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COPEPODID STAGES OF *EURYTE LONGICAUDA* (CYCLOPOIDA, CYCLOPIDAE, EURYTEINAE) FROM THE WHITE SEA ASSOCIATED WITH THE BRYOZOAN *FLUSTRA FOLIACEA*

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ABSTRACT

The copepodid phase of development of *Euryte longicauda* Philippi, 1843, is described from six stages associated with the bryozoan *Flustra foliacea* Linnaeus, 1758 Distinctive character states of the species include: distal teeth of mandibular gnathobase perpendicular to proximal teeth; distal seta of maxillular praecoxa with multiple cusps is perpendicular to proximal setae with one cusp; coxa of maxillule as a gnathobase perpendicular to praecoxa; maxillular palp comprised of two setae; fluted setae medially on the distal segment complex of both rami of swimming legs 1–4. The segmental homologies of the maxilla of *E. longicauda* are an unarmed syncoxa, a basis with two setiferous lobes, and a ramus of three segments. A re-examination of type specimens of *E. bellatula* Humes, 1991, and *E. verecunda* Humes, 1992, revealed a 2-segmented protopod for leg 5, confirming their inclusion in *Euryte*. *Euryte longicauda* retains the ancestral state for development of swimming legs 1–4. Development of the maxilliped suggests that *E. longicaudata* shares with *Troglocyclops janstocki* Rocha and Iliffe, 1994, and *Neocyclops vicinus* (Herbst, 1955) more states expressed during endopodal development of primitive cyclopoids, while endopodal development of the maxilliped of the remaining Cyclopidae is truncated. *Euryte longicaudata*, *T. janstocki*, and *N. vicinus* appear to belong to a monophyletic lineage at the base of the Cyclopidae; *T. janstocki* is most closely related to *E. longicaudata*.

Species of *Euryte* Philippi, 1843, usually are found in shallow, marine or brackish waters, and are collected as free-living copepods from the benthopelagic zone or in association with algae or scleractinian corals. There are ten nominal species (Table 1); *E. longicauda* Philippi, 1843, the oldest, originally was described from the vicinity of the Bay of Naples and later reported from the eastern North Atlantic Ocean and from the Arctic Ocean off islands west of Greenland (Sars, 1913). Other species of the genus have been found in the Southern Ocean (Brady, 1910), in tropical and subtropical waters of the Indian and Pacific Oceans (Sewell, 1949; Humes, 1991, 1992), and most recently from caves of the Mediterranean Sea (Jaume and Boxshall, 1996).

Derived states of *Euryte* that appear to separate its species from species in the remaining genera of the family Cyclopidae include a maxillule with toothed segment (Monchenko, 1974, 1975) and two distal claw-like setae originating on different endopodal segments of maxilliped (Ferrari and Ivanenko, 2001). Species of *Euryte* were removed from subfamily Halicyclopinae to a new subfamily Eurytcinae by Monchenko (1974, 1975). The monotypic genus *Ancheuryte* Herbst, 1989, was placed by its author in Euryteinae. The maxilliped is the only appendage of *Euryte* whose development is known (Ferrari and Ivanenko, 2001); illustrations of this appendage here were derived from the earlier study.

Species of Eurytcinae usually are considered basal to the other three subfamilies of the Cyclopidae (viz., Halicyclopinae Kiefer, 1927, Eucyclopinae Kiefer, 1927, and Cyclopinae Kiefer, 1927). However, a recent analysis of development patterns of cyclopid thoracopods (Ferrari, 1998), which did not include a member of Euryteinae, suggested that the number of armature elements on leg 5 used to diagnose the subfamilies often is convergent within the Cyclopidae. In this paper adults and juvenile copepodid stages of *Euryte longicauda* are described from the White Sea, development of the thoracopods is analyzed, changes in the presumed derived states of the genus are discussed, and the taxonomic status of *E. bellatula* Humes, 1991, and *E. verecunda* Humes, 1992, is re-examined.

MATERIALS AND METHODS

Bryozoans from the Karelian coast of the Gulf of Kandalaksha, White Sea, near the Marine Station of Moscow State University, 66°31′N, 33°07′W were isolated in plastic bags underwater by SCUBA divers. At the surface, ethanol or freshwater was added to the contents of each bag, and the fluid filtered through a 20 micron mesh net. In the laboratory, copepods were cleared and dissected in lactic acid following the method of Humes and Gooding (1964) and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% freshwater (Ferrari, 1995), and examined in glycerin with bright-field or differential interference optics. Drawings were made using *camera lucida*.

