

NAUPLII OF *TEGASTES FALCATUS* (NORMAN, 1869) (HARPACTICOIDA, TEGASTIDAE),
A COPEPOD WITH AN UNUSUAL NAUPLIAR MOUTH AND MANDIBLE

Viatcheslav N. Ivanenko, Frank D. Ferrari, and Hans-Uwe Dahms

(VNI) Department of Invertebrate Zoology, Biology Faculty, Moscow State University, MOSCOW 119 899, Russia;
(FDF) IZ/MSC; MRC-534, National Museum of Natural History, Smithsonian Institution, 4210 Silver Hill Road,
Suitland, Maryland 20746, U.S.A. [correspondence, ferrarif@si.edu];
(H-UD) National Taiwan Ocean University, Institute of Marine Biology, 2 Pei-Ning Road, KEELUNG, Taiwan, 202

A B S T R A C T

There are six stages in the naupliar phase of development of *Tegastes falcatus* (Norman, 1869). The labrum is expressed as a simple fold which does not cover the mouth. A poorly-sclerotized mouth tube was observed on some specimens of all stages except NI (= naupliar stage 1); NI and NII are the only stages without an anus and presumably do not feed. The antennal endopod is a subchela against itself at NII; its distal endopodal segment becomes bifurcate at NIII. A chela on the naupliar mandible consists of the endopod opposite a distoventral attenuation of the basis on NII-NVI. The segmental elements of a chela are present at NI, although the endopod does not oppose the basis at this stage. The maxillule is a unilobe bud with one seta at NIII that gains a second seta at NV and is transformed into a simple bilobe bud with three setae at NVI. The maxilla and maxilliped are each an asetose, ventral attenuation at NVI. Naupliar stages, found in large numbers along with all six copepodid stages of *T. falcatus*, apparently feed on suctorian ciliates growing on colonies of the bryozoan *Flustra foliacea* (Linnaeus, 1758). This is the first description of six naupliar stages for a species of Tegastidae Sars, 1904.

KEY WORDS: Copepoda, development, Harpacticoida, *Tegastes falcatus*

INTRODUCTION

The harpacticoid genus *Tegastes* Norman, 1903 presently includes 43 nominal species of small, laterally compressed copepods usually found in shallow marine waters (Bodin, 1997; Ivanenko and Defaye, 2004). Species of *Tegastes* often are associated with algae, bryozoans and cnidarians (Humes, 1981a, b; Humes, 1984; Bartsch, 1999). Naupliar stages have not been reported for any species of *Tegastes* although naupliar stage I (= NI) of *Parategastes sphaericus* (Claus, 1863) has been described and compared to NI of the peltidiid *Alteutha oblonga* (Goodsir, 1845) (see Dahms, 1990). Here we describe six naupliar stages of *Tegastes falcatus* (Norman, 1869), a species previously reported from the White Sea (Chislenko, 1967) and now found there attached to an unidentified suctorian ciliate living on colonies of the bryozoan *Flustra foliacea* (Linnaeus, 1758).

MATERIALS AND METHODS

Colonies of the bryozoan *Flustra foliacea* were collected underwater by SCUBA divers from boulders at depths of 18–20 m off the Karelian coast of the Gulf of Kandalaksha, White Sea, near the Marine Station of Moscow State University, 66°33'21N, 33°06'04E. *F. foliacea* also occurs in the North Sea, Barents Sea and other shallow waters of the Arctic Ocean. Its colonies consist of flat, branching fronds reaching up to 10 cm; these were placed in plastic bags at depth. At the surface, live colonies were kept in a refrigerator and observed under dissecting microscope on the day of collection. Ethanol was added to each bag (about 15% by volume). After 30 min the fluid plus bryozoan was shaken and the fluid filtered through a 20 micron mesh net. Thousands of specimens of naupliar and copepodid stages of the harpacticoid copepod *T. falcatus* were isolated from the washings. Adult females of this harpacticoid copepod are identified by a lancet-like terminal seta on the caudal ramus; this was the only species of *Tegastes* found in the samples. In the laboratory, nauplii were cleared and dissected in lactic acid and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% freshwater (Ferrari, 1995). For line drawings made with a camera lucida, specimens were examined in glycerin with

bright-field or differential interference optics. For electron micrographs, specimens were dried out of ethanol in a critical point dryer, mounted, sputter coated with 10–15 nm gold/palladium alloy and imaged with a scanning electron microscope with emitter. In general, descriptive terms and abbreviations follow Ferrari and Dahms (2007). Specimens of the six naupliar stages of *Tegastes falcatus* are deposited under USNM 1102497 in the Smithsonian Institution's National Museum of Natural History, Washington D.C.; specimens also have been retained by the senior author (VNI).

RESULTS

Naupliar stages of *Tegastes falcatus* (Norman, 1869)
Figures 1–9

NVI (Fig. 1A, E).—Body length 0.147–0.158 mm, width 0.122–0.125 mm (4 specimens); arthroal membrane between adjacent somites absent; labrum a simple fold which does not cover the mouth; tube-like extension from mouth present in some specimens (Fig. 3A, D); anus present.

Antennule (Fig. 1D): 1 articulating segment with 5 terminal and 6 ventral setae; a seta on body adjacent to articulating segment.

Antenna (Fig. 2A, B): coxa with medial, naupliar arthritis articulating proximally, anteriorly and posteriorly, but not distally; basis with 1 proximoventral seta, 2 distoventral setae and 5 setae on a complex dorsal lobe. Endopod a subchela against itself; proximal endopodal segment with 2 groups of 2 proximoventral setae, 1 distoventral seta and 1 distodorsal seta; distal endopodal segment bi-attenuate, ventral prong smaller.

