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SEVEN NEW SPECIES OF *TORTANUS* (*ATORTUS*) (COPEPODA, CALANOIDA, TORTANIDAE) FROM NORTH SULAWESI, INDONESIA

BY

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ABSTRACT

Seven new species of the planktonic copepod genus and subgenus *Tortanus* (*Atortus*) are described from North Sulawesi, Indonesia. Four of these species, *T. (A.) indonesiensis*, *T. (A.) omorii*, *T. (A.) processus* and *T. (A.) lukmani*, belong to the *brevipes* species complex sensu Ohtsuka & Kimoto (1989). Two species, *T. (A.) sulawesiensis* and *T. (A.) manadoensis*, can be placed in the *recticauda* species complex. The seventh species, however, *T. (A.) bilobus*, belongs to neither group, which will necessitate a revision of the current morphology-based grouping with the aid of a genetically-based phylogeny. The co-occurrence of multiple closely-related congeners in a relatively small area suggests possible microhabitat segregation among these species.

RÉSUMÉ

Sept nouvelles espèces du genre et sous-genre de copépode planctonique *Tortanus* (*Atortus*) sont décrites du nord de Sulawesi, Indonésie. Quatre de ces espèces, *T. (A.) indonesiensis*, *T. (A.) omorii*, *T. (A.) processus* et *T. (A.) lukmani*, appartiennent au complexe d'espèces *brevipes* sensu Ohtsuka & Kimoto (1989). Deux espèces, *T. (A.) sulawesiensis* et *T. (A.) manadoensis*, peuvent être placées dans le complexe d'espèces *recticauda*. La septième espèce cependant, *T. (A.) bilobus*, n'appartient à aucun groupe, ce qui nécessitera une révision de l'actuel groupement fondé sur la morphologie avec l'aide d'une phylogénie basée sur la génétique. La co-occurrence de congénères étroitement apparentés dans une petite zone suggère une possible ségrégation du microhabitat parmi ces espèces.

INTRODUCTION

Planktonic copepods of the genus *Tortanus* Giesbrecht, 1898, mainly inhabit tropical or subtropical coastal waters of the Indo-West Pacific region and the

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Atlantic Ocean, and encompass 40 known species (see, e.g., Ohtsuka et al., 1987; Ohtsuka & Kimoto, 1989; Ohtsuka, 1992; Chen & Hwang, 1999; Nishida et al., 2015; Walter & Boxshall, 2016). The species of the genus are classified into five subgenera: *Tortanus* (*Tortanus*) Giesbrecht, 1898, *Tortanus* (*Eutortanus*) Smirnov, 1933, *Tortanus* (*Boreotortanus*) Ohtsuka, 1992, *Tortanus* (*Acutanus*) Ohtsuka, 1992 and *Tortanus* (*Atortus*) Ohtsuka, 1992. Of these, the subgenus *Atortus* comprises 25 species (Nishida et al., 2015), all of which are distributed exclusively in the Indo-West Pacific and many of which inhabit oligotrophic, clear waters, often associated with coral reefs and sea-grass beds (Ohtsuka & Kimoto, 1989; Ohtsuka & Reid, 1998; Ohtsuka et al., 2000; Nishida & Cho, 2005).

During the course of a study on the biodiversity of pelagic copepods in Indonesian waters, seven species of *Tortanus* (*Atortus*), so far unknown, were collected from North Sulawesi. Herein these species are described with remarks on a morphological comparison between these and other, allegedly related species. Insights gained from the co-occurrence of multiple closely-related species in a relatively small area are also discussed.

MATERIAL AND METHODS

Plankton samples were collected from nearshore waters off Tanjung Merah near Bitung along the southern coast of North Sulawesi, Indonesia, during daytime on 20-25 March 2003 by 2-min surface tows of a larval net (mesh size 0.5 mm; mouth diameter 50 cm). While sea-grass beds and coral colonies were present along shore of Tanjung Merah, the present samples were collected from the area of sea-grass beds (1-2 m deep), wherein *Thalassia hemprichii* (Ehrenberg) Aschers was the dominant sea-grass species. All samples were fixed and preserved in 2% formaldehyde/seawater. *Tortanus* (*Atortus*) specimens were sorted from the original samples, dissected with needles in 10% glycerol/distilled water under a stereo microscope, and the body and appendages were observed under a compound microscope and illustrated with the aid of a camera lucida.

Both the female and male are described for two of the seven species discovered in the present study, on the basis of co-occurrence in appreciable numbers of both sexes in the same tows. However, although suspected corresponding females of the other five species were collected, only males are described for these species, due to their mixed occurrence in small numbers, which made it impossible to determine their female-male correspondence, awaiting further research applying genetic analysis.

The morphological terminology follows Huys & Boxshall (1991) and, in particular, Ohtsuka & Reid (1998) for the segmental homology of the antennules

in both sexes and the male leg 5. Abbreviations used in the text are: TL, total length; A1, antennule; A2, antenna; Pdg1-Pdg5, pedigerous somites 1-5; Ur1-Ur5, urosomal somites 1-5; CR, caudal rami; P1-P5, legs 1-5; Re, exopod; Ri, endopod. The prosome length was measured from the anterior apex to the mid-posterior end of the prosome, and the urosome length from the mid-anterior end of urosome to the posterior end of the caudal rami. The type-specimens are formalin-preserved and deposited at the Museum Zoologicum Bogoriense (MZB), Research Center for Biology, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia.

DESCRIPTIONS

Order CALANOIDA Sars, 1903
 Superfamily DIAPTOMOIDEA Baird, 1850
 Family TORTANIDAE Sars, 1902
 Genus *Tortanus* Giesbrecht, 1898

***Tortanus (Atortus) sulawesiensis* sp. nov.** (figs. 1-3)

Material examined.— Holotype (MZB Cru. Cop. 113) female (TL: 2.28 mm), paratypes (MZB Cru. Cop. 114) 1 female (2.39 mm) and 2 males (1.96 and 2.22 mm); collected off Tanjung Merah (1°23.491'N 125°06.460'E) on 20 March 2003.

Female.— Prosome (fig. 1a, b) about 3.2 times as long as urosome; posterior corners produced into symmetrical, rounded lobes, reaching anterior 1/3 of genital compound somite. Urosome (fig. 1c) 2-segmented; genital compound somite symmetrical, about twice as long as anal somite, with large ventral process, parallelogramic in lateral view (fig. 1b); anal somite asymmetrical, right margin more convex and longer than left. CR (fig. 1c) asymmetrical, right ramus slightly wider and shorter than left, anterior part of left ramus curved medially.

A1 (fig. 1d) symmetrical, 15-segmented (ancestral segments I-IX, XI-XIV, XXVI-XXVIII fused), reaching mid-length of urosome when extended posteriorly. A2 (fig. 1g), coxa naked; basis incompletely fused with proximal segment of Ri. Re shorter than Ri and 2-segmented, 1st segment extremely short with no seta, 2nd segment ca. 6 times as long as 1st segment and furnished with short mediobasal seta and 4 apical setae. Ri 3-segmented, proximal segment furnished with tuft of setules; 2nd segment incompletely fused with distal segment; distal segment bearing 6 distal setae. Mandible (fig. 1h) palp with elongate basis (more than twice as long as Ri and Re). Re and Ri 2-segmented, distal segment with 5 and 6 apical setae, respectively; gnathobase bearing 5 cuspidate teeth and 4 rows of spinules. Maxillule (fig. 2e) praecoxal arthrite with 13 stout setae; distal segment elongated with 3 strong, pectinate terminal setae, tips of which serrated, medial

