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Naupliar development of *Nitocra karanovici* (Copepoda, Harpacticoida)

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Abstract.—All six naupliar stages of the harpacticoid copepod *Nitocra karanovici* are described. A key to the identification of the naupliar stages is provided. Stages can be distinguished by number of segments of the exopod of antenna 2, setation of the limbs including the bud of the caudal ramus, and presence and setation of the bud of maxilla 1. A particular naupliar character was found in the nauplii of *N. karanovici* that is in common for all Ameiridimorpha, except Ameiridae and otherwise not known from other Harpacticoida. This is a pair of bean-shaped, bare medial cuticular areas of the ventral body wall present in Parastenocarididae, Cylindropsyllidae, and as in *Canthocamptus*, *Attheyella*, *Moraria*, and *Mesochra* of the Canthocamptidae.

Keywords: development, evolution, Harpacticidae, naupliar characters, phylogeny, systematics

Whoever has treated bottom deposits in search of small animals has been impressed by the abundance and variety of larvae obtained in this process. Most of them belong to the Copepoda and in particular to the Harpacticoida (Schminke 1982). The life of the nauplii is exposed to different selection pressures and nauplii, therefore, have experienced remarkable adaptive radiation. These larvae vary of forms, shapes, particular structures, and behavioral characteristics (Dahms et al. 2009). Due to their great abundance and variety, nauplii may play an important ecological role (Dahms 2004a, 2004b). Many meiofaunal food chains must begin with nauplii (Dahms & Qian 2004). Life-history studies in the field and the investigation of stage-specific phenomena in the laboratory are in need of information of naupliar biology (Dahms et al. 2012, 2013). Knowledge of postembryonic development is also important for phylogenetic and evolutionary analysis (Dahms et al. 2009).

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Materials and Methods

Collection data.—Ovigerous females of *Nitocra karanovici* which provided the developmental stages were collected from a seaweed *Padina* sp. at Bangsaen beach, Chonburee Province in Thailand (12°45′N, 100°53′E) in April 2008 by use of a beaker

in which substratum from the field was stirred and subsequently decanted over a screen (100 μm mesh-size). The residue containing, e.g., harpacticoids, was rinsed into smaller bowls for transport to the laboratory. The developmental stages used in this study represent the offspring exclusively of single-female cultures unless indicated otherwise. The classification used is that of Lang (1948, 1965).

Cultivation.—Ovigerous females of *Nitocra karanovici* were transferred to individual petri dishes containing filtered seawater. These were kept at 20°C to 24°C with a light-dark cycle of 12:12 hours. Water renewal was about 50% per week. Seawater was obtained and prepared as described by Dahms (2000). When nauplii emerged, some of them were isolated in watch glasses and the exuviae of subsequent moults were collected. *Dunaliella salina* was used as algal food. A few drops of food-suspension were added every few days.

Preparation.—Stages were fixed in 5% buffered formaldehyde and embedded in glycerine which clears the natural color of nauplii, and color and shape of the red nauplius-eye is lost quite soon and the eye is, thus, not figured. Nauplii were mounted whole, broken cover-glass pieces being added to prevent them from being compressed and to facilitate rolling to allow inspection from all sides. Body lengths were measured from the anterior to the posterior end of the naupliar body; body width is given as the widest part of the nauplius. Drawings were made from single specimens; others (2–5) were checked for variability.

Descriptive terminology.—The following terms are defined according to their usage in the chapters (see Ferrari & Dahms 2007): The harpacticoid nauplius has at least three pairs of appendages: the antennules, antennae, and mandibles. The body is completely covered by a usually smooth nauplius 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 one caudal seta on both sides of the anal area. The labrum originates as a lobular flap near the frontal margin of the body, between the bases of the antennules, 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 protopodite. The antennule is uniramous. The antenna is noticeably different from that of the adult (and copepodids) in having a precoxa in some cases and a coxal masticatory process (= gnathobase), which is called prognathobasal when it is indicated only as an Anlage in NI. The antenna further consists of a coxa, basis, endopodite, and exopodite. The mandible is composed of the same elements, except the precoxa. The endopodite consists of an inner process and usually an outer lateral field of setae arising on the outer lateral margin (except in *Polyarthra* where it is homologous to the second segment and in Ectinosomatidae where it is vestigial). The postmandibular appendages (maxillule, maxilla, maxilliped, leg 1 and leg 2) may develop successively from NII onwards. For all appendages the singular form is used. 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. The 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 1930) are presumed sensory elements of the antennule with sclerotized bases and are more transparent than normal setae with blunt or rounded ends. The complement of setae, setules, spines and aesthetascs is called element of a particular structure

and is referred to as the armature. In addition to setae, setules and spines, the body segments or appendages present a variety of ornamenting cuticular projections. Spinules could be very fine hair-like cuticular extensions of setae and spines, labrum and ventral body wall, or, small, pointed, conical processes. Denticles are minute triangular outgrowths. The spinules and denticles are considered as the ornamentation.

Results

Description of naupliar stages of *Nitocra karanovici*

Figs. 1–6

The nauplii are creeping larvae and not able to swim. The nauplii of *Nitocra karanovici* have a pear-shaped habitus at early stages, the hind-body emarginating later to provide an elongate appearance. Nauplii have a remarkably elongate antennule. Hind-body armed on either side with 4 setae at NIV and with 5 at NV, and NVI. Labrum bears a prominent apex. Borderlines of ventral body wall are not visible, only a curved row of spinules beneath labral apex remains of it. Third antennular segment increases its armature from 9 elements (including aesthetasc) at NIV, 11 at NV, to 15 elements at NVI.