Mandible (Figs. 2C, D, 3B): coxa with 1 ventral seta; basis with 1 dorsal lobe with 2 setae, distoventrally drawn out into a complex structure (fixed finger of chela) with 2 setae and 2 large attenuations, 1 small attenuation with tiny points and 1 poorly-sclerotized small attenuation with a few

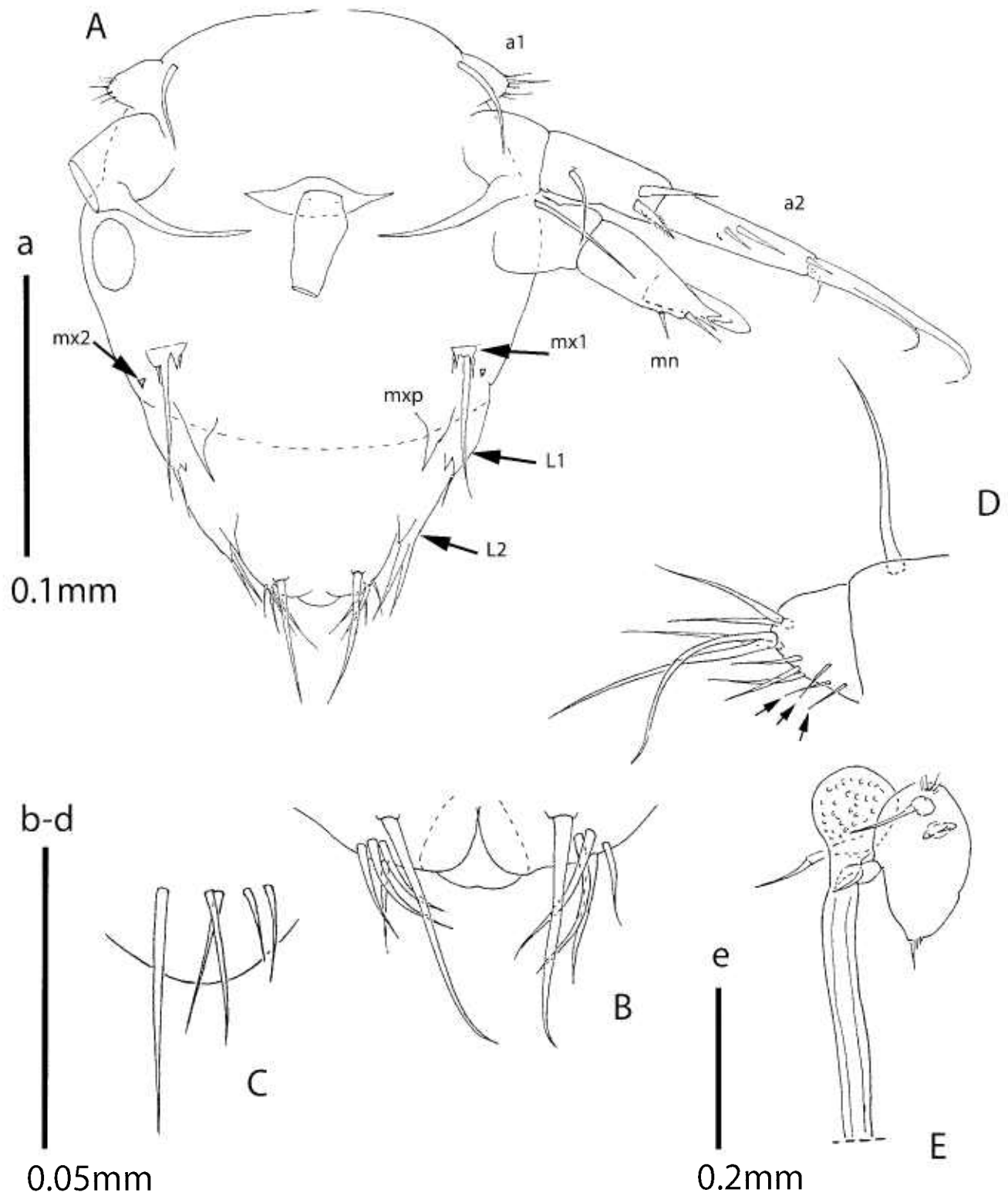


Fig. 1. *Tegastes falcatus*. Nauplius VI. A, habitus, ventral, left arrow to attenuation representing maxilla; B, caudal rami, ventral; C, right caudal ramus, lateral; D, antennule, arrows to setae assumed to be added from Nauplius V; E, nauplius, left lateral, holding suctorium with right mandible and striking with left antenna. Abbreviations: A1-antennule, A2-antenna, Mn-mandible, Mx1-bud of maxillule, Mx2-bud of maxilla, Mxp-bud of maxilliped, L1-bud of Leg 1, L2-bud of Leg 2.



Fig. 2. *Tegastes falcatus*. Nauplius VI. A, antenna, arrow to seta added from Nauplius V; B, setae of presumptive exopod of antenna; C, right mandible, anterior, with two muscles to proximal rim of proximal endopodal segment; D, right mandible, medial; E, right maxillule, arrow to seta added from Nauplius V; F, bud of right maxilliped; G, bud of right Leg 1; H, bud of right Leg 2.