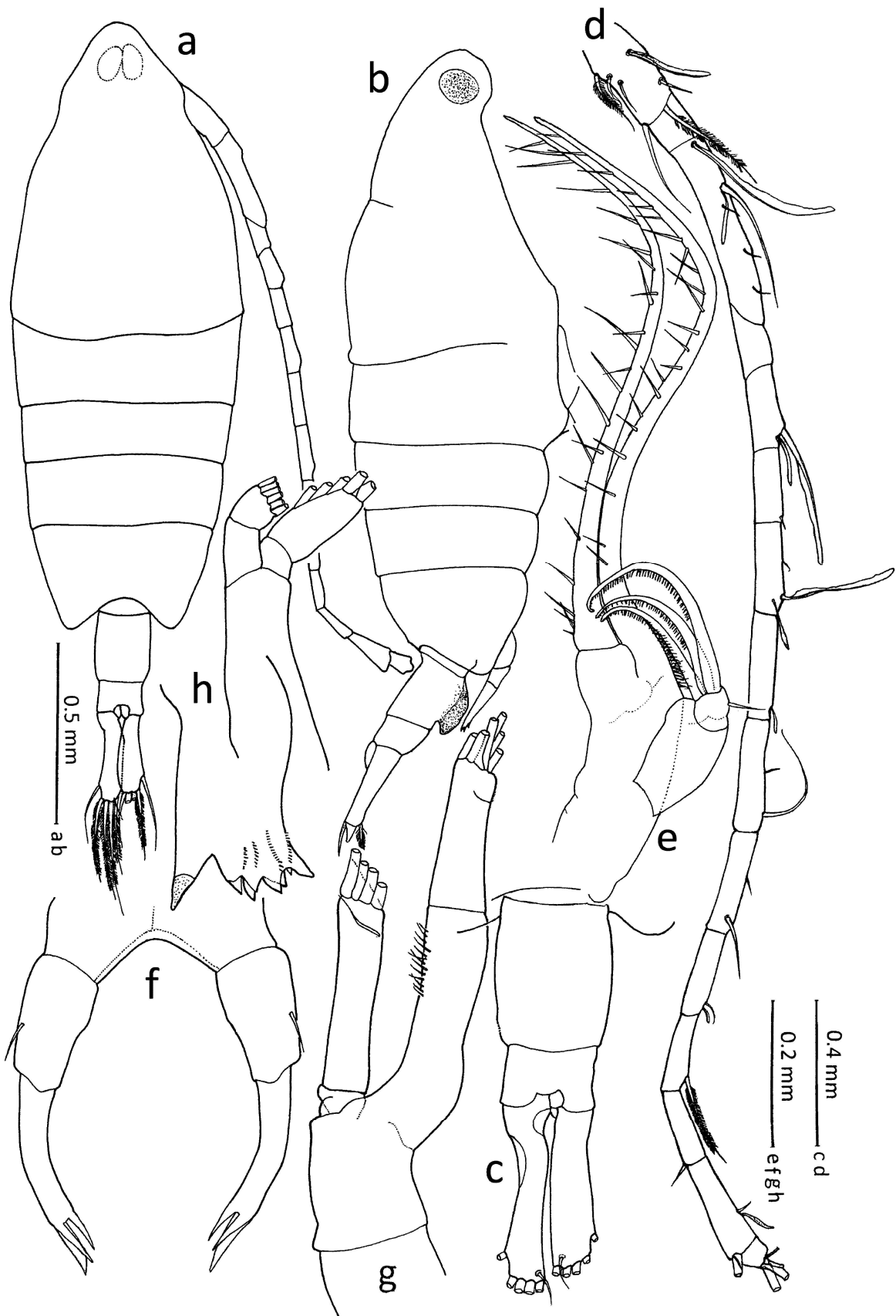


Fig. 1. *Tortanus (Atortus) sulawesiensis* n. sp., female (holotype). a, habitus, dorsal view; b, habitus, right lateral view; c, urosome, dorsal view; d, antennule; e, maxilliped; f, leg 5; g, antenna; h, mandible palp and gnathobase.

margin with row of spinules. Maxilla (fig. 2f) syncoxal endites with 1, 2, 2 and 3 setae from proximal to distal; basal endite with 1 developed and 2 rudimentary setae; Ri with 5 stout setae with claw-like tip and 2 rudimentary setae. Maxilliped (fig. 1e) syncoxa with two endites, each with spinulose seta; basis unarmed; Ri with 3 medial spinulose setae and lateral seta.

P1-4 (fig. 2a-d) biramous with 3-segmented Re and 2-segmented Ri; distal endopod segment of P1-4 with hair tuft on subdistal, anterior surface. Seta and spine formula as follows:

| | Coxa | Basis | Exopod segment 1; 2; 3 | Endopod segment 1; 2 |
|-------|------|-------|------------------------|----------------------|
| Leg 1 | 0-1 | 1-0 | 0-1; 0-1; I, I, 4 | 0-3; 1, 2, 3 |
| Leg 2 | 0-1 | 0-0 | I-1; I-1; III, I, 5 | 0-3; 1, 2, 3 |
| Leg 3 | 0-1 | 0-0 | I-1; I-1; III, I, 5 | 0-3; 1, 2, 3 |
| Leg 4 | 0-1 | 1-0 | I-1; I-1; III, I, 5 | 0-3; 1, 2, 3 |

P5 (fig. 1f) symmetrical, 3-segmented including common coxa; basis with seta near middle of lateral margin; Re slightly curved medially, ending in 3 semi-parallel prongs; central prong longest.

Male.— Prosome (fig. 3a, b) about 2.8 times as long as urosome; posterior corners not extending posteriorly as in female. Urosome symmetrical with 5 somites, devoid of any lateral protrusions. CR symmetrical, 5.3 times as long as wide.

Appendages similar to those of female, except right A1 and P5.

Right A1 (fig. 3c, d) geniculate, with segments XVI-XIX swollen. Segment XX equal in length to fused segments XXIV-XXVIII and slightly longer than fused segments XXI-XXIII. Anterior surface of segment XX furnished with ridge bearing denticles. Ridge extending just short of distal end of segment. Distal end of ridge slightly raised from surface plane of segment. Fused segments XXI-XXIII also furnished with ridges devoid of denticles on anterior surfaces. Hinge joint formed between segment XX and fused segments XXI-XXIII. Latter segment with indent on anterior surface near proximal end. Distal end of segment with a long spinous process extending almost entire length of fused segments XXIV-XXVIII.

P5 right leg (fig. 3e) coxa swollen without any processes; basis swollen, curved medially and bearing large acutely pointed process arising near inner proximal end; medial margin of segment with 3 lamellae, proximal one with 3 rounded processes, middle one triangular, and distal one digitiform with rounded tip and subterminal setule; Re claw-like with main curvature at proximal 1/3, furnished with setule on medioproximal margin, and subdistal spinule on lateral margin, medial margin with subdistal tongue-like process running toward and short of distal end, segment ending in two pointed tips, lateral tip longer and more acute

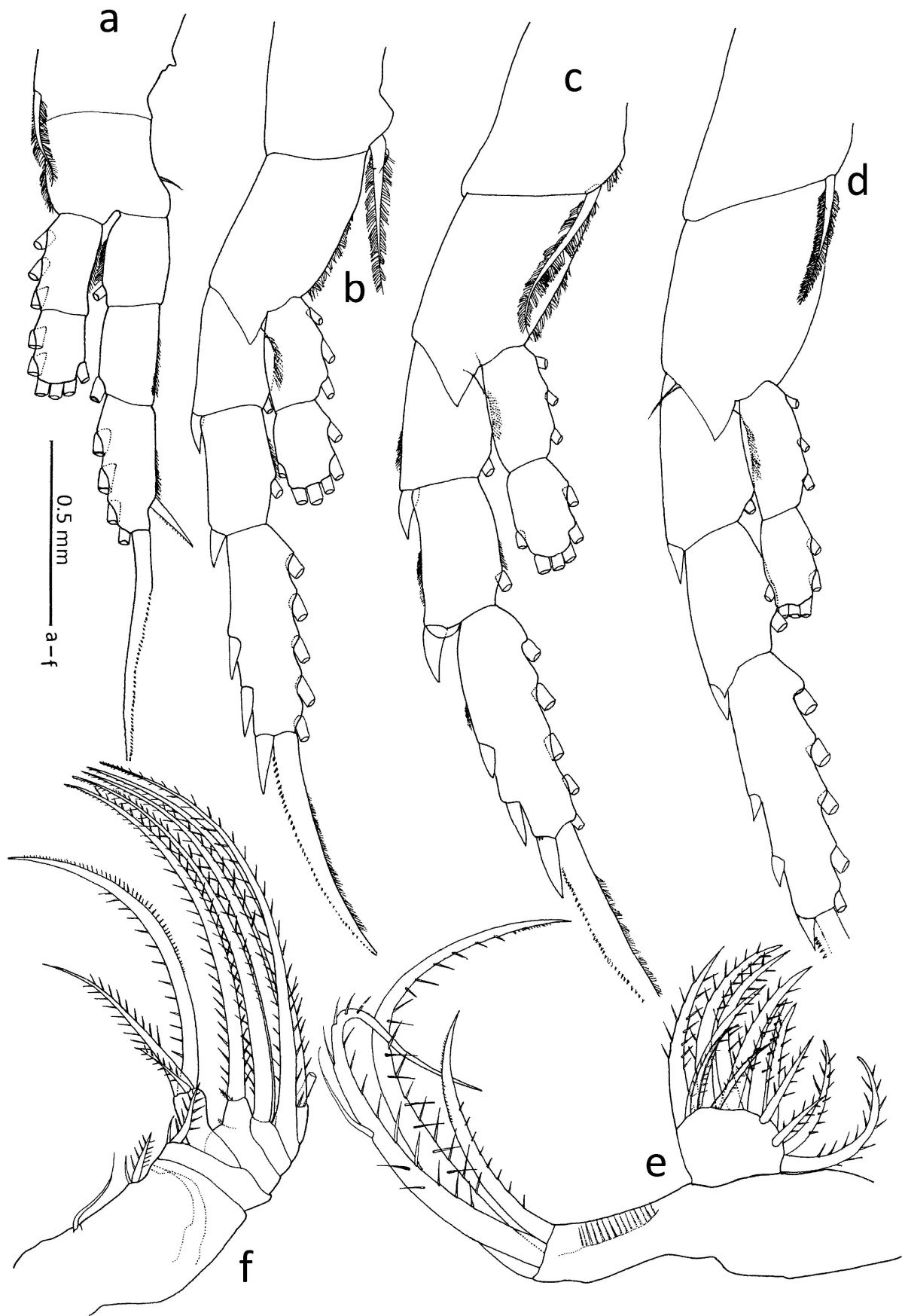


Fig. 2. *Tortanus (Atortus) sulawesiensis* n. sp., female (holotype). a-d, legs 1-4; e, maxillule; f, maxilla.

