



## Discovery of the male of the rare caligiform copepod *Kabataia Kazachenko, Korotaeva & Kurochkin, 1972* (Copepoda: Siphonostomatoida), with a reconsideration of its phylogenetic affinities

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### Abstract

We report the discovery of the male of the rare caligiform copepod *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972 on the gills of the type-host *Oplegnathus woodwardi* (Waite, 1900) captured in the Southern Ocean, off Australia. Light and scanning electron microscopy confirmed the unusual body plan of *Kabataia* Kazachenko, Korotaeva & Kurochkin, 1972, where only the first pedigerous somite is incorporated into the cephalothorax and the second and third pedigerous somites are fused to form a double-somite, visible both dorsally and ventrally. The adult female carries paired dorsal plates originating from the second pedigerous somite within this double-somite. In the male the second and third pedigerous somites are free and paired dorsal plates are present on the former. *Kabataia* exhibits sexual dimorphism in an unusually wide range of limbs. Most remarkable is the tubular extension from the exit pore of the maxillary gland at the base of the maxilla which reaches beyond the anterior margin of the mouth tube; this is present in the male only. *Kabataia* exhibits a functional articulation between the first and second pedigerous somites and thus lacks the diagnostic apomorphy of the family Trebiidae (incorporation of both first and second pedigerous somites into the cephalothorax). We propose to transfer *Kabataia* to the Pandaridae, since it shares the key synapomorphies of this family. Furthermore, we propose to transfer *Innaprokofevnas* Kazachenko, 2001 to the Dissonidae, which leaves *Trebius* Krøyer, 1838 as the only genus within the Trebiidae. The correct spelling of *Philorthratoriscus* Horst, 1897 is noted.

**Key words:** *Kabataia*, Trebiidae, caligiform, Pandaridae, copepod parasite, *Oplegnathus* host, *Philorthratoriscus*

### Introduction

*Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972 is a rare parasite of an oplegnathid fish, *Oplegnathus woodwardi* (Waite, 1900), found in Australian waters. It has been reported on just a single occasion and was originally described from adult females only (see Kazachenko *et al.* 1972). Its host was originally reported as *Ostorhinchus conwaii* by Kazachenko *et al.* (1972). Boxshall & Halsey (2004) could not trace this name but the confusion concerning the taxonomy of this fish host was resolved by Gomon *et al.* (2008). *Kabataia* Kazachenko, Korotaeva & Kurochkin, 1972 was placed in the copepod family Trebiidae Wilson, 1905 (Copepoda: Siphonostomatoida), a family diagnosed by the incorporation of the first and second pedigerous somites into the dorsoventrally flattened caligiform cephalothorax, combined with the retention of separate third and fourth pedigerous somites between the cephalothorax and the genital complex (Kabata 1979; Boxshall & Halsey 2004).

Until the discovery of *Kabataia* in 1972, the family Trebiidae comprised only its type genus *Trebius* Krøyer, 1838, and the family diagnosis was identical with that of this genus. All the species of *Trebius* utilise elasmobranchs as hosts (Boxshall & Halsey 2004) unlike *Kabataia* which was found on an actinopterygian host. Changes in the diagnosis of the family were required by the discovery of *K. ostorhynchi* which differed from

*Trebius* species in having paired dorsal plates on the second pedigerous somite of the female and in lacking a sternal furca, as well as in using an actinopterygian host. Subsequently a third genus, *Innaprokofevnas* Kazachenko, 2001, reported from a pleuronectid actinopterygian host, was placed in the Trebiidae (see Kazachenko 2001). The only species, *Innaprokofevnas orientcolae* Kazachenko, 2001, is parasitic on the roughscale sole *Clidoderma asperrimum* (Temminck & Schlegel, 1846). The validity of the placement of *Kabataia* and *Innaprokofevnas* in the Trebiidae has never been analysed.

The discovery of the male of *Kabataia* plus additional female specimens has provided the opportunity to expand our knowledge of the morphology of this interesting genus and to re-examine its phylogenetic relationships in order to better estimate its classification within the cluster of caligiform families.

## Materials and methods

Four knifejaw, *Oplegnathus woodwardi*, were captured by recreational fishers on the slopes of the continental shelf off Port MacDonnell, South Australia, in May 2007 and May 2008. Copepods were recovered from host gills using a dissecting microscope and fixed in 70% ethanol. Specimens were cleared in lactophenol prior to morphological examination. Selected specimens were measured (14 ♀♀ and 4 ♂♂, unless indicated otherwise) using a calibrated eyepiece micrometer and drawings were made with the aid of a drawing tube. The anatomical terminology follows Huys & Boxshall (1991). Parasite prevalence and intensity, followed by the range of parasites recovered in parentheses, are given in whole numbers and follow Bush *et al.* (1997). The total length (*LT*) range of parasitised hosts is presented in millimetres, followed in parentheses by the total length range of all fish examined and the total number of hosts studied. Five female and three male specimens were prepared for scanning electron microscopy (SEM). Specimens were dehydrated through a graded acetone series (70; 80; 90; 95; 100; 100%) before critical point drying using liquid carbon dioxide as the exchange medium, and sputter coating with gold-platinum alloy. Representative specimens have been deposited in the Natural History Museum, London (NHMUK) and the Crustacean collection at the South Australian Museum, Australia (SAMA C).

## Taxonomic account

### Order Siphonostomatoida Burmeister, 1835

### Family Pandaridae Milne Edwards, 1840

### Genus *Kabataia* Kazachenko, Korotaeva & Kuroshkin, 1972

### *Kabataia ostorhynchi* Kazachenko, Korotaeva and Kurochkin, 1972 (Figs. 1–7)

**Host.** *Oplegnathus woodwardi* (Waite, 1900), Oplegnathidae (Perciformes).

**Locality.** Slopes of the continental shelf, off Port MacDonnell, South Australia, Australia.

**Site.** Gills; attached to gill lamellae.

**Prevalence and intensity.** 100, 38 (6–89); *LT* 401 (385–430) mm; *n* = 4.

**Material examined.** 35 ♀♀; nine ♂♂ (including three ♂♂ and five ♀♀ studied by SEM).

**Material accessioned.** Five ♀♀, one ♂ (NHMUK reg. no. 2007.947); two ♂♂ (NHMUK reg. nos 2009.263–264); ten ♀♀ (NHMUK reg. nos 2009.265–274); 15 ♀♀ (SAMA C8283); three ♂♂ (SAMA C8284).