Nauplius I.—Body length 57 μm, body width 66.8 μm. Antennule (Fig. 4A) 3-segmented. Segment 1 unarmed, segment 2 with 2 small and 1 long medial seta distally with longer spinules distally that are far extending caudally. Segment 3 with 1 subterminal seta and 2 long setae and an aesthetasc distally.

Antenna (Fig. 5A) with coxa and basis, 3-segmented exopod and 1-segmented endopod. Coxa with row of denticles dorsally and naupliar arthrite but no seta as yet. Basis with 2 setae. Exopod shorter than endopod; segment 1 longest without ornamentation, segment 2 very short with 1 seta, and segment 3 with 1 medial seta and 2 distal setae. Endopod robust with 1 inner bare seta on middle, and 1 short seta and 1 stout claw bearing a setule row on inner margin.

Mandible (Fig. 5A) with coxa and basis. Coxa without seta. Basis with 1 inner seta on inner margin, and 1 setule row dorsally. Exopod 2-segmented, segment 1 with 1 lateral seta proximally and segment 2 with 1 small seta and 1 big seta distally. Endopod 1-segmented, with 3 outer setae and 2 stout claws bearing a setule row along inner margin.

Caudal rami (Fig. 2A) with 1 seta.

Nauplius II.—Body length 65.9 μm, body width 74.6 μm. Antennule (Fig. 4B) 3-segmented. Segment 1 with 1 smooth seta, segment 2 with 2 setae. Segment 3 with 3 long setae and an aesthetasc distally.

Antenna (Fig. 5B) with coxa and basis, 3-segmented exopod and 1-segmented endopod. Basis with 1 plumose seta and 2 smooth setae. Exopod 3-segmented, segment 1 longest without ornamentation, segment 2 with 1 seta, and segment 3 with 1 medial seta and 3 distal setae. Endopod robust with 1 inner bare seta on middle, and 1 short seta and 1 stout claw bearing setule row on inner margin.

Mandible (Fig. 6B) with coxa and basis. Coxa with 1 inner seta. Basis with 1 inner seta 1 setule row on inner margin. Exopod 2-segmented, segment 1 with 2 setae proximally and segment 2 with 2 setae distally. Endopod 1-segmented, with 3 outer setae and 1 stout claw bearing a setule row along the inner margin.

Caudal rami (Fig. 2B) with 2 setae.

Nauplius III.—Body length 80.4 μm, body width 80.2 μm. Antennule (Fig. 4C) 3-segmented. Segment 1 with 1 smooth seta, segment 2 with 2 small setae. Segment 3 with 4 setae and an aesthetasc distally.

Antenna (Fig. 5C) with coxa and basis, 3-segmented exopod and 1-segmented endopod. Coxa with row of denticles dorsally