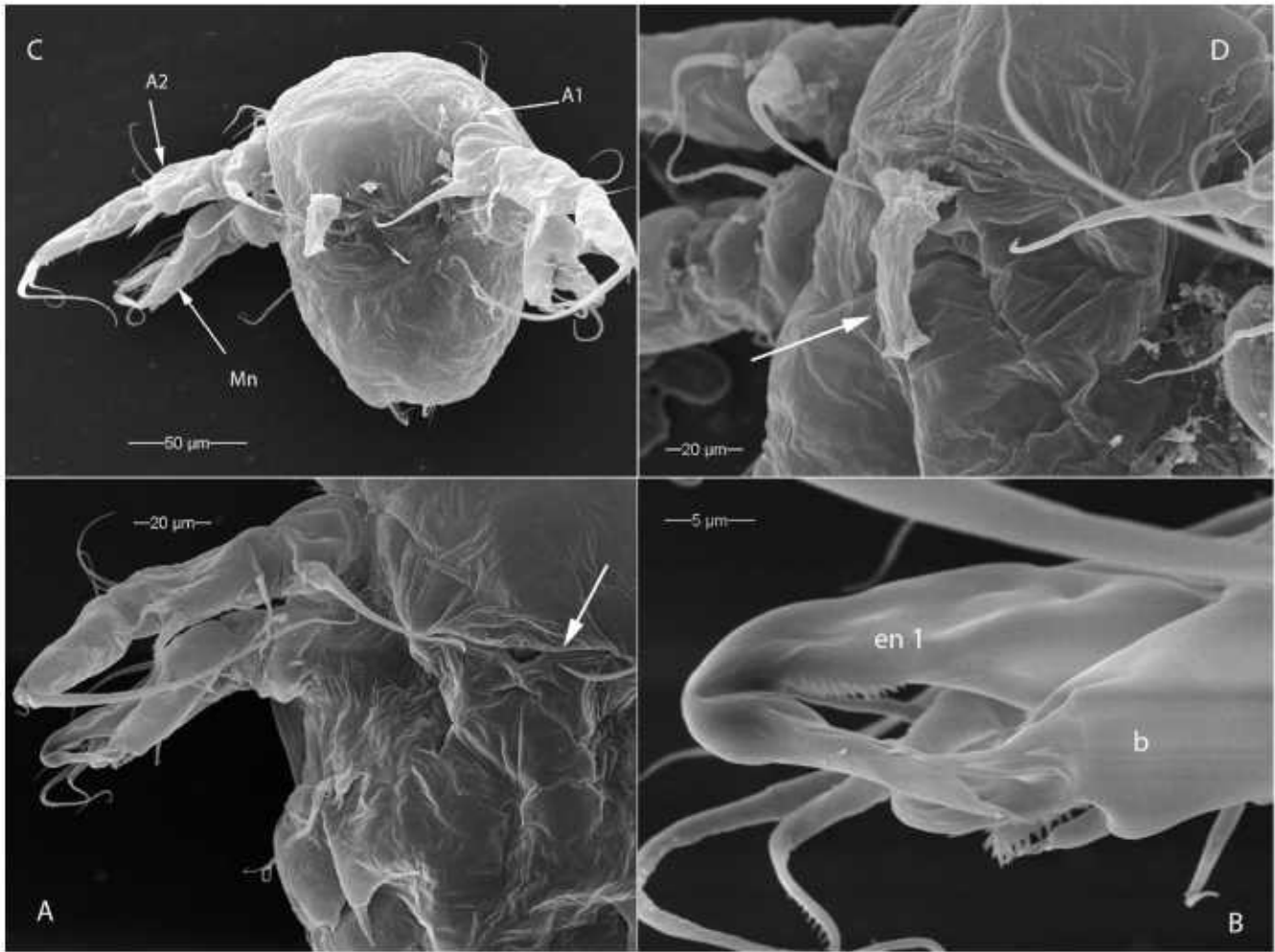


Fig. 3. *Tegastes falcatus*. A, Nauplius VI, ventral; arrow to fold representing labrum; B, left mandible, medial, showing relation of tip of proximal endopodal segment to distoventral attenuation of basis; C, Nauplius IV, ventrolateral; D, mouth area of Nauplius VI, ventral, arrow to poorly-sclerotized mouth tube. Abbreviations: A1-antennule, A2-antenna, Mn-mandible, en1-proximal endopodal segment, b - basis.

points. Proximal endopodal segment (moveable finger of chela) with 1 seta and attenuate distally, distal half of attenuation perpendicular to proximal half, tip of attenuation opposes distoventral complex structure of basis; distal endopodal segment with 1 ventral and 3 terminal setae.

Maxillule (Fig. 2E): bilobe bud with 2 setae on dorsal lobe (presumptive exopod); ventral lobe (presumptive endopod) with dorsal attenuation and 1 ventral seta.

Maxilla (Fig. 1A): small attenuation of ventral body exoskeleton.

Maxilliped (Fig. 2F): thick attenuation of ventral body exoskeleton.

Leg 1 (Fig. 2G): bilobe bud with 2 setae on dorsal lobe (presumptive exopod); 3 attenuations on ventral lobe (presumptive endopod).

Leg 2 (Fig. 2H): bilobe bud with 2 setae and 1 attenuation on dorsal lobe (presumptive exopod); 2 setae on ventral lobe (presumptive endopod).

Caudal Ramus (Fig. 1B, C): unilobe bud with 5 setae.

NV (Fig. 4A).—Differs from NVI as follows:

Body length 0.125-0.148 mm, width 0.111-0.120 mm (4 specimens).

Antennule (Fig. 4C): unarticulated with 1 basal and 3 ventral setae.

Antenna (Fig. 4D, E): Proximal endopodal segment with 1 seta in proximal group.

Maxillule (Fig. 4F): unilobe bud with 2 setae.

Maxilla, Maxilliped, Leg 1, and Leg 2 absent.

Caudal Ramus (Fig. 4B): unilobe bud with 4 setae.

NIV (Figs. 3C, 5A).—Differs from NV as follows:

Body length 0.103-0.109 mm, width 0.103-0.107 mm (2 specimens).

Antennule (Fig. 5C): without ventral setae on articulating segment, and 1 terminal seta bifurcate.

Antenna (Fig. 5D, E): basis not as elongate; complex dorsal lobe with 4 setae. Proximal endopodal segment without distoventral seta.

Maxillule (Fig. 5A): unilobe bud with 1 seta.

Caudal Ramus (Fig. 5B): unilobe bud with 3 setae.

NIII (Fig. 6A).—Differs from NIV as follows:

Body length 0.103-0.107 mm, width 0.092 mm (2 specimens).

Antennule (Fig. 6B): 3 terminal setae, 1 bifurcate.

