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Copepodid development of *Tegastes falcatus* (Norman, 1868) (Copepoda, Harpacticoida, Tegastidae) with a discussion of the male genital somite

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Abstract.—The lateral face of the cephalosome deepens progressively during the six stages of copepodid development of *Tegastes falcatus*. A simple aesthetasc on the second from the proximal segment of the antennule is transformed into a bifurcate aesthetasc during the molt to copepodid II. Copepodids II–VI bear eight setae on the caudal ramus, a number unique to copepods. Formation of the arthrodial membrane separating the middle segment and distal complex of the endopod of swimming legs 2–4 is delayed until CVI, one stage later than the exopod. Gender dimorphism initially is observed in antennular segmentation, setation of the maxilliped and rami present on leg 5 at copepodid IV. At copepodid V, males and females differ in antennular segmentation, rami present on leg 5 and the shape of leg 6. Gender dimorphism at copepodid VI also includes the shape of the cephalosome, of the genital triple-somite complex, and of one seta on the caudal ramus. The morphology of the ventral attenuation of the sixth and seventh thoracic somites, the anterior abdominal somite, and the degree of rotation of leg 6 are compared for males of *Tegastes falcatus*, *T. gemmeus*, *T. ctenidus*, *Parategastes conexus* and *Syngastes* sp. *Tegastes* is composed of species whose females and males have a genital triple-somite (sixth and seventh thoracic somites plus the anterior abdominal somite not separated by arthrodial membranes). Tegastidae are diagnosed as species with the rami of leg 1 unsegmented and basis elongate; male genital somite (seventh thoracic) extended ventrally; male leg 6 present only on one side; protopod of male leg 6 unarmed; female embryo sac with 3–4 embryos; female leg 5 with broad baseoendopod forming embryo sac chamber. Species of the lineage Tegastidae plus Peltidiidae have males with an asymmetrical leg 6 in addition to the rectangular distal basal endite of the maxillule noted by Seifried (2003). A stout ventral spine with hyaline membrane on the distal segment complex of the exopod of swimming leg 4 also may be a synapomorphy for this lineage.

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Species of *Tegastes* are small, laterally compressed harpacticoid copepods usually associated with algae and cnidarians (Humes 1981a, b); there are 43 nominal species in the genus. The last new species of the genus were described over two decades ago (Humes 1984), although a redescription is recent (Ferrari et al. 2007). Recent reports of a species of *Tegastes*, *T. acroporanus*, as the ''red bug pest'' on aquarium corals (e-mail: Eric Borneman to VNI) should increase interest in these peculiar harpacticoid copepods.

Tegastes falcatus is frequently encountered in nearshore, benthic habitats of the North Atlantic and Arctic oceans. This paper describes copepodid development of *T. falcatus* from the White Sea; these are the first set of complete observations and illustrations for copepodid development for any species of Tegastidae although Dahms (1993) provided abbreviated observations of the copepodid development of *T. clausii*. Development of the naupliar stages of *Tegastes falcatus* is presented in a separate paper (Ivanenko et al. 2008). The symmetry and asymmetry of the male genital somite, including leg 6, of *T. falcatus* are compared to four other species in two genera of Tegastidae, viz., *Tegastes gemmeus* Humes, 1984, *Tegastes cnidicus* Humes, 1981, *Syngastes* sp., and *Parategastes conexus* Humes, 1984, as well as from two species, *Alteutha oblonga* (Goodsir, 1845) and *Alteuthellopsis corallina* Humes, 1981, and from two genera of its presumed sister family Peltidiidae Sars, 1904. *Tegastes falcatus* is the fourth species of relatively rare copepods, including *Euryte longicauda*, *Dermatomyzon nigripes*, and *Asterocheres flustrae*, described as associated with the bryozoan *Flustra foliacea* (see Ivanenko & Smurov 1997, Ivanenko & Ferrari 2003, and Ferrari & Ivanenko 2005); with the exception of *Asterocheres flustrae*, all copepodid stages of these species also are described from this byrozoan.

Materials and Methods

Colonies of flat, branching fronds of the bryozoan *Flustra foliacea* (Linnaeus, 1758) on boulders at depths of 18–20 m off the Karelian coast of the Gulf of Kandalaksha, White Sea, in front of the Marine Station of Moscow State University (66°33′21″N, 33°06′04″E) were collected underwater and placed in plastic bags at depth by SCUBA divers. At the surface, live colonies were refrigerated and observed with a dissecting microscope on the day of collection. Later, 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 μm mesh net. No difference in copepod species was detected in the treatment with ethanol or fresh water. In each treatment, many specimens of naupliar and copepodid stages of *Tegastes falcatus* were isolated from the washings. In the laboratory, copepodids were cleared and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% fresh water (Ferrari 1995). For line drawings made with a camera lucida, whole or dissected specimens were examined in glycerin with bright-field or differential interference optics. For scanning electron micrographs (SEM), 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.

The somite complex consisting of the head somites, and first and second thoracic somites is the cephalosome. Somites are numbered according to their relative developmental age, following Hulsemann (1991). Thoracic and abdominal somites increase in developmental age anteriorly from the posterior abdominal (or anal) somite, which is the oldest and first to appear during development. The anterior abdominal somite is the

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second abdominal somite to appear. The first thoracic somite bears the maxilliped, and the genital openings are found on the seventh. In general, descriptive terms follow Ferrari (1995). Segments of the antennule cannot be easily separated from segment complexes, so the phrase "articulating part" is used here for both. Interpretations of segmentation of the maxillule, the maxilla, and the maxilliped follow Ferrari & Ivanenko (2008); the protopod of these three limbs has a coxa with one setiferous endite. Abbreviations are: CI–CVI, copepodid stages one through six (for copepods like *Tegastes falcatus*, CVI is the adult stage); Th, thoracic somite; Abd, abdominal somite. Ramal segments of swimming legs 1–4 (thoracopods 2–5) are proximal and middle; the distal part is a segment complex. The terms "seta" and "spine" are used for articulating cuticular elements connected by an arthrodial membrane to an appendage segment; setae appear less rigid than spines. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment. In order to maintain continuity among descriptive publications, tables of setae and spines on swimming legs 1–4 in the descriptive section generally follow the formula introduced by Lang (1934). Roman numerals indicate spines and Arabic numerals indicate setae. Numerals to the left of a comma or dash indicate dorsal elements; numerals between two commas indicate terminal elements, and numerals to the right of a comma or dash indicate ventral elements. A semicolon separates ramal segments, and an asterisk indicates that the segment is absent. Homologous segments and setae cannot be compared from these tables (see Ferrari & Ivanenko 2005) because setae on the proximal and middle segments of the rami of swimming legs initially appear proximally on the distal segment complex (see setal precedence in Ferrari & Dahms 2007).

Localities reflect our understanding of correct identifications of this species. Only authors who have contributed descriptions and/or illustrations are cited in the synonymy section. Specimens of the six copepodid stages of *Tegastes falcatus* are deposited under USNM 1104744 in the National Museum of Natural History (USNM), Smithsonian Institution; specimens also have been retained by the senior author (VNI).

Order Harpacticoida Sars, 1904
Family Tegastidae Sars, 1904
Genus *Tegastes* Norman, 1903
Tegastes falcatus (Norman, 1869)
Figs. 1–21

Amymone falcata Norman, 1869:256, 257, 296.
Amymone sphaerica: Brady, 1880:28, pl. XLIX, figs.1–11; 1903:4, 5, pl. I, fig. 13.
Tegastes falcata: Scott, 1905:801, fig. 11.
Tegastes falcatus: Sars, 1904:69, pl. XLI.—Lang, 1948:469, pl. 196, fig. 4.—Chislenko, 1967:122–124, fig. 33.—Huys et al., 1996:296, fig. 116e, f.
? *Tegastes falcatus*: Pesta, 1932:43, fig. 43; 1959:115, fig. 43.

Specimens.—CVI–CIV females, CVI–CIV males, CIII, CII, CI separated from the bryozoan *Flustra foliacea* Linnaeus.

CVI adult female.—Length (body plus caudal ramus) 0.43–0.49 mm, maximum dorsoventral width 0.29–0.36 mm (10 specimens); of 5 articulating sections. Cephalosome (Fig. 1A) including Th1&2 tapering to sharp point ventrally; Th3–5 articulate; small rounded projection from sternite of Th2; arthrodial membrane absent laterally and ventrally between Th6&7 and between Th7&abd2 forming a genital triple-somite complex; Th7 with 1 small and abd2 with 1 large hollow, ventral, hook-like attenuation. Abd3,4,1 small and articulating. Cephalosome, Th2–7 and abd2 with irregularly shaped depressions on surface of cuticle. Anal opening terminal between caudal rami on

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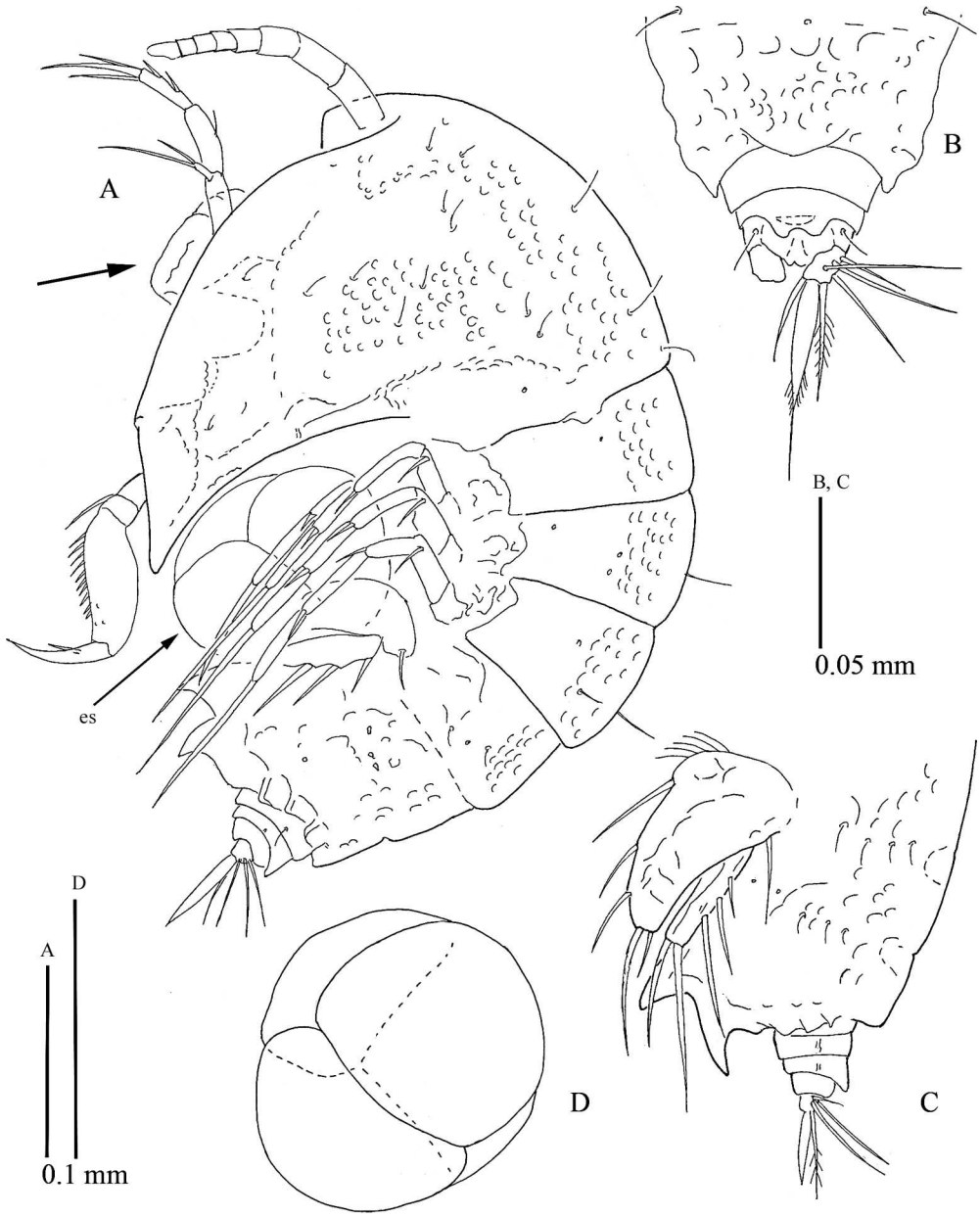


Fig. 1. *Tegastes falcatus* (Norman, 1903). Adult female. A, Habitus, lateral, arrow to labrum; *es*, embryo sac. B, Posterior part of genital triple-somite complex, 3 abdominal somites and caudal rami, dorsal (eighth seta not shown). C, Leg 5, genital triple-somite complex, 3 abdominal somites and caudal ramus, lateral (eighth seta not shown). D, Embryo sac including 4 embryos.

abd1; copulatory pore and oviducal openings not seen. Embryo sac, with 4 embryos, within embryo sac chamber (Fig. 1A, D) formed by baseoendopod of leg 5 and sternites of genital triple-somite complex.

Rostrum (Fig. 2A): simple, blunt extension of cuticle between A1s.

Labrum (Figs. 1A, 2B): sclerotized with platelets, elongate, narrower and bilobate anteriorly; major axis anteroposterior.

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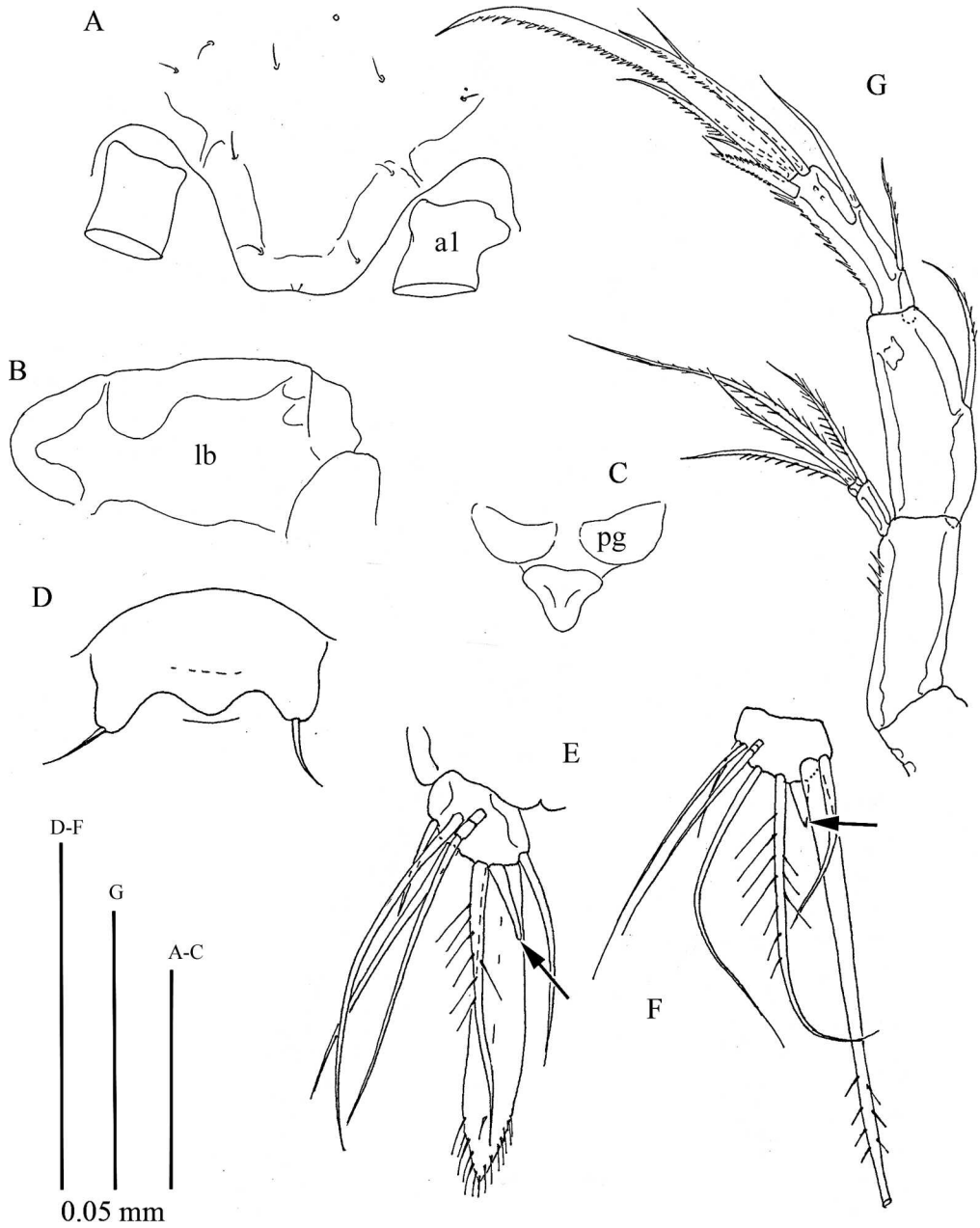


Fig. 2. *Tegastes falcatus* (Norman, 1903). Adult female. A, Rostral area, anterior. B, Labrum and paragnath, lateral. C, Paragnaths, ventral. D, Genital area and setae of leg 6. E, Caudal ramus, dorsal, arrow to eighth seta (distal tip of broad seta absent). F, Aberrant caudal ramus (broad seta replaced with narrow seta), dorsal, arrow to eighth seta. G, Antenna. Abbreviations.—a1, antennule; lb, labrum; pg, paragnath.