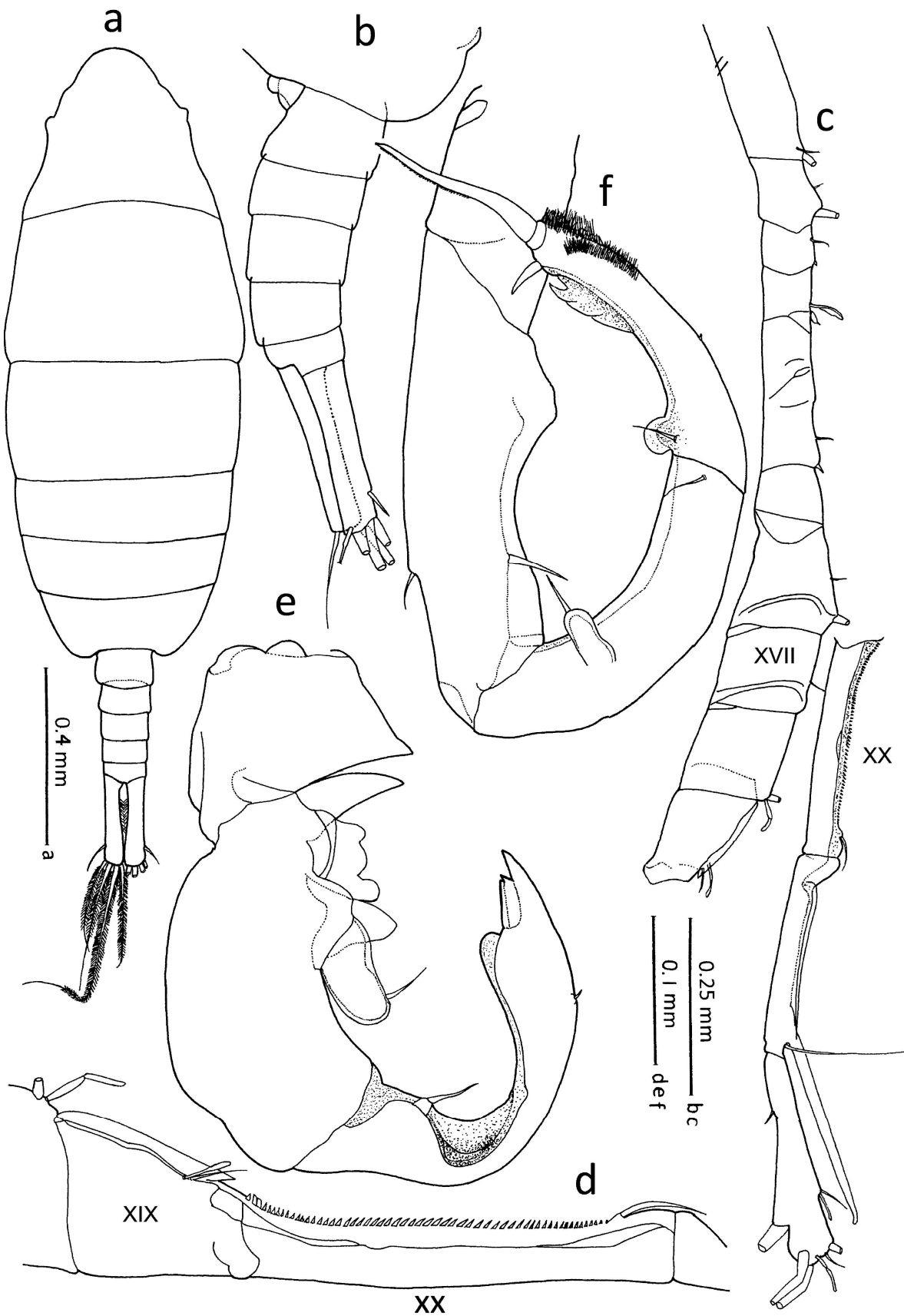


Fig. 3. *Tortanus (Atortus) sulawesiensis* n. sp., male (paratype). a, habitus, dorsal view; b, urosome, right lateral view; c, d, right antennule (number of ancestral segment is indicated by Roman numerals); e, right leg 5; f, left leg 5.

than medial one. Left leg (fig. 3f) coxa devoid of any processes; basis medial margin swollen near proximal and distal ends, furnished with one seta each near distal 1/3 of lateral and medial margins; Re1 with digitiform process with terminal seta near proximal 1/3 of medial margin and subdistal seta; Re2 bearing rounded process on proximomedial margin with seta at its base, lateral margin hirsute on distal 1/5, medial margin bearing series of lamellae running from mid-length to distal end of segment and subterminal spine, apex with long sinuate spine.

Etymology.— The specific name *sulawesiensis* refers to Sulawesi Island where the species was collected. It thus is a geographical adjective, agreeing in gender with the masculine generic name.

Remarks.— The subgenus *Atortus* can be classified into two morphological groups as defined by Bowman (1971), followed by Othman (1987), and revised by Ohtsuka & Kimoto (1989). The first group sensu Bowman (1971) (= the *tropicus* group sensu Othman, 1987) is characterized by (1) the right side of Ur2 of the male with a process, (2) the anterior end of the serrate margin of segment XX of the right A1 of the male produced proximally over segment XIX, (3) the distal segment of P5 of the female either slender and asymmetrical or sub-quadrate. The second group sensu Bowman (1971) (= the *murrayi* group sensu Othman, 1987) is featured by (1) the absence of a lateral process on the right side of Ur2 of the male, (2) segment XX of right A1 of the male not produced proximally, (3) P5 of the female 3-segmented, its terminal segment tapering distally and furnished with 1-3 distal prongs. Ohtsuka & Kimoto (1989) subdivided the first (*tropicus*) group into the *longipes*- and *rubidus* species groups (plus unassigned species) and the second (*murrayi*) group into the *murrayi* and *recticauda* species groups, and re-named the first and second group as the *brevipes*- and *recticauda* species complex, respectively.

Tortanus (A.) *sulawesiensis* is assigned to the *murrayi* species group of the *recticauda* species complex and closely resembles *T.* (A.) *murrayi* Scott, 1909, *T.* (A.) *scaphus* Bowman, 1971, *T.* (A.) *lophus* Bowman, 1971, and *T.* (A.) *bonjol* Othman, 1987, by the absence of characteristic processes on Pdg5 and the genital compound somite of the female, and the basic structure of P5 in both sexes, but is distinguished from the latter four species by the ventral process on the genital compound somite and the shape of CR in the female, and the characteristic shape of the tongue-like process on the Re of the right P5 and of the lamellae of Re2 of the left P5 in the male.

***Tortanus (Atortus) bilobus* sp. nov.** (figs. 4-5)

Material examined.— Holotype (MZB Cru. Cop. 115) female (TL: 2.11 mm), paratypes (MZB Cru. Cop. 116) 2 females (1.97 and 2.00 mm) and 2 males (1.58 and 1.61 mm); collected off Tanjung Merah (1°24.265'N 125°07.219'E) on 22 March 2003.

Female.— Prosome (fig. 4a) about 3.5 times as long as urosome, posterior corners produced into asymmetrical, rounded lobes, left corner wider and produced more posteriorly than right. Urosome 2-segmented, anal somite coalesced with CR (fig. 4a, b). Genital compound somite elongated, left margin irregular with spinule near posterior 1/4 (fig. 4b, c), right margin with 2 obtuse processes (fig. 4a, c), genital operculum oval and located at anterior 1/3 (fig. 4b, c). CR asymmetrical, left ramus longer than right.

Other features of body, i.e., trunk, A1 (fig. 4d), A2, maxillule, maxilla, maxilliped, and P1-4 similar to those in female *T. (A.) sulawesiensis*.

P5 rudimentary (fig. 4e); proximal segments of right and left legs fused to form common base; apical segment lamellar and sub-quadrate with distolateral seta.

Male.— Prosome (fig. 5a) about 2.7 times as long as urosome; posterior corners produced into asymmetrical, rounded lobes, left lobe wider and produced more posteriorly than right. Genital somite asymmetrical, left side produced posteriorly. Right margin of Ur2 without any processes.

Other features of body, i.e., of trunk and appendages as in male *T. (A.) sulawesiensis*, except right A1 and P5.

Right A1 (fig. 5b) serrate ridge of segment XX produced proximally to mid-length of segment XIX; anteroproximal process on segment XIX slender, reaching midpoint of segment.

P5 (fig. 5c) right leg coxa broad without ornament; basis bearing semi-trapezoid medial process with 2 setules along proximal margin, distal half of segment broadened; Re straight on outer margin and slightly concave at middle part of medial margin, furnished with 1 proximal outer spine and 3 spines on inner margin. Left leg coxa unarmed; basis elongate with mid-lateral seta and proximally 3 semi-circular processes, proximal one with terminal setule; Re1 with medial spinule located at proximal 1/4 of segment; Re2 medial margin with basal and sub-distal setae and terminal spine, tip of segment lamellate.