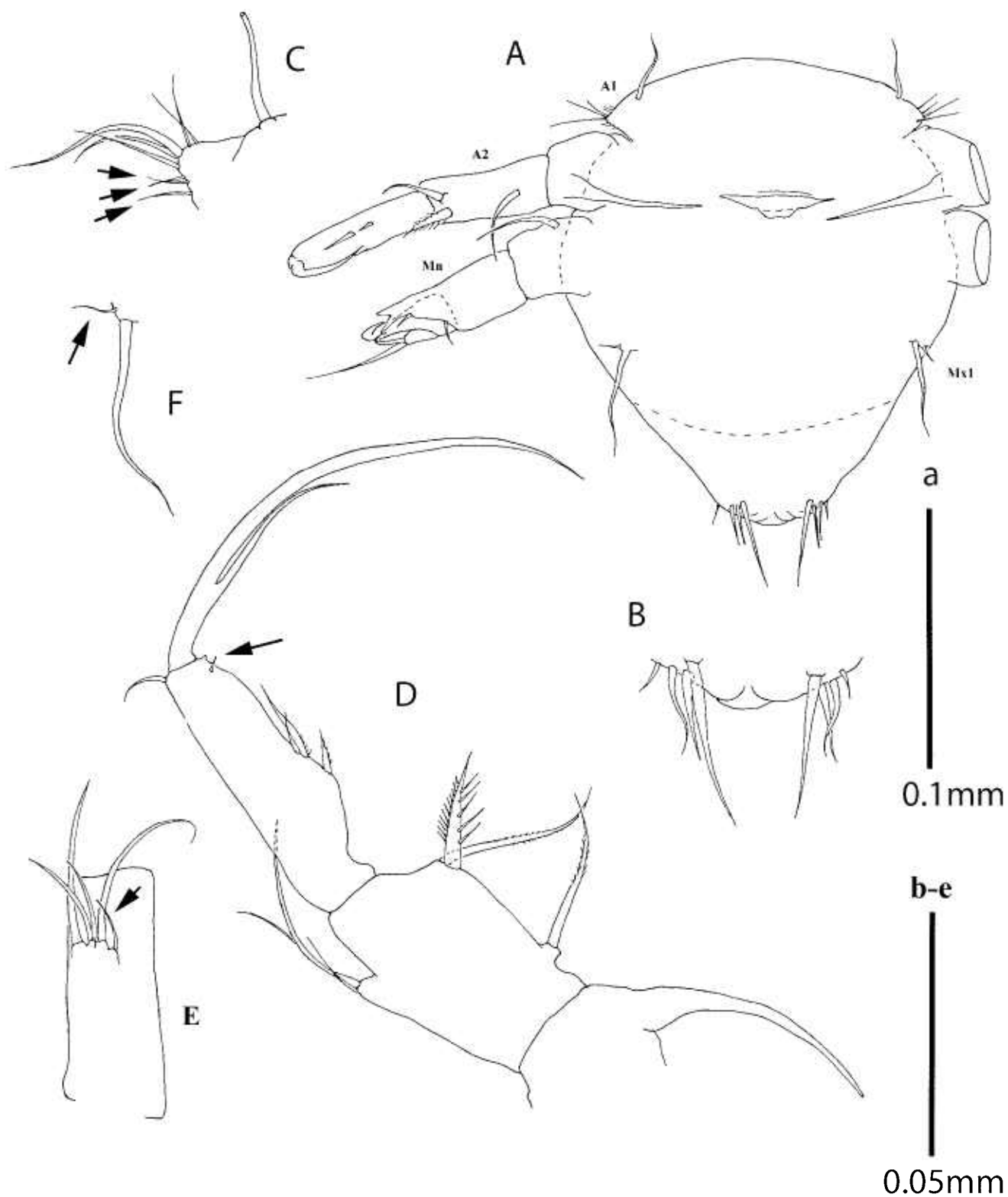


Fig. 4. *Tegastes falcatus*. Nauplius V. A, habitus, ventral; B, caudal rami, ventral; C, antennule, arrows to setae added from Nauplius IV; D, antenna, arrow to seta added from Nauplius IV; E, presumptive exopod of antenna, arrow to seta added from Nauplius IV; F, right maxillule, arrow to seta added from Nauplius IV.