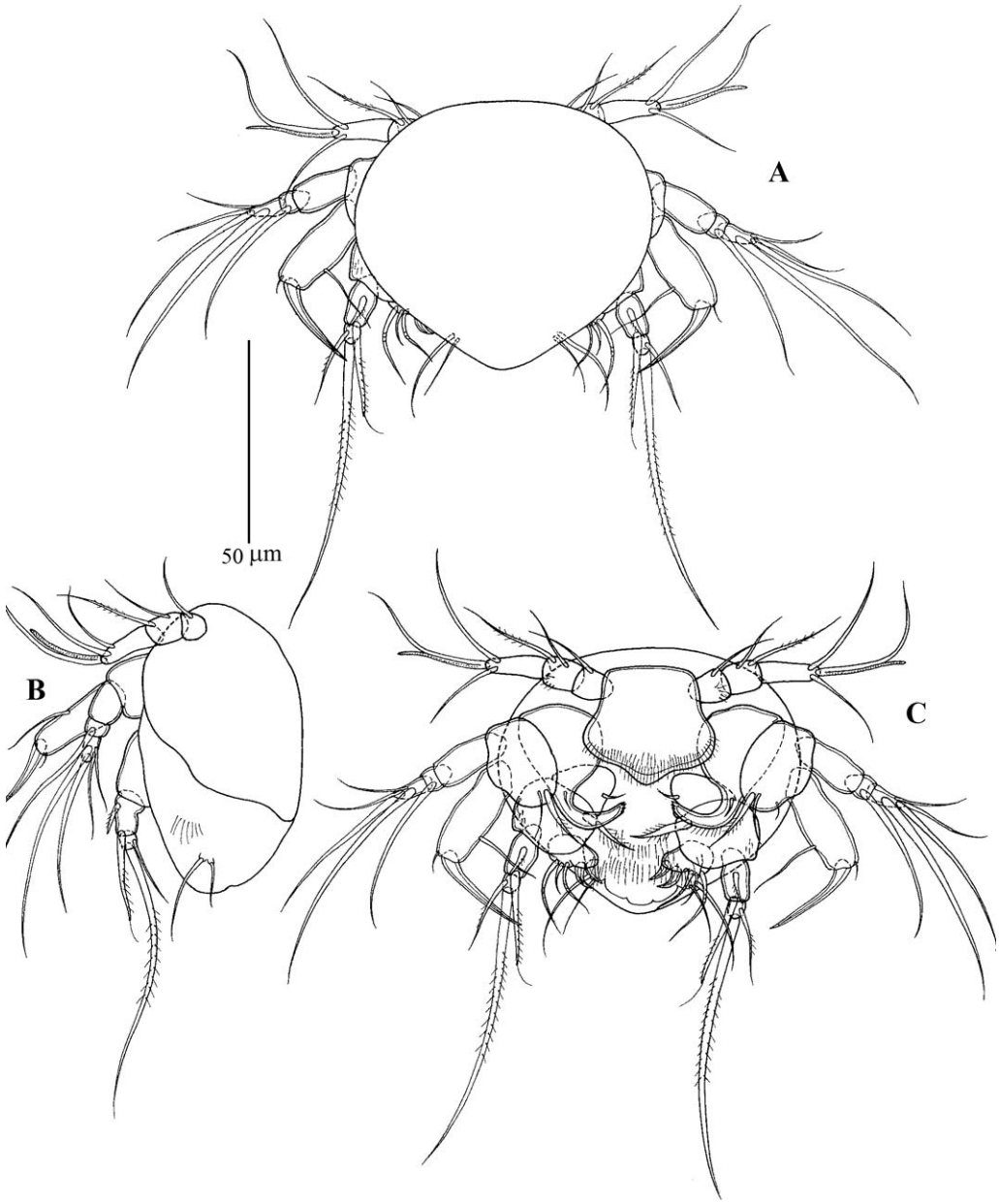

Fig. 1. *Nitocra karanovici,* habitus. A, dorsal; B; lateral; C, ventral view.

and 1 small seta. Basis with 1 small seta and 2 plumose setae. Exopod longer than endopod; segment 1 with 1 seta, segment 2 with 1 plumose seta, and segment 3 with 2 medial plumose setae and 2 plumose distal setae. Endopod robust with 1 inner bare seta on middle, and 1 short seta and 1 stout claw bearing setule row on inner margin.

Mandible (Fig. 6C) with coxa and basis. Coxa with 1 inner seta. Basis with 2 inner setae and 1 setule row dorsally. Exopod 2-segmented, segment 1 with 2 lateral setae proximally and segment 2 with 3 setae

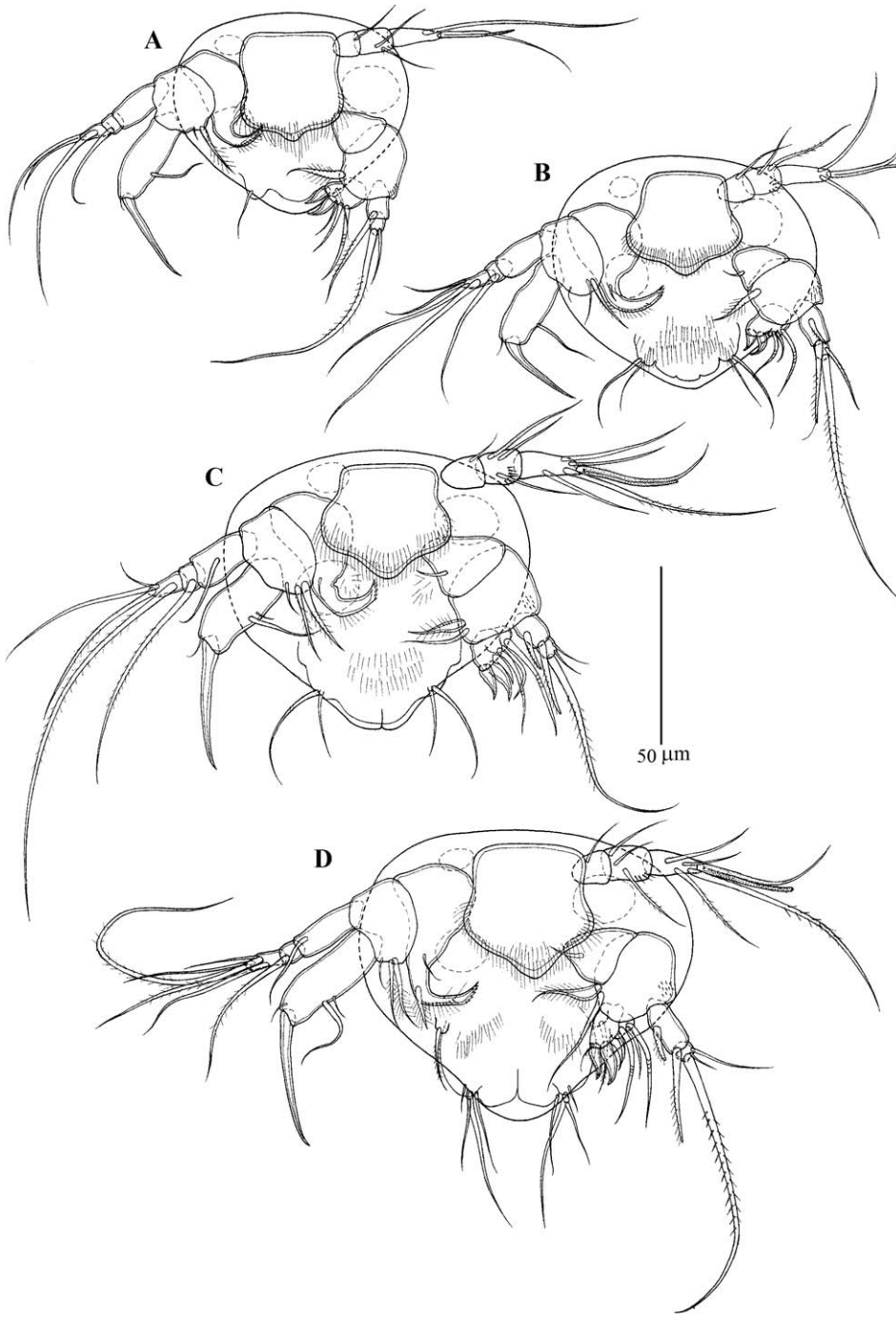

Fig. 2. *Nitocra karanovici,* habitus in ventral view. A, nauplius I; B, nauplius II; C, nauplius III; D, nauplius IV. Appendages are shown alternately (left A1, right A2, left Md).