Somites are numbered according to their relative developmental age following Hulsemann (1991); thoracic and abdominal somites, except the most posterior anal somite, increase in age and decrease in numeral designation anteriorly. The anal somite bearing caudal ramus is designated the first and developmentally oldest abdominal somite. The first thoracic somite bears the maxilliped; the genital openings are found on the seventh. The number of segments of antennule often is difficult to determine because the arthrodial membranes separating the segments may be very thin. Ramal segments of swimming legs 1–4 (thoracopods 2–5) are proximal, middle, and distal. The terms "seta" and "spine" are used for articulating cuticular elements connected by an arthrodial membrane to an appendage segment; setae appear to be less rigid than spines. In order to maintain continuity among descriptive publications, tables of setae and spines on swimming legs 1–4 in the descriptive section follow the formula introduced by Lang (1934). In the formula, Roman numerals indicate spines and Arabic numerals are setae. Numerals to the left of a comma or dash indicate lateral elements; numerals between two commas are terminal elements, and numerals to the right of a comma or dash are medial elements. A semicolon separates ramal segments and an asterisk indicates that the segment is absent. It should be noted, however, that this kind of formula is not derived from the way a swimming leg is patterned during development, in which the distal arthrodial membrane of a segment is formed one copepodid stage later than the formation of the initial seta of the segment (Ferrari and Benforado, 1998; Ferrari, 2000). Thus, setal and segmental homologies cannot be determined correctly from the formula. Ferrari and Benforado

Table 1. List of the nominal species of *Euryte*.

E. longicauda Philippi, 1843 (cosmopolitan?)
E. robusta Giesbrecht, 1900 (cosmopolitan?);
  Syns. *E. similis* T. Scott, 1912 (Antarctic: South Orkneys);
  E. propinqua Brady, 1910 (Antarctic)
E. curticornis Sars, 1913 (off Norway)
E. longiseta Grandori, 1926 (Mediterranean Sea)
E. brevicauda Sewell, 1949 (off Maldives)
E. sewelli Vervoort, 1964 (off Maldives)
E. pseudorobusta Vervoort, 1964 (North Pacific: off Caroline Islands)
E. grata Herbst, 1989 (off Puerto Rico)
E. bellatula Humes, 1991 (Indo-Pacific)
E. verecunda Humes, 1992 (Pacific coast off Panama)

(1998) suggest that the distal segment of the exopod or endopod of swimming legs 1–4 may be a complex of more than one segment; here the term 'segment complex' is used to identify this part of each ramus. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. Only authors who have contributed descriptions and/or illustrations are cited in the synonymy section.

Abbreviations: Abd–abdominal somite; C1–C6–copepodid stages 1–6; CR–caudal ramus; Th–thoracic somite.

Order Cyclopoida Sars, 1913

Family Cyclopidae Rafinesque, 1815
Subfamily Euryteinae Monchenko, 1974
Genus *Euryte* Philippi, 1843

Philippi, 1843: 64; Giesbrecht, 1900, 52–57; Sars, 1913: 23; Kiefer, 1929: 22–23; Sewell, 1949: 30–31; Vervoort, 1964: 39–40, key; Monchenko, 1974: 25; Herbst, 1989: 54–55, key; Humes, 1991: 105, 107.

Euryte longicauda Philippi, 1843
Figures 1–15

Euryte longicauda Philippi, 1843: 64, pl. 3, figs. a–d; Giesbrecht, 1900: 57–58, pl. 4, figs. 15, 17, 19–21; T. Scott, 1905: 143, pl. 10, figs. 10–12; Sars, 1913: 24, pl. 12; Jaume and Boxshall, 1996: 92–98, figs. 8–11.
Euryte longicauda var. *minor* T. Scott, 1905: 143, pl. 10, figs. 13, 14.
Euryte minor Sars, 1921: 106, pl. 70, fig. 2.
? *Euryte longiseta*; Grandori, 1926: 49, pl. 1, figs. 16–23.
? *Cyclopina clausi* Czerniavsky, 1868: 39, pl. 1.
? *Cyclops nigricauda* Norman, 1869: 295.
? *Cyclops pallidus* Norman, 1869: 295.
? *Thorellia brunea* Boeck, 1864: 25.
? *Thorellia brunea* var. *antarctica* Thomson, 1883: 95 pl. 5, figs. 15–19.

Type Locality.—Sorrento, Naples bay, Mediterranean Sea.

