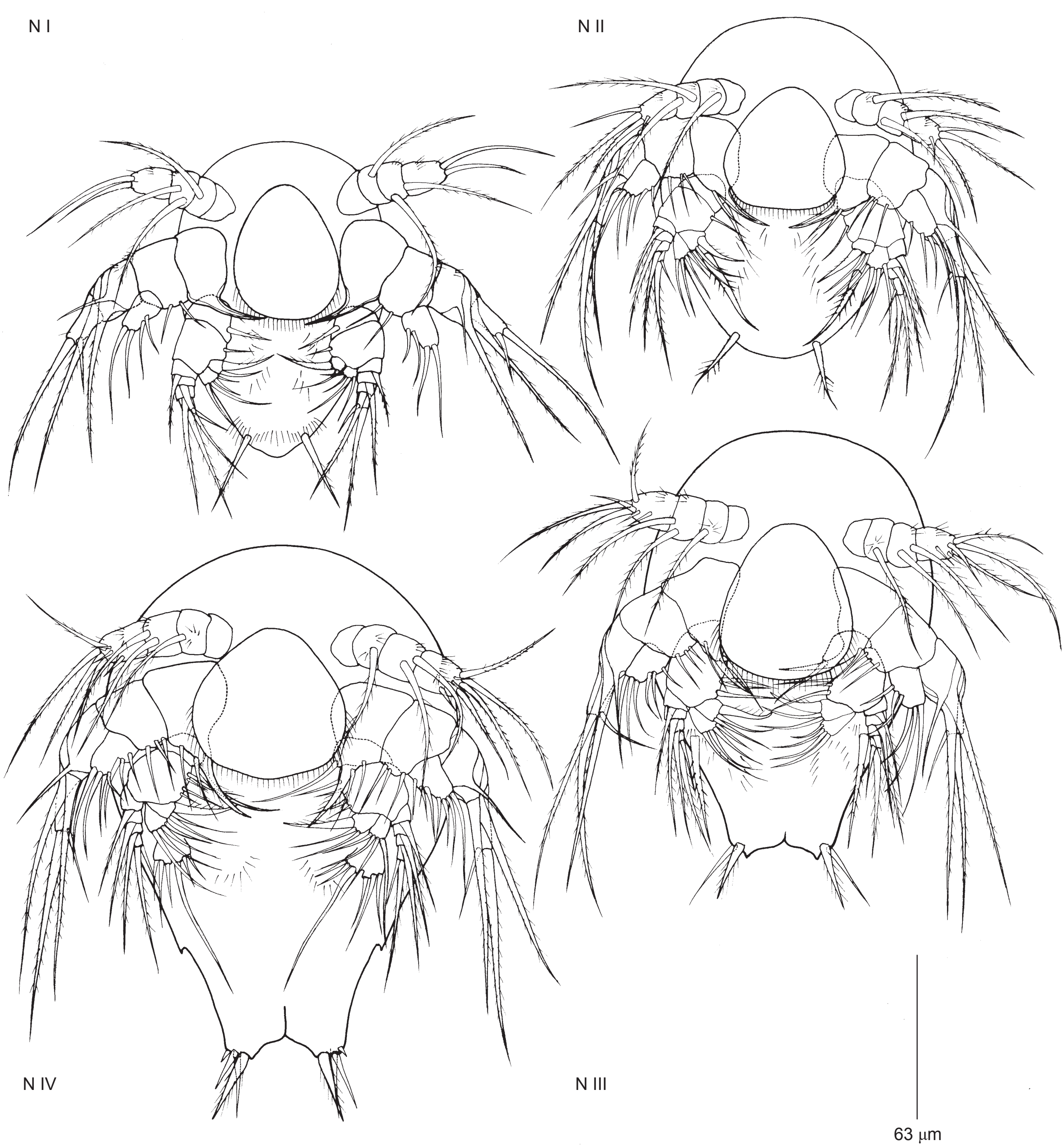

Fig. 1. *Eucyclops* cf. *serrulatus tropicalis*. Naupliar stages I to IV in ventral view. Scale bar = 63 µm.

whereas the 2nd maxilla and maxilliped do not appear externally at any stage. Throughout the naupliar phase, there is no visible segmentation of the body. The red median eye and yolk droplets were not figured because the embedding medium cleared these structures before the investigation (Figs. 1-12).

Eucyclops cf. serrulatus tropicalis (Figs. 1-5)

Nauplius I (Figs.1, 3-5)

Body length 121 μm, body width 63 μm. Body more nearly round in cross-section than at later stages. Labrum furnished with some spinules along its lateral and frontal margin, as well as transversely at proximal base, being slightly longer than wide. Sternal field bearing a row of spinules along lateral margins under caudal edge of labrum. Hindbody bearing 2 oblique rows of spinules frontally and a subterminal row of long spinules all along ventral and lateral sides. One spinulose seta (= initial furca) arising from a protuberance on each caudal side.

First antenna 4-segmented (Fig. 3). Proximalmost segment devoid of any conspicuous armature. Second segment bearing 1 anterior spinulose seta. Third segment bearing 2 anterior spinulose setae throughout the phase; outer 1 stronger than inner 1. Distal 4th segment bearing 2 smooth setae terminally of unequal length.

Second antenna bearing a rectangular-shaped coxa carrying a sword-shaped masticatory process (= gnathobase) (Fig. 4). Basis furnished with 2 setae along inner margin, and 3 anterior surface spinules at outer portion of basis. Endopod consisting of 1 segment armed with 2 inner lateral setae midway, and 2 setae of almost equal size terminally. Exopod 4-segmented, 1st segment with 1 small seta and 3 spinules on outer anterior surface, 2nd segment with 1 spinulose seta, 3rd segment with 1 spinulose seta, and distal 4th segment with 1 small inner seta and 1

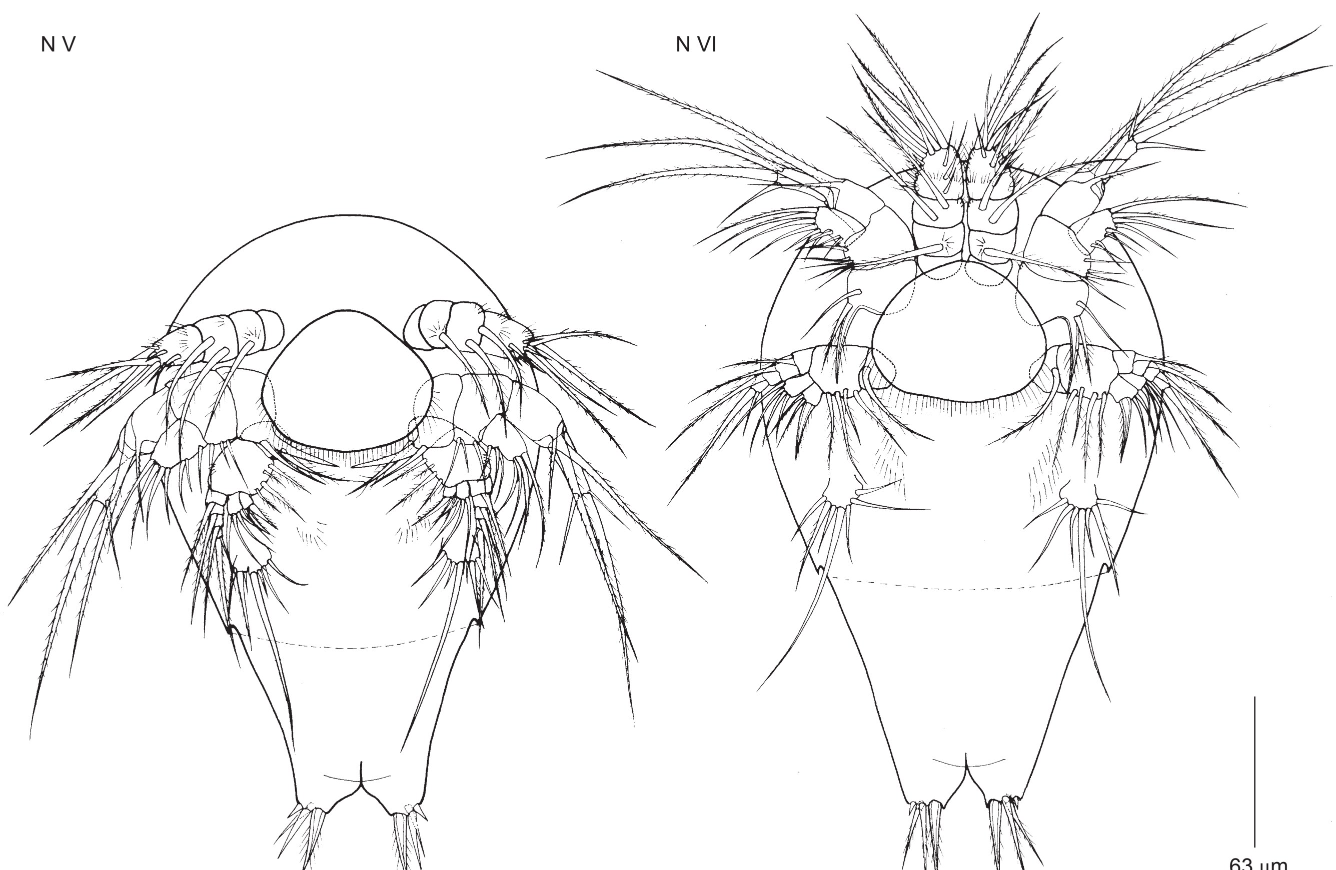

Fig. 2. *Eucyclops* cf. *serrulatus tropicalis*. Naupliar stages V and VI in ventral view. Scale bar = 63 μm.

spinulose seta at tip of segment.