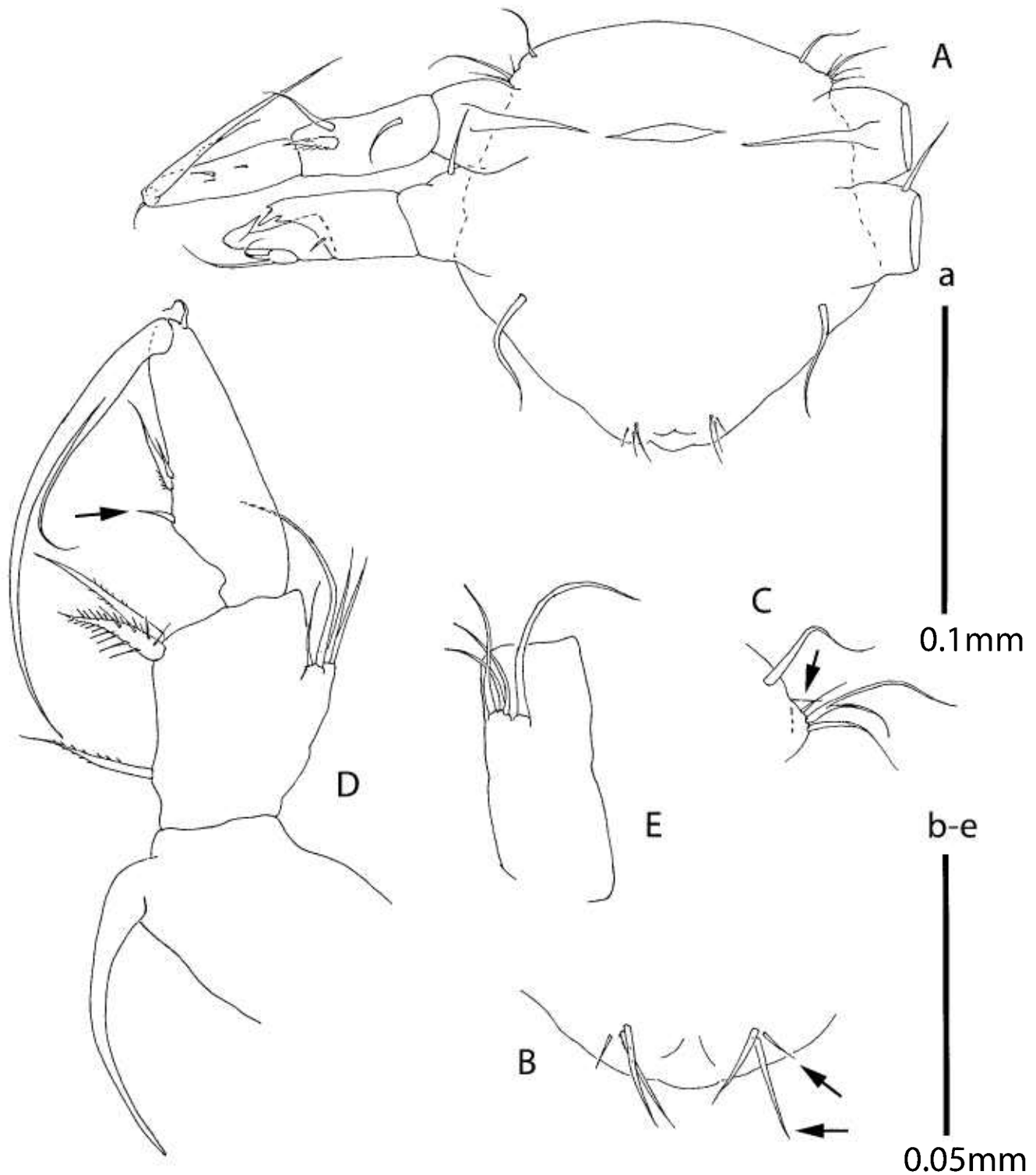


Fig. 5. *Tegastes falcatus*. Nauplius IV. A, habitus, ventral; B, caudal rami ventral, arrows to setae added from Nauplius III; C, antennule, arrow to seta added from Nauplius III; D, antenna, arrow to seta added from Nauplius III; E, presumptive exopod of antenna.

Antenna (Fig. 6C, D): proximal group of setae absent on proximal endopodal segment.

Caudal Ramus (Fig. 6A): unilobe bud with 1 seta.

NII (Fig. 7C, D).—Differs from NIII as follows:

Body length 0.082 mm, width 0.070 mm (1 specimen); anus absent.

Antennule (Fig. 7B): 2 terminal setae, 1 bifurcate.

Antenna (Fig. 7C, D): dorsal lobe of basis with 3 setae. Distal endopodal segment with 1 attenuation.

Mandible (Fig. 7E-G): complex structure of basis without small attenuation and poorly-sclerotized attenuation.

NI (Fig. 8A).—Differs from NII as follows:

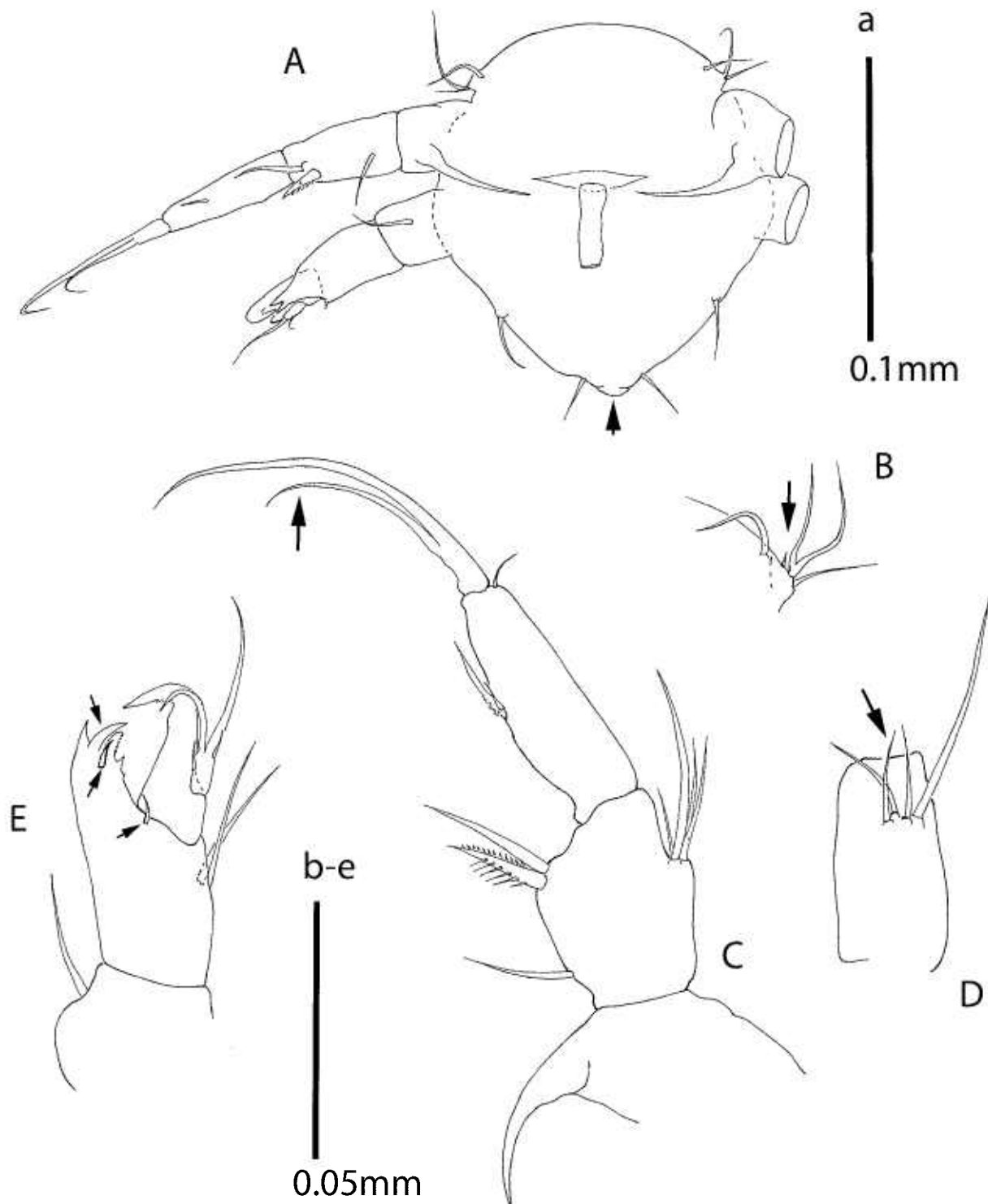


Fig. 6. *Tegastes falcatus*. Nauplius III. A, habitus, ventral, arrow to anus; B, antennule, arrow to setae added from Nauplius II; C, antenna, arrow to endopodal segment changed from Nauplius II; D, presumptive exopod of antenna, arrow to seta added from Nauplius II; E, mandible, arrows to structure and setae added from Nauplius II.