Paragnath (Fig. 2B, C): 2 lobes between a median lobe.

Antennule (Fig. 18A, D): 8 articulating parts; setation 1, 11, 10, 3 + bifurcate aesthetasc, 2, 4, 4, 6 + bifurcate aesthetasc.

Antenna (Fig. 2G): protopod 2-segmented, coxa unarmed, basis with dorsal

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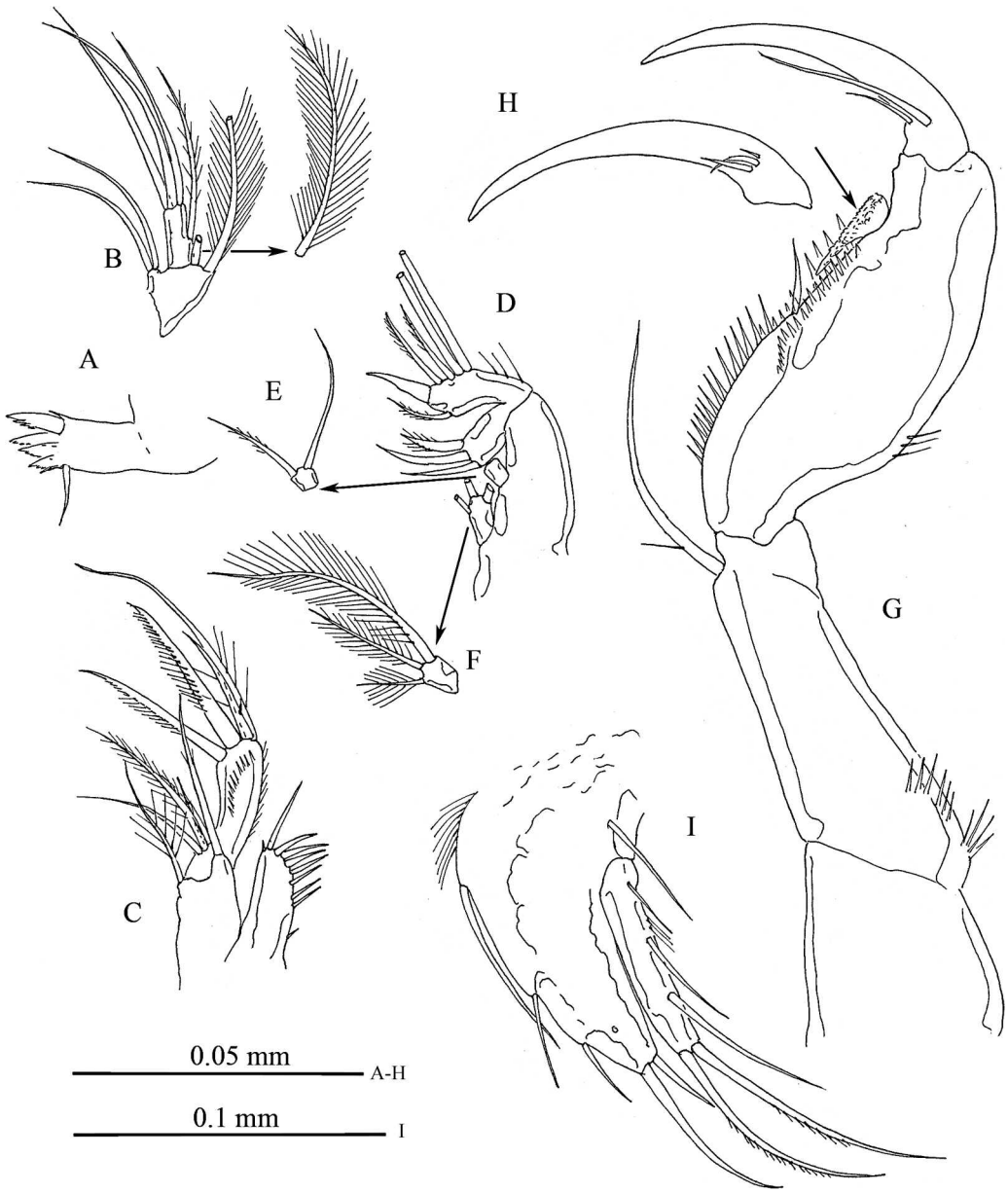


Fig. 3. *Tegastes falcatus* (Norman, 1903). Adult female. A, Mandibular gnathobase. B, Mandibular palp, one seta illustrated separately. C, Maxillule. D, Maxilla. E, Coxal endite of maxilla. F, Praecoxal endite of maxilla. G, Maxilliped, posterior, arrow to anvil-shaped seta. H, Claw of maxilliped, anterior. I, Left leg 5.

and ventral denticles. Exopod 2-segmented with 1 and 3 setae; endopod 2-segmented; proximal segment with 1 mid-ventral seta, distal segment with 1 dorsal, 5 terminal and 2 ventral setae.

Mandible (Fig. 3A, B): gnathobase with 3 tooth-like attenuations and 2 setae; basis with 2 ventral setae. Exopod of 2 dorsally inserting setae; endopod with 1 mid-ventral and 3 terminal setae.

Maxillule (Fig. 3C): praecoxal endite elongate, with 10 setae; coxal exite and endite each with 1 seta; proximal and

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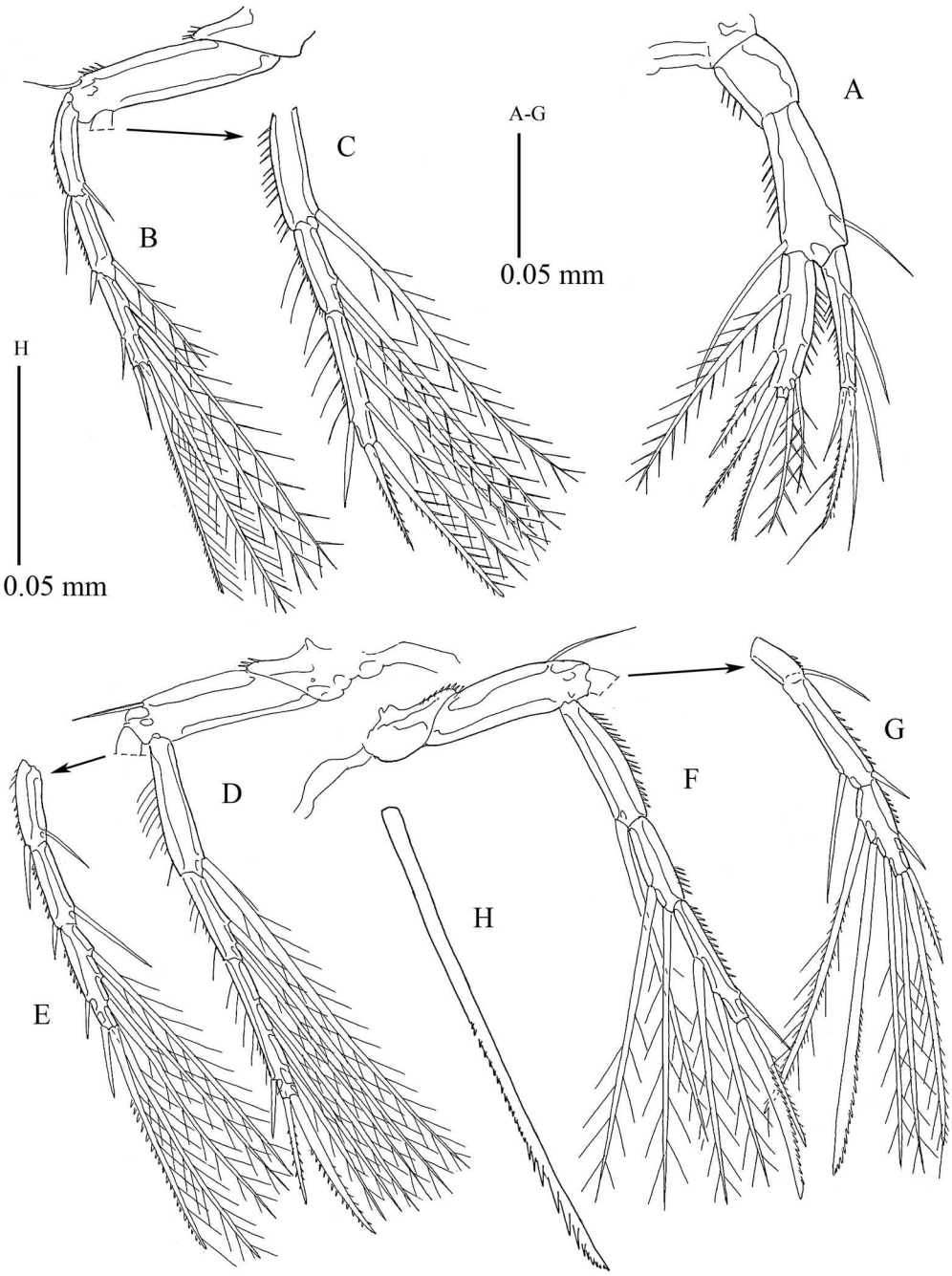


Fig. 4. *Tegastes falcatus* (Norman, 1903). Adult female. A, Leg 1. B, Leg 2. C, Endopod of leg 2. D, Leg 3. E, Exopod of leg 3. F, Leg 4. G, Exopod of leg 4. H, Modified seta of exopod of leg 4.

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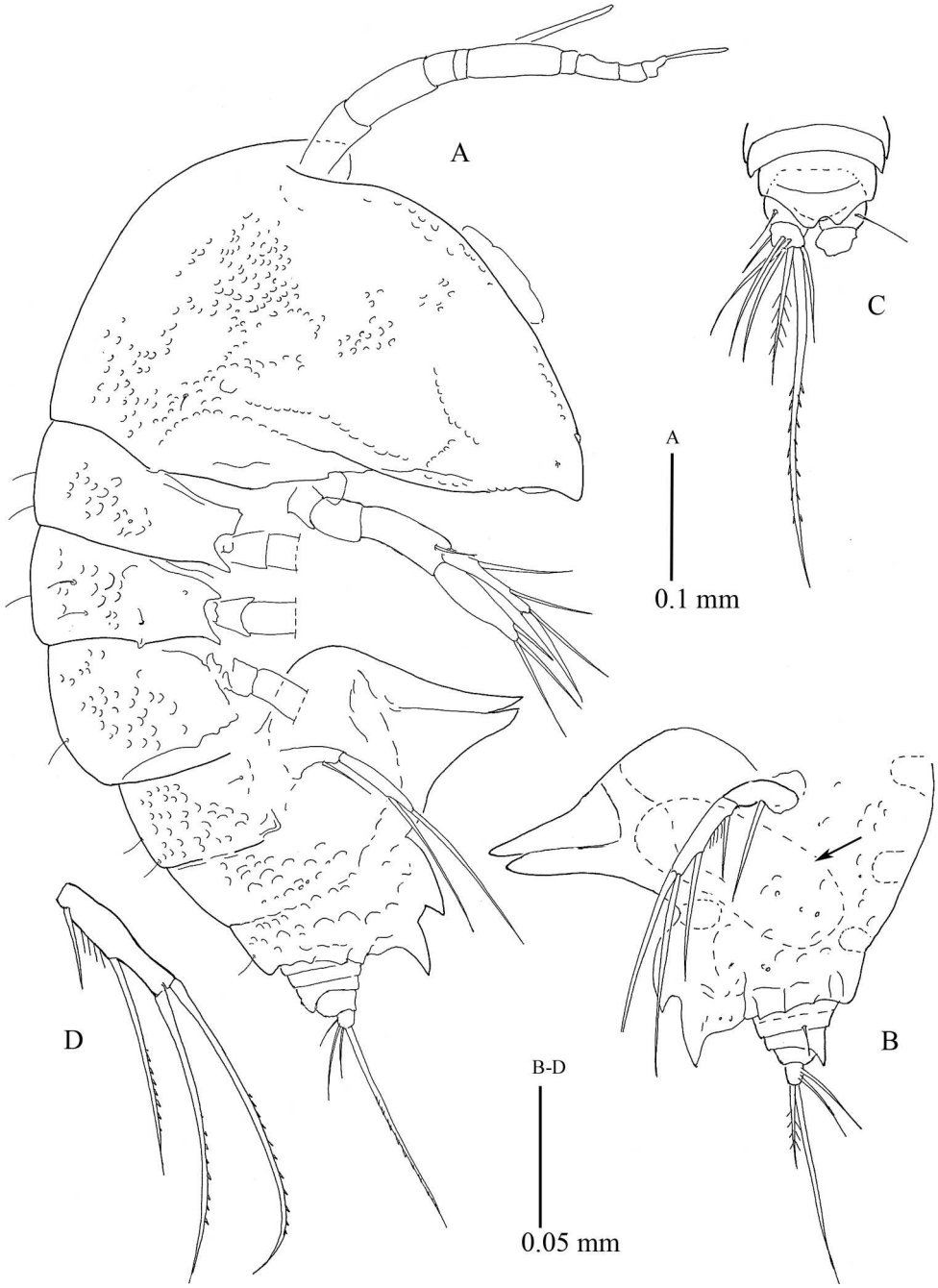


Fig. 5. *Tegastes falcatus* (Norman, 1903). Adult male. A, Habitus, lateral. B, Leg 5, genital triple-somite complex, 3 abdominal somites and caudal ramus, lateral, arrow to spermatophore, broken lines. C, Posterior part of genital triple-somite complex, 3 abdominal somites and caudal rami, dorsal. D, Exopodal segment of leg 5.