Mandible made of a short proximal portion (= initial coxa) with 1 spinulose seta at inner margin (Fig. 5). Basis armed with 1 small seta. Endopod 2-segmented. First segment ornamented with 1 spinulose spine and 1 spinulose seta, 2nd segment bearing 4 smooth setae of subequal length. Exopod 4-segmented with 1 spinulose seta

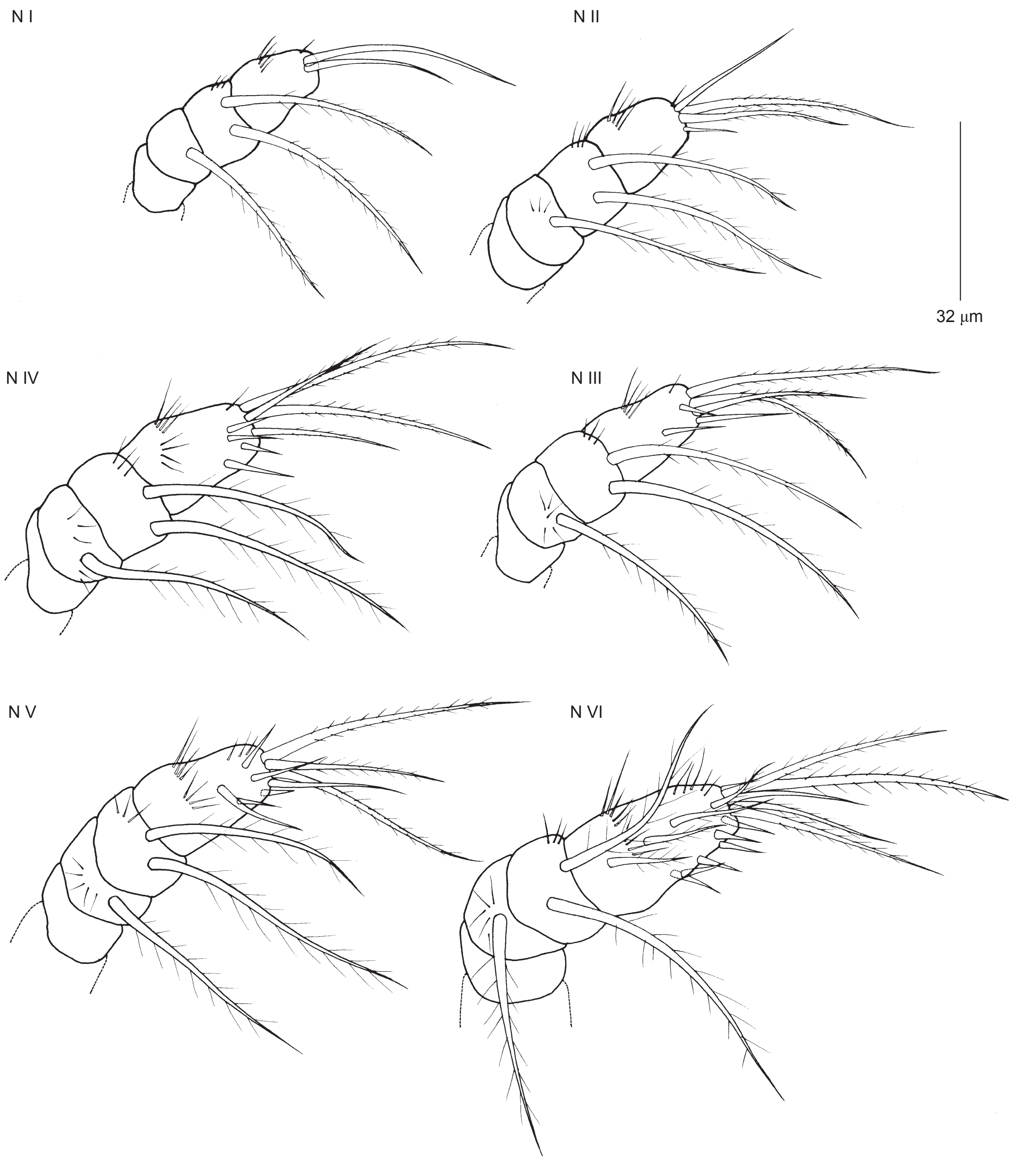

Fig. 3. *Eucyclops* cf. *serrulatus tropicalis*. Development of the naupliar left 1st antenna of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

at tip of inner margin of each segment. Distal 4th segment bearing 1 additional small smooth seta at tip.

Nauplius II (Figs.1, 3-5).

Body length 136 μm, body width 93 μm. N II

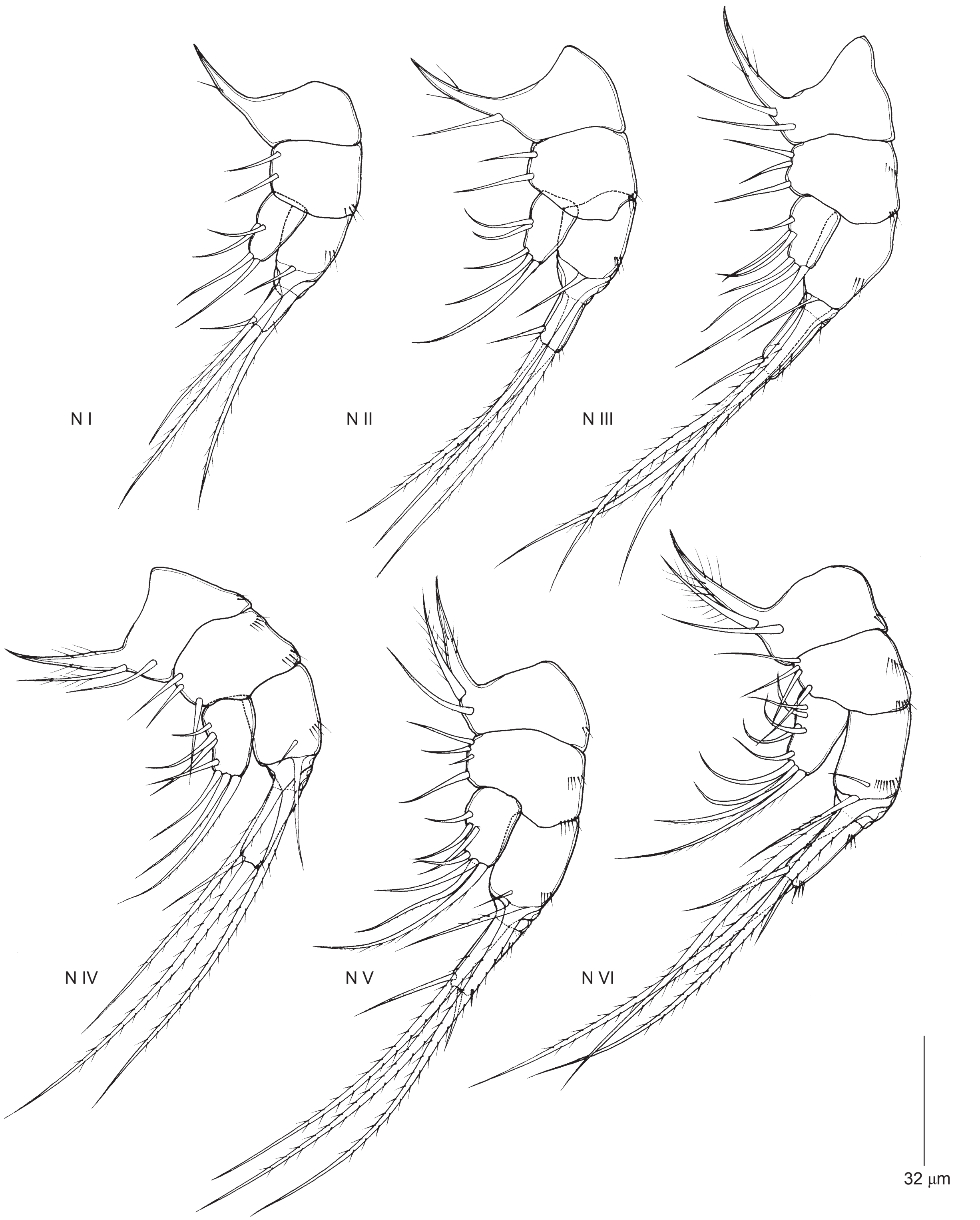

Fig. 4. *Eucyclops* cf. *serrulatus tropicalis*. Development of the naupliar left 2nd antenna of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

differing from N I in the following aspects.