**Description of adult female.** Body (Figs. 1A–C, 2A) dorsoventrally flattened; body length 2.63 mm (2.43–2.85 mm) measured from anterior margin of frontal plates to posterior margin of caudal rami, excluding caudal setae; maximum width 1.31 mm (1.25–1.4 mm), measured at widest point of dorsal cephalothoracic shield. Body comprising anterior cephalothorax, fused second and third pedigerous somites forming double-somite, free fourth pedigerous somite, genital complex, and abdomen (Figs. 1A, 2A–E). Cephalothorax incorporating first pedigerous somite, covered by dorsal cephalothoracic shield provided with conspicuous strips of membrane along margins of lateral areas; paired frontal plates, provided with marginal membrane; lunules absent (Fig. 1A). Nauplius eye

visible dorsally (Fig. 1A). Second and third pedigerous somites fused, with plane of fusion marked dorsally by transverse suture (arrowed in Fig. 2B). Paired dorsal plates present on second pedigerous somite, originating laterally and extending posteriorly beyond posterior border of fourth pedigerous somite and overlapping onto anterior dorsal surface of genital complex. Fourth pedigerous somite short, forming waist separating double (second-third) pedigerous somite from genital complex, lacking dorsal plates. Genital complex slightly broader than cephalothorax; about 1.4 times wider than long ( $n = 12$ ); bearing fifth legs ventro-laterally (Fig. 3F, 4E).

Free abdomen comprising anal somite; about twice wider than long, with median anal slit, bearing caudal rami posteriorly. Caudal rami (Fig. 1C) dorsoventrally flattened, about 1.2 times longer than wide; medial margin ornamented with row of long setules; armed with three long plumose setae on distal margin, two shorter pinnate setae on lateral margin and naked inner distal seta. Egg sacs linear, uniseriate (Figs. 1A, 2A).

Antennule two-segmented (Fig. 1A, D); first segment with total of 27 irregularly plumose setae, arranged with 25 along anterior and anteroventral surfaces, plus two dorsal setae: second segment slender, cylindrical, with one seta located near middle of posterior margin plus apical array of 12 setal elements (no aesthetasc identifiable).

Antenna uniramous (Figs. 1E, 3A), comprising coxa, basis and curved, laterally directed subchela formed by fusion of endopod and distal claw; coxa unarmed; basis unarmed but with finely striated integument; subchela forming strong claw with sclerotized tip, armed with short slender seta proximally and longer seta in mid-region near anterior margin.

Postantennal process (Figs. 1F, 3B) well-developed, claw-like, with two papillae bearing multiple sensillae, plus similar multi-sensillate papilla on adjacent ventral cephalothoracic surface.

Mouth tube (Fig. 3C) tapering distally, formed by labrum and labium, with narrow distal opening surrounded by marginal membrane.

Mandible (Fig. 1G) elongate, stylet-like, bearing 12 teeth on one side near apex.

Maxillule (Fig. 1H) with basal portion incorporated into ventral cephalothoracic wall; anterior papilla bearing three unequal setae; posterior lobe forming curved spiniform process.

Maxilla (Figs. 1I, 3D) slender, brachiform; armed with two elements at tip, calamus ornamented with three spiral rows of serrated membrane; canna shorter, ornamented with single strip of finely serrated membrane; pore of maxillary gland simple, without tubular extension.

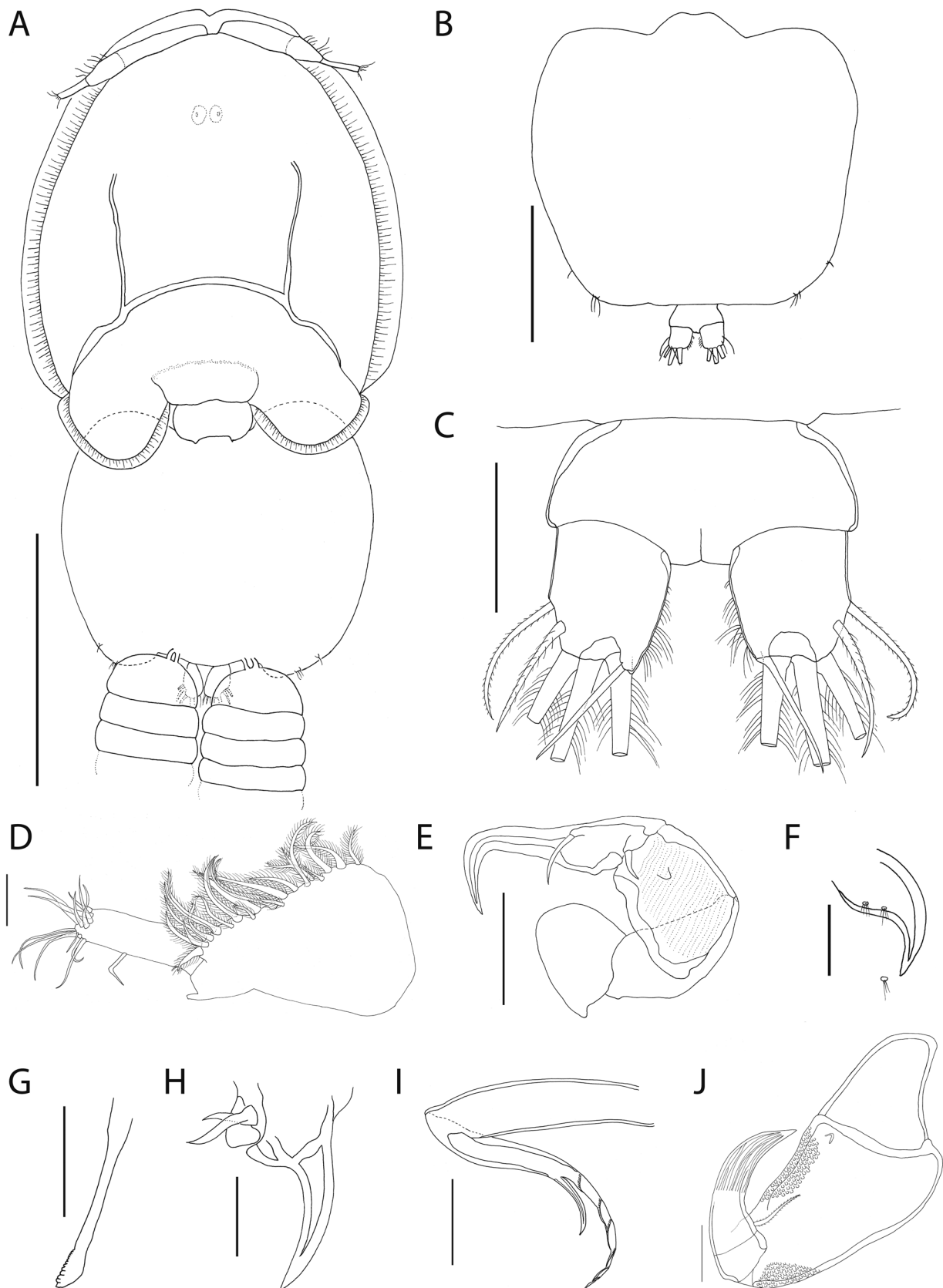
Maxilliped (Figs. 1J, 3E) comprising robust corpus and distal subchela representing fused endopodal segments plus heavily sclerotized terminal claw; corpus ornamented with patches of minute denticles on distal outer margin; subchela subdivided by incomplete suture line, and bearing single seta about at level of suture; reduced myxal process present on corpus opposing tip of claw; claw finely ridged distally (Fig. 3E).

Sternal furca absent.