Other Localities.—Antarctic (Brady, 1910); Barents Sea (Sars, 1913; Yashnov, 1948); Black Sea (Czerniavsky, 1868; Ulomsky, 1940); France (Lindberg, 1949; Canu, 1892); Franz Josef Land (Scott, 1899); Greenland (Buchholz, 1874); Ireland, Scotland, England (Brady, 1872, 1978; Wells, 1965; Hamond, 1968); Mediterranean Sea (Philippi, 1843; Grandori, 1926; Giesbrecht, 1900; Schirl, 1973, Jaume and Boxshall, 1996); North Atlantic, Faroes (Stephensen, 1929); North Sea (Sars, 1913, 1921; Lindberg, 1950); Polar Islands north of Grinnell Land (Sars, 1913); Samoa and Suez Canal (Gurney, 1927); New Zealand (Thomson, 1883); White Sea (Ivanenko and Smurov, 1997).

Other Mediterranean Sea Reports.—Grandori, 1926; Giesbrecht, 1900; Schirl, 1973; Jaume and Boxshall, 1996.

Specimens.—15 CVI females, 4 CVI males, 5 CV, 4 CIV, 4 CIII, 4 CII, 3 CI separated from the bryozoan *Flustra foliacea* Linnaeus collected 15–25 m in Kandalaksha Bay, White Sea in the vicinity of the Biological Station of Moscow State University, 66°31′N, 33°07′W, 08 August 2000.

CVI Female.—Body length range 0.86–0.91 mm; ratio length of prosome to urosome 1.2:1 (10 specimens).

Prosome (Fig. 1A): 4 parts: first a complex of 5 cephalic somites plus Th1&2; Th3–5 articulating.

Urosome (Fig. 1C–E): 5 parts: Th6; genital complex of Th7 fused to Abd2; Abd3, 4, 1 articulating. Anal opening mid-dorsal on Abd1. Genital complex in dorsal view with constriction posterior to leg 6 followed by symmetrical lateral process. Paired oviducal openings dorsolateral; 1 copulatory pore midventral.

Egg sacs (Fig. 3F): with 2–9 eggs. Rostrum (Fig. 1B), labrum (Fig. 2E), and paragnath (Fig. 2F), as figured.

Antennule (Fig. 2A): 21 articulating segments with 8, 4, 2, 2, 2, 2, 2, 2, 2, 1, 1, 1,1, 0, 1, 1+1, 0, 1, 2, 2, 4, 1+1 setae + aesthetasc; some females with second segment partially subdivided by arthrodial membrane.

Antenna (Fig. 2D): 4 segmented, with 3, 1, 5, 7 setae and denticles laterally on all segments; 1 curved seta on third segment and 5 curved setae on fourth.

Mandible (Fig. 2G, H): with proximal seta and 11 tooth-like attenuations medial on gnathobase; distal set of 4 tooth-like attenuations from single base perpendicular to proximal set. Palp represented by 3 setae.

Maxillule (Fig. 3A–C): praecoxal endite with 6 stout setae [distal with multiple cusps] and 2 thin setae, praecoxal exite with 1 seta; coxa with thin gnathobase perpendicular to praecoxal endite, with 6–7 tooth-like attenuations medially and 2 setae; palp represented by 2 setae.

Maxilla (Fig. 3D, E): 5-segmented: first segment unarmed; second segment with 2 endites, proximal endite with 1 seta, distal endite attenuate proximally with 1 seta distally; third segment with 3 setae on ventro-distal endite; fourth segment with 3 setae, each on a small lobe; fifth segment with 2 setae.

Maxilliped (Fig. 3F): 5-segmented: syncoxa with 2 lobes, each bearing 1 seta; basis with lateral denticles, medial denticles proximally and distal lobe with 1 seta. Proximal endopodal segment unarmed; middle segment complex with 3 setae, lateral seta thick and curved; distal endopodal segment with 3 setae, 1 terminal seta thick and curved.

Swimming legs 1–4 (Fig. 4A, C–E): protopod 2-segmented; rami 3-segmented. Spine and setal formula as in Table 2; medial setae fluted on distal segmental complex of both rami.

Leg 5 (Fig. 2I): 3-segmented; contralateral coxal segments joined by intercoxal sclerite; basis with 1 lateral seta with setules; exopod with 1 terminal seta with setules, and 1 medial, 1 terminal and 1 lateral setae distinctly fluted.

Leg 6 (Fig. 1E): unilobe bud with 2 long setae with setules and 1 short, thick seta near oviducal opening.

CR (Fig. 1A, B): length to width ratio 9:1 with distal and proximal sections wider than middle section; 4 large, terminal setae and 2 thinner, lateral setae.