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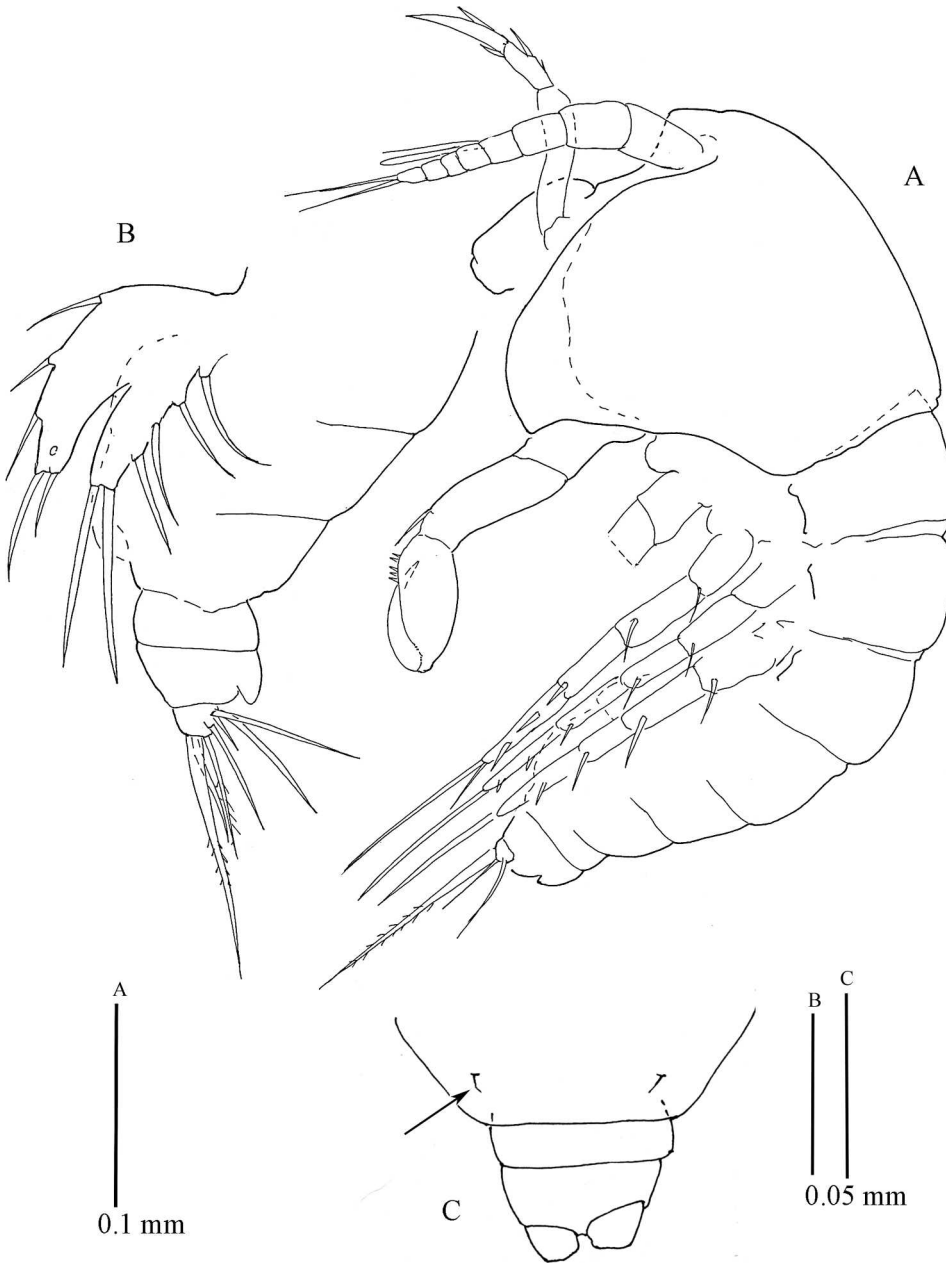


Fig. 6. *Tegastes falcatus* (Norman, 1903). CV female. A, Habitus, lateral. B, Leg 5, genital triple-somite complex, 2 abdominal somites and caudal ramus, lateral. C, Posterior part of genital triple-somite complex, 2 abdominal somites and caudal rami, ventral, arrow to seta of leg 6.

distal basal endites indistinguishable, each with 4 ventral setae and denticles; ramus with 3 setae inserting on unsclerotized area of basis.

Maxilla (Fig. 3D–F): praecoxal endite of syncoxa with 3 setae, coxal endite of syncoxa with 2 setae; proximal lobe of basis elongate, with 3 setae; distal lobe of

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Table 1.—Spines and setae on swimming legs 1–4 of *Tegastes falcatus* CVI female; p = proximal segment; m = middle segment; d = distal segment complex; * = segment not expressed.

	Coxa	Basis	Exopod p;m;d	Endopod p;m;d
Leg 1	0–0	1–1	*; *; II, I, I + 1	*; *; II, I, I + 2
Leg 2	0–0	1–0	I–I; I–1; II, I, 3	0–1; 0–2; II, I, 2
Leg 3	0–0	1–0	I–I; I–I; II, I, 4	0–1; 0–2; II, I, 3
Leg 4	0–0	1–0	I–0; I–I; II, I, I + 3	0–1; 0–2; II, I, 2

basis elongate, with 1 ventral, 1 stout terminal, and 1 dorsal setae toward tip of lobe; ramus of 3 setae inserting on unsclerotized area of basis.

Maxilliped (Figs. 3G, H, 17D): praecoxa unarmed, coxa with 1 distoventral seta; basis with anterior and posterior line of denticles, posterior longer and thicker; with a small, unmodified seta mid-ventrally and a small, anvil-shaped seta distoventrally. Endopod apparently 1-segmented; posteroproximally with 2 setae, one long; anterodistally with 3 setae, one of which is very small.

Swimming legs 1–4 (Fig. 4A–G): protopod 2-segmented; swimming leg 1 with 1-segmented rami; swimming legs 2–4 with 3-segmented rami. Spine and setal formula, Table 1; second from proximoventral seta on exopod of leg 4 spine-like, with distal hyaline membrane (Fig. 4G, H).

Leg 5 (Fig. 3I): baseoendopod with 1 dorsal, 2 terminal and 3 ventral setae; exopod 1-segmented, with 2 terminal and 3 dorsal setae (lengths vary among specimens).

Leg 6 (Figs. 2D, 17A): simple, ventral lobe-like flap with 1 seta.

Caudal ramus (Figs. 2E, F, 13B, 17F): short with 4 terminal, 1 distolateral, 1 lateral and 2 dorsal setae; 1 middle terminal seta broad at base with narrow terminal part [often broken]; setules distally on broad section, terminal part without setules; second middle seta small, less than half length of other terminal setae.

CVI adult male.—Differs from female CVI as follows: length range (body plus caudal ramus) 0.41–0.48 mm, maximum dorsoventral width 0.29–0.34 mm (10 specimens). Cephalosome (Fig. 5A) not tapering; genital triple-somite complex protruding ventrally (Figs. 5B, C, 21A, B) as a beak-like structure ventrally, consisting of articulating protopod of leg 6 anterior to a ventral attenuation of Th7; copulatory pore ventral, between protopod of leg 6 and attenuation of Th7.

Spermatophore (Fig. 5B): large, bean-shaped, within genital triple-somite complex.

Antennule (Fig. 18E–J): 9 articulating parts with 1, 11, 8 + aesthetasc, 2, 7 + bifurcate aesthetasc, 1, 2, 1, 10 + bifurcate aesthetasc; articulation between seventh and eighth part.

Leg 5 (Figs. 5B, D, 21A): endopodal lobe absent; basis with 1 dorsal seta; exopod 1-segmented with 2 terminal and 2 dorsal setae.

Leg 6 (Figs. 5B, 21A, B): unarmed protopod of leg 6.

Caudal Ramus (Figs. 5C, 17D): middle terminal seta elongate, simple.

CV female.—Differs from CVI female as follows: length (body plus caudal ramus) 0.38 mm, maximum dorsoventral width 0.22 mm [1 specimen]; cephalosome including Th1&2 rounded, with blunt point ventrally, not tapering as in female (Fig. 6A); arthrodial membrane developed between Th6&7 and between Th7&abd2; ventral, hook-like attenuation absent from Th6 and from Th7; abd4 absent.

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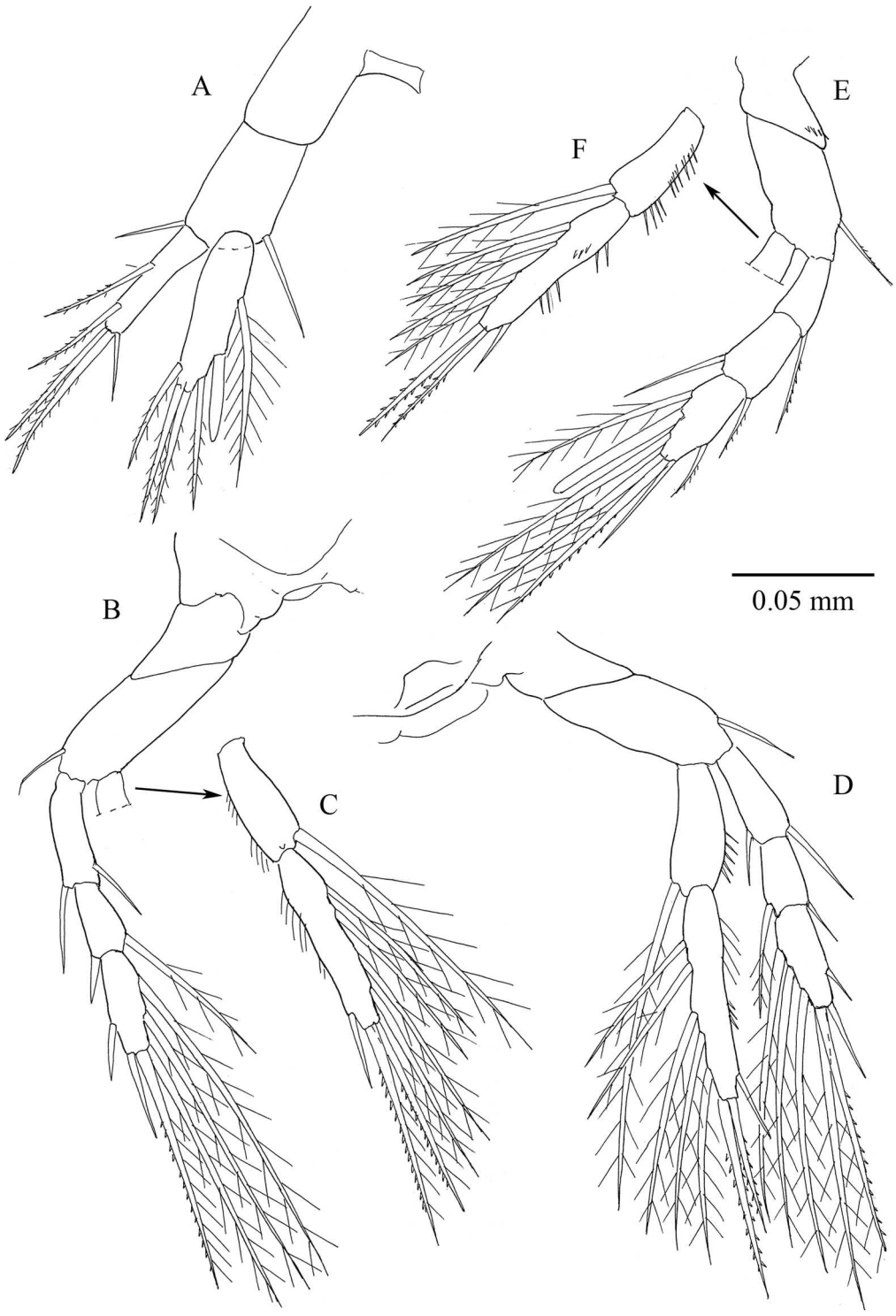


Fig. 7. *Tegastes falcatus* (Norman, 1903). CV female. A, Leg 1. B, Leg 2. C, Endopod of leg 2. D, Leg 3. E, Leg 4. F, Endopod of leg 4.

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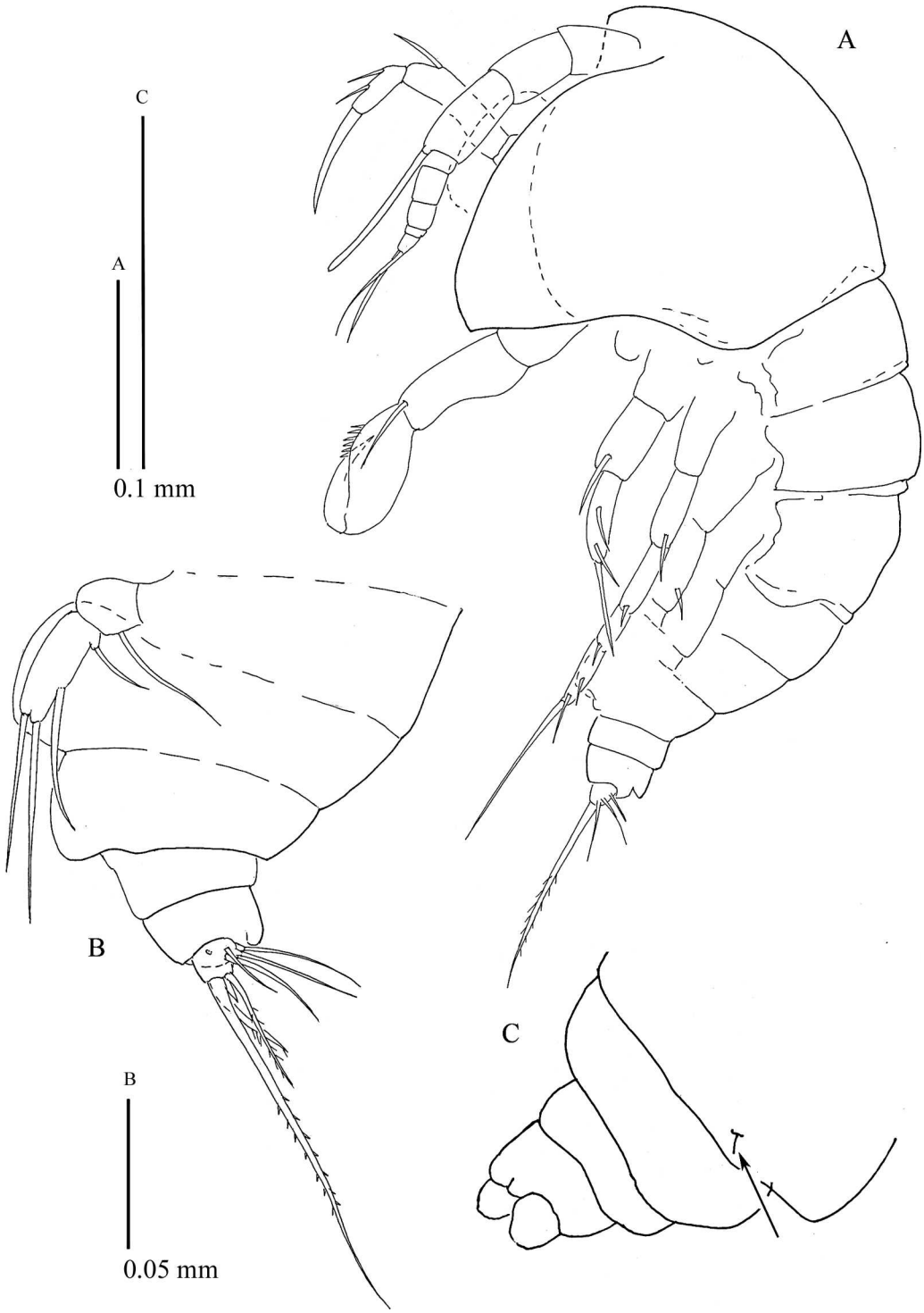


Fig. 8. *Tegastes falcatus* (Norman, 1903). CV male. A, Habitus, lateral. B, Leg 5, genital triple-somite complex, 2 abdominal somites and caudal ramus, lateral. C, Posterior part of genital triple-somite complex, 2 abdominal somites and caudal ramus, lateral, arrow to seta of leg 6.

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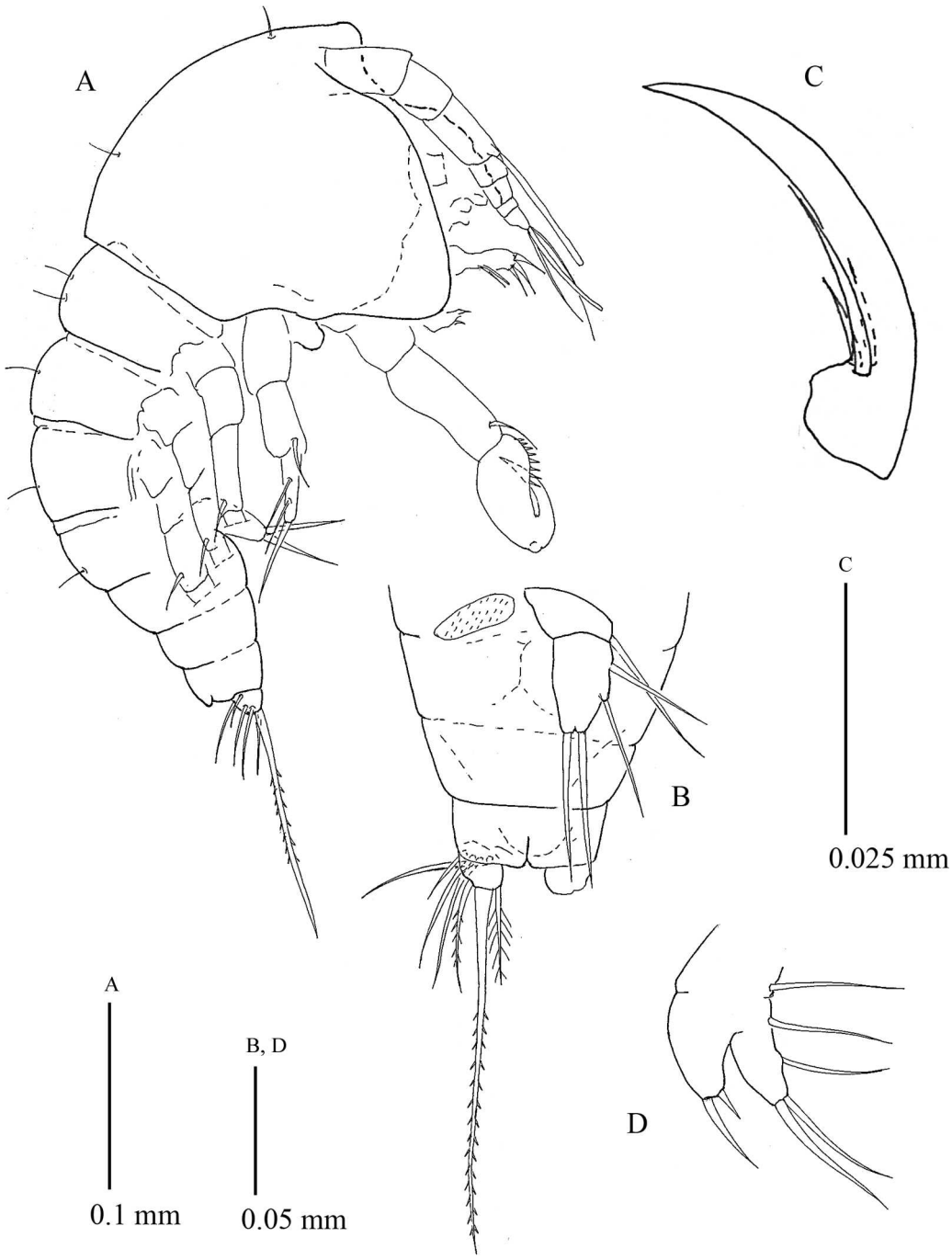


Fig. 9. *Tegastes falcatus* (Norman, 1903). CIV male. A, Habitus, lateral. B, Leg 5, genital somite, 2 articulating somites and caudal rami, ventral. C, Claw of maxilliped, posterior. CIV female. D, Leg 5.