Etymology.— The specific name *bilobus* refers to the presence of two lobe-like processes on the right margin of genital compound somite in the female. The name is an adjective agreeing in gender with the masculine generic name.

Remarks.— The female P5 (simple, sub-quadrate) and the male A1 (serrate process on segment XX extending to segment XIX) of *T. (A.) bilobus* are in

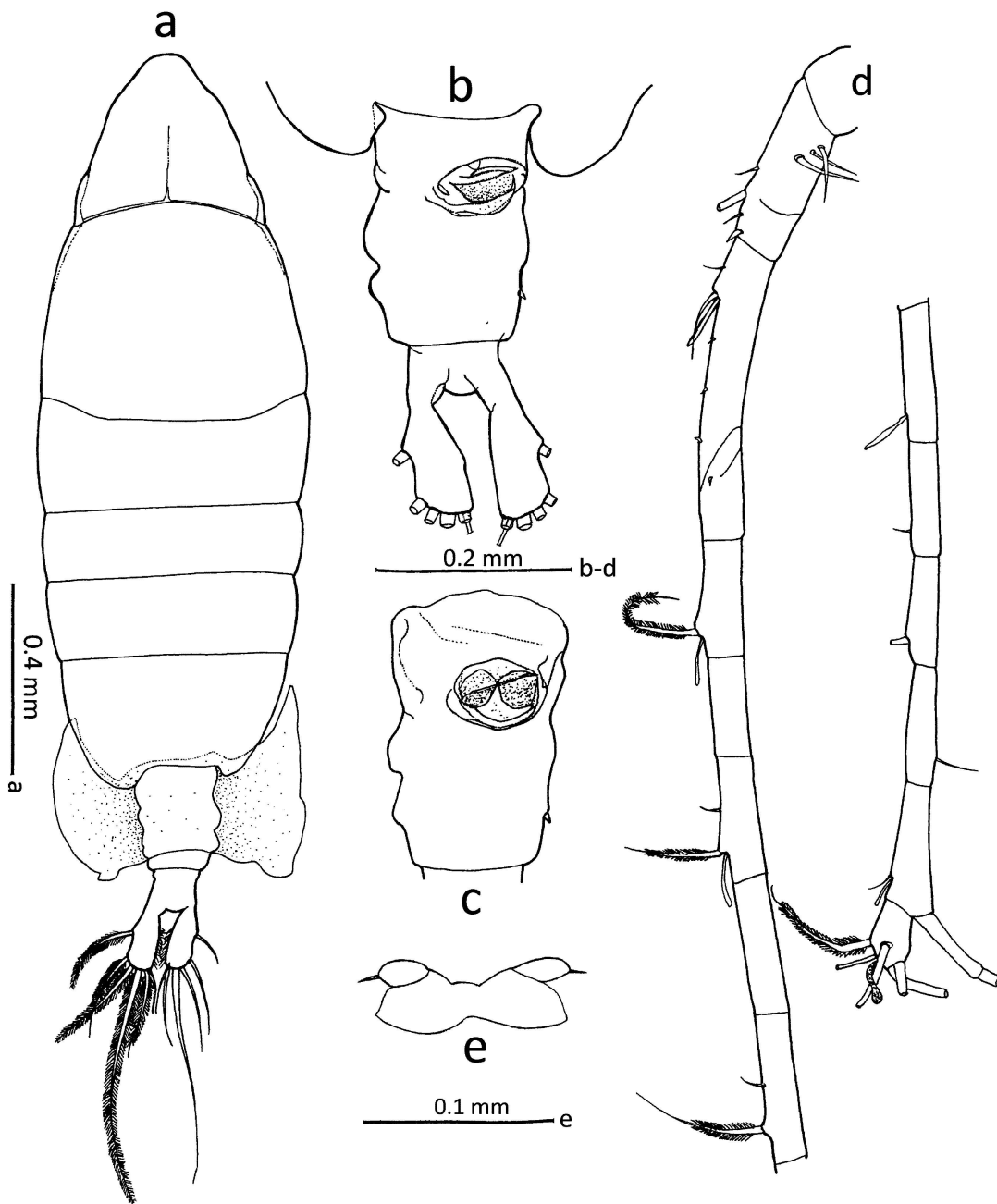


Fig. 4. *Tortanus (Atortus) bilobus* n. sp., female (holotype). a, habitus, dorsal view; b, pediger 5 and urosome, ventral view; c, genital compound somite, ventral view; d, antennule; e, leg 5.

accordance with those of the *brevipes* species complex, but the male Ur2 (absence of lateral process on right side) corresponds to the *recticauda* species complex. The new species thus has a mixture of both species complexes. Accordingly, it is impossible to assign this species to either of the two groups. Nevertheless, *T. (A.) bilobus* is distinguished from the other species of *Tortanus (Atortus)* by the combination of features in the A1 and Ur2 as above in the male, and the characteristic shape of the genital compound somite in the female.

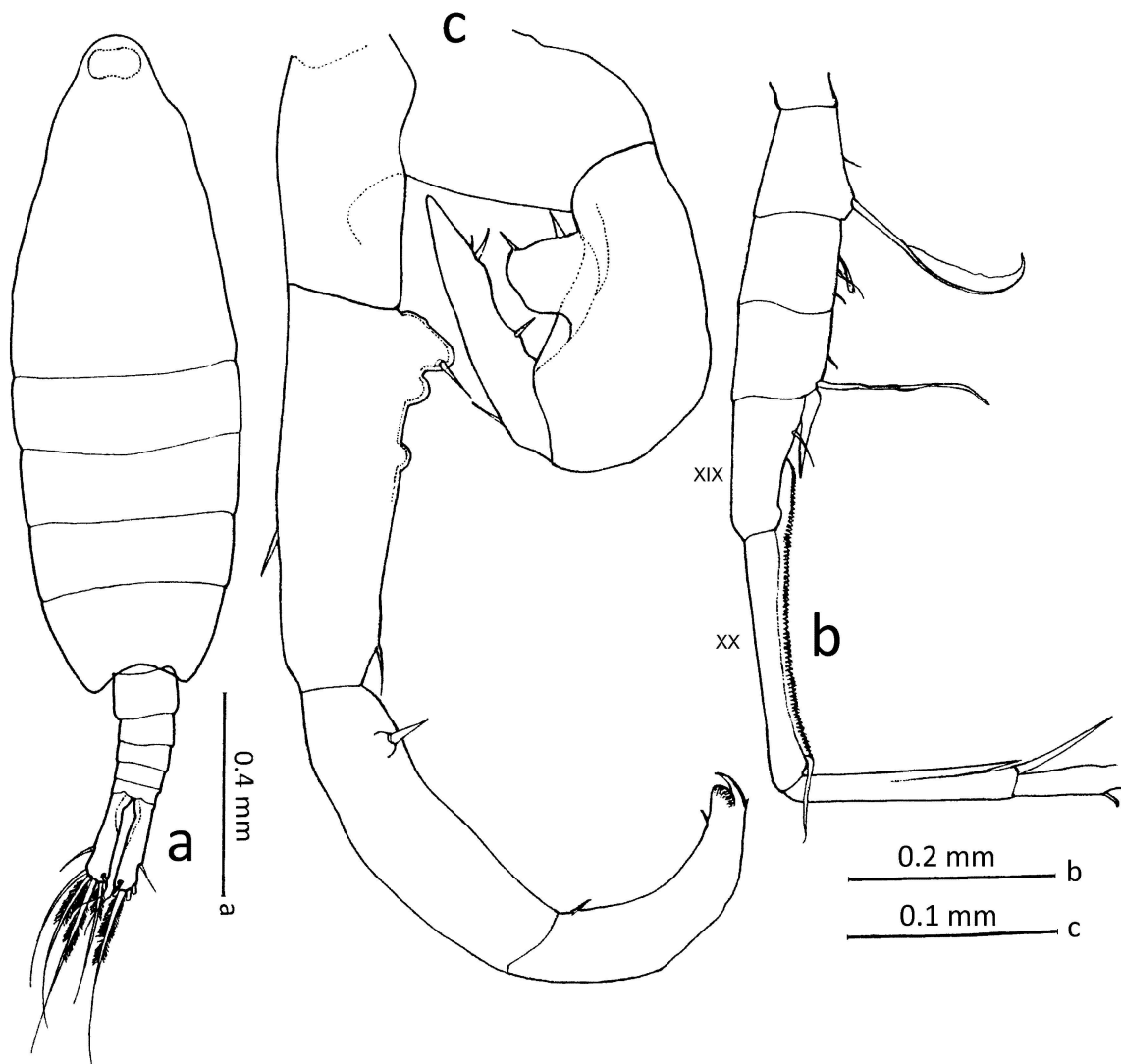


Fig. 5. *Tortanus (Atortus) bilobus* n. sp., male (paratype). a, habitus, dorsal view; b, right antennule (number of ancestral segment is indicated by Roman numerals); c, leg 5.

***Tortanus (Atortus) omorii* sp. nov. (fig. 6)**

Material examined.— Holotype (MZB Cru. Cop. 117) male (TL: 1.97 mm); collected off Tanjung Merah (1°24.265'N 125°07.219'E) on 22 March 2003.