Body length 0.070 mm, width 0.0640 mm (1 specimen).

Antennule (Fig. 8A): 3 terminal setae.

Antenna (Fig. 8B, C): shaft of naupliar arthrite on coxa uneven, not smoothly tapering. Proximal endopodal segment with 1 ventral seta.

Mandible (Fig. 8D-F): complex structure of basis without setae. Proximal endopodal segment without setae; distal endopodal segment with 2 terminal setae. Endopod not directly opposing attenuation of basis.

Maxillule absent.

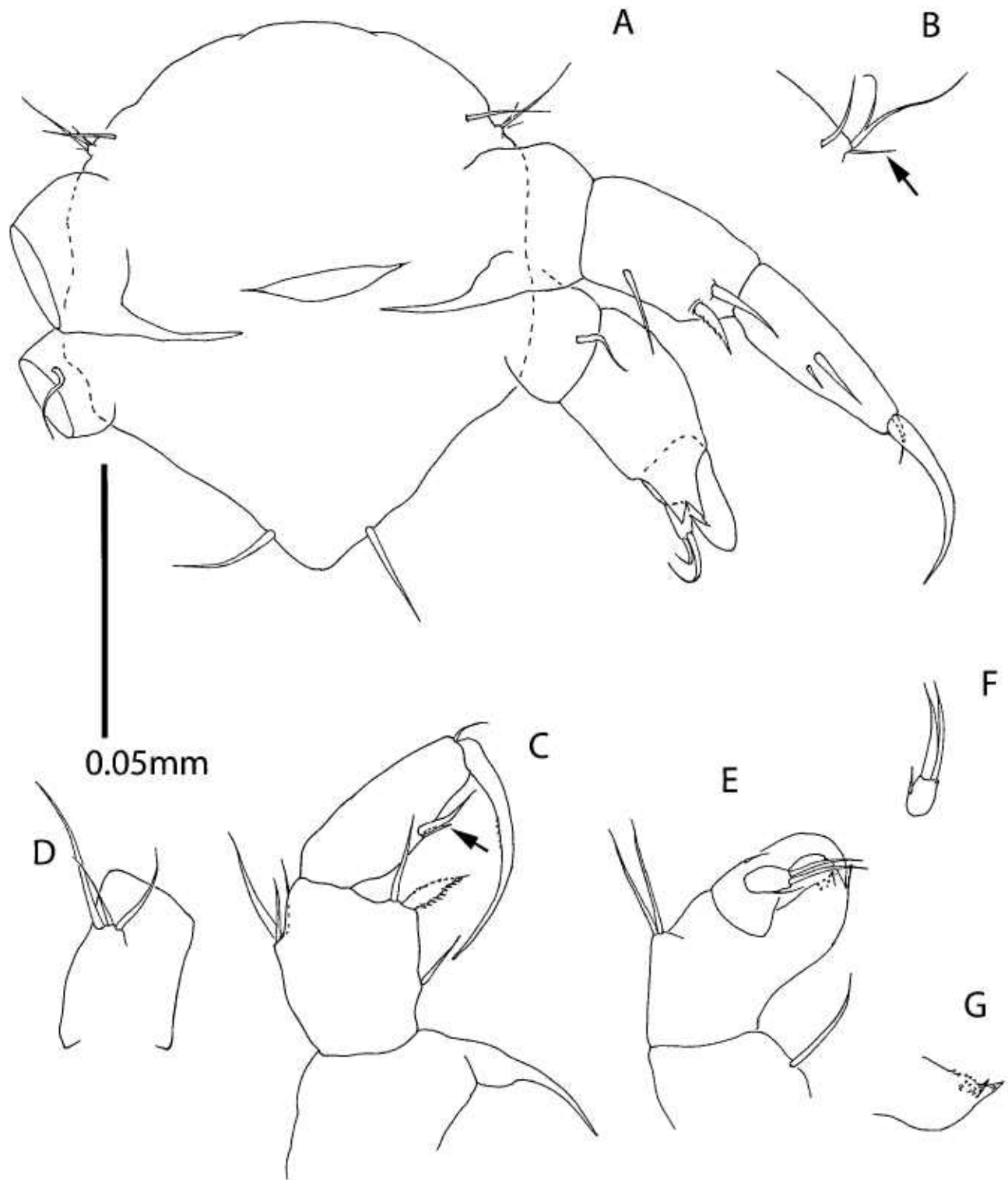


Fig. 7. *Tegastes falcatus*. Nauplius II. A, habitus, ventral; B, antennule, arrow to seta added from Nauplius I; C, antenna, arrow to seta added from Nauplius I; D, presumptive exopod of antenna; E, mandible; F, second endopodal segment of antenna; G, attenuation of mandibular basis.