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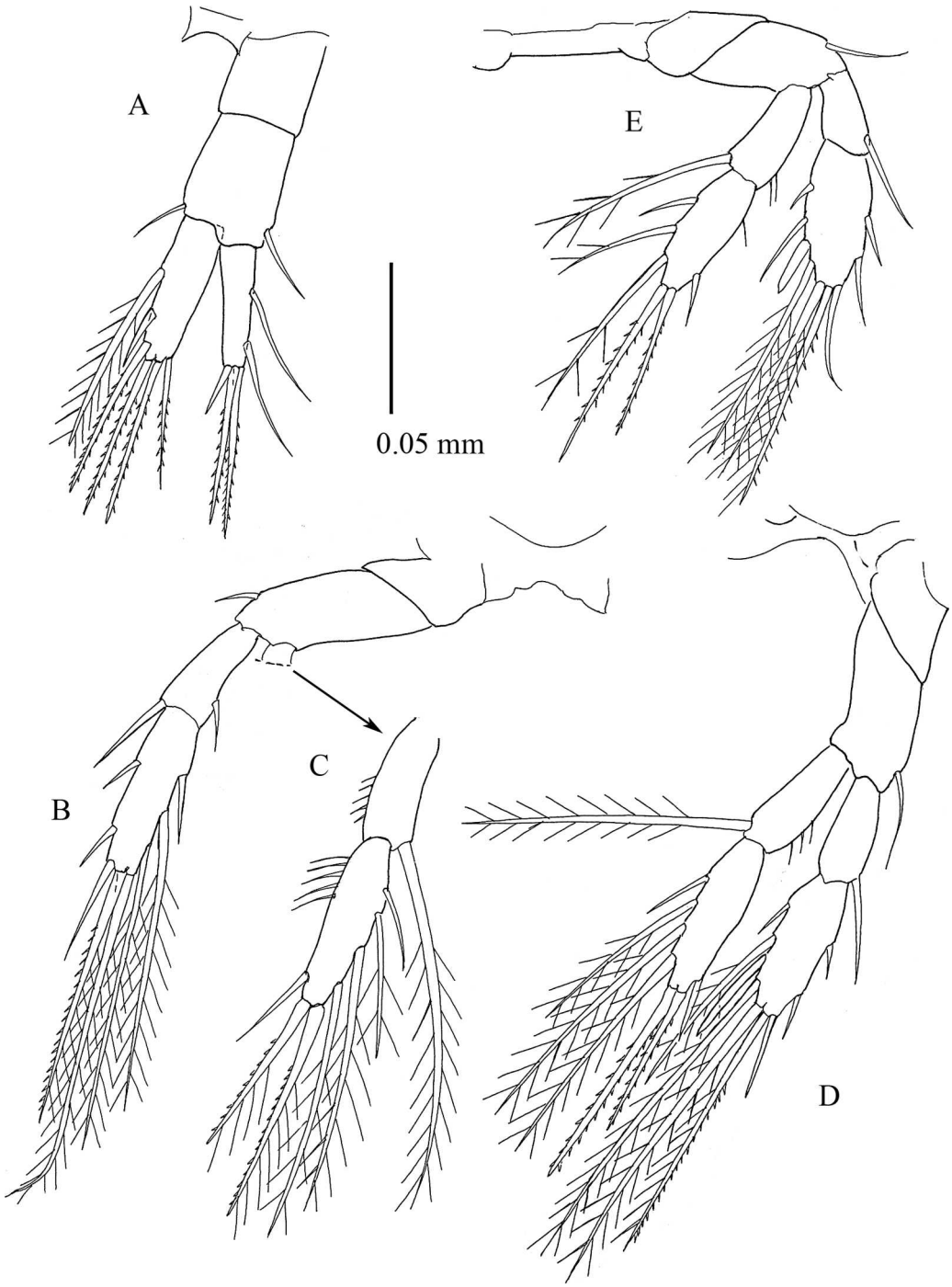


Fig. 10. *Tegastes falcatus* (Norman, 1903). CIV female. A, Leg 1. B, Leg 2. C, Endopod of leg 2. D, Leg 3. E, Leg 4.

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Table 2.—Spines and setae on swimming legs 1–4 of *Tegastes falcatus* CV; p = proximal segment; m = middle segment; d = distal segment complex; * = segment not expressed.

	Coxa	Basis	Exopod p;m;d	Endopod p;m;d
Leg 1	0–0	1–1	*; *; II, I, I + 1	*; *; 1, 2, I + 2
Leg 2	0–0	1–0	0–1; *; I, II, 5	0–1; *; I, II, 4
Leg 3	0–0	1–0	I–I; I–1; II, I, 4	0–1; *; I, II, 5
Leg 4	0–0	1–0	I; I–I; II, I, I + 3	0–1; *; I, II, 4

Antennule (Fig. 19A, B): 8 articulating parts; setation 1, 11, 10, 3 + bifurcate aesthetasc, 2, 4, 4, 6 + bifurcate aesthetasc.

Swimming legs 1–4 (Fig. 7A–F): Spine and setal formula, Table 2.

Leg 5 (Fig. 6B): exopod not articulating with baseoendopod.

Leg 6 (Fig. 6C): 1 seta ventrally, protopod of leg 6 not distinct.

Caudal ramus: middle terminal seta simple, as CVI male.

CV male (Fig. 8A).—Differs from CV female as follows: length (body plus caudal ramus) 0.37–0.42 mm, maximum dorsoventral width 0.23–0.24 mm [4 specimens].

Antennule (Fig. 19C–F): 8 articulating parts with 1, 11, 17 + small, midventral and bifurcate aesthetascs, 1, 3, 4, 10 + bifurcate aesthetasc.

Leg 5 (Fig. 8A): endopod absent.

Leg 6 (Fig. 8C): 1 seta laterally.

CIV female.—Differs from CV female as follows: length (body plus caudal ramus) 0.31–0.32 mm, maximum dorsoventral width 0.18–0.20 mm (2 specimens).

Antennule (Fig. 20A, B): 7 articulating parts with 1, 7, 9 + bifurcate aesthetasc, 2, 4, 4, 6 + bifurcate aesthetasc.

Swimming legs 1–4 (Fig. 10A–E): protopod 2-segmented; swimming leg 1 with 1-segmented rami; swimming legs 2–4 with 2-segmented rami. Spine and setal formula, Table 3.

Leg 5 (Fig. 9): protopod 1-segmented with distodorsal seta; exopod with 2 dorsal and 3 terminal setae; endopod with 2 terminal setae.

CIV male.—Differs from CIV female as follows: length (body plus caudal ramus) 0.31–0.37 mm, maximum dorsoventral width 0.20 mm (3 specimens); arthrodial membrane poorly developed between Th6&7, between Th7&abd2 and between abd2&abd1; abd3 absent (Fig. 9A, B).

Antennule (Fig. 19G–I): 6 articulating parts with 1, 7, 10 + bifurcate aesthetasc, 3, 4, 10 + bifurcate aesthetasc.

Maxilliped (Fig. 9C): endopod posteroproximally with 1 long seta; anterodistally with 2 setae.

Leg 5 (Fig. 9B): endopod absent.

CIII.—Differs from CIV female as follows: length (body plus caudal ramus) 0.30–0.36 mm, maximum dorsoventral width 0.16–0.20 mm, (8 specimens); cephalosome including Th1&2 rounded ventrally; Th3–7 and abd1 articulate although arthrodial membrane not well-developed between Th6&7 and between Th7&abd1; abd2 absent (Fig. 11A, B).

Antennule (Fig. 20C): 6 articulating parts with 1, 10 + bifurcate aesthetasc, 2, 4, 4, 6 + bifurcate aesthetasc.

Maxilliped (Fig. 11C): endopod posteroproximally with 1 short seta; anterodistally with 2 setae.

Swimming legs 1–4 (Figs. 11B, 12A–D): protopod 2-segmented; swimming leg 1 with 1-segmented rami, swimming legs 2&3 with 2-segmented rami, swimming leg 4 with 1-segmented rami. Spine and setal formula, Table 4; without stout seta on the exopod of leg 4.

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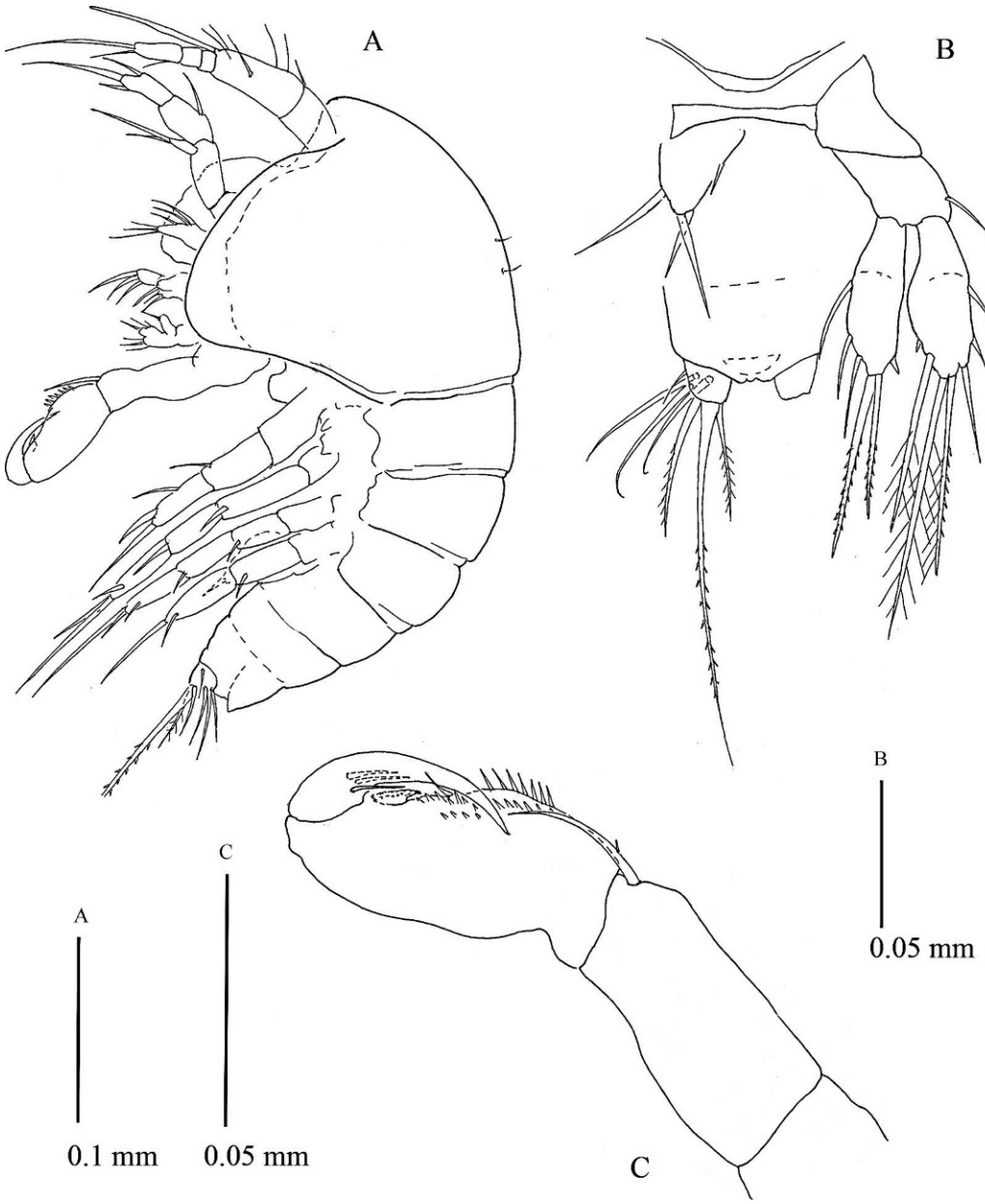


Fig. 11. *Tegastes falcatus* (Norman, 1903). CIII. A, Habitus, lateral. B, Leg 4, leg 5, posterior somites, and caudal rami, ventral. C, Maxilliped, posterior.

Leg 5 (Fig. 11B): bilobate bud, large dorsal lobe with 1 dorsal and 2 terminal setae; small ventral lobe with 1 terminal seta.

Leg 6: absent.

CII.—Differs from CIII as follows: length (body plus caudal ramus) 0.27–0.31 mm, maximum dorsoventral width 0.13–0.18 mm, (8 specimens); Th3–6 and abd1 articulate; Th7 absent (Fig. 13A).

Antennule (Fig. 20D): 6 articulating parts with 1, 4 + bifurcate aesthetasc, 1, 3, 4, 6 + bifurcate aesthetasc.

Maxilliped (Fig. 14A): endopod posteroproximally with 1 very small seta.

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Table 3.—Spines and setae on swimming legs 1–4 of *Tegastes falcatus* CIV; p = proximal segment; m = middle segment; d = distal segment complex; * = segment not expressed.

	Coxa	Basis	Exopod p;m;d	Endopod p;m;d
Leg 1	0–0	1–0	*; *; II, I, I + 1	*; *; 1, 2, I + 2
Leg 2	0–0	1–0	I–I; *; III, I, I + 3	0–1; *; I, II, I + 3
Leg 3	0–0	1–0	I; *; III, I, II + 3	0–1; *; I, II, I + 3
Leg 4	0–0	1–0	I; *; III, I, III + 2	0–1; *; I, II, 3

Swimming legs 1–3 (Fig. 14B–D): Spine and setal formula, Table 5.

Swimming leg 4 (Fig. 13C): bilobate bud; dorsal lobe with 1 dorsal and 2 terminal setae; ventral lobe with 2 terminal setae.

Leg 5: absent.

Caudal ramus: length of second middle seta one-fifth of remaining terminal setae.

CI.—Differs from copepodid stage II as follows: length (body plus caudal ramus) 0.24–0.28 mm, maximum dorsoventral width 0.12–0.14 mm (7 specimens); Th6 absent (Fig. 15A).

Antennule (Fig. 20E): 5 articulating parts with 1, 3 + aesthetasc, 2, 3, 6 + bifurcate aesthetasc.

Antenna (Fig. 16A, B): distal endopodal segment with 1 proximoventral, 3 mid-ventral, 1 distodorsal and 4 terminal setae; exopod unsegmented.

Mandible (Fig. 16C): palp poorly sclerotized; basis with 2 ventral setae; lobe-like exopod with 2 terminal setae; wrinkled endopod with 3 terminal setae on a distal segment, and 2 ventral setae on 1 or 2 undistinguishable segments.

Maxillule (Fig. 16D): praecoxal endite with 4 setae; coxal exite with 3 setae, endite with 1 seta; proximal and distal basal endites indistinguishable, with 4 ventral setae; ramus of 3 setae inserting on unsclerotized area of basis.