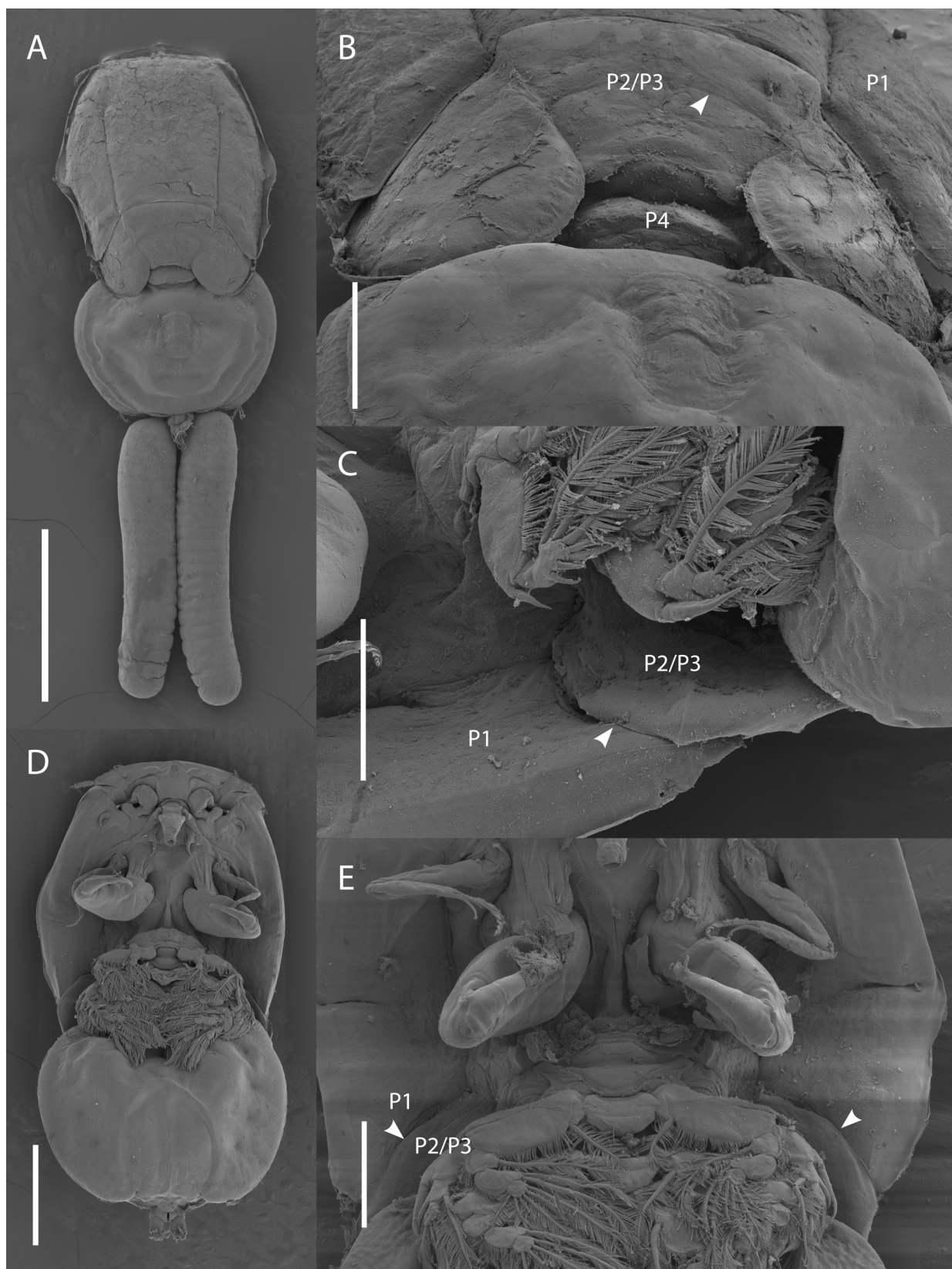
Swimming legs 1–4 biramous (Fig. 4A–E); armature on rami of legs 1–4 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Endopod	Exopod
leg 1	0–0	1–1	0–0; 3	I–0; II–5
leg 2	0–1	1–0	0–1; 0–2; 6	I–I; I–I; III–4
leg 3	0–1	1–0	0–1; 0–1; 4	I–I; I–I; III–4
leg 4	0–1	1–0	0–1; 4	I–I; I–I; III–4

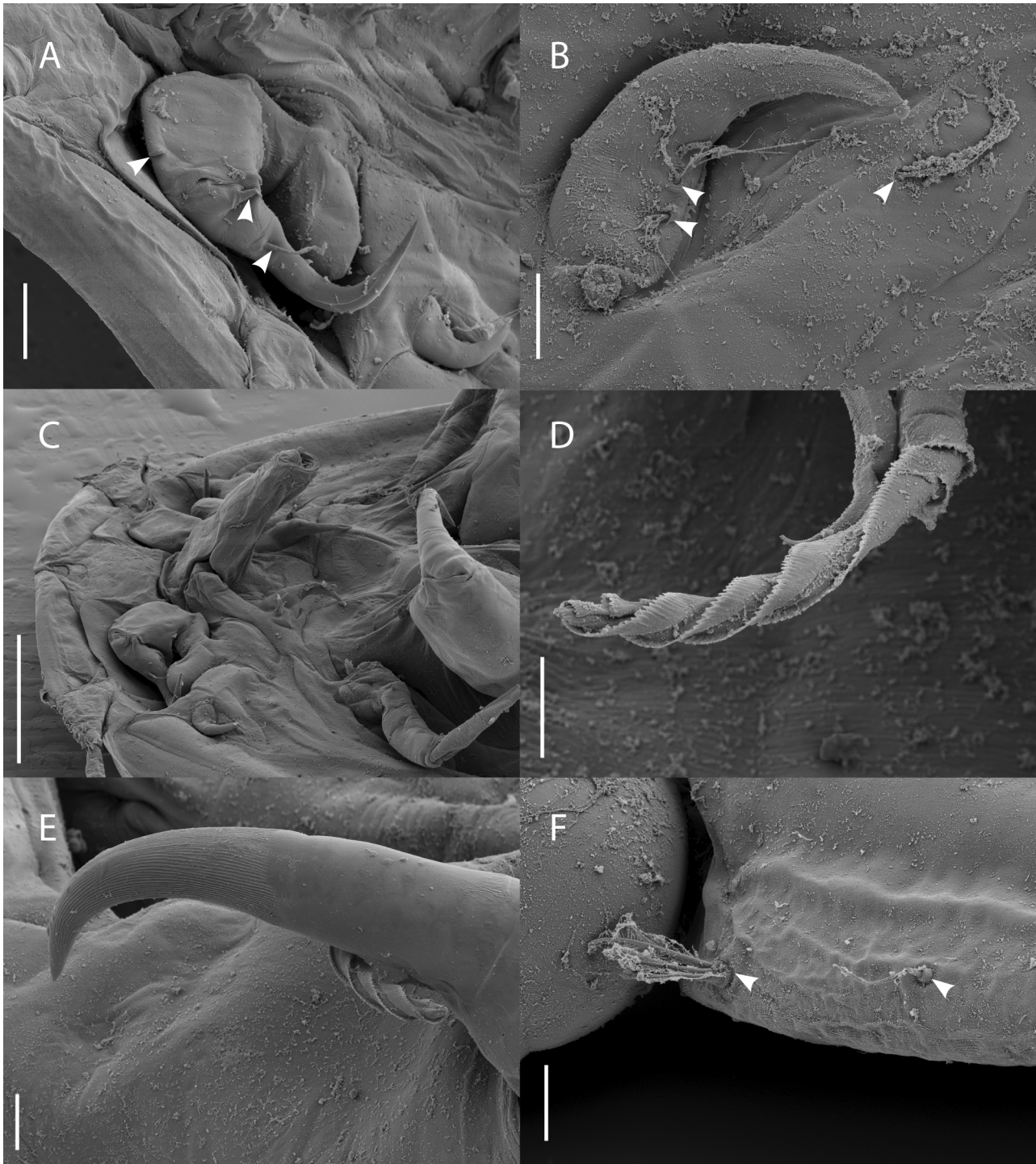
Leg 1 (Fig. 4A) joined by slender intercoxal sclerite forming interpodal bar, without marginal membrane. Protopod comprising incompletely separated coxa and basis; coxa unarmed; basis rectangular with outer plumose seta and inner basal plumose seta located near to origin of endopod. Endopod two-segmented; first segment unarmed, second segment armed with three plumose setae distally and ornamented with setule row along lateral margin. Exopod two-segmented; first segment elongate, robust, armed with slightly curved, spinulate spine at outer distal angle, lacking inner seta but with inner marginal row of long setules; second segment with two curved outer margin spines, two mid-length plumose setae distally, plus three long plumose setae and ornamented with setule row along inner margin.