Sternal field bearing 1 spinulose seta on each side, but 1 row of spinules on hind body disappeared. One additional smooth and slender caudal seta on either side (Fig. 1).

Proximal segment of 1st antenna (Fig. 3) bearing 3 spinules on anterior surface. Two more smooth setae of unequal length on terminal edge

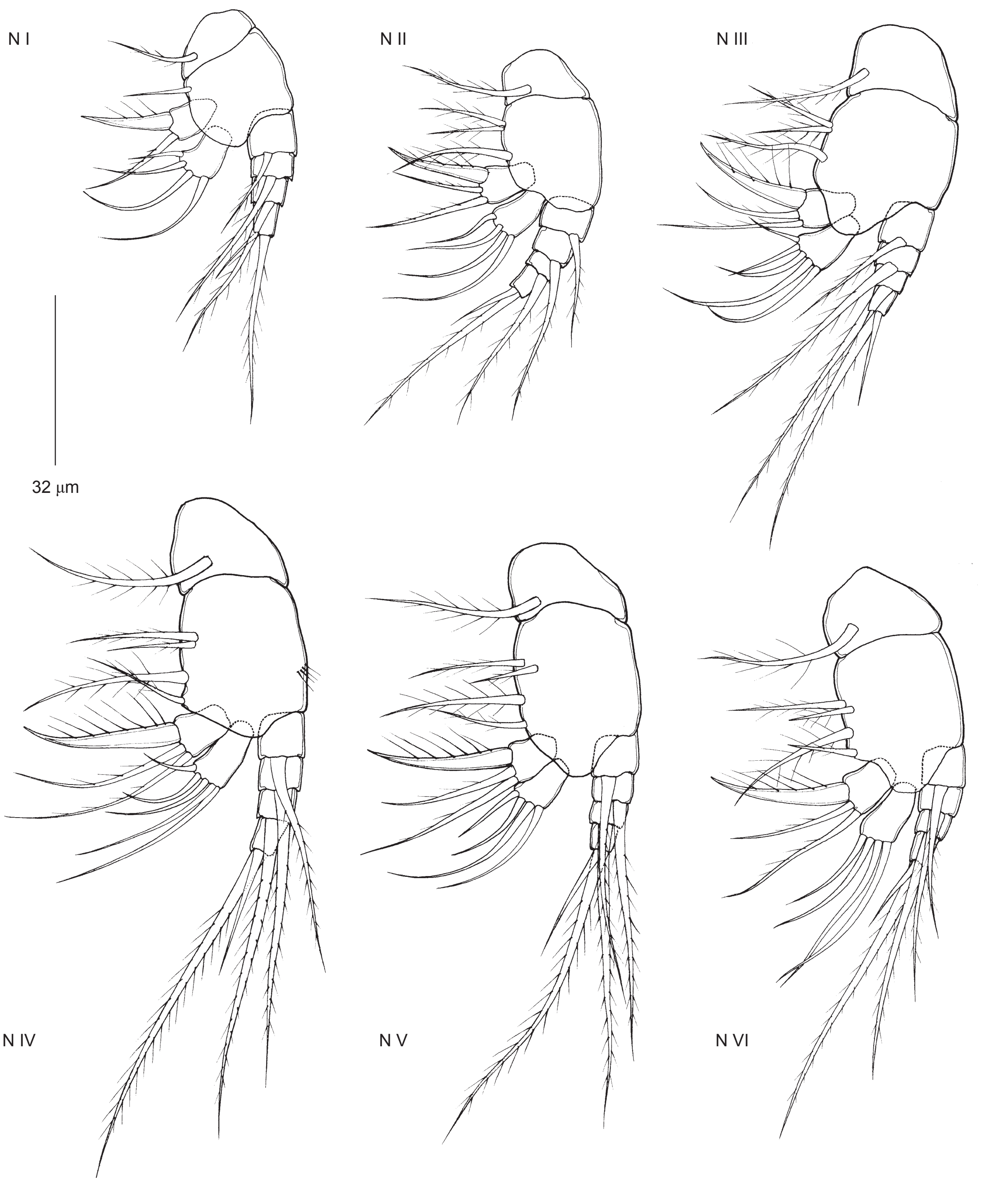

Fig. 5. *Eucyclops* cf. *serrulatus tropicalis*. Development of the naupliar left mandible of naupliar stages I to VI in anterior view. Scale bar 32 = µm.

of its distal segment. Former 2 smooth setae becoming spinulose.

Second antenna (Fig. 4) carrying 1 smooth seta at base of its masticatory process. A 3rd seta terminally on its endopod.

Mandible (Fig. 5) acquiring 2 more spinulose setae and former smooth seta becoming spinulose at its basis. Lobe of 1st endopod segment bearing 1 additional spinulose seta.

First maxilla (Fig. 1) making its first appearance as a spinulose seta originating from a protuberance.

Nauplius III (Figs. 1, 3-5).

Body length 164 μm, body width 111 μm. N III differs from N II in the following aspects.

Hindbody grooved medially.

First antenna (Fig. 3) acquiring 2 subterminal elements on distal segment.

Second antenna (Fig. 4) bearing additional smooth seta at base of masticatory process; endopod acquiring a 3rd, subterminal smooth seta.

Mandible (Fig. 5) bearing 1 additional smooth seta on 2nd endopodal segment.

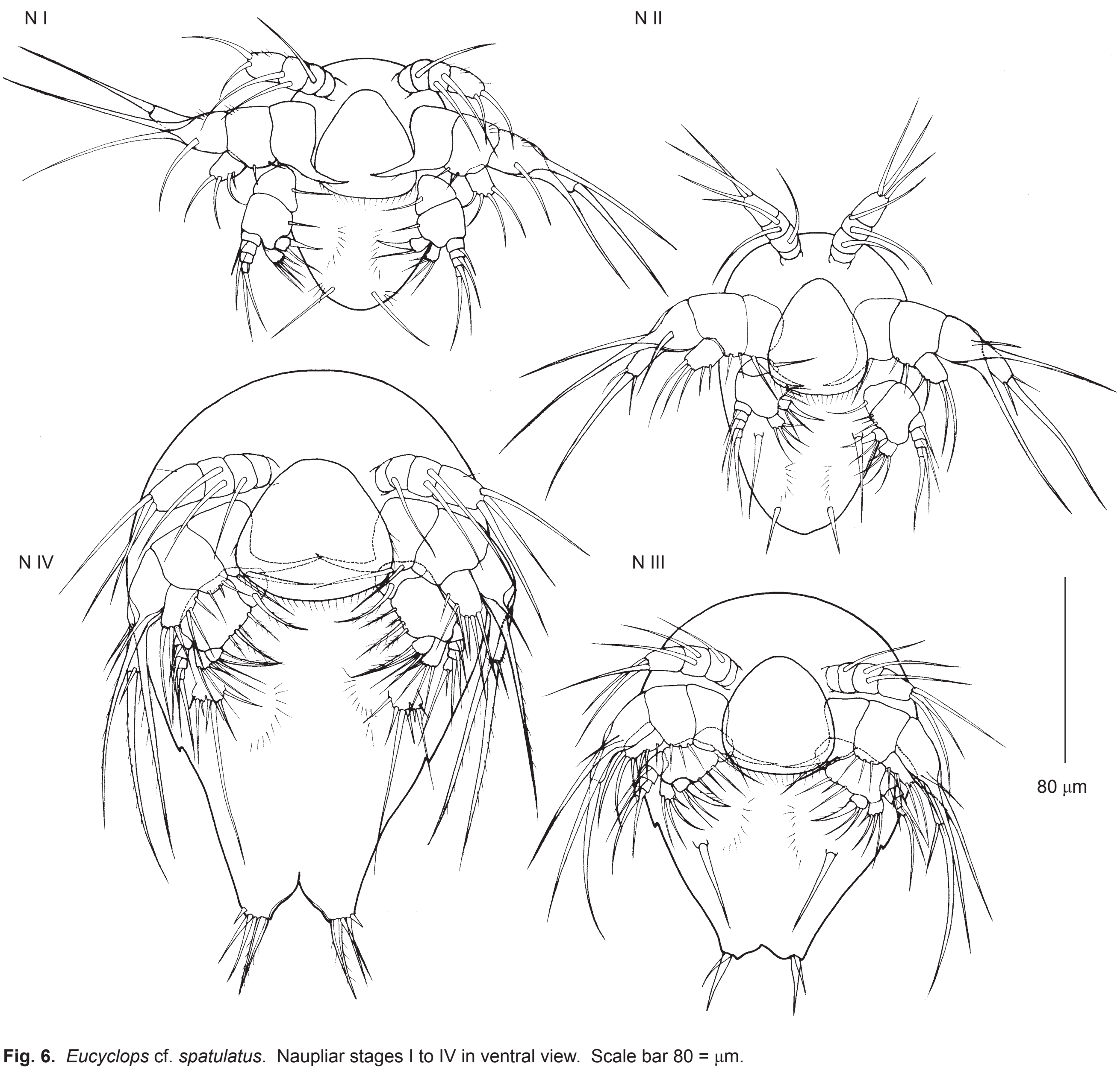

Fig. 6. *Eucyclops* cf. *spatulatus*. Naupliar stages I to IV in ventral view. Scale bar 80 = μm.