Maxilla (Fig. 16E): distal praecoxal endite of syncoxa with 1 seta, coxal endite of syncoxa with 1 seta.

Maxilliped (Fig. 16F): posteroproximal seta absent.

Swimming legs 1–2 (Fig. 16G, H): Spine and setal formula, Table 6.

Swimming leg 3 (Fig. 15B): bilobate bud; dorsal lobe with distal spine and distal seta; ventral lobe with 2 setae.

Leg 4: absent.

Caudal ramus: with 7 setae (Fig. 15C).

Remarks.—Females of *T. falcatus* can be separated from other species of the genus by the lanceolate seta on the caudal ramus, the shape of the small, ventral, hook-like attenuation on the posterior thoracic somite (simple, curved posteroventrally) and the large ventral, hook-like attenuation on the anterior abdominal somite (simple, curved posteriorly). Males can be separated by the shape of these attenuations, as well as the shape of the protopod of leg 6 (pointed distally) and the shape of the ventral attenuation of the posterior thoracic somite (pointed posteriorly).

An embryo sac with four embryos is carried in a chamber formed by the anteroventral face of the genital somite and the endopod of leg 5 of the female. Eight setae are present on the caudal ramus. All setae are hollow, including the smallest (Figs. 2E, F, 13B, 17F) and are interpreted here as true setae, and not as attenuations of the caudal ramus.

Dark-red adults of *T. falcatus* have been recorded from many localities in the North Atlantic and Arctic oceans: coasts of Britain, North Sea, Norwegian Sea, including the Shetland Islands between the North and Norwegian seas, which is the type locality, Barents Sea, White Sea,

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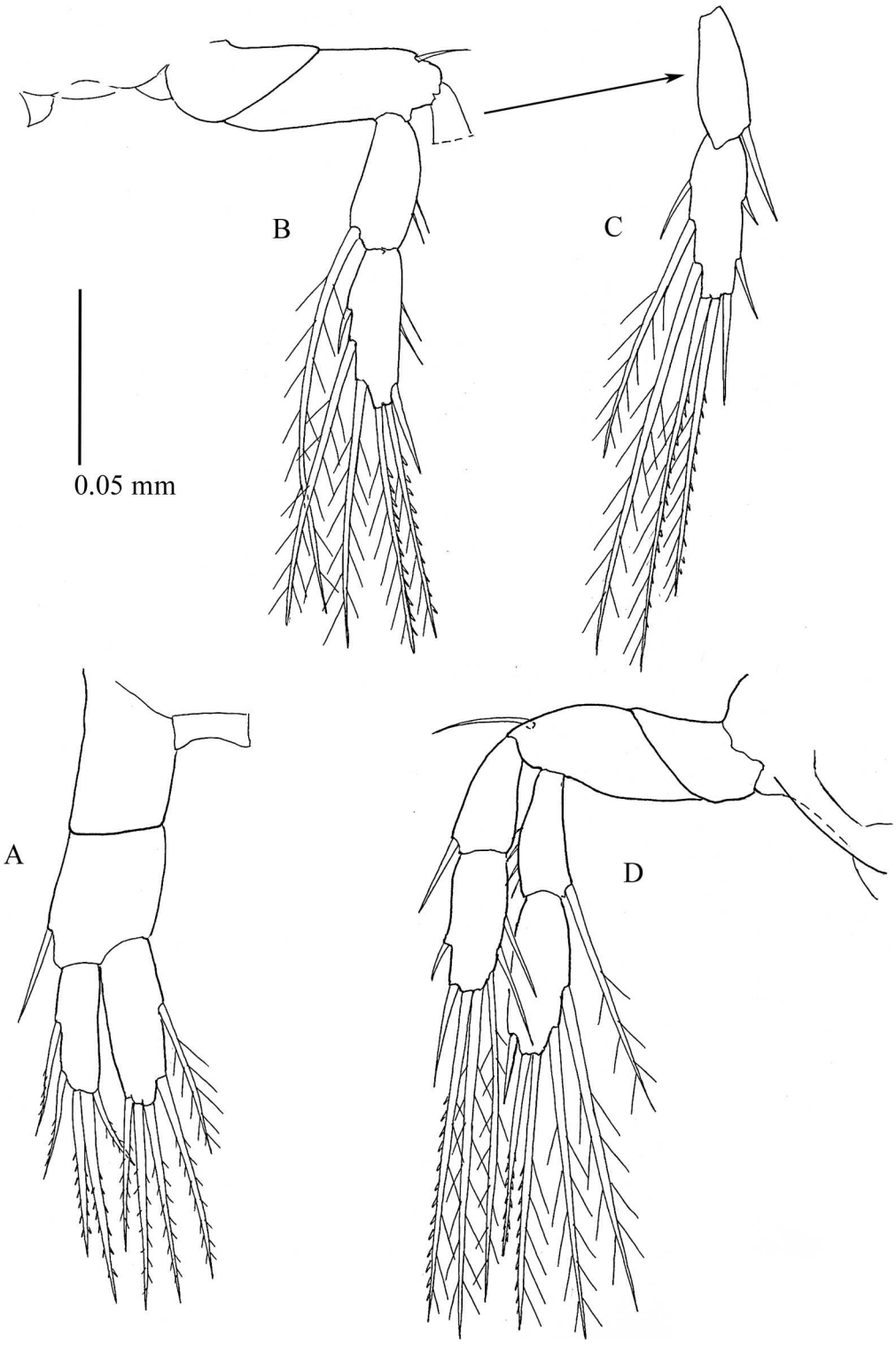


Fig. 12. *Tegastes falcatus* (Norman, 1903). CIII. A, Leg 1. B, Leg 2. C, Exopod of leg 2. D, Leg 3.

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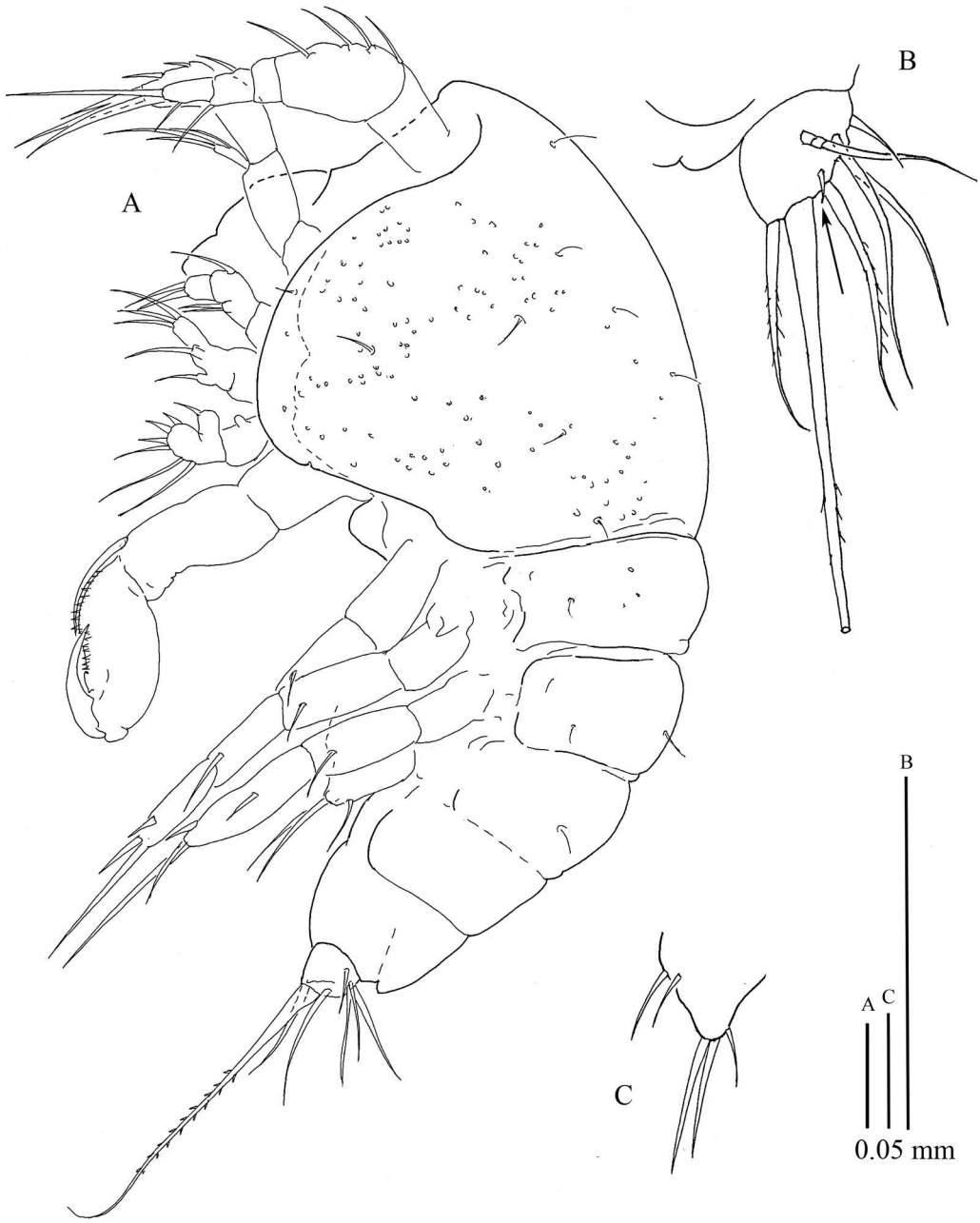


Fig. 13. *Tegastes falcatus* (Norman, 1903). CII. A, Habitus, lateral. B, Right caudal ramus, dorsal, arrow to eighth seta. C, Leg 4.

Laptev Sea, east coast of the United States, the Hudson Bay, and the coast of Greenland (see Sars 1904, Wilson 1936, Chislenko 1967, 1977; McAlice & Coffin 1990). However, specimens reported from the Mediterranean and around Sri Lanka (Ceylon before 1972) require additional study.

Tegastes falcatus previously has been collected from sand or in association with different macro algae, as well as from plankton samples, all from shallow wa-

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Table 4.—Spines and setae on swimming legs 1–4 of *Tegastes falcatus* CIII; p = proximal segment; m = middle segment; d = distal segment complex; * = segment not expressed.

	Coxa	Basis	Exopod p;m;d	Endopod p;m;d
Leg 1	0–0	1–0	*; *; II, I, I + 1	*; *; 1, 2, 2
Leg 2	0–0	1–0	I; *; III, I, I + 3	0–1; *; I, II, I + 2
Leg 3	0–0	1–0	I; *; II, I, II + 2	0–1; * ; I, II, 2
Leg 4	0–0	1–0	*; *; III, I, II + 1	* ; *; I, II, III

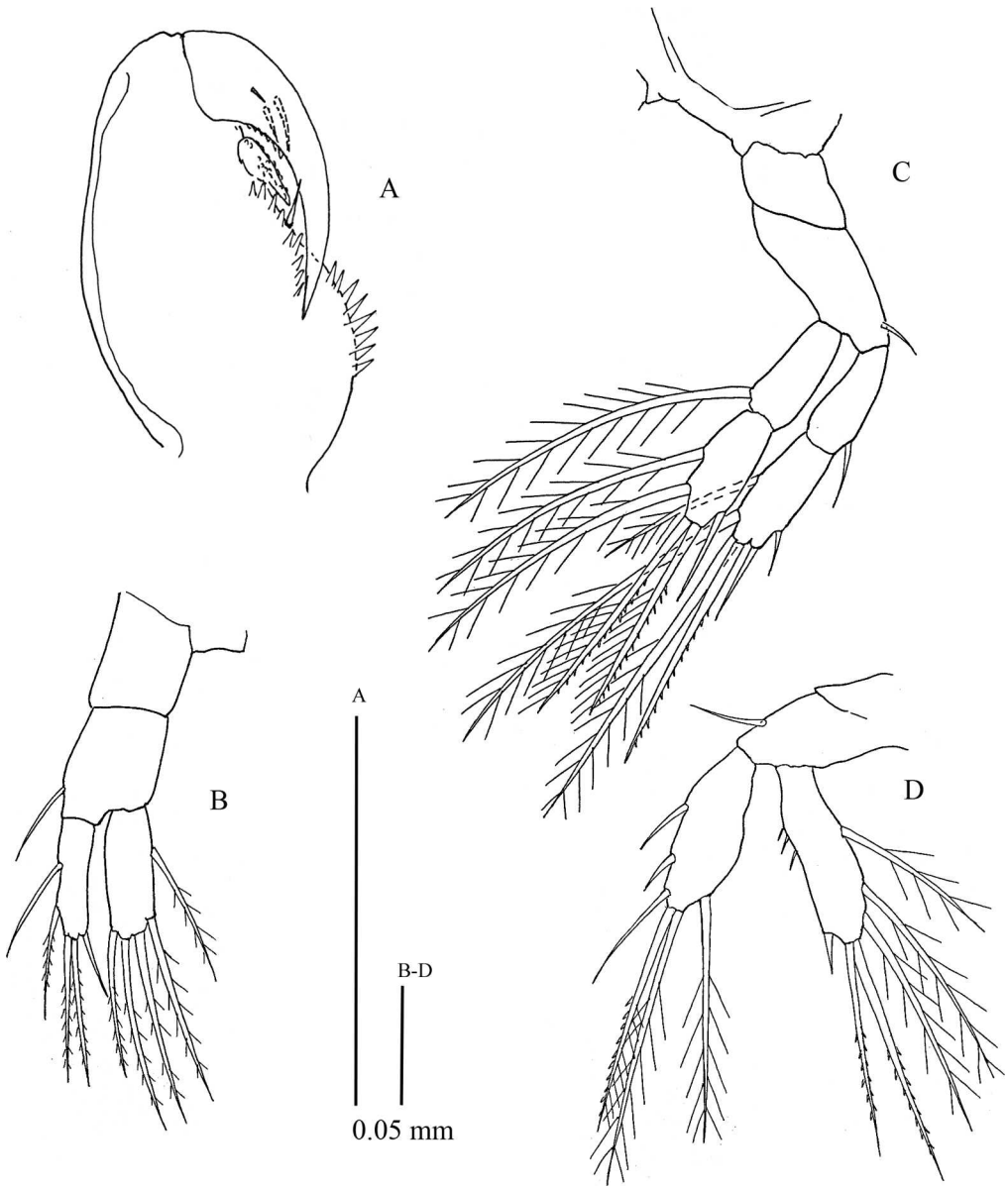


Fig. 14. *Tegastes falcatus* (Norman, 1903). CII. A, Basis and claw of maxilliped, posterior. B, Leg 1. C, Leg 2. D, Leg 3.