DISCUSSION

The nauplii are unusual in general appearance and in the morphology of their appendages compared to other harpacticoid and copepod nauplii. Their shape is circular

but their outreaching antennae and mandibles present a foreshortened appearance. Labrum and ventral body wall are unfurnished. They appear unable to swim or creep efficiently over surfaces. A poorly-sclerotized mouth tube

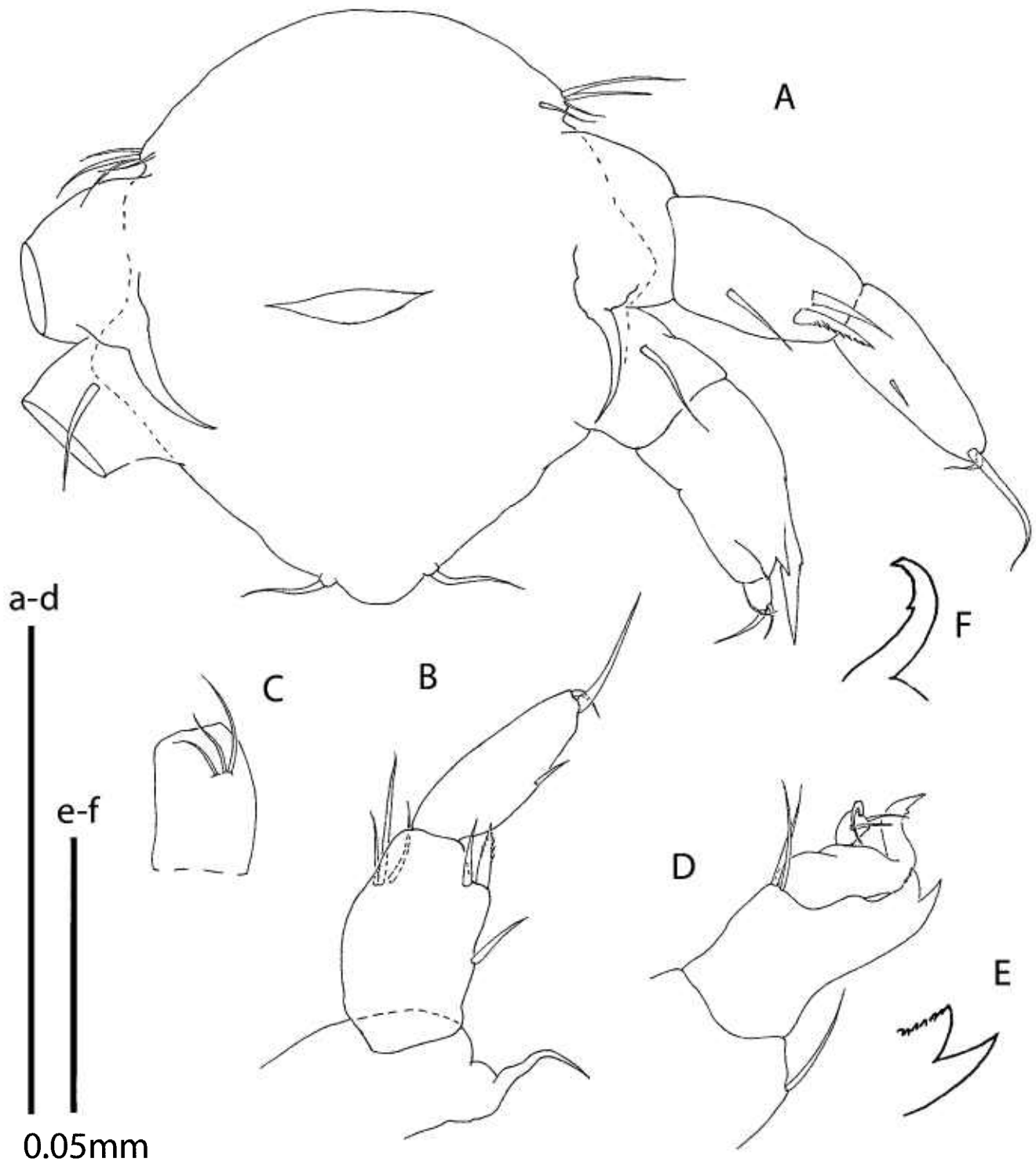


Fig. 8. *Tegastes falcatus*. Nauplius I. A, habitus, ventral; B, antenna; C, presumptive exopod of antenna; D, mandible; E, attenuation of mandibular basis; F, attenuation of proximal endopodal segment of mandible.

has not been reported for nauplii of any other copepod. This structure was not observed on all specimens of NII-NVI, and it is not clear whether it has been withdrawn into the mouth of some specimens or, alternately, whether this presence-absence represents a dimorphism. A mouth tube was not observed on the few specimens available for study

of NI. NI and NII of *T. falcatus* lack an anus, the shaft of naupliar arthrite is not smoothly tapering and the mandibular chela is not well-formed. NI apparently does not feed and this may explain the absence of a mouth tube for this stage. The mouth tube may be a part of the naupliar foregut which can be extruded or withdrawn.