Nauplius IV (Figs. 1, 3-5)

Body length 197 μm, body width 134 μm. N IV differs from N III in the following aspects. Two additional outermost subequal setae on either side of hindbody (Fig. 1).

First antenna with 2 additional smooth setae on anterior surface of distal segment (Fig. 3).

Cylindrical endopod of 2nd antenna (Fig. 4) bearing 1 additional seta proximally at inner margin of its endopod. First segment of exopod ornamented with 1 small seta on anterior surface.

Mandible (Fig. 5) bearing 1 small spinulose 4th seta at inner corner of basis.

First maxilla (Fig. 1) bearing a lobe ornamented with 5 small setae and 1 long seta.

Nauplius V (Figs. 2, 3-5)

Body length 234 μm, body width 158 μm. N V differs from N IV in the following aspects. Hindbody (Fig. 2) grooved and elongate.

First antenna (Fig. 3) bearing 12 setae, with the addition of 1 smooth seta on the anterior surface of the distal 4th segment; and basis of 2nd antenna (Fig. 4) bearing 1 small seta on inner margin. Exopod ornamented with 1 small seta on tip of distal 4th segment.

Nauplius VI (Figs. 2, 3-5)

Body length 279 μm, body width 174 μm. N VI differs from N V in the following aspects.

First antenna (Fig. 3) bearing 18 setae with the addition of 6 setae on outer margin of distal 4th segment.

Naupliar stages of *Euc. spatulatus* are remarkably similar to those of *Euc. serrulatus*, except for their smaller size and the characters mentioned below. Hence, only differential characters between the 2 species are described here.

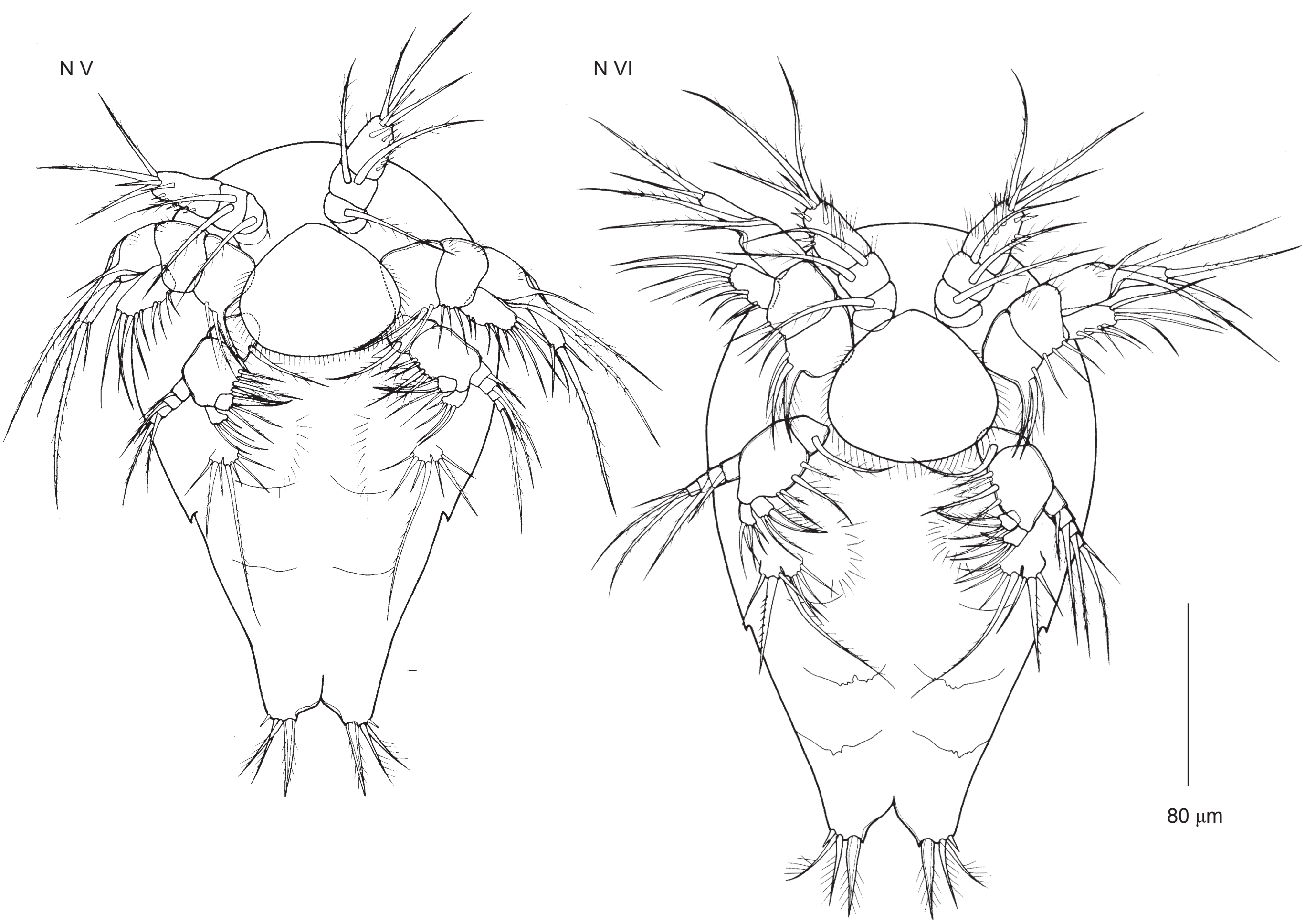

Fig. 7. *Eucyclops* cf. *spatulatus*. Naupliar stages V and VI in ventral view. Scale bar = 80 μm.

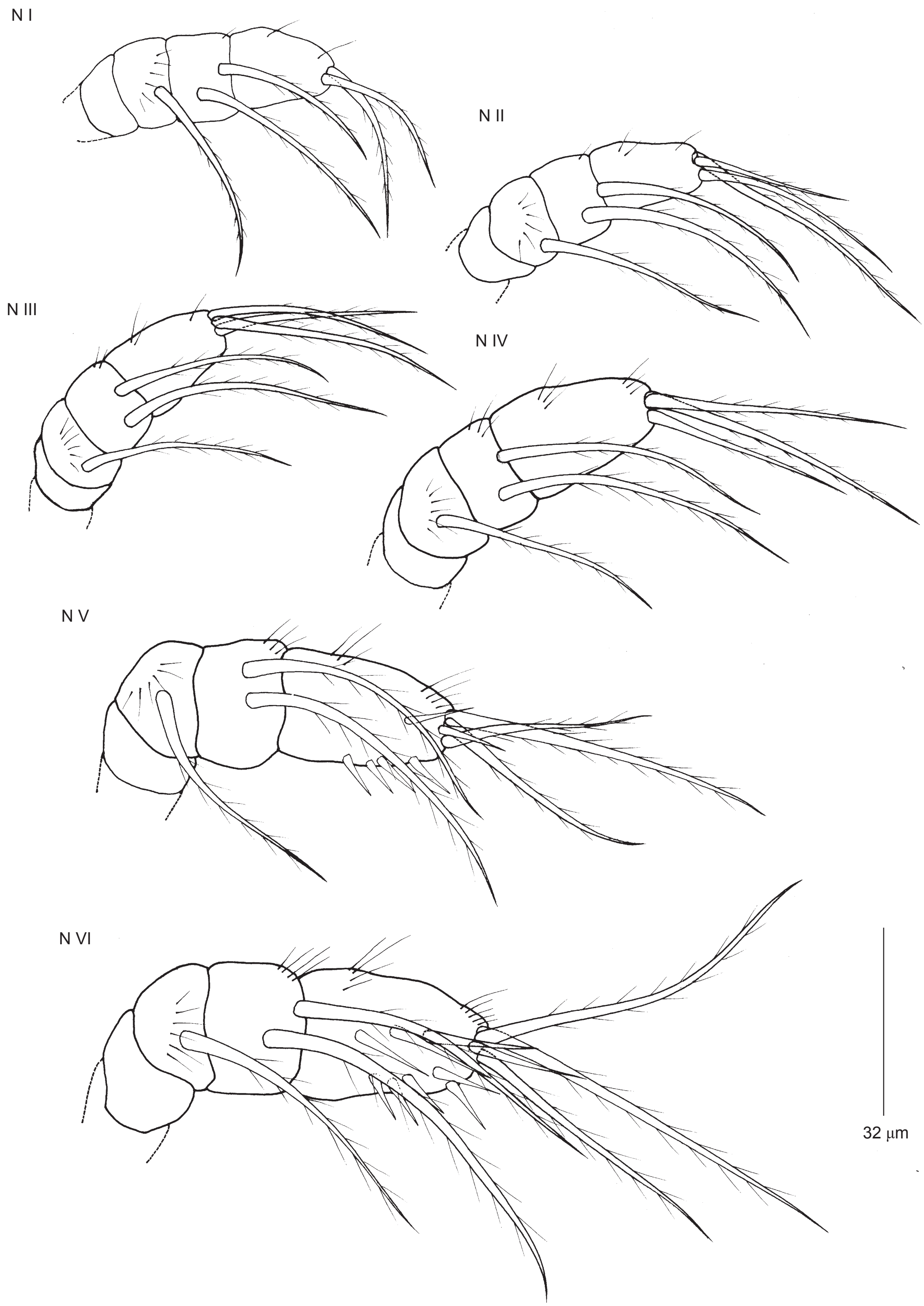

Fig. 8. *Eucyclops* cf. *spatulatus*. Development of the naupliar left 1st antenna of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