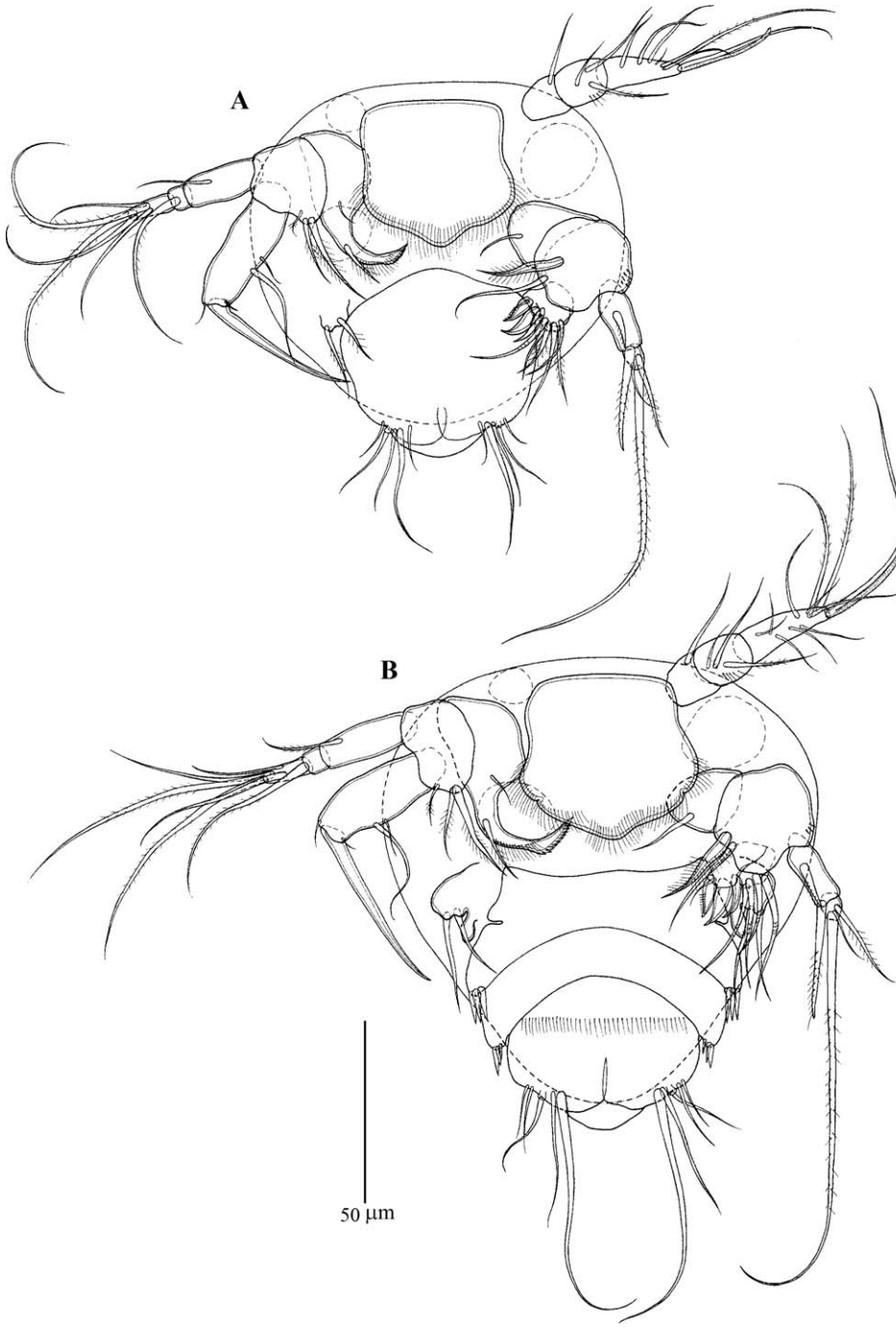

Fig. 3. *Nitocra karanovici,* habitus in ventral view. A, nauplius V; B, nauplius VI. Appendages are shown alternately (left A1, right A2, left Md).