Male.— Prosome (fig. 6a) about 2.7 times as long as urosome; posterior corners produced into asymmetrical lobes, right lobe wider than left. Genital somite asymmetrical, left sides lightly more produced posteriorly than right; Ur2 furnished with posterolateral process on right side (fig. 6a-c), bearing terminal setule. Anal somite partly fused with CR; CR asymmetrical, right ramus wider than left.

Other features of body, i.e., of trunk and appendages as in male *T. (A.) sulawesiensis*, except right A1 and P5.

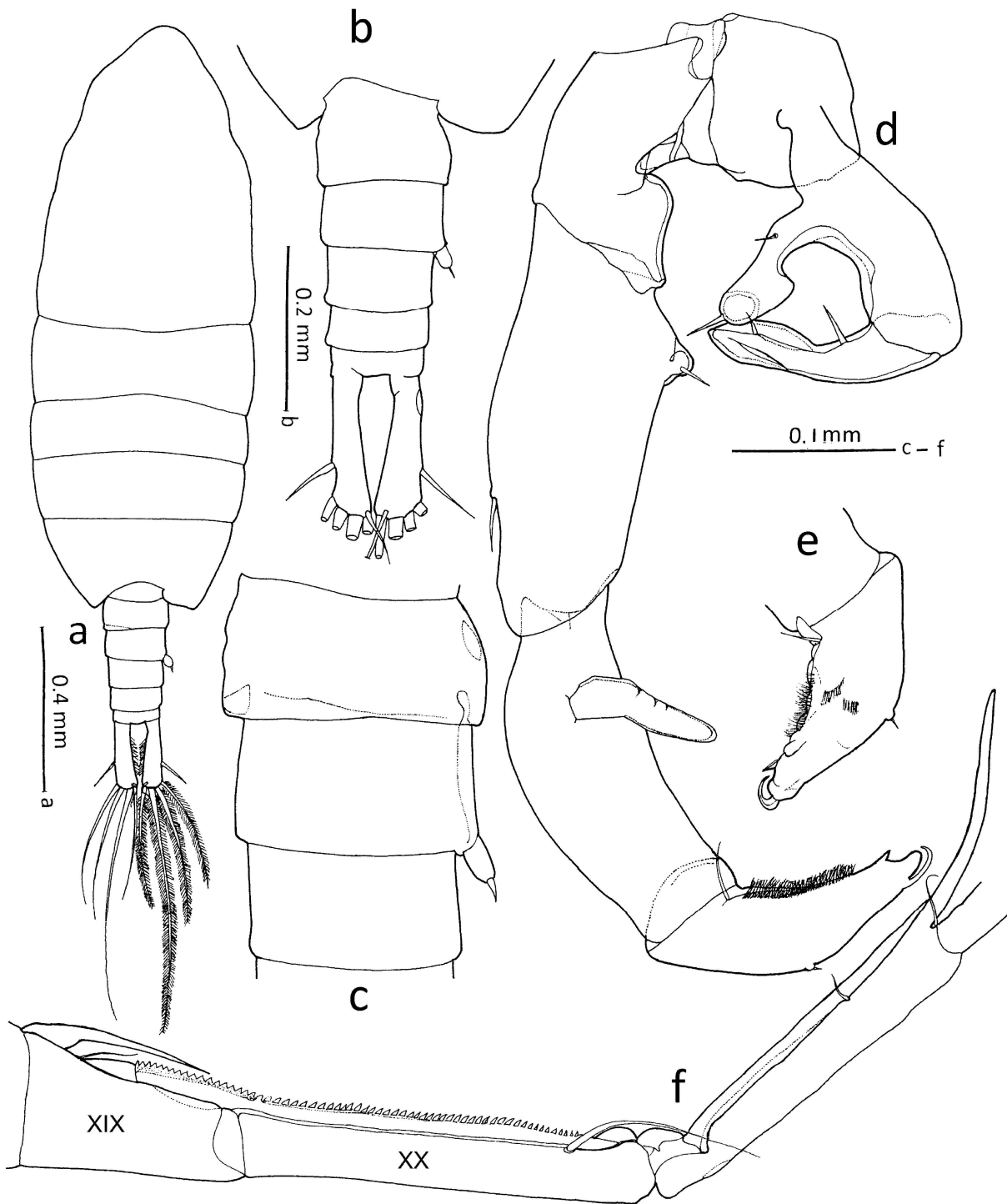


Fig. 6. *Tortanus (Atortus) omorii* n. sp., male (holotype). a, habitus, dorsal view; b, pediger 5 and urosome, dorsal view; c, urosomites 1-3, dorsal view; d, leg 5; e, exopod 2 of left leg 5; f, right antennule (number of ancestral segment is indicated by Roman numerals).

Right A1 (fig. 6f) serrate ridge of segment XX produced proximally to mid-length of segment XIX. Anteroproximal process on segment XIX slender, reaching near distal end of segment.

P5 (fig. 6d, e) right leg coxa broad without ornament; basis bearing large ladle-shaped medial process with proximal and distal setule, distal half of segment

broadened and curved medially; Re slightly curved medially with 2 setae, middle part of inner margin emarginated. Left leg coxa with medioproximal depression; basis elongate with medioproximal semi-circular process with terminal setule; Re1 with medial digitiform process located at proximal 1/4 of segment; Re2 with longitudinal row of setules on medial margin, proximomedial seta, minute lateral seta at mid-length, subdistal lateral seta, medial subdistal notch, and rounded tip.

Female.— Unknown.

Etymology.— The species is named in honour of Dr. Makoto Omori, Professor Emeritus of Tokyo University of Marine Science and Technology. The name thus is a noun in the genitive singular.

Remarks.— The male of *T. (A.) omorii* belongs to the *brevipes* species complex, but cannot be assigned to either the *longipes* or *rubidus* species groups within the species complex, because the posterior corners of the prosome are asymmetrical but of subequal length (left side longer in the *longipes* group, symmetrical in *rubidus* group), the coxa of the right P5 has no medial process (as in the *longipes* group; process present in the *rubidus* group), and the basis of the left P5 has no sinuate medial margin (as in the *rubidus* group; margin sinuate in the *longipes* group). However, *T. (A.) omorii* is distinguished from the other species of the *brevipes* species complex by the characteristic ladle-shaped process on the basis of the male right P5.

***Tortanus (Atortus) indonesiensis* sp. nov. (fig. 7)**

Material examined.— Holotype (MZB Cru. Cop. 118) male (TL: 1.87 mm), paratype (MZB Cru. Cop. 119) 1 male (1.82 mm); collected off Tanjung Merah (1°40'48"N 125°04'12"E) on 25 March 2003.

Male.— Prosome (fig. 7a) about 2.8 times as long as urosome; posterior corners rounded and asymmetrical, with left posterior margin produced more posteriorly than right (fig. 7b). Genital somite with genital aperture on left posterolateral margin. Ur2 with posterolateral and posteroventral processes on right side (fig. 7b, c), the latter of which smaller, each with minute seta on tip.

Other features of the body, i.e., trunk and appendages as in male of *T. (A.) sulawesiensis* except right A1 and P5.

Right A1 (fig. 7d, e) segment XX equal in length to fused segments XXIV-XXVIII and slightly longer than fused segments XX1-XXIII. Anterior surface of segment XX furnished with ridge bearing denticles extending proximally near proximal end of segment XIX. Proximal end of ridge slightly raised from surface plane of segment XIX. Anteroproximal process on segment XIX triangular. Fused segment XXI-XXIII furnished with ridge devoid of denticles on anterior surface,