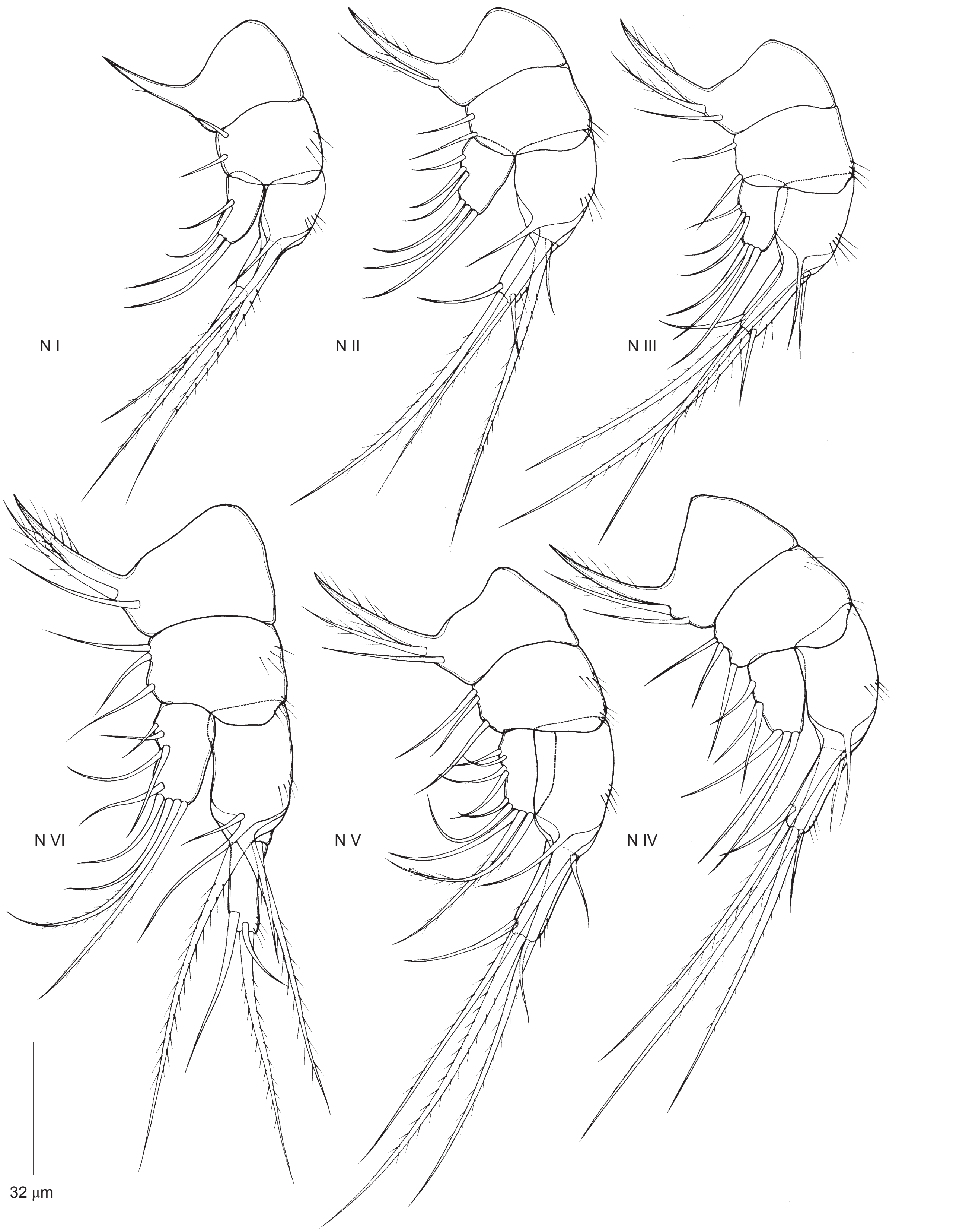

Fig. 9. *Eucyclops* cf. *spatulatus*. Development of the naupliar left 2nd antenna of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

Nauplius I of *Euc.* cf. *spatulatus* (Figs. 6, 8-10)

Body length 107 μm, body width 70 μm.

Distal 4th segment of 1st antenna (Fig. 8) bearing 2 spinulose setae.

Distal 4th segment of exopod of 2nd antenna (Fig. 9) bearing 1 spinulose seta.

Distal 4th segment of exopod of mandible (Fig. 10) bearing 1 spinulose seta.

No transverse row of small spinules along caudal rim (Fig. 6).

Nauplius II of *Euc.* cf. *spatulatus* (Figs. 6, 8-10)

Body length 128 μm, body width 82 μm.

Fourth segment of 1st antenna (Fig. 8) bearing 1 additional spinulose seta.

Third segment and distal 4th segment of exopod of 2nd antenna (Fig. 9) bearing 1 additional small smooth seta and 2 additional small smooth

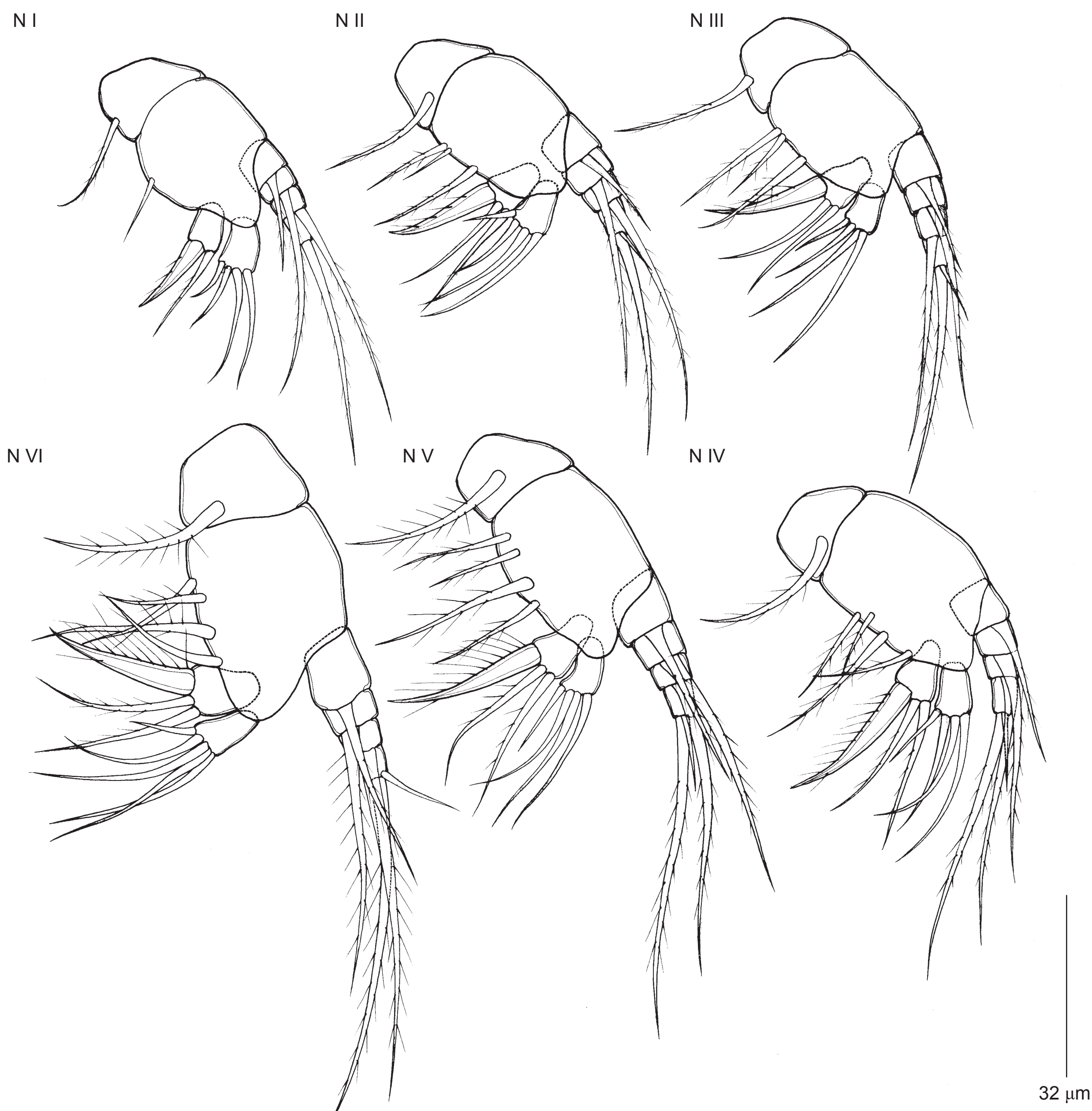

Fig. 10. *Eucyclops* cf. *spatulatus*. Development of the naupliar left mandible of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

setae, respectively.