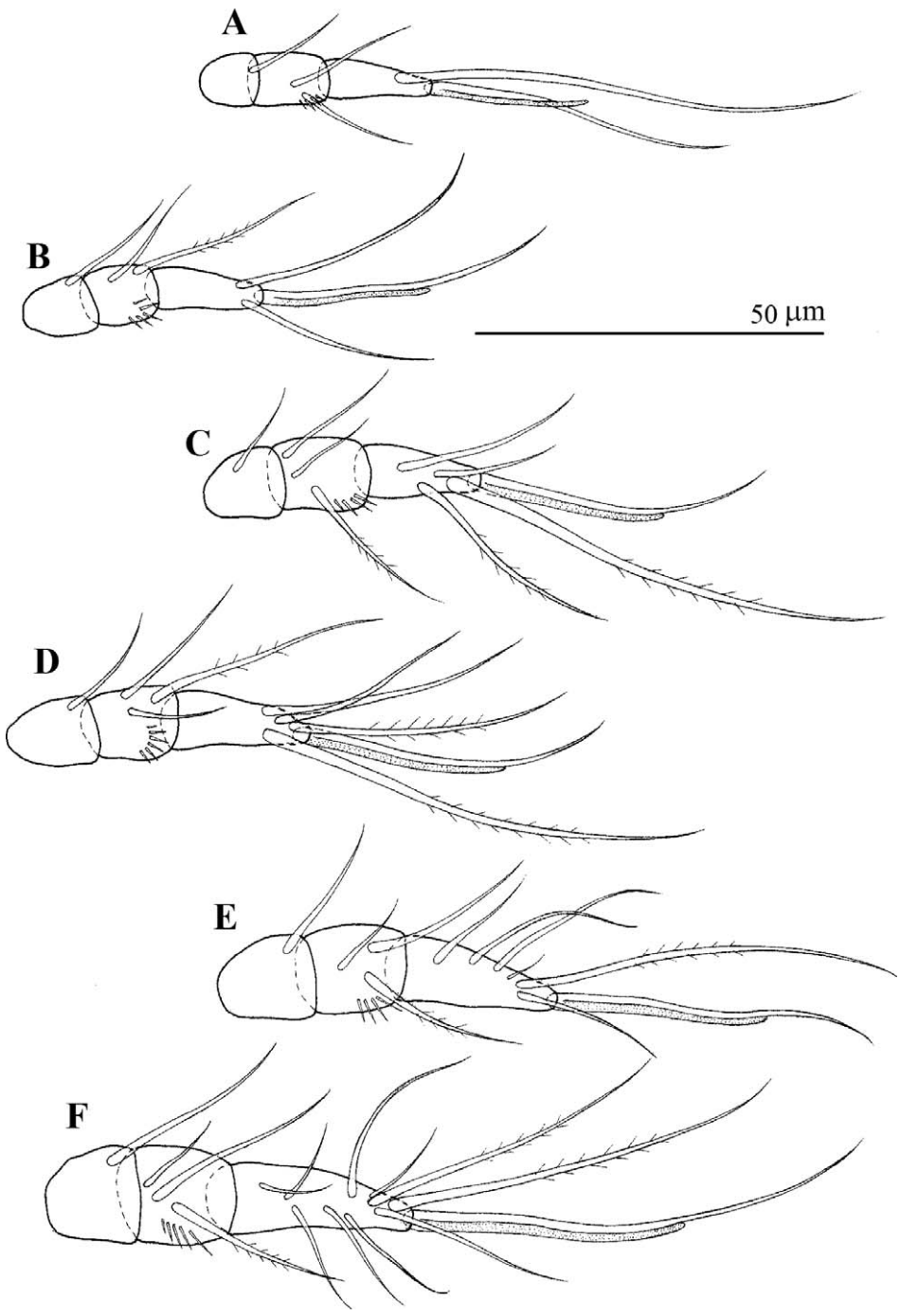

Fig. 4. *Nitocra karanovici,* antennule development in ventral view. A–F, NI to NVI (naupliar stage I to naupliar stage VI; left A1, right A2, left Md).