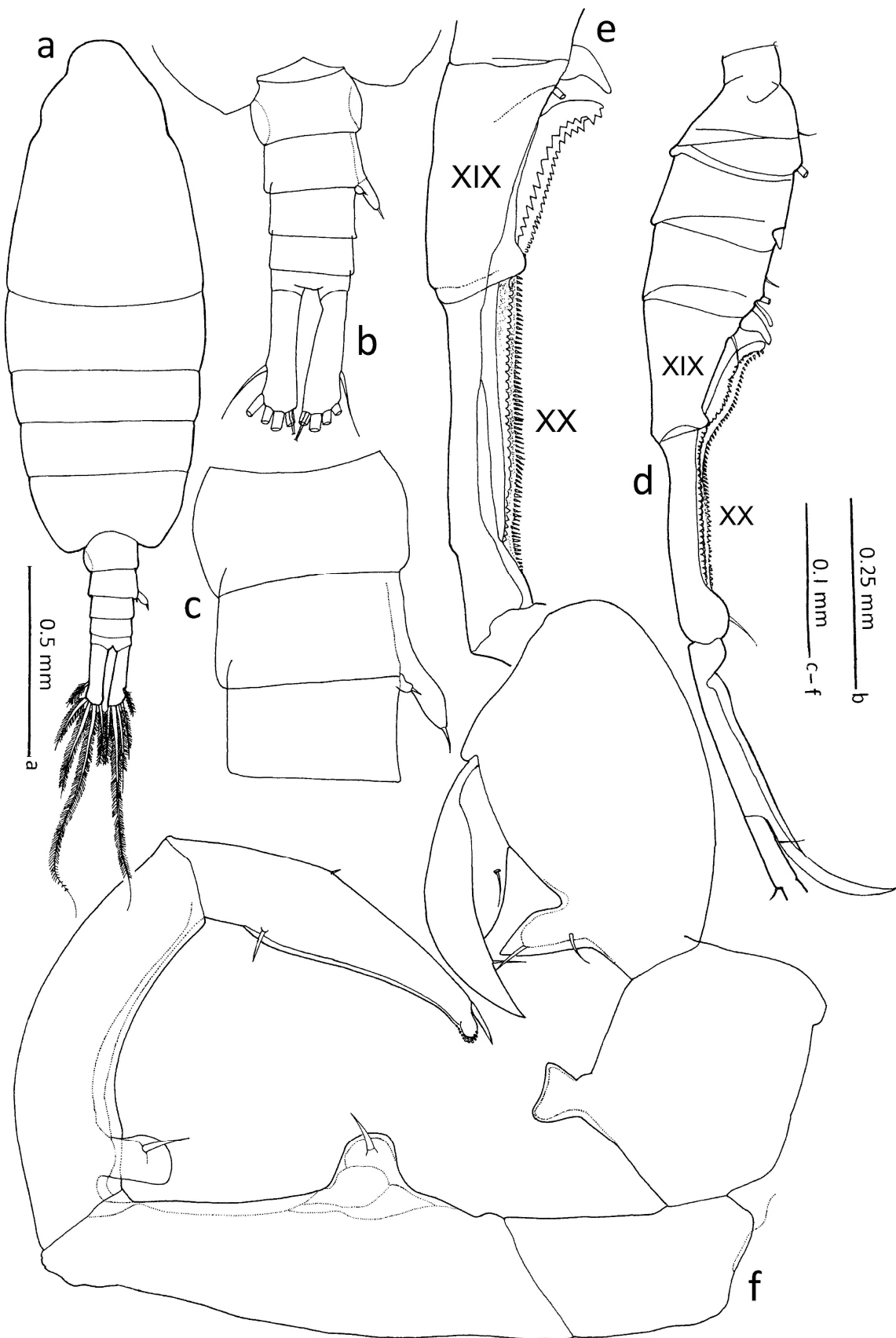


Fig. 7. *Tortanus (Atortus) indonesiensis* n. sp., male (holotype). a, habitus, dorsal view; b, pediger 5 and urosome, dorsal view; c, urusomites 1-3, dorsal view; d, e, right antennule (number of ancestral segment is indicated by Roman numerals); f, leg 5.

with indent on anterior surface near proximal end; distal end of segments with long spinous process extending almost entire length of fused segments XXIV-XXVIII.

Right P5 (fig. 7f) coxa semi-trapezoid with small distolateral process and semi-trapezoid medial process with concave distal margin; basis triangular and expanded laterally, with digitiform process bearing 2 setae on proximomedial margin; Re slightly curved medially, tapering distally into acute tip, and with 2 medial setae. Left leg coxa unarmed; basis elongate and straight, with cylindrical process bearing seta near proximal 1/3 of medial margin; Re1 with proximomedial, cylindrical process bearing seta; Re2 with proximomedial seta, mid-lateral seta, and subdistal lateral seta, tip of segment rounded with granular surface.

Female.— Unknown.

Etymology.— The specific name *indonesiensis* refers to the type locality, Indonesia. The name thus is an adjective agreeing in gender with the masculine generic name.

Remarks.— *Tortanus* (*A.*) *indonesiensis* belongs to the *brevipes* species complex, but cannot be assigned to either the *longipes* or the *rubidus* species group within that species complex, because the proximal end of the denticulate ridge of segment XX of the right A1 is raised from the surface plane of segment XIX (as in the *longipes* species group), but the medial margin of the basis of the left P5 is not sinuate (as in the *rubidus* species group). However, *T.* (*A.*) *indonesiensis* is distinguished from the other species of the species complex by the characteristic semi-trapezoid process on the coxa of the male right P5.

***Tortanus* (*Atortus*) *manadoensis* sp. nov. (fig. 8)**

Material examined.— Holotype (MZB Cru. Cop. 120) male (TL: 2.00 mm), paratype (MZB Cru. Cop. 121) 1 male (1.97 mm); collected off Tanjung Merah (1°23.943'N 125°07.162'E) on 21 June 2003.

Male.— Prosome (fig. 8a) about 3.1 times as long as urosome; posterior corners produced into symmetrical, rounded lobes. Genital somite asymmetrical, produced postero-laterally on left side; Ur2 without any lateral processes. CR asymmetrical, right ramus longer than left.

Other features of the body, i.e., the trunk and appendages as in the male *T.* (*A.*) *sulawesiensis*, except right A1 and P5.

Right A1 (fig. 8b) segment XX not produced proximally, anterior surface of segment with serrate ridge beginning from proximal end and ending near distal end of segment; fused segments XXI-XXIII produced into 2 processes, proximal one produced into short spine-like process, distal one produced into long spine-like process extending to mid-length of fused segments XXIV-XXVIII.

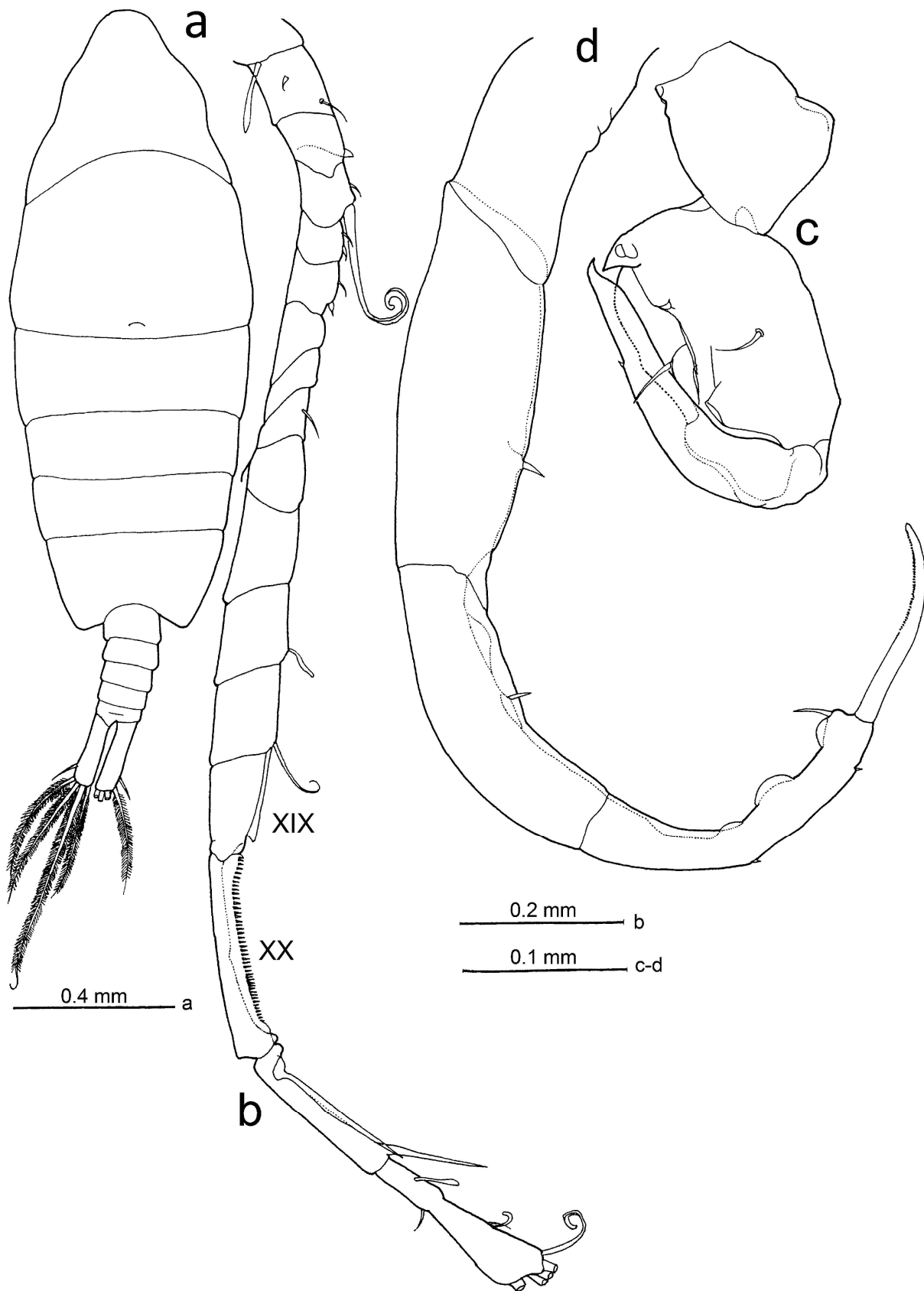


Fig. 8. *Tortanus (Atortus) manadoensis* n. sp., male (holotype). a, habitus, dorsal view; b, right antennule (number of ancestral segment is indicated by Roman numerals); c, right leg 5; d, left leg 5.