Only 1 caudal spine on each caudal side, being shorter than that of N I (Fig. 6).

First maxilla (Fig. 6) making its first appearance as a smooth seta originating from a protuberance.

Nauplius III of *Euc.* cf. *spatulatus* (Figs. 6, 8-10)

Body length 156 μm, body width 116 μm.

With 3 spinulose setae on 4th segment of 1st antenna (Fig. 6). With 2 subequal sized caudal setae on either side (Fig. 6).

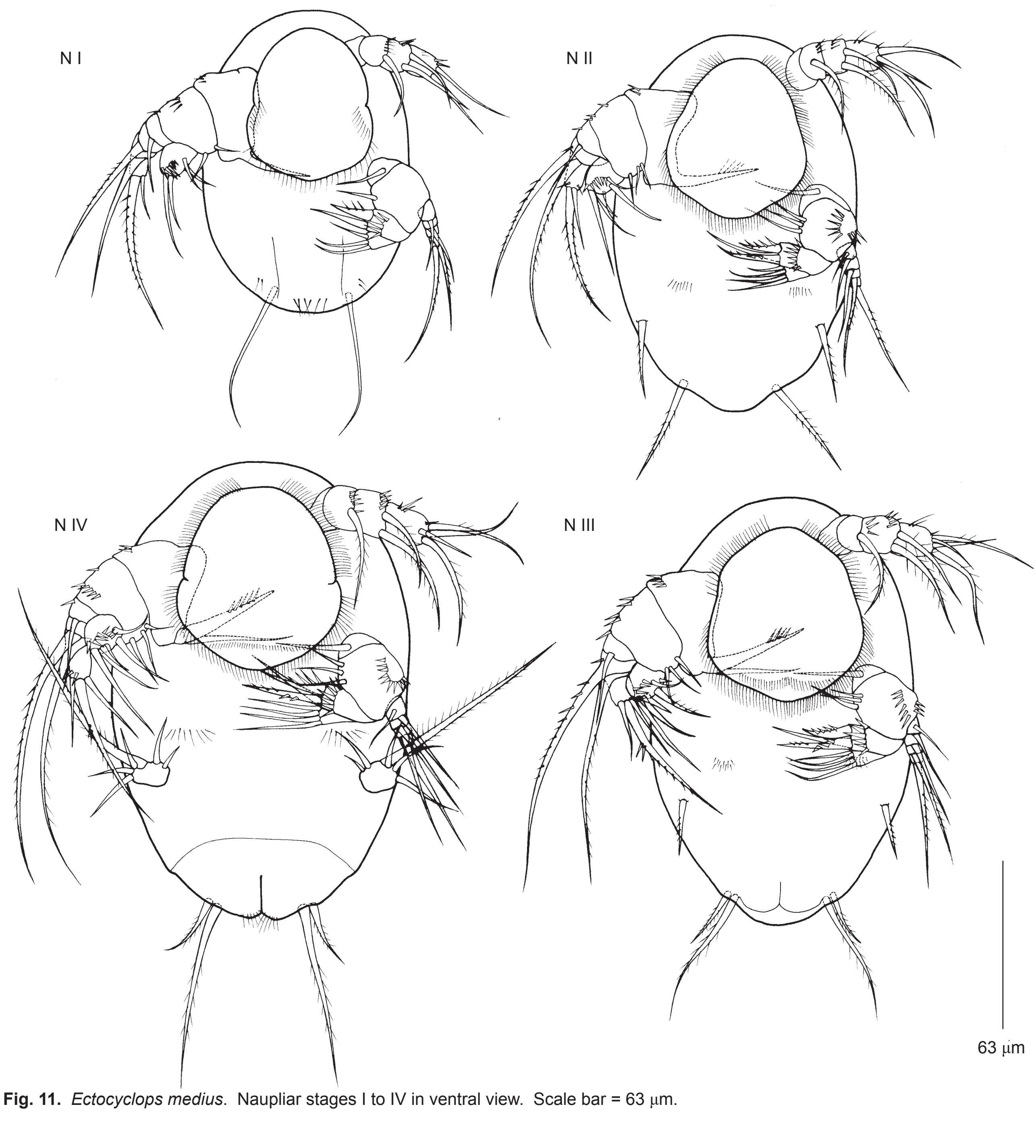

Fig. 11. *Ectocyclops medius*. Naupliar stages I to IV in ventral view. Scale bar = 63 μm.

Nauplius IV of *Euc.* cf. *spatulatus* (Figs. 6, 8-10)

Body length 234 μm, body width 152 μm.
No structural changes compared to nauplii of *Euc*. cf. *serrulatus tropicalis*.

Nauplius V of *Euc.* cf. *spatulatus* (Figs. 7-10)

Body length 255 μm, body width 156 μm.
First antenna (Fig. 3) bearing 12 setae, with 6 additional smooth setae on anterior surface and outer margin of distal 4th segment.
Hind body showing 2 suture lines indicating proliferation of somites (Fig. 7).

Nauplius VI of *Euc.* cf. *spatulatus* (Figs. 7-10)

Body length 274 μm, body width 171 μm.
First antenna (Fig. 8) bearing 15 setae, 3 additional smooth setae on anterior surface and outer margin of distal 4th segment.
First segment of exopod of 2nd antenna (Fig. 9) bearing 1 additional small smooth seta at tip.
Hind body showing 3 suture lines indicating segmentation (Fig. 7).

Naupliar stages of *Ect*. *medius* are remarkably similar to those of *Euc*. cf. *serrulatus tropicalis*, except for their slightly smaller size and characters mentioned below. Only differential characters between the 2 species are described here.

Nauplius I of *Ect. medius* (Figs. 11, 13-15)

Body length 113 μm, body width 68 μm.
Labrum rather large and round-shaped.
Each segment of 1st antenna (Fig. 13) furnished with strong spinules on anterior margin, except for 1st segment. With 2 spinulose setae on tip of distal 4th segment.
Anterior surfaces of coxa, basis, and endopod of 2nd antenna (Fig. 14) furnished with strong spinules.
Anterior surface of mandibular endopod furnished with strong spinules. First and 2nd segments of mandibular exopod with 1 smooth seta each. Third and distal 4th segments with 1

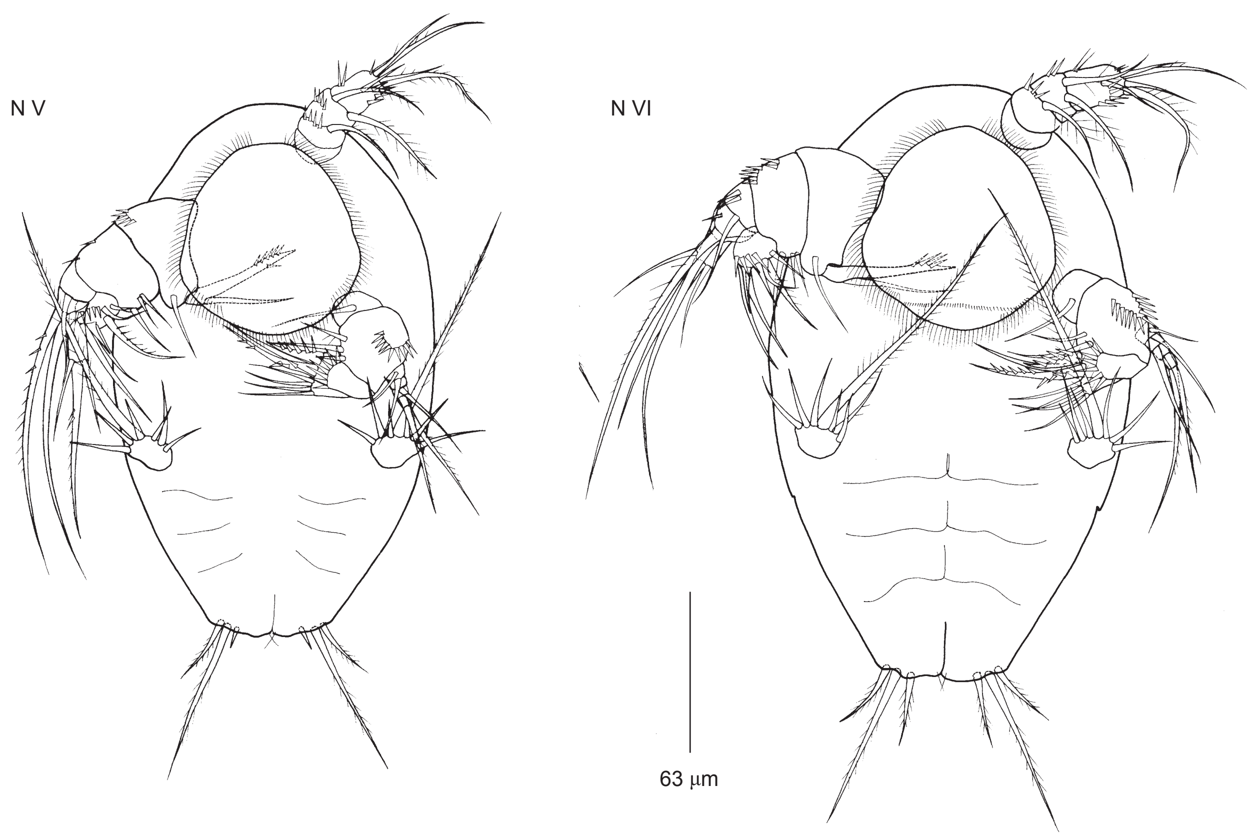

Fig. 12. *Ectocyclops medius*. Naupliar stages V and VI in ventral view. Scale bar = 63 μm.

spinulose seta each (Fig. 15).