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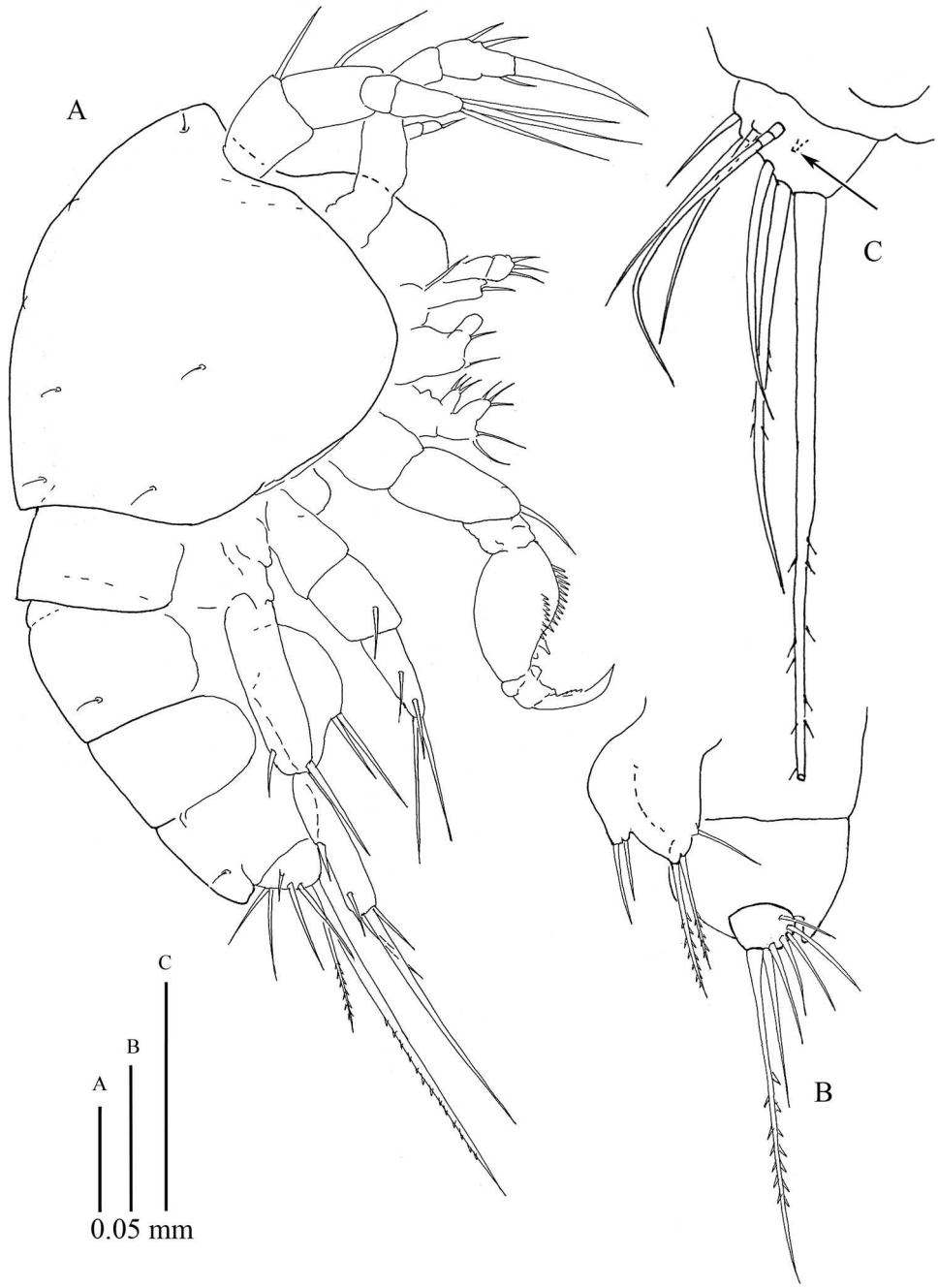


Fig. 15. *Tegastes falcatus* (Norman, 1903). CI. A, Habitus, lateral. B, Leg 3, anal somite and caudal ramus, lateral. C, Left caudal ramus, dorsal, arrow to eighth seta.

ters. A few adults of *T. falcatus* from the White Sea were associated with *Fucus inlatus*, *Ahnfeltia plicata*, *Ascophyllum nodosum*, and *Laminaria saccharina* (Chislenko, 1967). In the present study, many specimens of nauplii and the copepodid stages of *T. falcatus* were found in washings of the White Sea bryozoan

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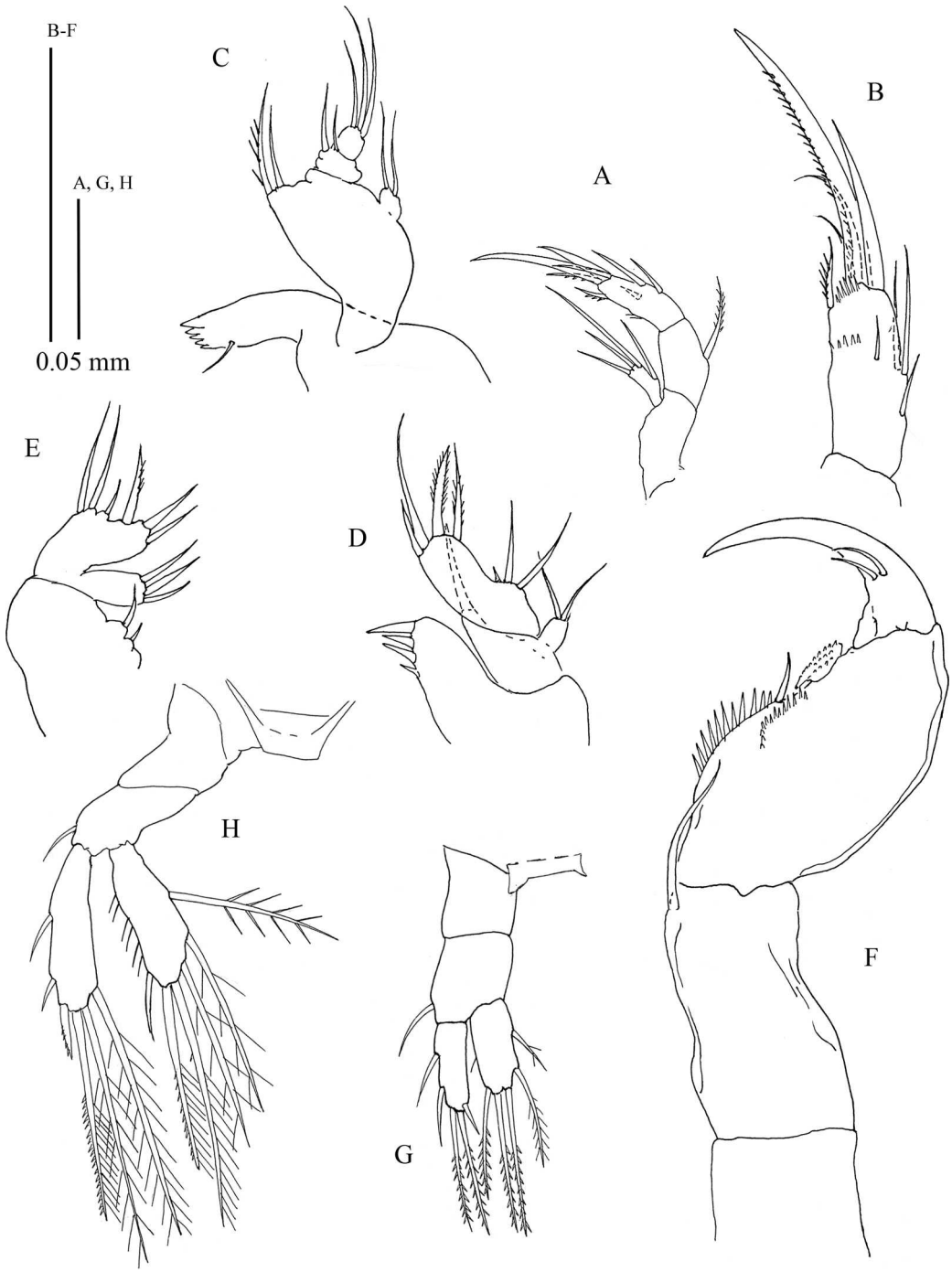


Fig. 16. *Tegastes falcatus* (Norman, 1903). CI. A, Antenna. B, Distal segment of antennal endopod. C, Mandible. D, Maxillule. E, Maxilla. F, Maxilliped, anterior. G, Leg 1. H, Leg 2.

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Table 5.—Spines and setae on swimming legs 1–3 of *Tegastes falcatus* CII; p = proximal segment; m = middle segment; d = distal segment complex; * = segment not expressed.

	Coxa	Basis	Exopod p;m;d	Endopod p;m;d
Leg 1	0–0	1–0	*; *; II, I, I + 1	*; *; 1, 2, 2
Leg 2	0–0	1–0	I; *; II, I, 3	0–1; *; I, II, 2
Leg 3	0–0	1–0	*; *; III, I, 2	*; *; I, II, 3

Flustra foliacea which served as a substrate for an unidentified suctorian protist. Previous samplings of this bryozoan from the same locality revealed neither suctorians nor tegastids (Ivanenko & Smurov 1997).

Observations of nauplii of *T. falcatus* indicate that they feed on the sessile suctorian growing on the bryozoan, a symbiotic relationship new for copepods. The nauplii use the chelae of the mandible to attach to the suctorian, and the long distal segment of the antennal endopod to damage and pierce the pellicle of the suctorians (Ivanenko et al. 2008, observations of VNI). The copepodids also are assumed to be associated directly with the suctorian and only indirectly with the bryozoan. The subchela of their maxilliped and the stout, unarmed seta on the basis of their maxilla may serve functions during the copepodid phase of development similar to those of the mandible and antenna of the nauplii.

Development and Relationships

The lateral face of the cephalosome deepens progressively during the copepodid phase of development. The simple aesthetasc on the second-from-proximal segment of the antennule of CI is transformed into a bifurcate aesthetasc on CII. Formation of the arthrodial membrane separating the middle segment and distal complex of the endopod of swimming legs 2–4 is delayed until CVI, one stage later than the exopod. The endopod of the maxilliped bears two groups of setae, posteroproximally and anterodistally; the number of setae in these two groups increases during the copepodid phase, but not in a pattern that can be related to changes in segmentation, as has been hypothesized for calanoids and polyarthrans (see Ferrari & Dahms 1998), cyclopoids (Ferrari & Ivanenko 2001), or siphonostomatoids (see Ivanenko et al. 2001, Ivanenko & Ferrari 2003). Copepodids II–VI bear eight setae on the caudal ramus. This number, unique to copepods, is an apomorphy for the species. The morphology of the long terminal seta on the female caudal ramus changes significantly during the molt to CVI. It is long and evenly tapered, with few well-spaced setules on CIV–V females, CIV–VI males and younger copepodids. On CVI females, this seta is broad proximally but narrow distally; most setules originate toward the distal part of the broad section.

Gender dimorphism initially is observed at copepodid IV for: antennular segmentation, male with one segment fewer and segments not homologous to those of the female; setation of the maxilliped, male 1 posteroproximal and 2 anterodistal (female 2 posteroproximal and 3 anterodistal); rami on leg 5, male endopod absent (female present). At copepodid V for: antennular segment homologies as observed in setation; rami present on leg 5, same situation; position of leg 6 seta, male lateral (female ventral). Gender dimorphism at copepodid VI includes, in addition to the structures at CV: shape of the cephalosome laterally, male with rounded ventral tip (female pointed); genital triple-somite complex,

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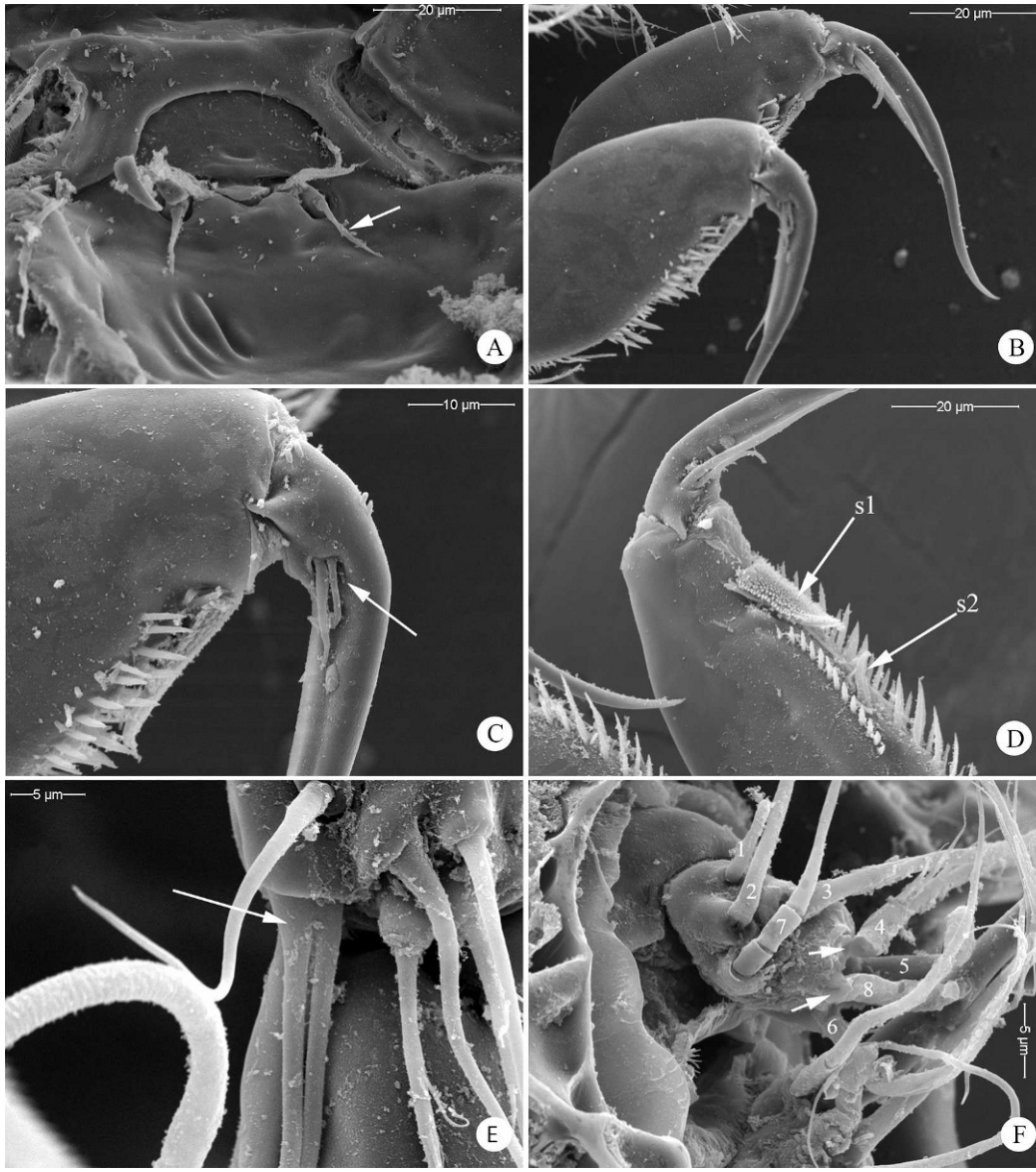


Fig. 17. SEM of *Tegastes falcatus* (Norman, 1903). A, Genital triple-somite complex of female, ventral, arrow to seta of left leg 6. B, Distal segments of male maxillipeds. C, Proximal part of male maxilliped, anterior, arrow to smallest of 3 setae. D, Basis of maxilliped of female, posterior, s1 arrow to anvil-shaped seta, s2 arrow to simple seta. E, Armature of segment 5 of male antennule, arrow to seta plus aesthetasc. F, Left caudal ramus of male with 8 setae, arrows to broken base of setae 4 and 8.

male produced ventrally (female not produced); a middle terminal seta on the caudal ramus, male long and simple (female broad base, narrow terminally).

The taxonomic importance of the morphology of leg 6 can be seen in the following species of Tegastidae (Figs. 21–23): *Tegastes falcatus* (Norman, 1903) [USNM 1104744] leg 6 with one distal point with concave lateral margins (Fig. 21B); *Tegastes gemmeus* Humes, 1984 [USNM 213824, paratype] leg 6 with one distal point with convex lateral margins (Fig. 22C); *Tegastes cnidicus*

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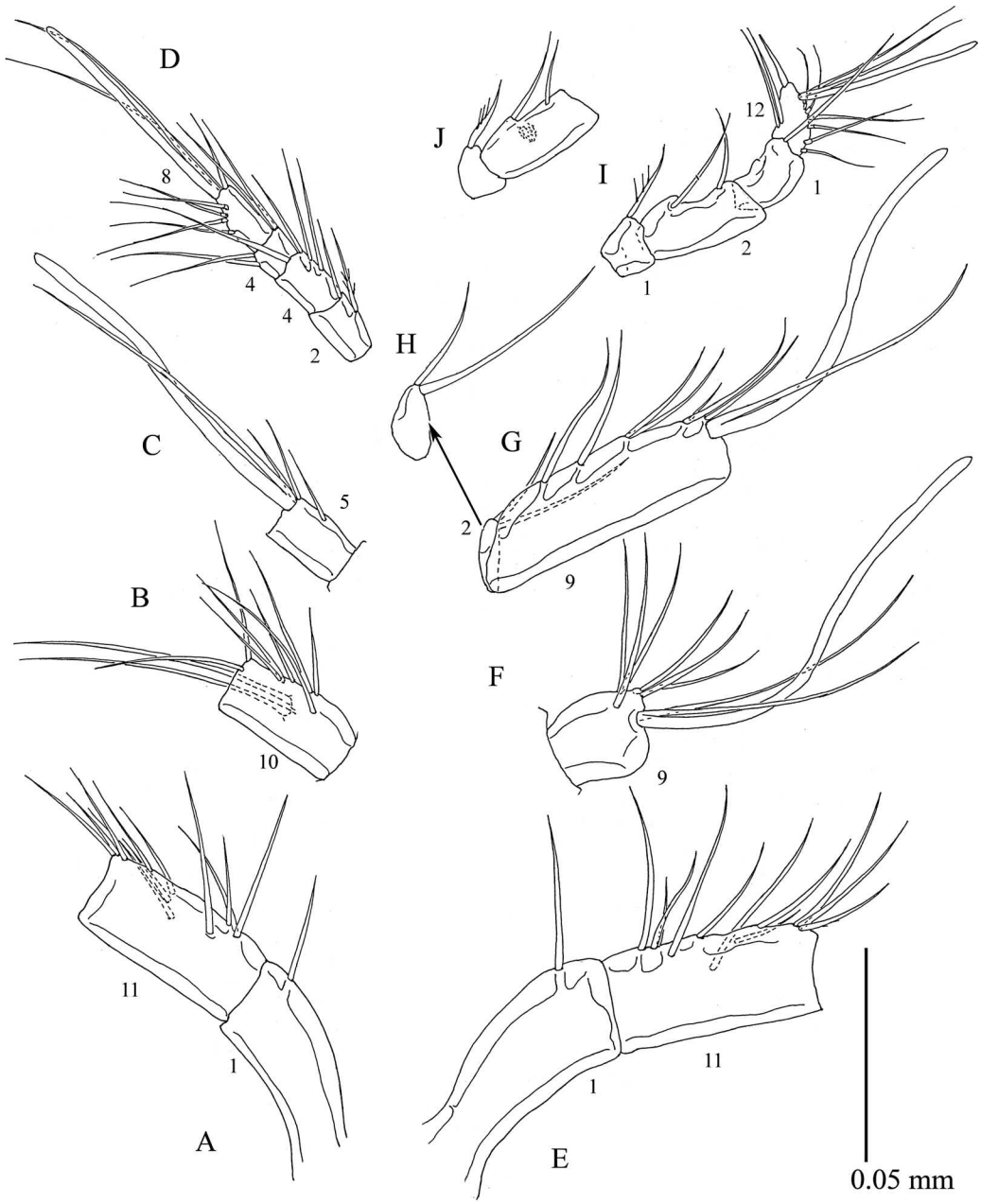


Fig. 18. *Tegastes falcatus* (Norman, 1903). A–D, Antennule, adult female. E–J, Antennule, adult male; numbers indicate total number of setal elements (setae plus aesthetascs).