P5 (fig 8c) right leg coxa short and swollen; basis expanded with triangular proximomedial process, medial margin produced medially into rounded process bearing long setule, posterior surface of segment with long setule; inner margin of Re lamellar with lateral spinule at distal 1/3. Left leg (fig. 8d) coxa unarmed; basis elongated and straight with medial setule at mid-length; Re1 curved medially with medial setule at mid-length; Re2 curved medially with 3 semicircular processes along distal half of medial margin and stout serrated seta at tip, subterminal medial setule, and midlateral and subdistolateral spinules.

Female.— Unknown.

Etymology.— The specific name *manadoensis* refers to Manado City, the provincial capital of North Sulawesi where the specimens of this species were collected. The name thus is an adjective agreeing in gender with the masculine generic name.

Remarks.— *Tortanus* (*A.*) *manadoensis* belongs to the *recticauda* species complex, and can be assigned to the *murrayi* species group by the characteristic processes on the basis and Re of the male right P5. *Tortanus* (*A.*) *manadoensis* is distinguished from the other species of the group by the triangular proximomedial process on the basis of the male right P5 and the semicircular processes on the Re2 of the male left P5.

***Tortanus* (*Atortus*) *processus* sp. nov. (fig. 9)**

Material examined.— Holotype (MZB Cru. Cop. 122) male (TL: 1.87 mm), paratypes (MZB Cru. Cop. 123) 2 males (1.89 and 1.89 mm); collected off Tanjung Merah (1°23.491'N 125°06.460'E) on 25 March 2003.

Male.— Prosome (fig. 9a) about 2.3 times as long as urosome; posterior corners produced into symmetrical, rounded lobes; left lateral side of Pdg5 (fig. 9b) with semicircular process on ventral margin. Genital somite (fig. 9c) asymmetrical, left margin more convex than right, and with semicircular process posteriorly; Ur2 (fig. 9a, c) with 2 right posterolateral processes furnished with setule, larger one of which reaching anterior 1/3 of Ur3. CR asymmetrical, right ramus wider than left.

Other features of the body, i.e., trunk and appendages as in male *T.* (*A.*) *sulawesiensis*, except right A1 and P5.

Right A1 (fig. 9d) serrate ridge of segment XX produced proximally to proximal 1/4 of segment XIX; anteroproximal process on segment XIX triangular; fused segments XXI-XXIII produced distally into long and curved spine-like process.

P5 right leg (fig. 9e) coxa broad and acute at its base without ornament; distal half of basis broad and semicircular, bearing digitiform process with proximal and terminal setules on medial margin; Re stout and claw-like, furnished with 2 setules on medial margin. Left leg (fig. 9f) medial margin of coxa with large

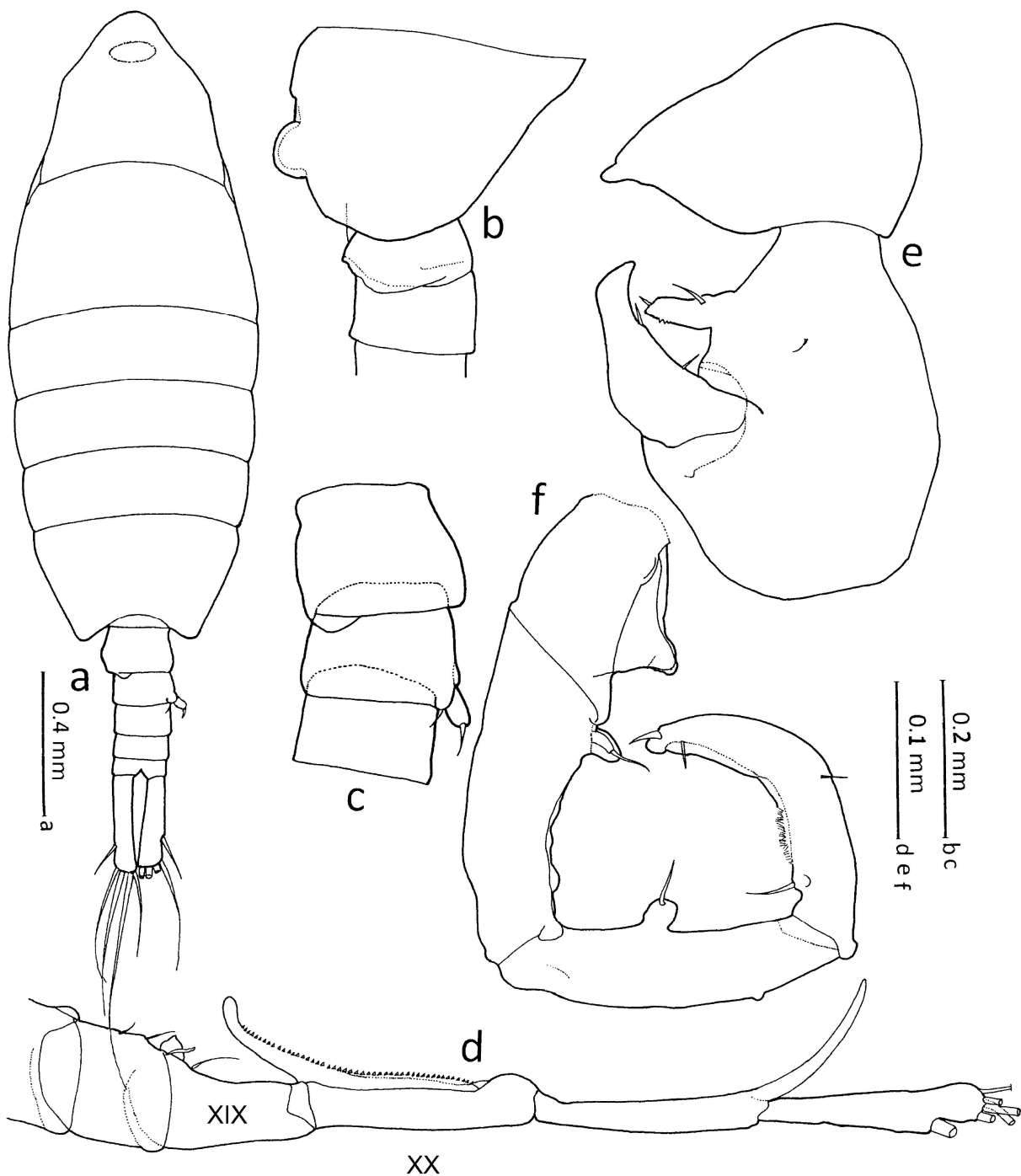


Fig. 9. *Tortanus (Atortus) processus* n. sp., male (holotype). a, habitus, dorsal view; b, pediger 5 and urosomites 1-2, left lateral view; c, urosomites 1-3, dorsal view; d, right antennule (number of ancestral segment is indicated by Roman numerals); e, right leg 5; f, left leg 5.

triangular process from its base to anterior 3/4; basis elongate, with proximomedial papilla with terminal setule and irregular, rounded processes along inner margin; Re1 slightly curved medially with papilla bearing terminal setule at proximal 2/5 of medial margin; Re2 curved inwards with subterminal lateral spine, 3 (each proximomedial-, distomedial- and mid-lateral) setules, and 2 hairy rows on proximal half of medial margin.

Female.— Unknown.

Etymology.— The specific name *processus* refers to the characteristic semicircular process on the ventral margin of the left lateral side of Pdg5. The name is an adjective agreeing in gender with the masculine generic name.

Remarks.— *Tortanus* (*A.*) *processus* belongs to the *brevipes* species complex, but can not be assigned to either the *rubidus* or the *longipes* species group, since the posterior end of its prosome is symmetrical (as in the *rubidus* group), but the basis of the male right P5 is broad and semicircular and the medial margin of the basis of the male left P5 has a series of processes (as in the *longipes* group). Nevertheless, *T. (A.) processus* is distinguished from the other species of the species complex by the semicircular ventrolateral process of the fused Pdg5 and the large triangular process on the coxa of the left P5.

***Tortanus* (*Atortus*) *lukmani* sp. nov. (fig. 10)**

Material examined.— Holotype (MZB Cru. Cop. 124) male (TL: 1.79 mm), paratypes (MZB Cru. Cop. 125) 2 males (1.87 and 1.88 mm); collected off Tanjung Merah (1°23.491'N 125°06.460'E) on 25 March 2003.

Male.— Prosome (fig. 10a, b) about 2.9 times as long as urosome; posterior corners produced into asymmetrical, rounded lobes, left side wider than right. Genital somite slightly asymmetrical, left margin more convex than right, and with process distally; Ur2 right lateral side with small posterior process with distal setule; CR asymmetrical, right ramus longer than left.

Other features of the body, i.e., trunk and appendages as in male *T. (A.) sulawesiensis*, except right A1 and P5.

Right A1 (fig. 10c) serrate ridge of segment XX produced proximally to mid-length of segment XIX; anteroproximal process on segment XIX acutely triangular, extending to proximal 1/3 of segment; fused segments XXI-XXIII produced into 2 processes, proximal one produced into short spine-like process, distal one produced into long spine-like process extending near distal end of fused segments XXIV-XXVIII.