**FIGURE 1.** *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972 (adult female). A, habitus, dorsal; B, genital complex, ventral; C, anal somite and caudal rami, ventral; D, antennule, ventral; E, antenna, ventral; F, postantennal process, ventral; G, mandible, ventral; H, maxillule, ventral; I, maxilla, ventral; J, maxilliped, posterior. Scale bars: A = 1 mm; B = 500  $\mu$ m; C, E, H–J = 100  $\mu$ m; D, G = 50  $\mu$ m.



**FIGURE 2.** Scanning electron micrographs of adult female *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972. A, female with egg sacs, dorsal; B, double-somite, comprising fused second and third pedigerous somites (P2/P3), and free fourth pedigerous somite (P4), dorsal, with arrowhead indicating suture; C, functional articulation (arrowhead) between first pedigerous somite (P1) and double-somite (P2/P3), ventral view; D, habitus, ventral; E, ventral surface of cephalothorax with leg 1 removed to reveal articulation between first pedigerous and double P2/P3 somites (arrowheads). Scale bars: A = 1 mm; D = 500  $\mu$ m; B, C, E = 200  $\mu$ m.



**FIGURE 3.** Scanning electron micrographs of adult female *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972. A, antenna *in situ*, showing blunt projection on basis (left arrowhead) and setae (other two arrowheads); B, postantennal process showing multi-sensillate papillae (arrowheads); C, oral region, ventrolateral; D, tip of maxilla, showing spirally-arranged serrated membranes; E, maxilliped, showing finely ridged tip of claw; F, posterolateral corner of genital complex, lateral view showing components of leg 5 (arrowhead). Scale bars: A, F = 50  $\mu\text{m}$ ; B, D, E = 20  $\mu\text{m}$ ; C = 200  $\mu\text{m}$ .

Leg 2 (Fig. 4B) joined by slender intercoxal sclerite ornamented with large flap of marginal membrane along free posterior margin. Protopod comprising coxa and basis; coxa armed with long plumose inner seta; basis armed with short spinulate outer plumose seta, and ornamented with row of setules along posterior margin. Endopod three-segmented; each segment with setule row along lateral margin; first segment armed with inner long plumose seta, second with two long plumose setae, and third segment bearing six long plumose setae. Exopod three-

segmented; each segment with row of setules along inner margin and short setules present on lateral margin of second and third segment. First segment with enlarged outer spinulate distal spine and inner plumose seta, second segment with medium distal spine and inner plumose seta; third segment smallest, armed with three spinulate outer spines, increasing in size distally, plus four long plumose setae.

Leg 3 (Fig. 4C) joined by slender intercoxal sclerite ornamented with large flap of marginal membrane along free posterior margin. Protopod comprising coxa and basis; coxa armed with long plumose inner seta; basis armed with long spinulate outer spine, and ornamented with row of setules along posterior margin. Endopod three-segmented; each segment ornamented with setule row along lateral margin; first and second segments each armed with inner plumose seta; third segment bearing four long plumose setae. Exopod three-segmented; each segment with row of long setules along inner margin (not drawn in segments one or two in Fig. 4C) and short setules on lateral margin of second and third segments. First and second segments each with outer distal spine and inner plumose seta; third segment smallest, armed with three spinulate outer spines, increasing in size distally, plus four long plumose setae.

Leg 4 (Fig. 4D) joined by slender intercoxal sclerite, lacking marginal membrane. Protopod comprising coxa and basis; coxa armed with very long, curved, inner plumose seta; basis armed with spinulate outer spine, and ornamented with row of long setules along posterior margin. Endopod two-segmented; both segments ornamented with setules along lateral margin; first segment with inner plumose seta; second segment with four plumose setae. Exopod three-segmented; each segment with row of long setules along inner margin and short setules on lateral margin of second and third segments. First and second segments each with spinulate outer spine and inner plumose seta; third segment with three spinulate outer spines, increasing in size distally, plus four plumose setae.

Leg 5 (Figs. 3F, 4E) vestigial, represented by isolated (protopodal) seta on surface of genital complex and small exopodal lobe bearing three small plumose setae.

**Description of adult male.** Dorsoventrally flattened as in female; body length 2.25 mm (1.825–2.775 mm) measured from anterior margin of frontal plates to posterior margin of caudal rami, excluding caudal setae; maximum width 1.49 mm (1.125–1.9 mm), measured at widest point of dorsal cephalothoracic shield. Dorsal cephalothoracic shield and frontal plates provided with marginal membrane as in female (Figs. 5A, 6A). First pedigerous somite incorporated into cephalothorax. Second and third pedigerous somites free, separated by functional articulation (arrowed in Fig. 6B–C). Second pedigerous somite with paired dorsal plates originating laterally, as in female. Fourth pedigerous somite short, forming waist separating distinct third pedigerous somite from genital complex; lacking dorsal plates. Genital complex (Figs. 5B, 7A) about as wide as long, with widest point about at mid-length; bearing legs 5 and 6 ventrally; genital apertures paired, each closed off by flattened operculum representing leg 6.

Abdomen comprising two free somites; anal somite wider than preceding somite. Caudal rami (Fig. 5B) ornamented and armed as in female.

Antennule (Fig. 7B) as for female.

Antenna (Fig. 7C–D) three-segmented; first segment with surface striations; second segment with five large crenulated adhesion pads and corrugated processes; third segment forming curved claw bearing accessory claw proximally (Fig. 7D), one large naked seta, plus projecting corrugated adhesion pad.

Postantennal process (Fig. 5C) as in female except with additional large basal papilla bearing multiple sensillae.