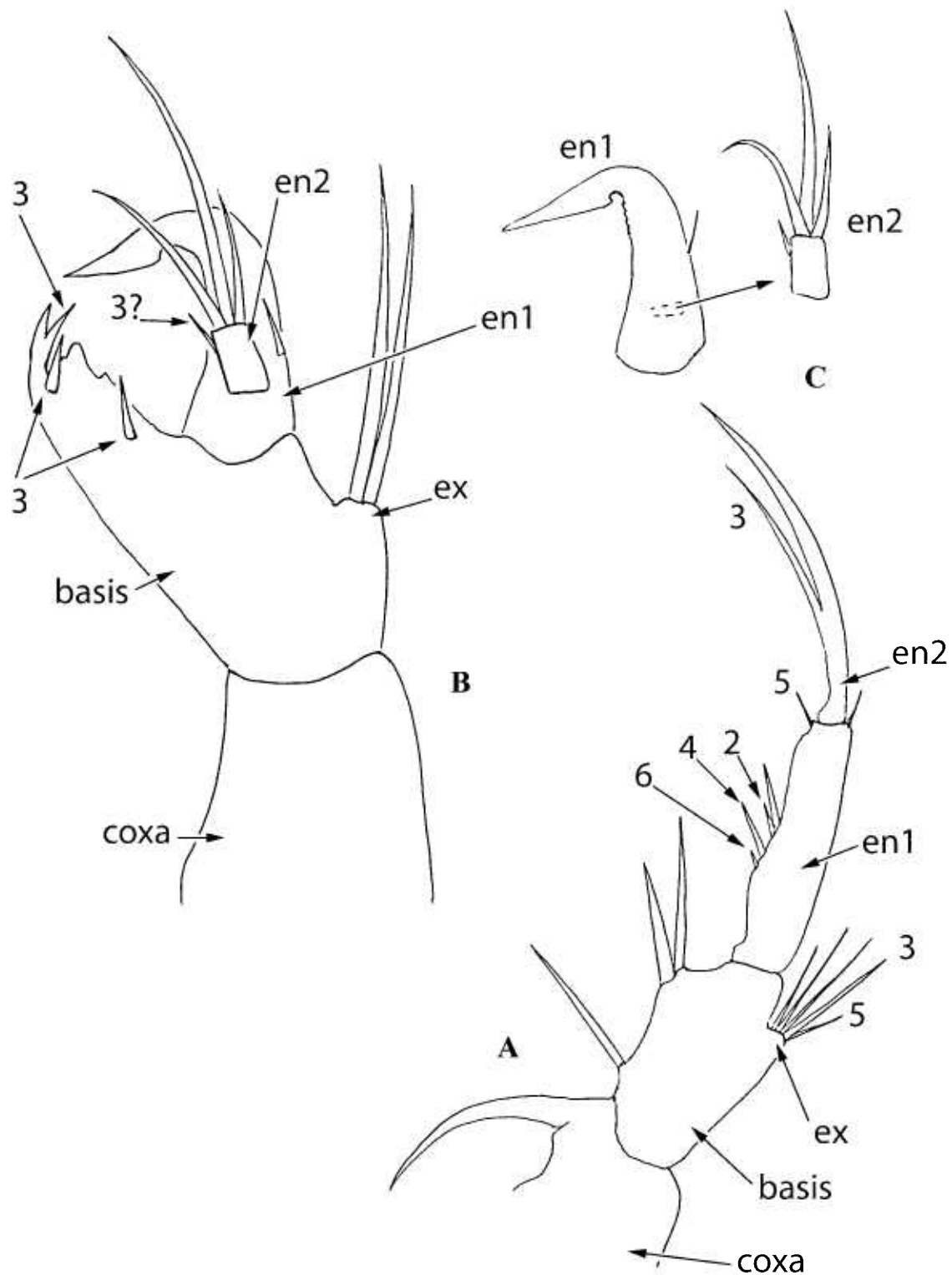


Fig. 9. *Tegastes falcatus*. Nauplius VI. A, generalization of segmental homologies of antenna; B, generalization of segmental homologies of mandible. Arrows to setae assumed to be added at the numbered stage. Abbreviations: en1-proximal endopodal segment, en2-distal endopodal segment, ex-presumptive exopod.

Chelae are not known for copepod naupliar limbs. A chela-like configuration can be observed on the mandible of NI of the tegastid *Parategastes sphaericus* and of the peltidiid *Alteutha oblonga* (see Dahms, 1990) although

segmental homologies for these species were not elucidated (Dahms, 1993). The mandibular chela on nauplii of *T. falcatus*, formed from endopodal segments, may be a synapomorphy for species within this lineage of families.

Chelae, in general, are not well-represented on the limbs of copepods. A chela may be present on the leg 5 of some adult male calanoid copepods, particularly the centropagoideans (Ferrari and Ueda, 2005), but this kind of chela is not formed with segments of the endopod; rather segments of the exopod are involved. Chela-like structures also are known on the geniculate antenna 1 of some adult males of *Pontella* and *Labidocera* that are genera within the centropagoidean family Pontellidae, but these structures result from the opposition of a distal endopodal segment on a seta of a proximal endopodal segment (unpublished observations of FDF).

The naupliar labrum of *T. falcatus* may be reduced to a simple, thin fold of tissue which does not cover the mouth, an unusual morphology for copepod nauplii (Dahms, 2004). Alternately, the tissue fold may not be homologous to the labrum which may fail to develop during the naupliar phase. A labrum is present during the copepodid phase of development (personal observations of authors). The naupliar antennule appears to consist of a single segment, although a seta on body adjacent to the articulating segment may be the seta of a proximal segment which does not articulate with its somite. This configuration is unique to copepod nauplii.

An arthroal membrane separates the naupliar arthrite only proximally, anteriorly and posteriorly, from the coxa of the antenna. However, muscles attached to the base of this structure are retained, supporting the suggestion (Ferrari and Dahms, 2007) that it is not a seta. Bifurcation of the terminal endopodal segment of the antenna during the molt to the third naupliar stage is unusual for copepod nauplii. During the naupliar phase, 3-5 setae dorsal to the endopod of the antenna are assumed to be setae of the exopod (Fig. 9A). The distoventral attenuation of the mandibular basis, which forms the palm of the chela, becomes more complex in shape as setae are added during naupliar development. Two setae dorsal to the endopod of the naupliar mandible are assumed to be exopodal (Fig. 9B). During the naupliar phase of development, the maxillule remains a unilobe or simple bilobe bud with no more than three setae. The maxilla and the maxilliped are present as non-articulating extensions of their respective somite; neither is armed with setae.

A comparison of nauplii belonging to Tegastidae and Peltidiidae revealed a remarkable number of specialized features common to both families (Dahms, 1990) which might represent synapomorphies for a lineage of these two families: antennule 1-segmented in tegastids and 2-segmented in peltidiids; disproportionate enlargement of coxa and basis of antenna; reduced exopods of antenna and mandible; mandibular endopod with strong hook-like structures. Although Tegastidae and Peltidiidae swim well as copepodids; they are clumsy in this locomotory pattern as nauplii.

Living nauplii of *T. falcatus* were observed in the laboratory during the first hours after sampling of colonies of the bryozoan *Flustra foliacea*. The living nauplii were attached to the shaft of an unidentified suctorian protistan

(Ciliophora) covering the surface of the bryozoan in a dense layer. The cell body of the ciliate and the naupliar body are comparable in size. The distal part of the attachment stalk of the suctorian ciliate is held by a nauplius with its mandibular chela (see Fig. 1E); the pointed distal segment of antenna 2 was observed to poke at the spherical cell body of the suctorian ciliate. Many copepods are known to directly parasitize invertebrates (Ho, 2001), and a habit of clasping larger invertebrates was inferred for nauplii of tegastids and peltidiids (Dahms, 1990). However, *T. falcatus* is the only crustacean reported as associated with a protistan during its naupliar phase of its development.

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