Hindbody with 1 smooth long caudal seta on each side (Fig. 11).

Nauplius II of *Ect. medius* (Figs. 11, 13-15)

Body length 141 μm, body width 89 μm.

Labrum furnished with additional small

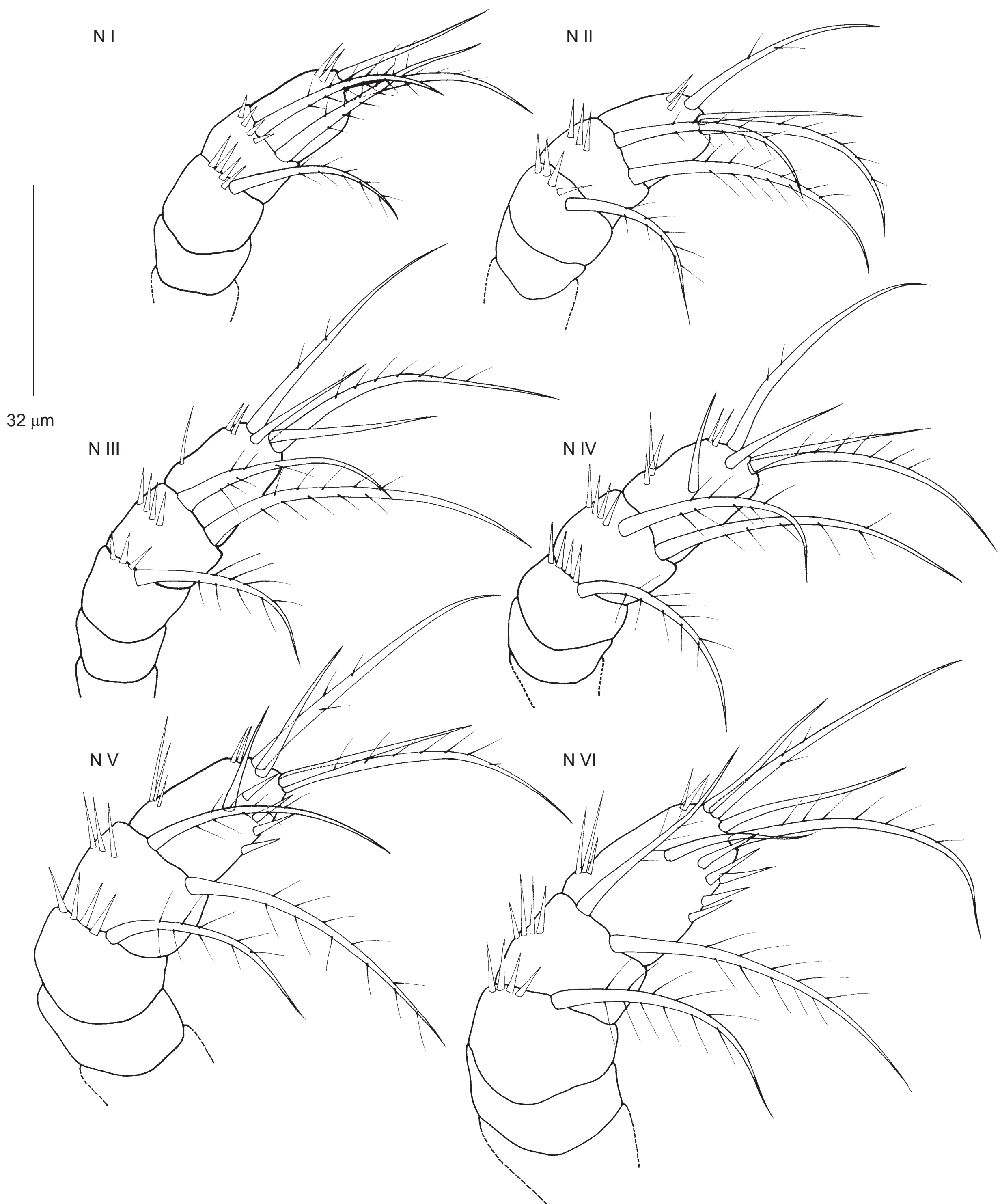

Fig. 13. *Ectocyclops medius*. Development of the naupliar left 1st antenna of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

spinules around its rim (Fig. 11).

With 1 additional smooth seta on distal 4th segment of 1st antenna (Fig. 12).

Anterior surfaces of coxa, basis, and endopod of 2nd antenna (Fig. 14) furnished with stronger spinules.

Fig. 14. *Ectocyclops medius*. Development of the naupliar left 2nd antenna of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

Anterior surface of mandibular basis furnished with strong spinules. First segment of mandibular exopod with 1 additional smooth seta on anterior surface (Fig. 15).

Nauplius III of *Ect. medius* (Figs. 11, 13-15)

Body length 162 μm, body width 95 μm.

With 1 additional strong smooth seta on distal 4th segment of 1st antenna (Fig. 13).

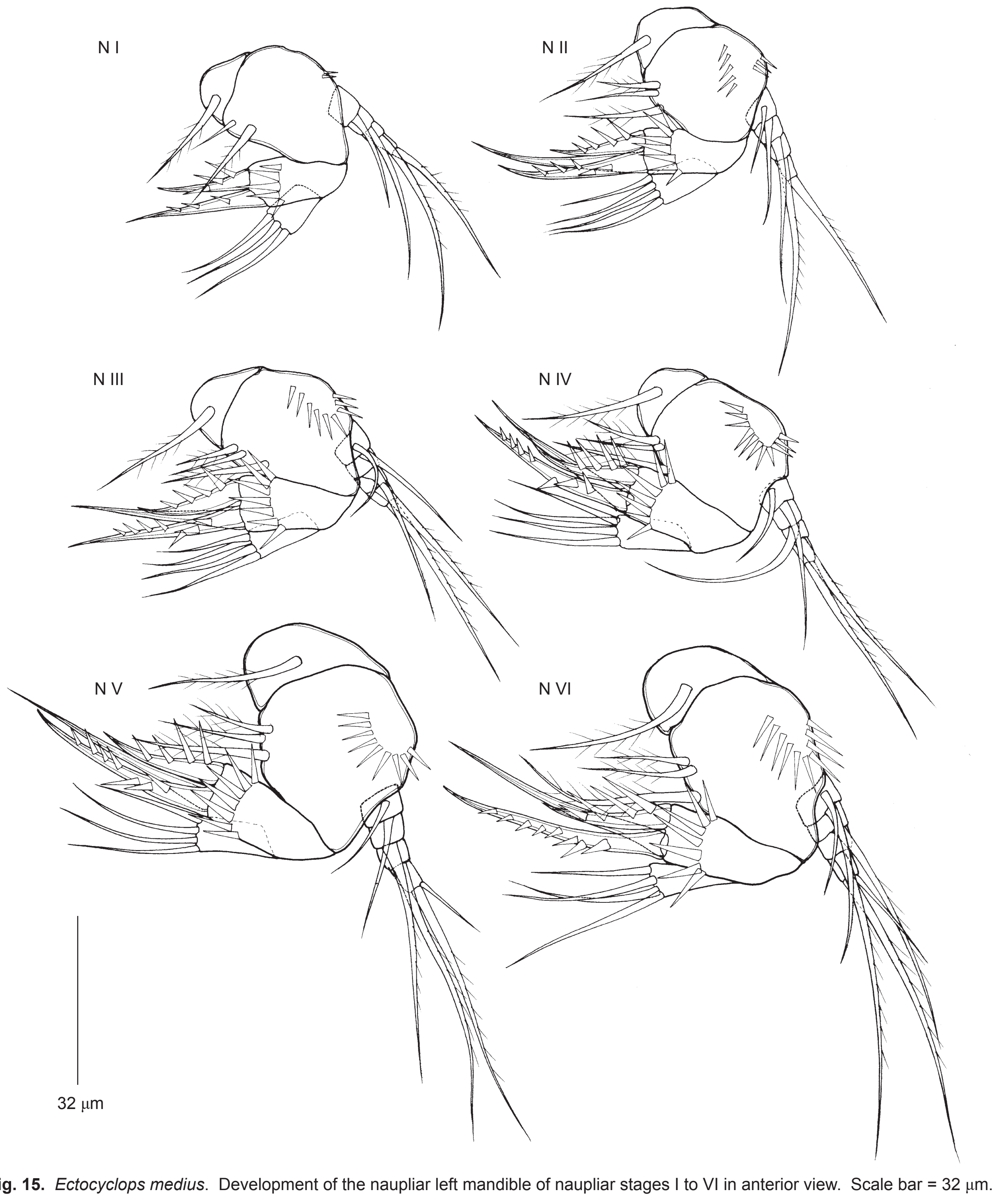

Fig. 15. *Ectocyclops medius*. Development of the naupliar left mandible of naupliar stages I to VI in anterior view. Scale bar = 32 μm.