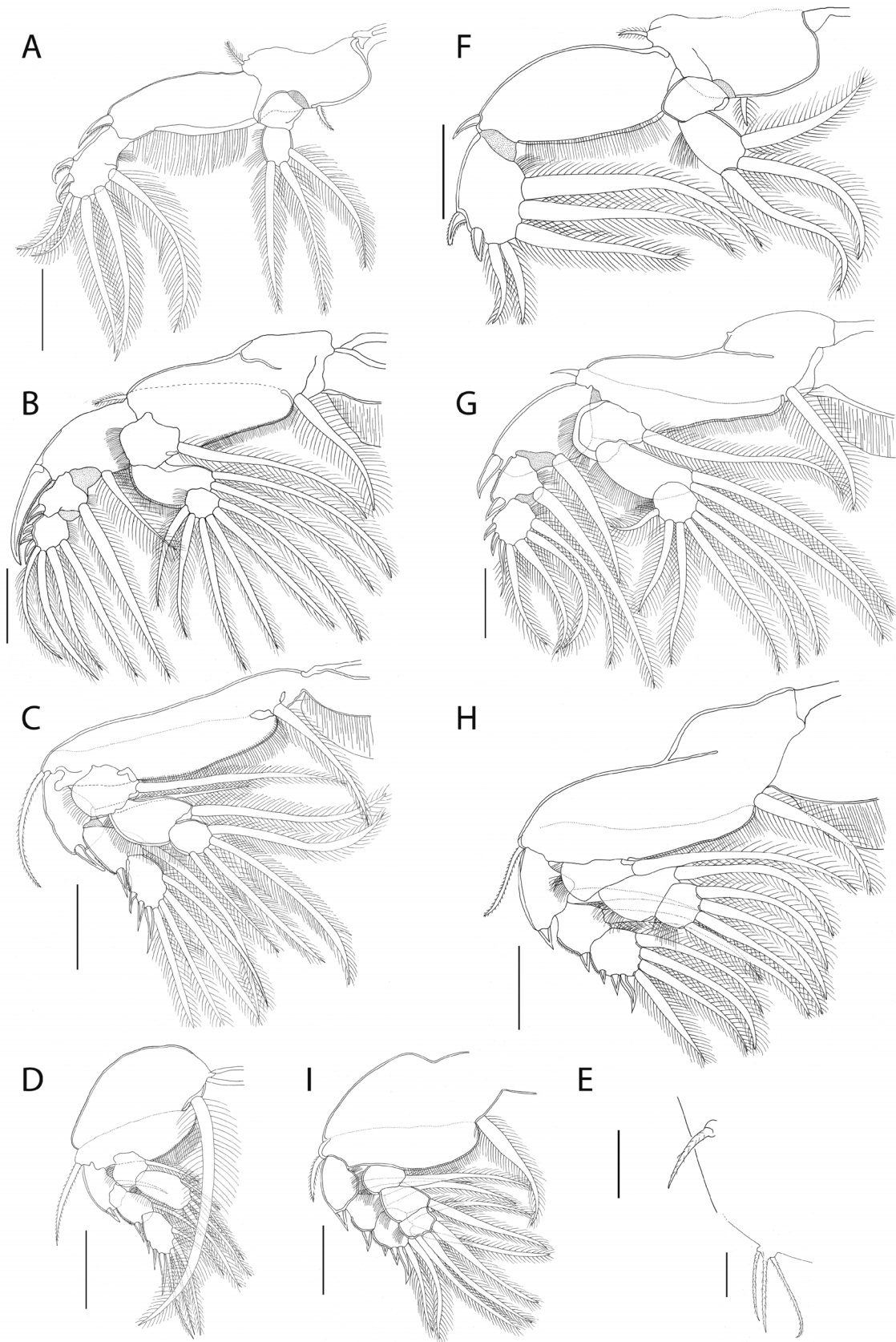
Mouth tube (Fig. 7E–F) and mandible as for female.

Maxillule (Figs. 5D, 7E) with robust swollen basal part carrying tapering posterior process plus three accessory processes of different sizes; anterior papilla armed with one small and two large setae.

Maxilla (Figs. 5E, 7D) brachiform; with large excretory pore at base of syncoxa opening into elongate tube pore extending 237 to 257  $\mu\text{m}$  medially ( $n = 3$ ), reaching beyond anterior edge of mouth cone (arrowed in Fig. 7D); calamus with three spirally-arranged rows of serrated membrane; canna with two rows of serrated membrane.

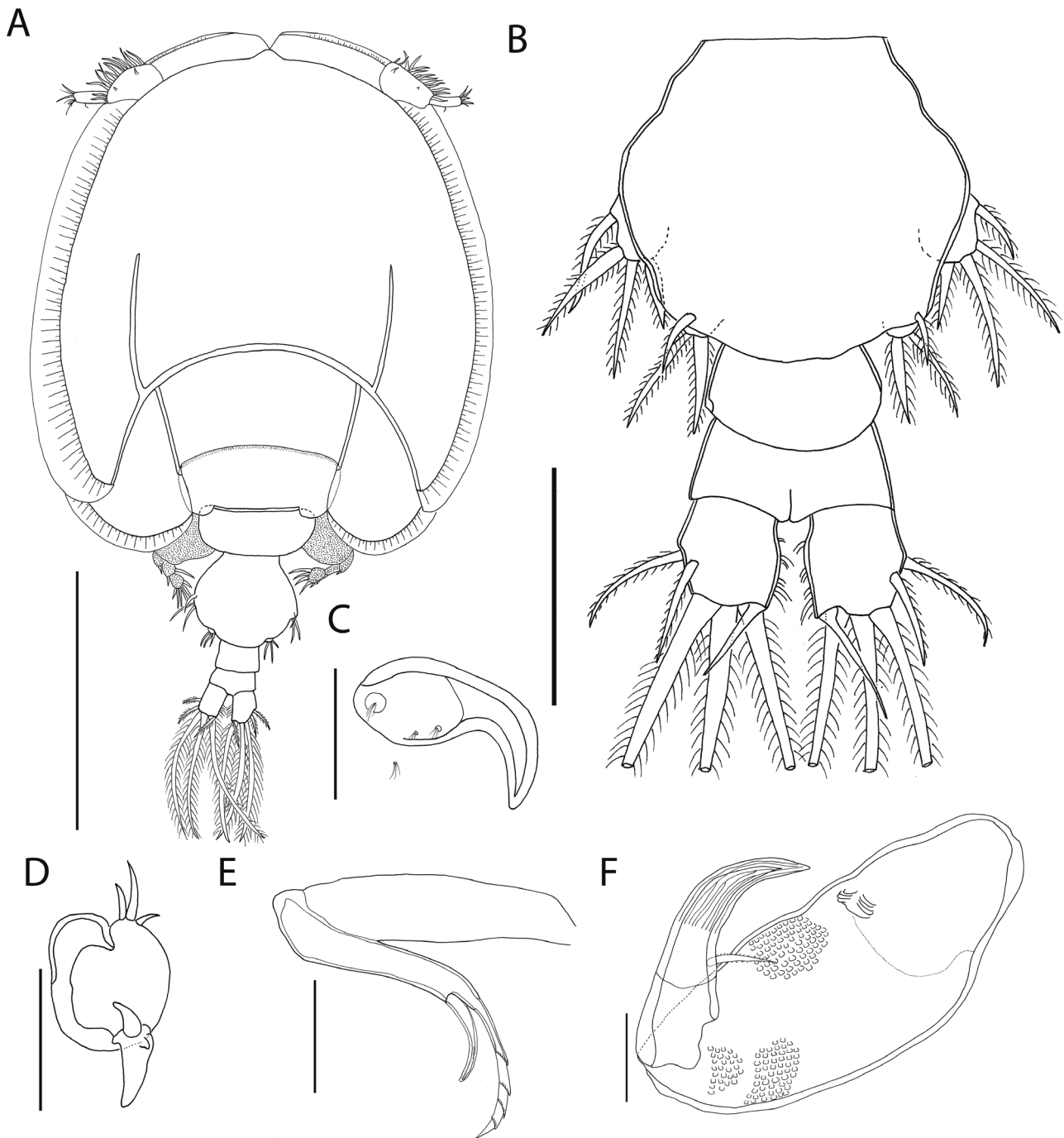
Maxilliped (Figs. 5F, 7G, H) comprising robust corpus and distal subchela; corpus ornamented with three large patches of epicuticular scales on distal outer surface; claw of subchela ridged at tip; small corrugated myxal process present on corpus, opposing tip of claw (Fig. 7H).