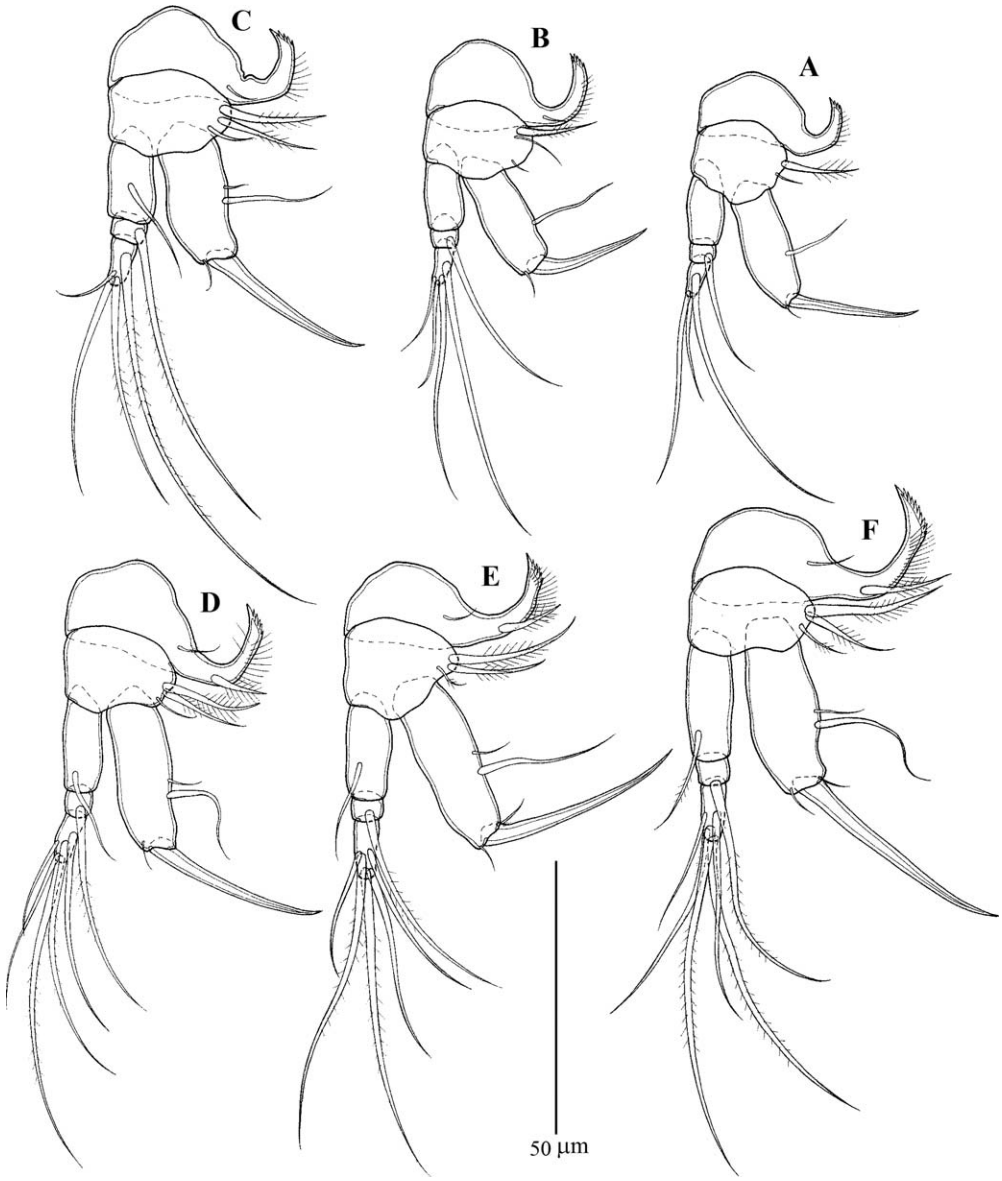

Fig. 5. *Nitocra karanovici,* antenna development in ventral view. A–F, NI to NVI (naupliar stage I to naupliar stage VI; left A1, right A2, left Md).

distally. Endopod 1-segmented, with 3 outer setae and 3 stout claws bearing setule row along the inner margin.

Maxillule (Fig. 2C) with 1 thick seta.

Caudal rami (Fig. 2C) with 1 seta.

Nauplius IV.—Body length 82.3 µm, body width 94.9 µm. Antennule (Fig. 4D) 3-segmented. Segment 1 with 1 smooth seta, segment 2 with 3 setae. Segment 3 with 5 setae and 1 aesthetasc distally.

Antenna (Fig. 5D) with coxa and basis, 3-segmented exopod and 1-segmented endopod. Coxa with row of denticles dorsally, 1 small seta, and naupliar arthrite with 1 seta. Basis with 1 small seta and 2 plumose setae. Exopod longer than endo-

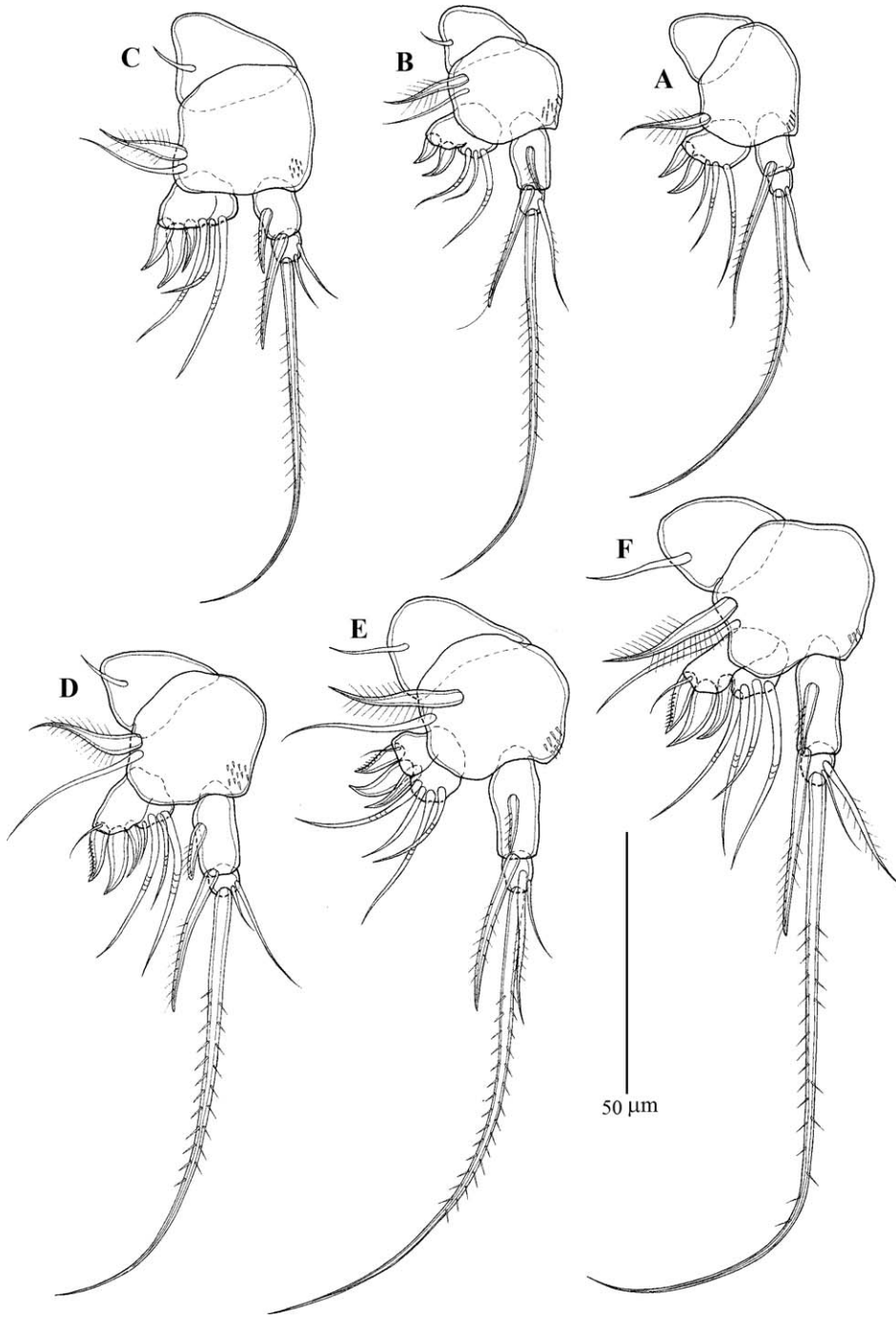

Fig. 6. *Nitocra karanovici,* mandible development in ventral view. A–F, NI to NVI (naupliar stage I to naupliar stage VI; left A1, right A2, left Md).

pod; segment 1 with 1 seta, segment 2 with 1 plumose seta, and segment 3 with 3 medial plumose setae and 2 plumose distal setae. Endopod robust with 2 inner bare setae on middle, and 1 short seta and 1 stout claw bearing setule row on inner margin.