Humes, 1981 [USNM 181821, paratype] leg 6 with three distal points (Fig. 23C); *Syngastes* sp. (Claus, 1863) [USNM 59591, as *Parategastes sphaericus* (Claus, 1863)] leg 6 with one distal point, teardrop-shaped (Fig. 23E); *Parategastes conexus* Humes, 1984 [USNM 213830, paratype] leg 6 rounded distally (Fig. 21C, D). Leg 6 also exhibits evidence of rotation (Figs. 21–23): a 45-degree counterclockwise rotation appears evident in *P. conexus*, *Smacigastes micheli* Ivanenko &

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Table 6.—Spines and setae on swimming legs 1–2 of *Tegastes falcatus* CI; p = proximal segment; m = middle segment; d = distal segment complex; * = segment not expressed.

	Coxa	Basis	Exopod p;m;d	Endopod p;m;d
Leg 1	0–0	1–0	*; *; II, 1, I + 1	*; *; 1, 2, 2
Leg 2	0–0	1–0	*; *; III, I, 2	*; *; I, I + 2, 3

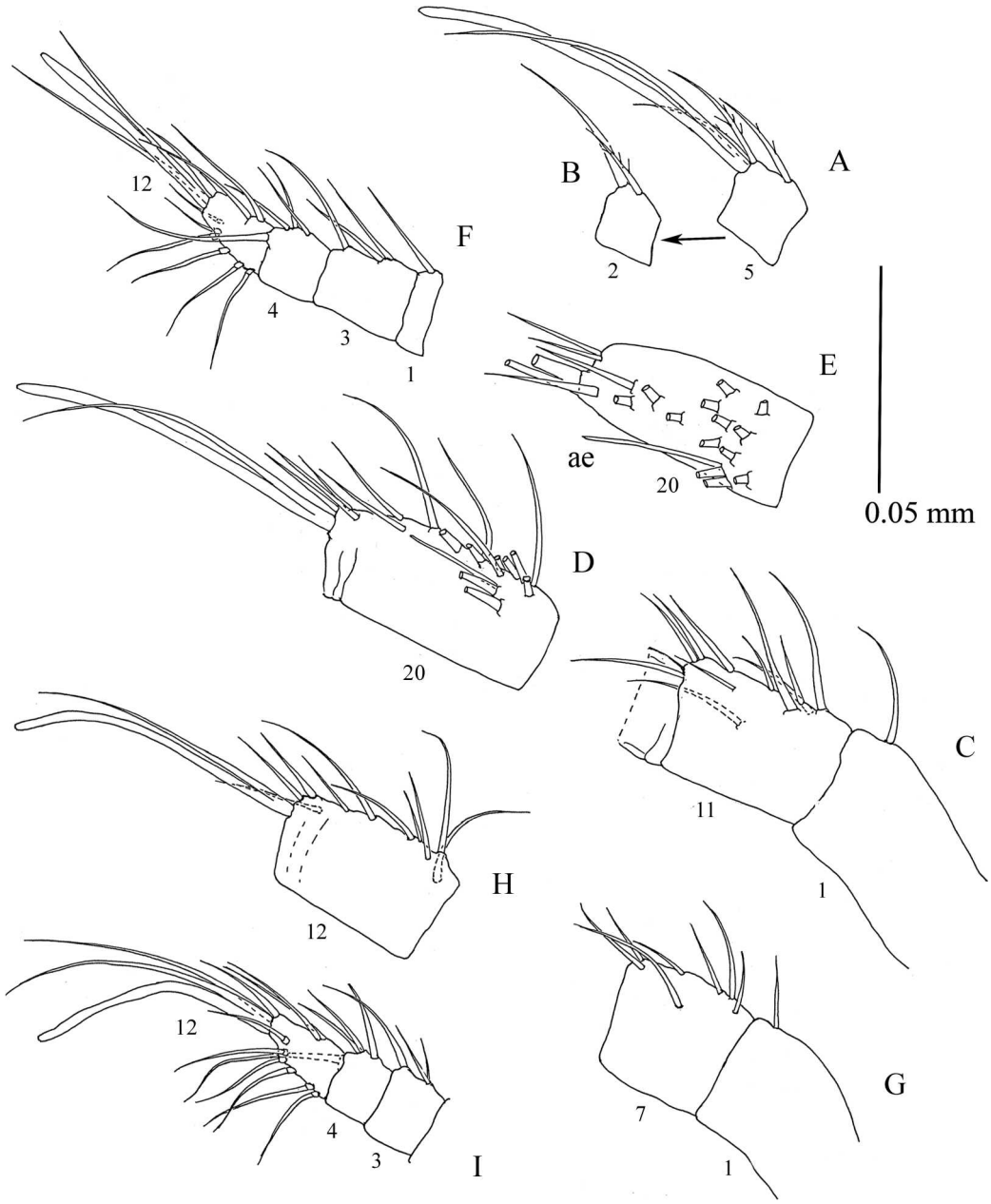


Fig. 19. *Tegastes falcatus* (Norman, 1903). A, Antennule segment 5 at CV of female. B, Segment 4 at CV of female. C–F, CV male. G–I, CIV male; numbers indicate total number of setae + aesthetascs.

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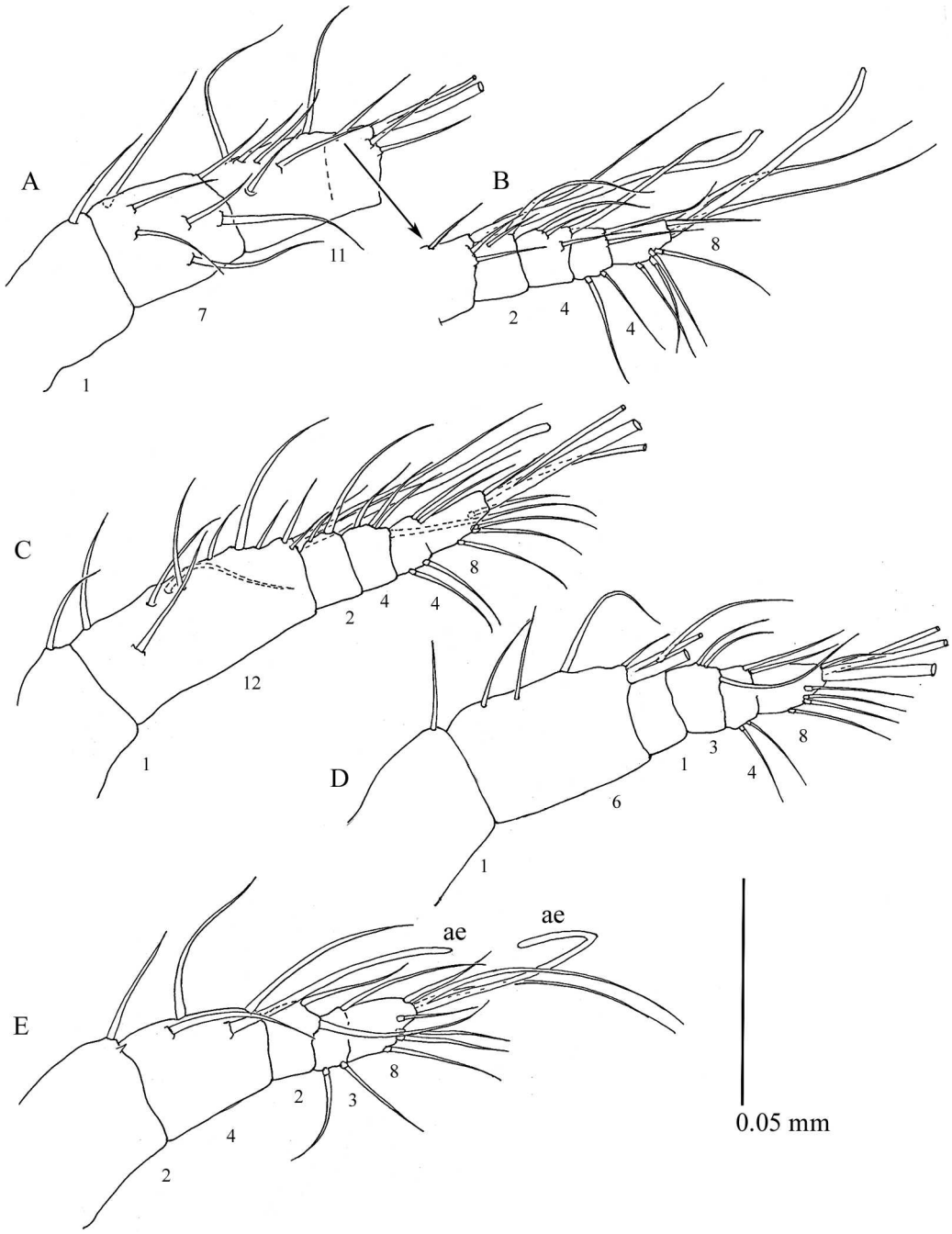


Fig. 20. *Tegastes falcatus* (Norman, 1903). A & B, Antennules CIV, female. C, CIII. D, CII. E, CI; numbers indicate total number of setae + aesthetascs.

Defaye, 2004, *Feregastes wellensi* Fiers, 1986, and *Tegastes gemmeus*, while a 45-degree clockwise rotation may explain the morphology of *T. cnidicus*. *Tegastes falcatus* and *Syngastes* sp. exhibit rotation of 180 degrees, so that the limb and somite appear symmetrical. Allocation of the same category of rotation to

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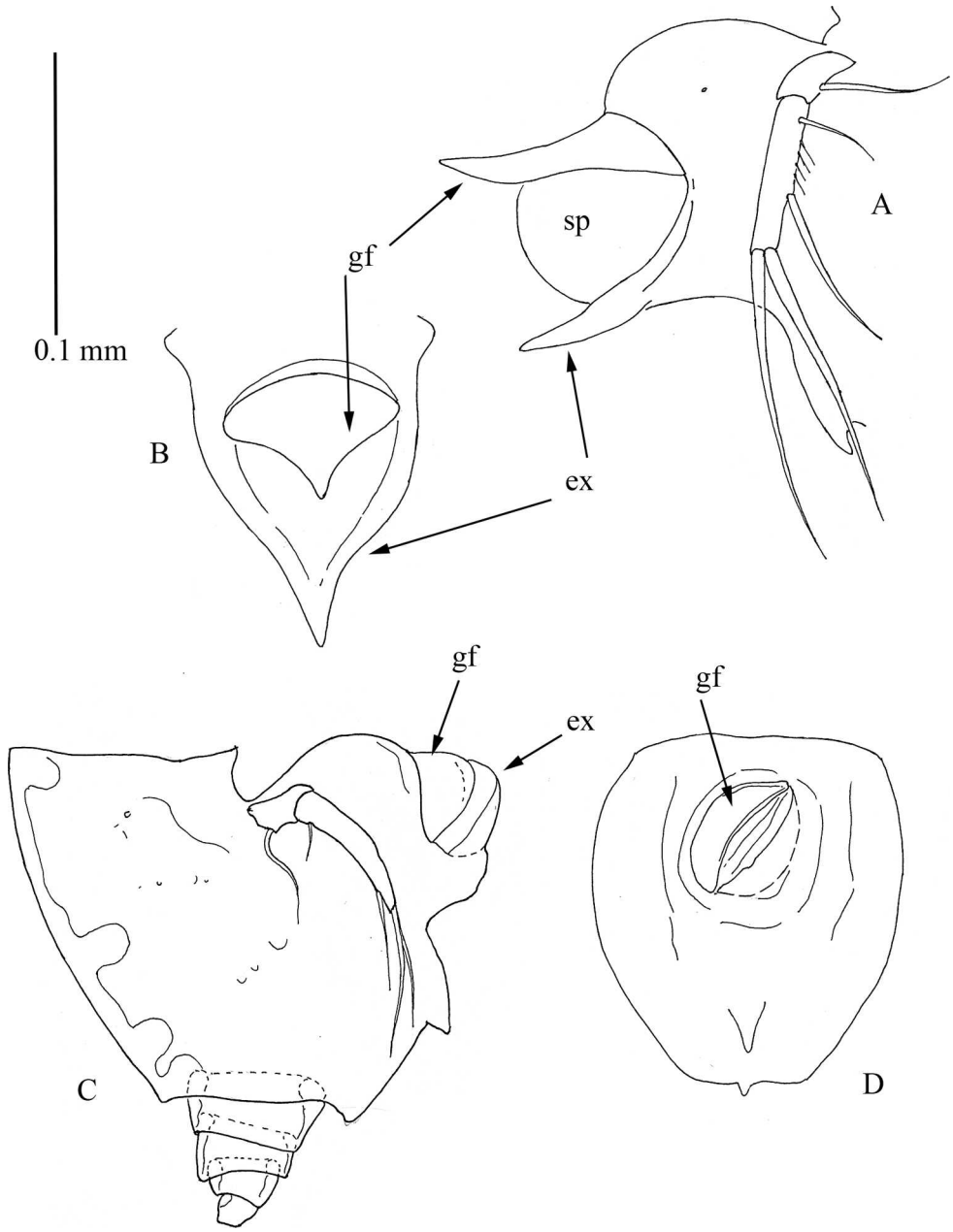


Fig. 21. *Tegastes falcatus* (Norman, 1903). A, Leg 5 and ventral attenuation of genital triple-somite complex of CVI male, lateral view. B, Ventral attenuation of genital triple-somite complex of CVI male, anterior view. *Parategastes conexus* Humes, 1984. C, Leg 5, genital triple-somite complex, abdominal somites, and caudal ramus of CVI male, lateral view. D, Genital triple-somite complex of male, ventral view. ex, ventral attenuation of genital triple-somite complex; gf (genital flap), protopod of leg 6; sp, spermatophore.

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Fig. 22. *Tegastes gemmeus* Humes, 1984. A, Leg 5, genital triple-somite complex, abdominal somites, and caudal ramus of CVI male, right lateral view. B, Same, left lateral. C, Ventral attenuation of genital triple-somite complex of CVI male, anterior view. ex, ventral attenuation of genital triple-somite complex; gf (genital flap), protopod of leg 6.

different genera suggests that the degree of torsion may be convergent. The morphology and degree of torsion of leg 6 has not been described for *Arawalla* and most species of *Parategastes*, *Syngastes* and *Tegastes*.