Sternal furca absent.



**FIGURE 4.** Legs of *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972 (adult female and adult male). A, female leg 1; B, female leg 2; C, female leg 3; D, female leg 4; E, female leg 5; F, male leg 1; G, male leg 2; H, male leg 3; I, male leg 4. Scale bars: A–D, F–I = 100  $\mu$ m; E = 50  $\mu$ m.



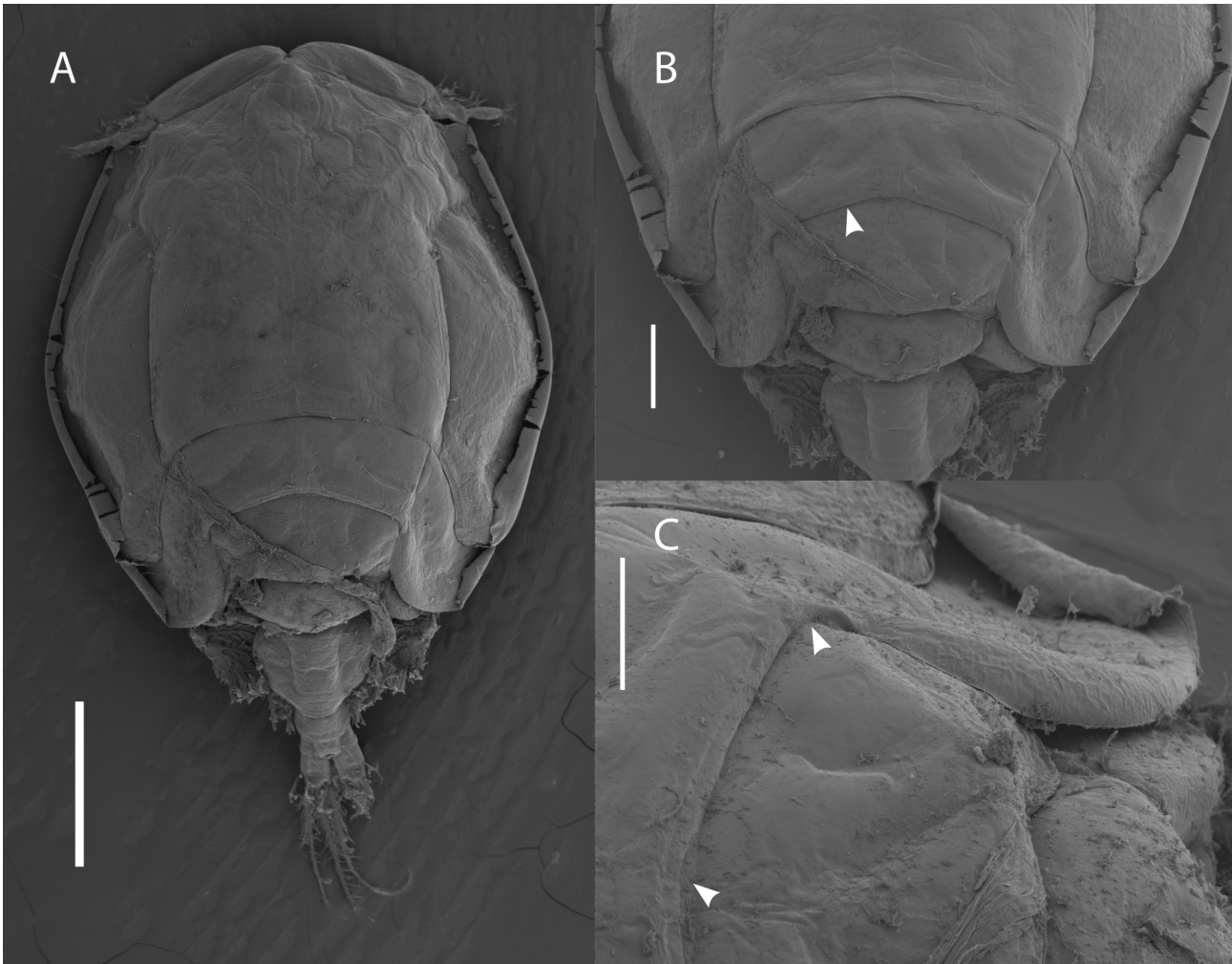


**FIGURE 5.** *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972 (adult male). A, habitus, dorsal; B, genital complex and free abdominal somites, dorsal, showing legs 5 and 6; C, postantennal process; D, maxillule; E, maxilla; F, maxilliped. Scale bars: A = 1 mm; B = 200  $\mu$ m; C–F = 100  $\mu$ m.

Legs as in female, with the following differences: leg 1 (Fig. 4F) basis with outer seta; outer spine on first exopodal segment shorter than in female; spines on second exopod segment not curved; leg 2 (Fig. 4G) basis with outer seta; spine on first exopodal segment reduced; distalmost spine on third segment longer than in female; leg 3 (Fig. 4H): basis with shorter outer seta, and distal spine on first exopodal segment shorter.

Leg 4 (Fig. 4I) with three-segmented endopod with setal formula 0 - 1, 0 - 1; 3; basis with shorter outer seta; inner plumose seta on coxa shorter than in female.

Leg 5 (Figs. 5B, 7A) represented by isolated plumose seta on surface of genital complex, plus posterior exopodal lobe bearing three plumose setae. Leg 6 (Figs. 5B, 7A) represented by flattened lobe closing off genital aperture, armed with one small and two large plumose setae.