Mandible (Fig. 6D) with coxa and basis. Coxa with 1 inner seta. Basis with 2 inner setae and with some setules dorsally. Exopod 2-segmented, segment 1 with 2 lateral setae proximally and segment 2 with 3 setae distally. Endopod 1-segmented, with 4 outer setae and 3 stout claws along the inner margin.

Maxillule (Fig. 2D) with 2 smooth setae.

Caudal rami (Fig. 2D) with 2 smooth setae.

Nauplius V.—Body length 104.6 μm, body width 103.7 μm. Antennule (Fig. 4E) 3-segmented. Segment 1 with 1 smooth seta, segment 2 with 3 setae. Segment 3 with 7 setae and an aesthetasc distally.

Antenna (Fig. 5E) with coxa and basis, 3-segmented exopod and 1-segmented endopod. Coxa with 1 row of denticles dorsally 1 small seta and naupliar arthrite with 1 seta. Basis with 1 small seta and 2 plumose setae. Exopod longer than endopod; segment 1 with 1 seta, segment 2 with 1 plumose seta, and segments 3 with 3 medial plumose setae and 2 plumose distal setae. Endopod robust with 2 inner bare setae on middle, and 1 short seta and 1 stout claw bearing setule row on inner margin.

Mandible (Fig. 6E) with coxa and basis. Coxa with 1 inner seta. Basis with 2 inner setae and with some setules dorsally. Exopod 2-segmented, segment 1 with 2 lateral setae proximally and segment 2 with 3 setae distally. Endopod 1-segmented, with 7 outer setae and 3 stout claws along inner margin.

Maxillule (Fig. 3A) with 1 smooth seta and 2 plumose setae.

Caudal rami (Fig. 3A) with 2 short setae and 2 long setae.

Nauplius VI.—Body length 131.8 μm, body width 120.1 μm. Antennule (Fig. 4F) 3-segmented. Segment 1 with 1 smooth seta, segment 2 with 3 setae. Segment 3 with 11 setae and 1 aesthetasc distally.

Antenna (Fig. 5F) with coxa and basis, 3-segmented exopod and 1-segmented endopod. Coxa with row of denticles dorsally 1 small seta and naupliar arthrite with 1 seta. Basis with 3 plumose setae. Exopod longer than endopod; segment 1 with 1 plumose seta, segment 2 with 1 plumose seta, and segments 3 with 3 medial setae and 2 distal setae. Endopod robust with 2 inner bare setae on middle, and 1 short seta and 1 stout claw bearing setule row on inner margin.

Mandible (Fig. 6F) with coxa and basis. Coxa with 1 inner seta. Basis with 2 inner setae and with some setules dorsally. Exopod 2-segmented, segment 1 with 2 lateral setae proximally and segment 2 with 3 setae distally. Endopod 1-segmented, with 4 outer setae and 1 seta and 3 stout claws along inner margin.

Maxillule (Fig. 3B) with 2 setae.

Swimming legs 1 (Fig. 3B) with 3 setae.

Intraspecific variability—For *N. karanovici* some variability within a stage is restricted to spinules, spinule rows, the length of setae and body size in general. Variability of ornamentation is not only restricted merely to different individuals but may be different for the two sides of the body. Generally it can be said that spinules of a spinule-row are smaller when supernumary. Teratogenic malformations have not been observed during the present study.

Key to naupliar stages of *Nitocra karanovici*

1. Almost circular in shape; first maxilla not indicated..... NI
– Not so; 1st maxilla visible with at least 1 seta 2
2. One caudal seta on each side..... NII
– More than 1 caudal seta on each side . 3

3. Two caudal setae ..... NIII
4. Four caudal setae on each side, first maxilla present as lobe with 4 setae, no indication of leg 1 ..... NIV
5. Leg 1 indicated as an abdominal fold; 5 caudal setae on each side . NV

– Legs 1 and 2 indicated as abdominal lobes with acutiform tips ..... NVI

Discussion

Comparative development of body form and appendages during the naupliar phase of *Nitocra karanovici*.—The body is oval in most representatives of Oligoarthra, at least in the later stages—so in *N. karanovici*. It is elongate in genera leading a pelagic life such as *Microsetella norvegica* (cf. Björnberg 1972) or *Macrosetella gracilis* (Krishnaswamy 1951) and in species living in the interstitial of sands such as *Paraleptastacus brevicaudatus* (Dahms 1990b). The foreshortened shape is restricted to Thalestridimorpha (Diosaccidae and Thalestridae). The nauplius shield covers the whole body at NI, but the hind-body protrudes in the later harpacticoid stages.

Once acquired (at NI or NII stage) the labrum does not usually change its ornamentation pattern during the naupliar phase in oligoarthran nauplii, such as in *N. karanovici*. The caudal edge may have a nose-like apex like in *N. karanovici*, so also in *Halectinosoma gothiceps* (Dahms 1990a), *Nitocra spinipes* (Dahms 1990a), or *Bryocamptus pygmaeus* (Dahms 1990a). The medial acutiform outgrowth of the labrum of *N. karanovici* is thus shared with other Ameiridae, Canthocamptidae, and Cylindropsyllidae.