Seifried (2003:10, 155) proposed the following synapomorphy for the mono-

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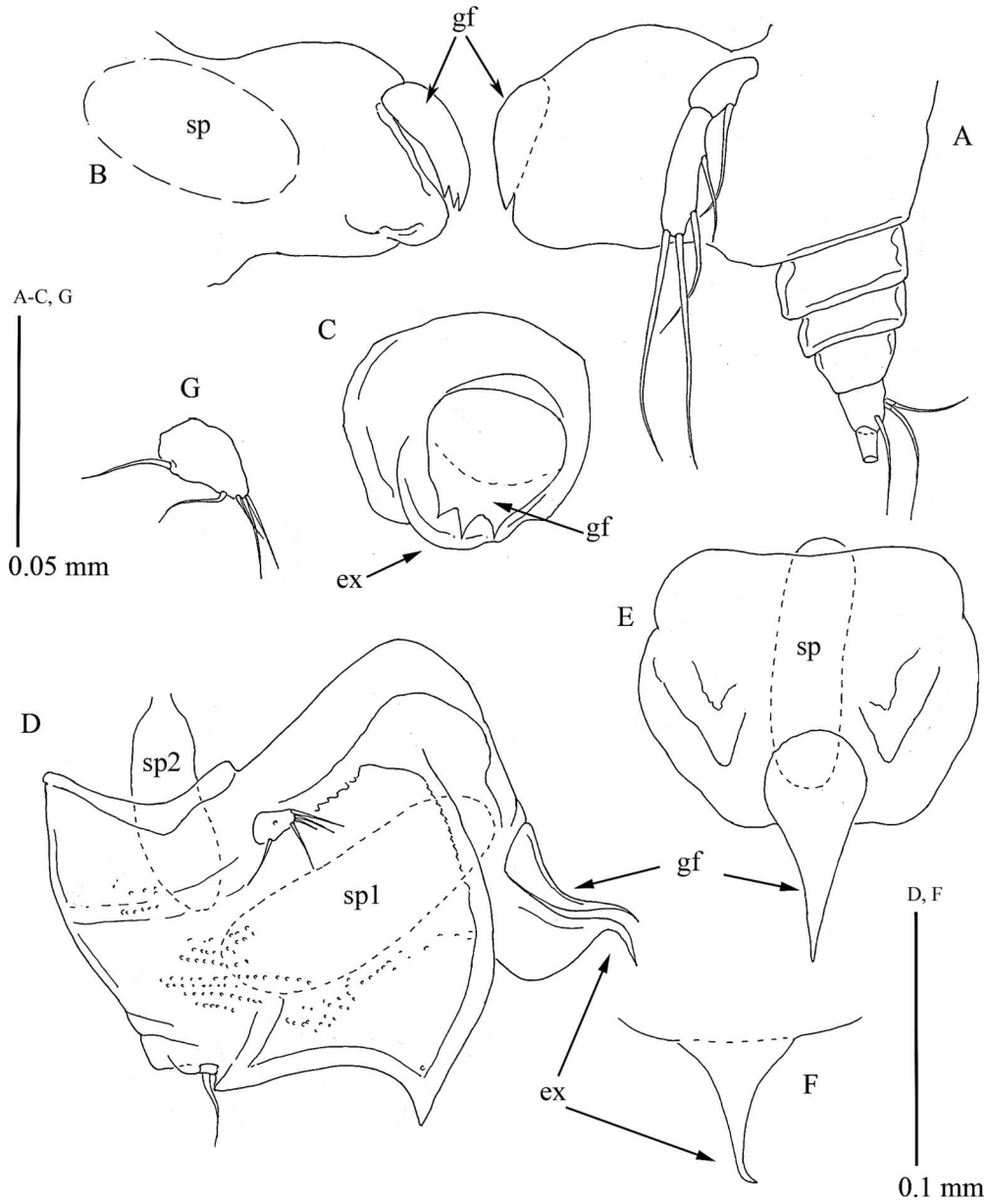


Fig. 23. *Tegastes cnidicus* Humes, 1981. A, Leg 5, genital triple-somite complex, abdominal somites, and caudal ramus of CVI male, left lateral view. B, Same, right lateral view; sp, spermatophore. C, Same, anterior view. *Syngastes* sp. D, Leg 5, genital triple-somite, abdominal somites and caudal ramus of CVI male, right lateral view; sp1, spermatophore near genital opening; sp2, spermatophore farther from genital opening. E, Genital triple-somite complex, ventral view. F, Asymmetrical extension of genital triple-somite complex, ventral view; sp, spermatophore. G, Leg 5; ex, ventral attenuation of genital triple-somite complex; gf (genital flap), protopod of leg 6.

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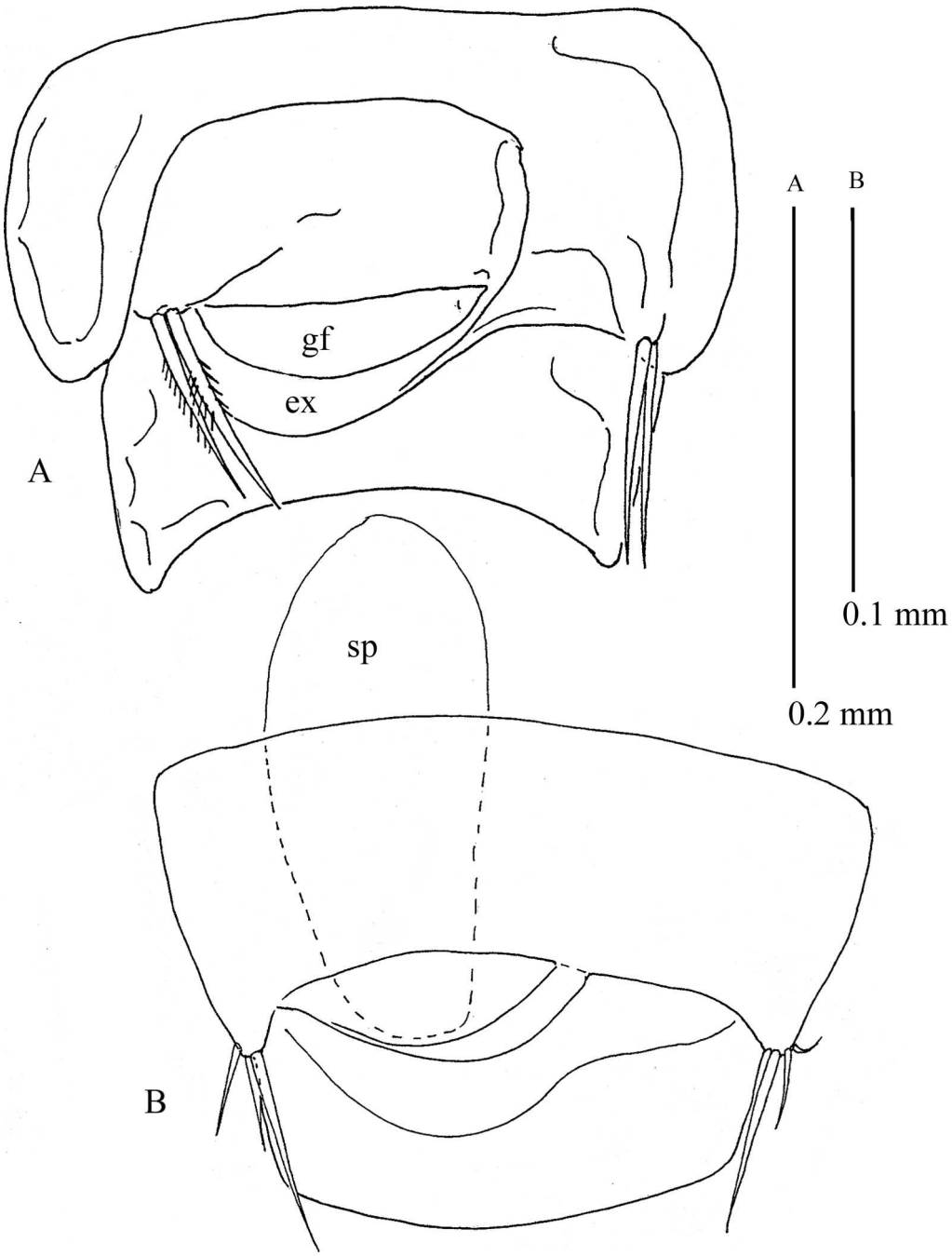


Fig. 24. *Alteutha oblonga* (Goodsir, 1845). A, Male genital somite, ventral view. *Alteuthellopsis corallina* Humes, 1981. B, Male genital somite, ventral view; ex, ventral attenuation of genital somite; gf (genital flap), protopod of leg 6; sp, spermatophore.

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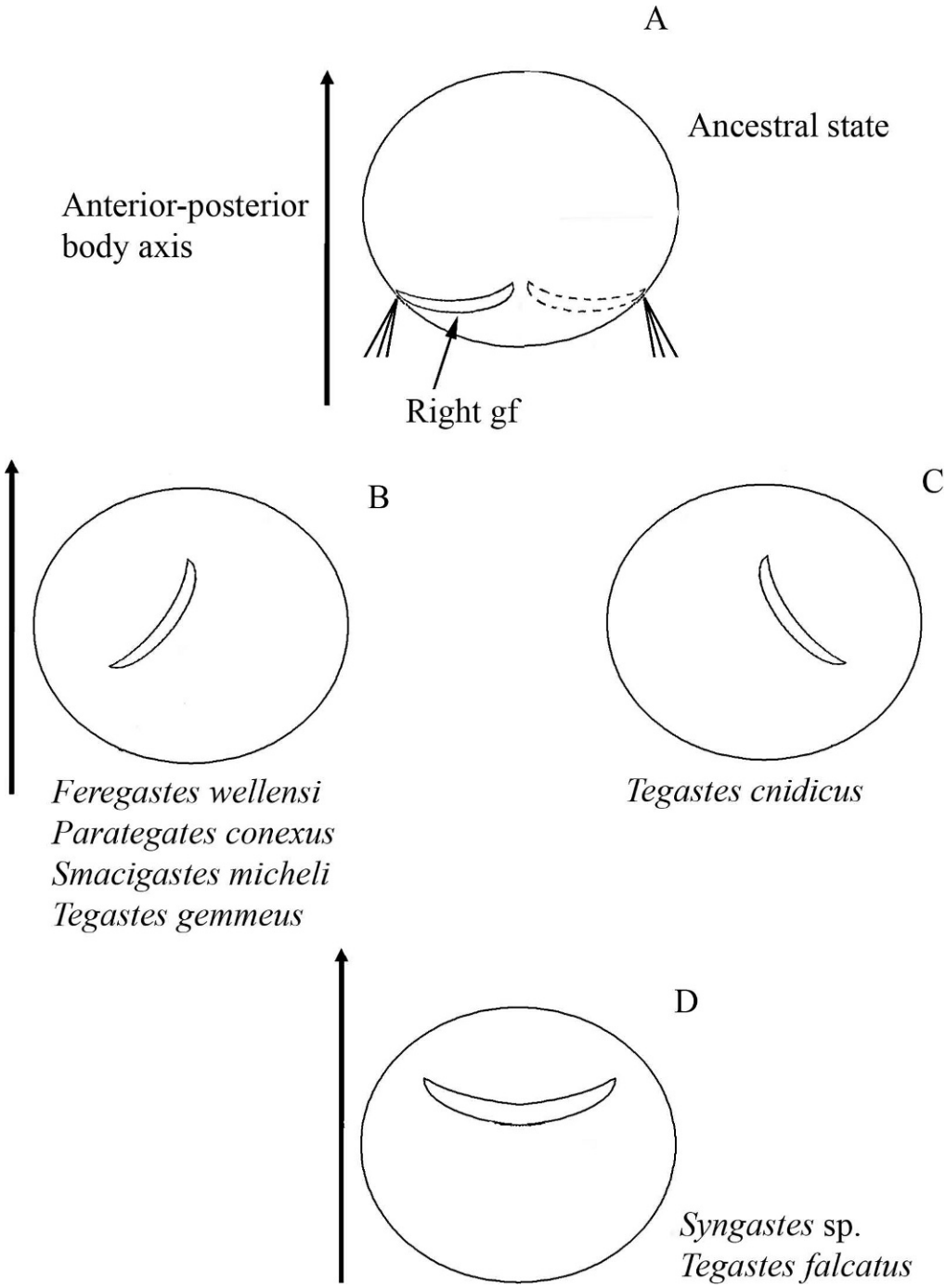


Fig. 25. Schematic comparison of position of right genital flap or protopod of leg 6 on genital triple-somite complex of male, ventral view; gf (genital flap), protopod of leg 6.

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phyletic lineage Peltidiidae and Tegastidae: ''endopod of maxillule fused with basis, forming a rectangular segment, and all setae inserting at distal edge.'' The rectangular segment here is interpreted as the distal basal endite, but the uniqueness of its morphology is not questioned. The lineage Peltidiidae and Tegastidae may be diagnosed further as species having males with leg 6 pair asymmetrical. A stout spine with hyaline membrane similar to that on leg 4, CIV–VI, of *T. falcatus* also has been reported on adults of some genera of Peltidiidae, e. g. *Alteuthellopsis corallina* Humes, 1981, *Eupelte aurulenta* Wells & Rao, 1987, *Alteutha polarsternae* Dahms, 1992, and *Alteutha depressa* (Baird, 1837) (see Sars 1904). Hicks (1986) proposed that species with this stout spine belong to a monophyletic lineage within Peltidiidae. Tegastid species which share this stout spine with hyaline membrane, presumably derived from a long flexible seta with setules, may be a part of that lineage, and this would suggest that species of Tegastidae should be allocated to Peltidiidae. An alternate hypothesis, that the derived stout spine was present on the ancestor of these two families, but has been lost secondarily in some lineages of Peltidiidae, would preserve the taxon Tegastidae. A derived stout spine, such as this one, would then be a second synapomorphy for the lineage Peltidiidae and Tegastidae.

Other possible synapomorphies of the lineage Peltidiidae plus Tegastidae are expressed in the asymmetry of the male leg 6 and its somite. Presumably, male leg 6 on the seventh thoracic somite was symmetrical in the last common ancestor of the taxon sister to the lineage Peltidiidae and Tegastidae. Symmetry of leg 6 is the condition for most other harpacticoids. The common ancestor of the lineage Peltidiidae and Tegastidae may have had a slightly asymmetrical pair of leg 6, similar to the peltidiid males *Alteutha oblonga* (Goodsir, 1845) [USNM 169633, paratype] (Fig. 24A) and *Alteuthellopsis corallina* Humes, 1981 [USNM 181336, paratype] (Fig. 24B). An extension on the ventral side of the genital somite below and posterior to the right protopod of leg 6 is clearly observed in the relatively large male of *A. oblonga*. In the presumed ancestor, the male genital somite may have articulated with both the sixth thoracic somite and the anterior abdominal somite and did not protrude ventrally. The male leg 6 of the ancestor would have been slightly asymmetrical, with the protopod of the right leg slightly larger than the left; both would have borne the same number of setae.

Derived features of female and male ancestor of Tegastidae include a genital double-somite formed by the seventh thoracic somite and the anterior abdominal somite (like those of the currently monotypic genera *Smacigastes* Ivanenko & Defaye, 2004, *Feregastes* Fiers, 1986, and *Arawella* Cottarelli & Baldari, 1987), and a left leg 6 absent; all armature on the articulating protopod of the right leg 6 also would be absent. The extent to which the male internal reproductive organs have been reduced within this lineage remains to be determined. Other proposed synapomorphies of Tegastidae include: body compressed laterally; basis of leg 1 elongate and rami unsegmented; eight setae on the caudal ramus; male genital-somite complex ventrally extended; protopod of male leg 6 an unarmed genital flap; female leg 5 with broad baseoendopod forming embryo sac chamber (not reported for *Arawella* Cottarelli & Baldari, 1987). Although Tegastidae have been described as expressing several of the character states mentioned above (see Lang 1948, Seifried 2003), we believe these are shared and derived within the family.

Among seven species in five of six known genera, only *T. falcatus* and

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Syngastes sp. (Fig. 23D–F) have leg 6 in a bilaterally symmetrical position, and only in males of *T. falcatus* is the position of both the protopod of leg 6 and the attenuation of the somite bilaterally symmetrical. All other species are characterized by different degrees and different directions of asymmetry of the right protopod of leg 6 and the attenuation of the somite (see Figs. 21C, D, 22, 23A–C), as summarized in the scheme of Fig. 25. The genital triple-somite complex observed in *T. falcatus* may represent the transformation of one of the asymmetrical states to a secondary bilateral symmetry, and this may be the most derived state in the family Tegastidae.

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