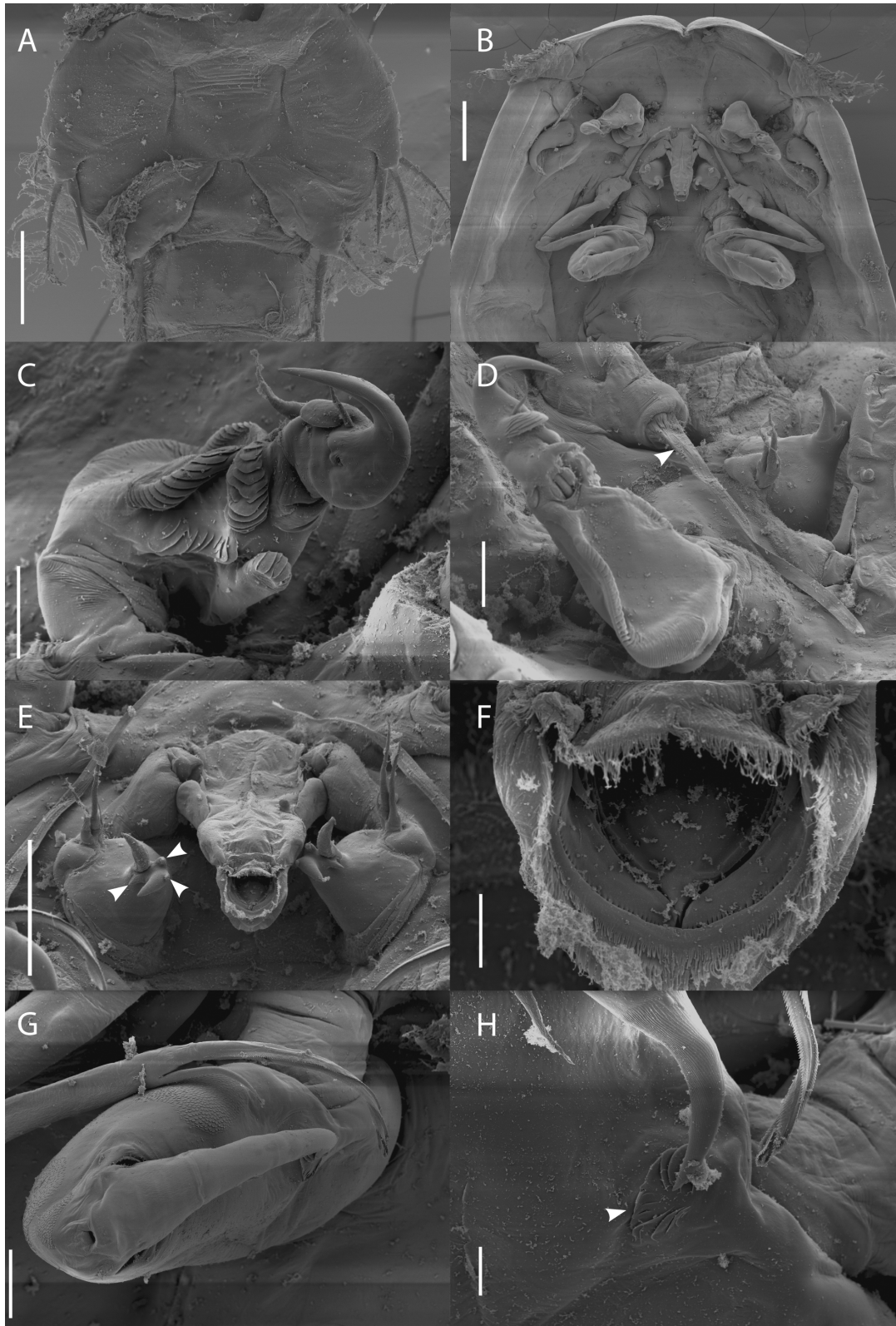


**FIGURE 6.** Scanning electron micrographs of adult male *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972. A, habitus, dorsal; B, posterior part of cephalothorax and free pedigerous somites, dorsal view showing surface sutures; C, same showing detail of functional articulation between second (P2) and third (P3) pedigerous somites (indicated by arrowheads). Scale bars: A = 500 µm; B, C = 200 µm.

## Discussion

*Kabataia* exhibits sexual dimorphism in an unusually wide range of characters. In the caligiform families it is common to find sexual dimorphism in the form of the genital complex plus legs 5 and 6 which it bears, in abdominal segmentation, in the form of the antenna and the maxilliped. Sexual dimorphism also occurs, but less commonly, in the postantennal process (e.g., Boxshall & El-Rashidy 2009) and in the maxillule (e.g., *Lepeophtheirus* von Nordmann, 1832, see Dojiri & Ho 2013). However, the form of the dimorphism exhibited in the maxillule of *Kabataia* is unusual. The female has a typical caligiform maxillule comprising an anterior papilla-like process bearing three unequal setae plus a tapering, spiniform posterior process. In the newly discovered male the posterior process is swollen, almost hemispherical, and carries four processes, one of which presumably represents the main posterior process and the other three are accessory processes. This is a unique expression of sexual dimorphism in the caligiform families.

The maxilla is a typical brachiform limb in both sexes in the caligiform families. Its primary role may be in grooming and it can also be involved in settling movements on the surface of the host (Kabata & Hewitt 1971), but it varies little in structure, rarely showing any sexual dimorphism. In *Kabataia* there is remarkable dimorphism: in the male only there is a tubular extension (referred to as a tube pore in harpacticoid literature) originating around the exit pore of the maxillary gland at the base of the maxilla, and extending about 248 µm antero-medially beyond



**FIGURE 7.** Scanning electron micrographs of adult male *Kabataia ostorhynchi* Kazachenko, Korotaeva & Kurochkin, 1972. A, genital complex, ventral view showing legs 5 and 6; B, mouthparts *in situ*, ventral; C, antenna showing corrugated adhesion pads; D, base of maxilla showing tube pore extension (arrowhead), plus claw of antenna; E, oral region with maxillule showing accessory processes (arrowheads); F, tip of mouth tube; G, maxilliped showing surface ornamentation of epicuticular scales; H, tip of claw of maxilliped and myxal process (arrowhead) opposing tip. Scale bars: A, E = 100 $\mu$ m; B = 200 $\mu$ m; C, D = 50  $\mu$ m; F = 10  $\mu$ m; G = 50  $\mu$ m; H = 10  $\mu$ m.

the anterior margin of the mouth tube. Such tube pore extensions have been reported in other siphonostomatoid copepods, such as the dinopontiid *Sinopontius aesthetascus* Boxshall, 1990 in which it was misinterpreted as an aesthetasc (Boxshall 1990a), but the sexual dimorphism exhibited in this feature in *Kabataia* is unique.

Sexual dimorphism in swimming legs is a phylogenetically informative character in caligiform copepods and has been used in phylogenetic analyses (e.g., Boxshall & Justine 2005). There is, for example, sexual dimorphism in the form of the exopodal spines of leg 2 of the caligid genera *Alebion* Krøyer, 1863 and *Pupulina* van Beneden, 1892, and Tang *et al.* (2012) noted that the male of *Prosaetes rhinodontis* (Wright, 1876) shares the possession of a modified terminal endopodal segment on leg 3 with other male pandarids (including the cecropids). *Kabataia* shows minor sexual dimorphism in swimming legs 1–3, and a difference in endopodal segmentation in leg 4; the endopod is two-segmented in the female and three-segmented in the male.