Hindbody slightly grooved and carrying 2 spinulose caudal setae of subequal length on each side (Fig. 11).

Nauplius IV of *Ect. medius* (Figs. 11, 13-15)

Body length 171 μm, body width 111 μm.

With 1 additional strong smooth seta on anterior surface of distal 4th segment of 1st antenna (Fig. 13).

Mandibular exopod with 1 additional smooth seta on anterior surface of distal 4th segment (Fig. 15).

Inner spinulose caudal seta much longer than outer 1 (Fig. 11).

Nauplius V of *Ect. medius* (Figs. 12-15)

Body length 212 μm, body width 126 μm.

First antenna (Fig. 13) bearing 12 setae with 4 additional strong setae.

Hindbody with 1 additional short innermost caudal seta on each side and 3 suture lines of segmentation (Fig. 12).

Nauplius V I of *Ect. medius* (Figs. 12-15).

Body length 236 μm, body width 144 μm.

First antenna (Fig. 13) bearing 13 setae with 1 additional seta midway.

Hindbody with 3 spinulose caudal setae of subequal length on each side and 3 suture lines indicating proliferation of somites (Fig. 12).

DISCUSSION

As apparently all free-living Copepoda, nauplii of *Euc*. cf. *serrulatus tropicalis*, *Euc*. cf. *spatulatus*, and *Ect. medius* have 6 naupliar instars in common. As with other but not all cyclopoid nauplii, they are dorsoventrally flattened (see Amelina 1927). The body shape is mostly circular in stage 1, then becomes elongated, and the hindbody emarginates in later stages. As in other copepods, the 1st stage nauplius (orthonauplius) of *Eucyclops* spp. and *Ectocyclops* spp. has 3 pairs of appendages: uniramous 1st antennae, biramous 2nd antennae with bimerous protopods and biramous mandibles with bimerous protopods. As in most other copepod nauplii, a median red naupliar eye is situated dorsally between the bases of the 1st antennae. The hind-body bears 1 seta on each side in N I and N II, whereas the seta number is remarkably variable in subsequent stages (see Dukina 1956).

The 2nd antenna and mandible increase their armature and ornamentation, usually until N V at the latest, when they reach their final naupliar appearance if no reduction occurs at the final molt. The 1st antenna and metanaupliar appendages, 1st and 2nd maxilla, maxilliped, and legs 1 and 2 change their shape and increase their armature and ornamentation until the final naupliar stage.

The armature and shape of the appendages on both sides of the body are symmetrical in the Cyclopoida as in all non-calanoid copepod nauplii (Dahms 2004b).

Larval peculiarities of the Cyclopoida within the Copepoda

The Copepoda is comprised of 6 naupliar stages at most, with stage reductions primarily in non-feeding taxa. Copepod nauplii bear a variable number of 1st antennal segments (as a rule 3 in most taxa, 5 or 6 in Polyarthra, 3-5 in Cyclopoida, and 1-3 in the Harpacticoida-Oligoarthra). The antennal endopod is 1-segmented (2-segmented in the Cyclopoida), the coxa of the 2nd antenna bears 2 setae, and the antennal exopod is 6-segmented. The mandibular exopod is 4-segmented, and the postmaxillar limbs of later stages are juxtaposed medially. At later stages, there are 6 furcal setae. A 1-segmented 2nd antennal endopod (Figs. 4, 9, 14) was argued to be an apomorphy of the Copepoda (where the 2-segmented state among the Cyclopoida is interpreted as a secondary acquisition; Dahms 2004a). There are spinule rows, possibly indicating a former 2-segmented state (or even a 4-segmented state at later stages) of this ramus in *Longipedia minor* T. and A. Scott, 1893, belonging to the Polyarthra (Dahms 1991).

In the Cyclopoida, postmandibular appendages vary greatly in the moment of their appearance as Anlagen, in the total number of Anlagen present at N VI, and in their shape and armature (Borutzky 1952, Dahms 2004a).

There are two 2nd antennal coxal setae in the Cyclopoida (Figs. 4, 9, 14). Besides the antennal enditic process of the coxa which is present (although rudimentary in N I) throughout the phase, there is a peculiar strong seta at the base of this process which develops in the N III stage in the Calanoida (Dahms and Fernando 1993a) and Cyclopoida (Dahms and Fernando 1992 1993b c 1994 1995). In some species of the Harpacticoida, a presumably homologous seta is present throughout the phase (Dahms 1990). However, if this is strongly developed, it appears also in harpacticoids but not before the N III stage (e.g., the Harpacticidae and Thalestridae; Dahms 1990).

Legs 1 and 2 are present in N VI (Figs. 2, 7, 12). The sudden external appearance of the 2nd and 3rd thoracic appendages as limb buds, as a rule not before N VI in all major copepod taxa, is a unique character compared to other crustacean nauplii and, therefore, a strong apomorphy for the Copepoda (Dahms 2004a). Exceptions in the form of reductions are provided by certain Oligoarthra (e.g., in *Macrosetella gracilis*) where naupliar postmaxillulary limb formation is reduced (Dahms 1990).

Postmaxillary appendages are medially juxtaposed in the Cyclopoida, Polyarthra, and Calanoida, whereas they are widely spaced secondarily in the derived Harpacticoida and Oligoarthra (Figs. 7, 12).

The caudal armature of non-copepod nauplii is difficult to ascertain, since spiniform processes might or might not have setal precursors. However, 6 naupliar setae are widespread, and this is the maximum number among all major copepod taxa. Six setae are present in primitive groups of the Harpacticoida, but often become reduced in derived taxa. A maximum number of 5 caudal setae was discernible in *Euc*. cf. *serrulatus tropicalis* studied here (Fig. 2).

Generic and specific naupliar distinctions among the Cyclopidae

According to Kiefer (1973), most cyclopoid species he studied from middle Europe are identifiable to the genus level once they reach the NIV, NV, or NVI stages. Kiefer (1973) claimed the 1st maxilla to be of most diagnostic value. The Eucyclopinae (comprising *Afrocyclops*, *Australoeucyclops*, *Austriocyclops*, *Ectocyclops,* *Eucyclops*, *Homocyclops*, *Macrocyclops*, *Ochridacyclops*, *Paracyclops*, *Thaumasiocyclops*, and *Tropocyclops*) show some peculiarities. An important naupliar descriminant in *Eucyclops*, *Tropocyclops*, and *Ectocyclops* is the relative length of the distal exopodal A2 segment (Alekseev 2002). Kiefer (1973) demonstrated that in *Macrocyclops* spp. and *Eucyclops* spp., the apical setae of the inner lobe of the 1st maxilla is longest, whereas the outer seta of the outer lobe is longest in all other cyclopoid subfamilies and genera. In *Tropocyclops* sp., the inner lobe of the 1st maxilla bears only 2, 3, or 4 setae, whereas there are more setae in other genera.

The cyclopoid nauplii studied here share a 4-segmented 1st antenna. This also holds for other cyclopoid genera investigated by H.U. Dahms as it does for *Macrocyclops fuscus* (Dahms and Fernando 1994). Both available naupliar descriptions of *Macrocyclops albidus* mention a 3-segmented 1st antenna (Manfredi 1925, Amelina 1927). Amelina (1927) figured the antennal exopod as 5-segmented throughout the phase with no addition of segments in *Mac. albidus*. We noted no increase in segment numbers in the species studied here. Dahms and Fernando (1994), however, found an increase of segments on the antennal exopod from 4 at N I to 5 at N III and 6 from N IV onwards in *Mac. fuscus*. Dahms and Fernando (1993b) showed the formation of 1 new segment on the antennal exopod from N II to N III in *Mesocyclops* cf. *thermocyclopoides*. Whereas the 2nd antennal exopod invariably becomes 5-segmented at the N III stage in both *Mes*. cf. *thermocyclopoides* and *Mes. aequatorialis similis* (Dahms and Fernando 1992), it stays 4-segmented in both *Eucyclops* species studied here and in *Ectocyclops*.

The 2nd naupliar stage of both *Eucyclops* species develops the Anlage of the 1st maxilla as a seta, usually arising from a protuberance. In the following stages, the number of appendage Anlagen increases by 1 at each stage so that at N VI the Anlage of leg 2 is present in most cases in both *Eucyclops* and *Ectocyclops*. Other postmandibular appendages are hidden under the cuticle throughout the naupliar phase.

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