P5 (fig. 10d, e) right leg (fig. 10d) coxa broad without ornament; distal half of basis much broadened and curved medially bearing semi-triangular medial process with proximal and terminal setules, proximolateral margin of segment armed with finger-like process, posterior surface with spine near base of Re; Re stout, curved medially at proximal 1/3, with 2 medial setules and subdistolateral setule. Left leg (fig. 10e) coxa smooth; basis elongate, with proximomedial broad-based digitiform process directed sub-distally with subterminal setule, and pillow-like process on distal half of medial margin; Re1 curved medially with medial papilla with distal

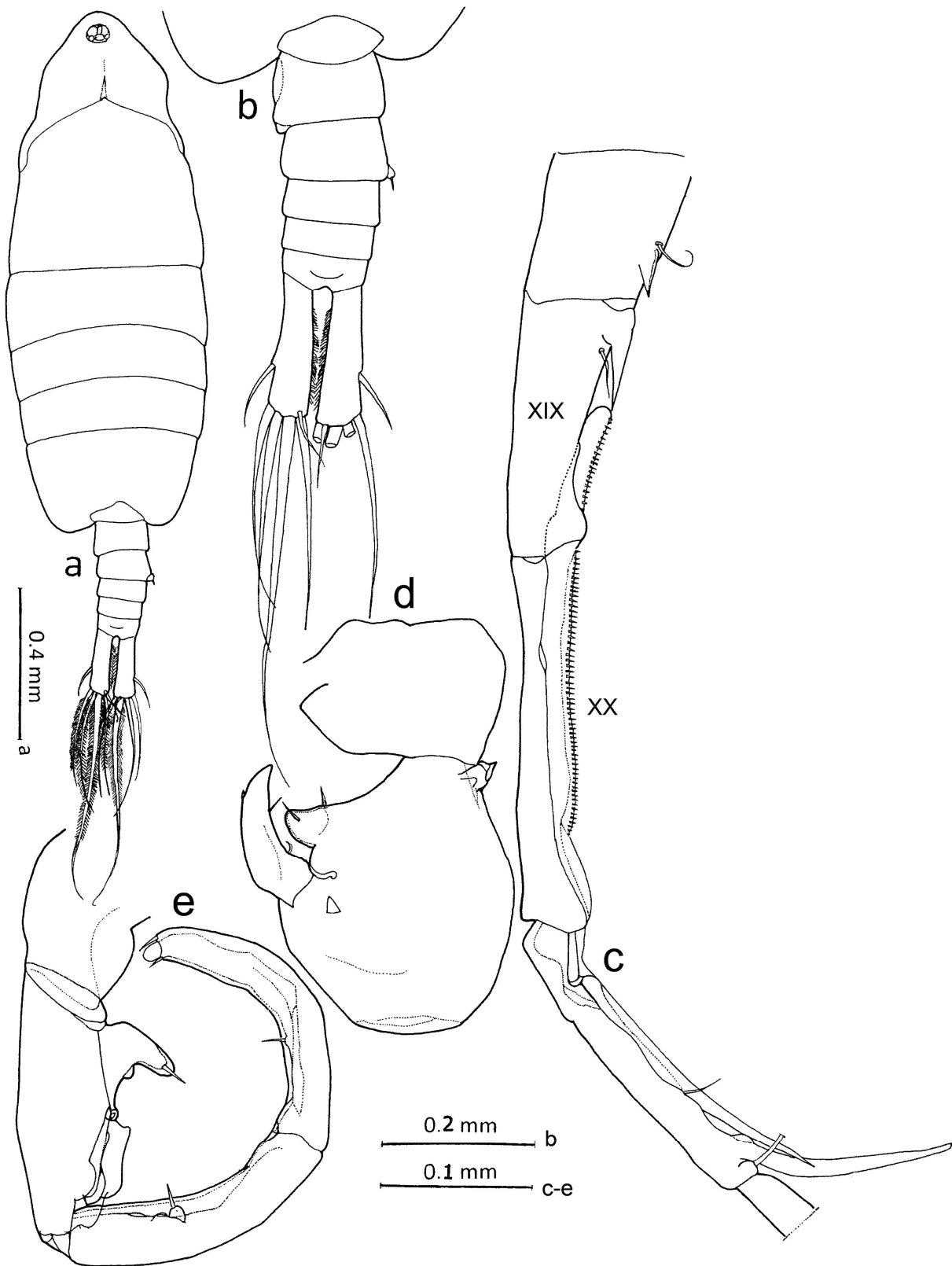


Fig. 10. *Tortanus (Atortus) lukmani* n. sp., male (holotype). a, habitus, dorsal view; b, pediger 5 and urosome, dorsal view; c, right antennule (number of ancestral segment is indicated by Roman numerals); d, right leg 5; e, left leg 5.

setule; Re2 curved medially with medial setule near midpoint, tip of segment produced into rounded process with 2 setae.

Female.— Unknown.

Etymology.— The species is named in honour of Professor Lukman Hakim, Director of the Indonesian Institute of Sciences (LIPI), Indonesia. The name thus is a noun in the genitive singular.

Remarks.— *Tortanus* (*A.*) *lukmani* belongs to the *brevipes* species complex, but can not be assigned to either the *rubidus* or the *longipes* species group, since the posterior end of its prosome is asymmetrical, with the left side longer, the medial margin of the basis of the male left P5 has a series of processes, and the basis of the male right P5 is broad and semicircular (as in the *longipes* group), but the proximal end of the denticulate ridge of segment XX of the right A1 is not strongly retroflexed (unlike in the *longipes* species group). Nevertheless, *T. (A.) lukmani* is distinguished from the other species of the species complex by the massive basis with characteristic proximolateral processes on the right P5 and the shape of the medial processes on the basis of the left P5.

DISCUSSION

As mentioned above, four of the seven new species, *Tortanus (Atortus) indonesiensis*, *T. (A.) omorii*, *T. (A.) processus* and *T. (A.) lukmani*, belong to the *brevipes* species complex sensu Ohtsuka & Kimoto (1989), which is identical to the first group sensu Bowman (1971) and the *tropicus* group sensu Othman (1987), while two species, *T. (A.) sulawesiensis* and *T. (A.) manadoensis*, are assigned to the *recticauda* species complex. However, the other species, *T. (A.) bilobus*, does not fit into either group, since the male A1 and female P5 coincide with the *brevipes* species complex but the male Ur2 conforms to the *recticauda* species complex. For better understanding of the evolution and phylogeny of the *Tortanus (Atortus)* species, further studies applying a molecular-genetic approach would be necessary, including revision of the species groups within *Tortanus (Atortus)*, not only for the species complex but also for the sub-grouping within the complexes, which apparently show considerable inconsistencies of character states in many species (see the remarks under the various species descriptions).

The occurrence records of *Tortanus (Atortus)* species, entirely restricted to the oligotrophic waters of the Indo-West Pacific, show a certain correspondence between geographic regions and morphology-based species complexes and groups (Ohtsuka & Kimoto, 1989; Ohtsuka & Reid, 1998). Namely, the *brevipes* species complex is restricted to the westernmost rim of the Pacific with the exception of the occurrence of *T. (A.) tropicus* Sewell, 1932, *T. (A.) andamanensis* Nishida,

Anandavelu & Padmavati, 2015, and *T. (A.) sigmoides* Nishida, Anandavelu & Padmavati, 2015, from the northeastern Indian Ocean (Sewell, 1932; Nishida et al., 2015), and *T. (A.) giesbrechti* Jones & Park, 1968, from the central Pacific. In contrast, the *recticauda* species complex comprises two groups, of which the *recticauda* species group is restricted to the western Indian Ocean and the *murrayi* group to the western most rim of the Pacific (Ohtsuka & Kimoto, 1989; Ohtsuka et al., 2000; Ohtsuka & Conway, 2003, 2005). Although *T. (A.) bilobus* shows features inconsistent with these groups, the present occurrences of the two species of the *murrayi* group and the four species of the *brevipes* group from North Sulawesi appear to be consistent with the above distributional patterns.

The co-occurrence of seven species of *Tortanus (Atortus)* in North Sulawesi calls for special attention, since, as far as we are aware, this may be among the largest numbers of co-occurring congeneric (more precisely, con-subgeneric) species of medium- to large-sized (ca. 1.5-2.5 mm) epipelagic copepods so far recorded in such a limited coastal area where depth may be too shallow (1-2 m) for efficient vertical segregation among closely-related species. This contrasts the occurrence patterns of pelagic copepods in the oceanic epipelagic and mesopelagic realms, wherein co-existence of multiple congeneric or morphologically similar species, such as those of the oncaeids (Nishibe et al., 2009; Itoh et al., 2014), scolecitrichids (Kuriyama & Nishida, 2006), and *Euaugaptilus* (Matsuura et al., 2010), is hypothesized to be maintained through vertical segregation and food-resource partitioning as possible major mechanisms. Possible mechanisms for the present co-occurrence of *Tortanus (Atortus)* may involve by-catch of species with different microhabitats and/or substrate preference (e.g., coral vs sea-grass areas), inviting a further study of their distribution at finer scales.

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