**Phylogenetic affinities of *Kabataia*.** *Kabataia* shares the basic caligiform body plan: it has a dorsoventrally flattened cephalothorax covered by a dorsal cephalothoracic shield that is expanded anteriorly to form frontal plates and laterally to form lateral expansions, the margins of which are provided with marginal membrane. This cephalothorax is separated from the genital complex by one to three free pedigerous somites. The genital complex comprises at least the fifth pedigerous, genital and first abdominal somites (see Boxshall 1990b). The number of caligiform families regarded as valid has recently decreased: currently only four are accepted: the Caligidae Burmeister, 1835, Dissonidae Yamaguti, 1963, Pandaridae, and Trebiidae. The family Euryphoridae Wilson, 1905 was considered to be a junior synonym of the Caligidae (see Boxshall & Halsey 2004; Boxshall & Justine 2005; Dojiri & Ho 2013) and both the Cecropidae Dana, 1849 and Amaterasidae Izawa, 2008 were reduced to synonymy with the Pandaridae by Tang *et al.* (2012).

The Caligidae is characterised by its advanced body form in which the first to third pedigerous somites are incorporated into the flattened cephalothorax, leaving the fourth pedigerous somite as the sole free somite anterior to the genital complex. This cephalization has created a cephalothoracic sucker which aids adhesion of caligids to the body surface of their hosts. The third pair of swimming legs is transformed into a flattened apron-like structure which functions to complete the membrane-lined rim of the cephalothoracic sucker posteriorly. *Kabataia* cannot be placed in the Caligidae because it does not share this key apomorphy of the family – only the somite bearing leg 1 is incorporated into the cephalothorax.

*Kabataia* does not belong in the Trebiidae where it was placed by Kazachenko *et al.* (1972). In *Trebius*, the type genus of the family Trebiidae, the first and second pedigerous somites are both incorporated into an extended cephalothorax leaving only two free pedigerous somites expressed between the cephalothorax and the genital complex. These two free somites are the third and fourth pedigerous somites. *Kabataia* does not share this body plan: instead only the first pedigerous somite is incorporated into the cephalothorax. The second pedigerous somite is separated from the first by an articulation visible both dorsally and ventrally (Fig. 2B–E), and is not incorporated into the cephalothorax. However, it is not a free somite as it is fused to the third pedigerous somite to form a double-somite in the female. The key character state here is that the articulation between first and second pedigerous somites is expressed. Thus, *Kabataia* lacks the diagnostic apomorphy of the Trebiidae and should be excluded from this family.

The remaining two caligiform families, the Dissonidae and Pandaridae could be considered as more basal as both typically retain discrete second, third and fourth pedigerous somites separating the flattened cephalothorax (which incorporates the first pedigerous somite as in all siphonostomatoids) from the genital complex. The Dissonidae currently comprises the genus *Dissonus* Wilson, 1906 only, and all species retain this basic plesiomorphic segmentation pattern (Boxshall *et al.* 2008). In addition, dissonids lack dorsal lobes on any of the free pedigerous somites. The fusion of the second and third pedigerous somites in adult female *Kabataia* plus the presence of paired dorsal plates derived from the second pedigerous somite indicate that *Kabataia* should not be placed in the Dissonidae.

In his review of the family, Cressey (1967) stated that all Pandaridae retained distinct second, third and fourth pedigerous somites, however Tang *et al.* (2012) stressed that the second and third pedigerous somites are fused in females of some pandarids of the genera related to *Dinemoura* Latreille, 1829. Since Cressey's (1967) review the family concept has changed and the former cecropid genera are now classified as members of the Pandaridae. A body plan in which the second and third pedigerous somites are fused to form a double-somite is also found in female *Prosaetes* Wilson, 1907 (Tang *et al.* 2010) and, as noted by Tang *et al.* (2012), only two free somites are expressed between the cephalothorax and the genital complex in the genera *Cecrops* Leach, 1816,

*Philorthratoriscus* Horst, 1897, and *Luetkenia* Claus, 1864. It is clear that *Kabataia* shares the same adult female segmentation pattern with several other pandarid genera.

Adults of both sexes of *Kabataia* also carry paired dorsal plates which originate on the second pedigerous somite (the anterior part of the double-somite in the female) and these extend posteriorly beyond the rear margin of the fourth pedigerous somite (Figs. 1A, 2A, 5A, 6A–B). The presence of paired dorsal plates is a feature typical of pandarid females and we propose to transfer *Kabataia* to the family Pandaridae.

At the suggestion of the editor, R. Huys, we note here that the generic name *Philorthratoriscus* has been misspelled [as *Philorthagoriscus*] by most authors since Horst (1897). In his revision, Wilson (1907) used the correct spelling and gave the derivation of the name, based on *Orthratoriscus* Bloch & Schneider, 1801 which was one of the old generic names of its host. Wilson (1922) continued to spell the name correctly but most other publications, including compendia such as Yamaguti (1963) and Boxshall & Halsey (2004), and revisions such as Kabata (1979) and Tang *et al.* (2010) used the incorrect spelling.

**Comments on the affinities of *Innaprokofevnas* Kazachenko, 2001.** The description of *Innaprokofevnas orientcolae* by Kazachenko (2001) did not critically assess its apomorphic character states or test the affinities of the new genus. Although material was not available for study, we consider that the original description contains sufficient information to prompt a reconsideration of its phylogenetic relationships. The body plan illustrated by Kazachenko (2001: Fig. 229) appears to show three free pedigerous somites between the cephalothorax and the genital complex, rather than only two as indicated in his text (2001: 19). This pattern is shared with *Dissonus*. Kazachenko also refers to the presence of paired dorsolateral plates on the second pedigerous somite of *Innaprokofevnas*. His figure shows a laterally extended tergite but this somite lacks any posteriorly-directed dorsal lobes like those present in *Kabataia* or other pandarids. Kazachenko (2001) demonstrated that the genital complex of *Innaprokofevnas* is ornamented with an array of conspicuous spinules on the ventral surface, as is typical for *Dissonus* species (Boxshall *et al.* 2008). While *Innaprokofevnas orientcolae* is in need of redescription, we consider that the evidence available suggests that it belongs in the family Dissonidae. We propose to transfer *Innaprokofevnas* to the Dissonidae, which leaves *Trebius* as the only genus within the Trebiidae. The validity of *Innaprokofevnas* as a genus distinct from *Dissonus* remains to be thoroughly tested.

## Acknowledgements

We thank Dennis and Kerry Heinicke and the Port MacDonnell Offshore Angling Club who assisted in the collection of fish for this research. Thierry Laperousaz from the South Australian Museum kindly curated accessioned material. Travel funds were awarded by the Australian Research Council and the National Health and Medical Research Council (ARC/NHMRC) Research Network for Parasitology to KSH for travel to London to work with GAB. This research was funded by an Australian Biological Resources Study (207-44) and Fisheries Research and Development Grant (207/225) awarded to KSH and Ian David Whittington.

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