A medial pair of bare bean-shaped lobules on the ventral body wall at naupliar stage NIII of *N. karanovici* is shared with other Ameiridae, Cylindropsyllidae, Parastenocarididae with the canthocamptid *Mesochra lilljeborgi*.

Number of antennular segments never exceeds 3 in Oligoarthra and all segments are cylindrical throughout the phase. Normal segment number is 3, but in Exanechentera (Tisbidimorpha) and in Podogennonta (Thalestridimorpha, Metidae, see Dahms 1990a) it is reduced. Peltidiidae bear 2-segmented and Tegastidae l-segmented antennules (Ivanenko et al. 2008). Within Thalestridae both 1- and 3-segmented antennules are common, whereas in Miracidae they are 1-segmented and in Metidae 2-segmented. A common type of 3-segmented oligoarthran antennule is also present in *N. karanovici* and is widespread within most of the families and consists of an unarmed short first segment sometimes furnished with a row of spinules on the frontal edge as in *Phyllognathopus viguieri* (Dahms 1990a). Segment 2 always bears 3 setae in oligoarthran nauplii—so also in *N. karanovici*.

The naupliar antennal exopodite of Oligoarthra is almost 1–4-segmented (in *Pseudotachidius* sp. it is 5-segmented, Dahms 1990a). The exopodite exhibits a trend of segment fusion within different groups of Exanechentera and Podogennonta. In Exanechentera the exopodite is 4-segmented, except in some species of *Scutellidium* (Clogston 1965, Dahms 1993) and Porcellidiidae (Bocquet 1948) where it is 3-segmented and in Tegastidae (Ivanenko et al. 2008) and Peltidiidae (Dahms 1990a) where it is reduced to an unsegmented lobe. In Harpacticidae the trend of segment reduction is indicated by a 3-segmented exopodite in *Harpacticus uniremis* (Dahms 1990a), whereas it is still 4-segmented in *Zaus spinatus* (Dahms 1990a). Segment number in Podogennonta never exceeds 3. In Miraciidae (except *Stenhelia* (*D.*) *palustris*, see Dahms & Bresciani 1993, Dahms & Hicks 1996) and Thalestridae (except *Idomene* sp.; and *Pseudotachidius* sp., Dahms 1990a) there are 2-segmented exopodites. In Metidae (Nicholls 1941) and in *Macrosetella gracilis* it is reduced to a simple seta. In Laophontidae

(Dahms 1991) and Cletodidae (Chullasorn et al. 2012) it is 1-segmented. Ameiridae and Canthocamptidae bear a 3-segmented exopodite whereas it is 2-segmented in Cylindropsyllidae (Dahms 1990a).

Naupliar peculiarities of the Ameiridae

The naupliar development of *Nitocra spinipes* was studied both by Griga (1960) and by Abraham & Gopalan (1975). Both descriptions are less detailed than would be necessary for comparative purposes. That the antennule is 4-segmented as reported by Abraham & Gopalan for NVI and the appearance of leg 1 (at NIV) before that of the maxillule (at NV) is doubted here.

A particular naupliar character was found in common for Ameiridimorpha, except Ameiridae, which is not known among other Harpacticoida. This is a pair of bean-shaped, bare medial cuticular areas of the ventral body wall present in Parastenocarididae (Schminke 1982), Cylindropsyllidae (Dahms 1990a) and as in *Canthocamptus*, *Attheyella*, *Moraria* (Sarvala 1977), and *Mesochra* of the Canthocamptidae.

In the Ameiridae the antennal coxa generally bears an inwardly curved masticatory process, a medial spinulose seta and a small proximal seta. The basis is armed with 2 distal spinulose setae and 1 small and plane proximal seta. The endopodite bears 1 long and 2 small setae midlength and 1 plane claw-like seta terminally with 1 setule at its outer base. The 3-segmented exopodite bears 1 small and plane seta subdistally on its elongate first segment and 1 spinulose seta on the distal edge of the second segment. Segment 3 of the exopodite is almost twice as long as segment 2 and peculiar in bearing a branched seta in the proximal third; one of the branches being remarkably long. This bifurcate seta probably is an apomorphy for the Ameiridae and is present on the antennal exopodite of *Ameiropsis* cf. *nobilis* but in no other harpacticoid nauplius. Borderline of mandibular coxa not distinct but its spinulose and proximally curved seta situated caudally of the labral edge. Endopodite armed with 3 claw-like setae on inner process proximalmost homologous to the anterior seta of other harpacticoids and 1 tiny seta at posterior base of the terminalmost seta. Outer lateral field with 6 setae, 2 of them being long and geniculate. Exopodite 2-segmented bearing 1 short spinulose seta proximally and 1 longer spinulose seta distally on segment, 1 long spinulose seta terminally on short distal segment, and 2 smaller, separate setae on outer face midlength.

At NIV and NV the maxillule is present as a lobe with 2 spinulose setae. At NVI it becomes bilobed bearing 2 plane inner setae and 2 spinulose outer setae. A field of tiny spinules frontomedially to the maxillule may represent the maxilla at NV. At NVI at least this should be represented by a protuberance medially to the maxillule. The maxilliped is probably represented at NV as a protuberance caudally of the maxillule. Anlagen of legs 1 and 2 are present at NVI as lateral lobes bearing 4 and 3 elements, respectively.

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