CVI Male.—Differs from female CVI as follows: Body length range 0.60–0.62 mm; ratio length of prosome to urosome 1.2:1 (5 specimens).

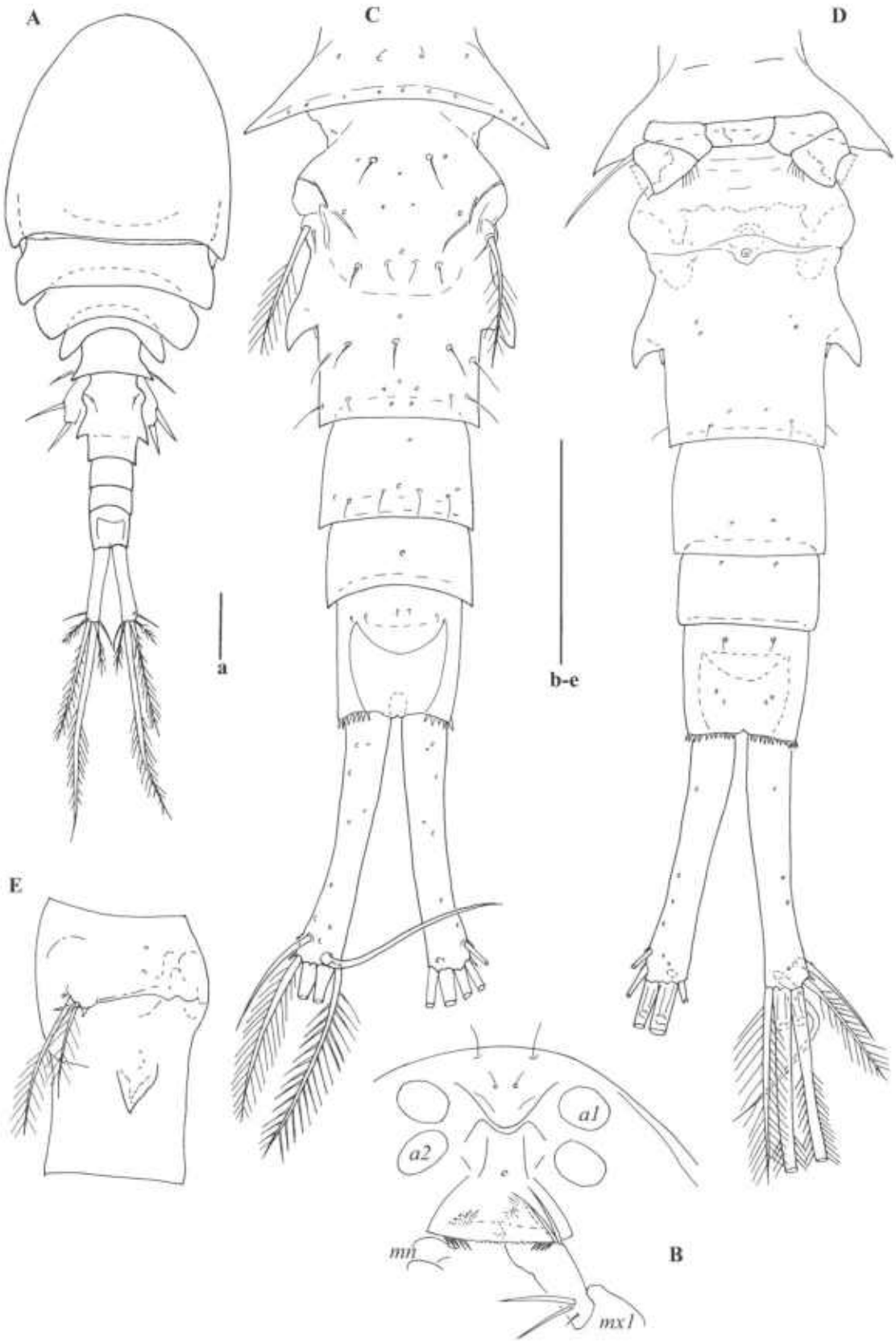

Fig. 1. *Euryte longicauda* Philippi, 1843, CVI Female: A, habitus, dorsal; B, anterior part of prosome (rostrum, labrum, and maxillule), ventral; C, urosome, dorsal; D, urosome, ventral; E, genital complex, lateral; *a1*–antennule, *a2*–antenna, *mn*–mandible, *mx1*–maxillule. Scale line "a" is 0.1 mm for A; line "b–e" is 0.1 mm for B–E.

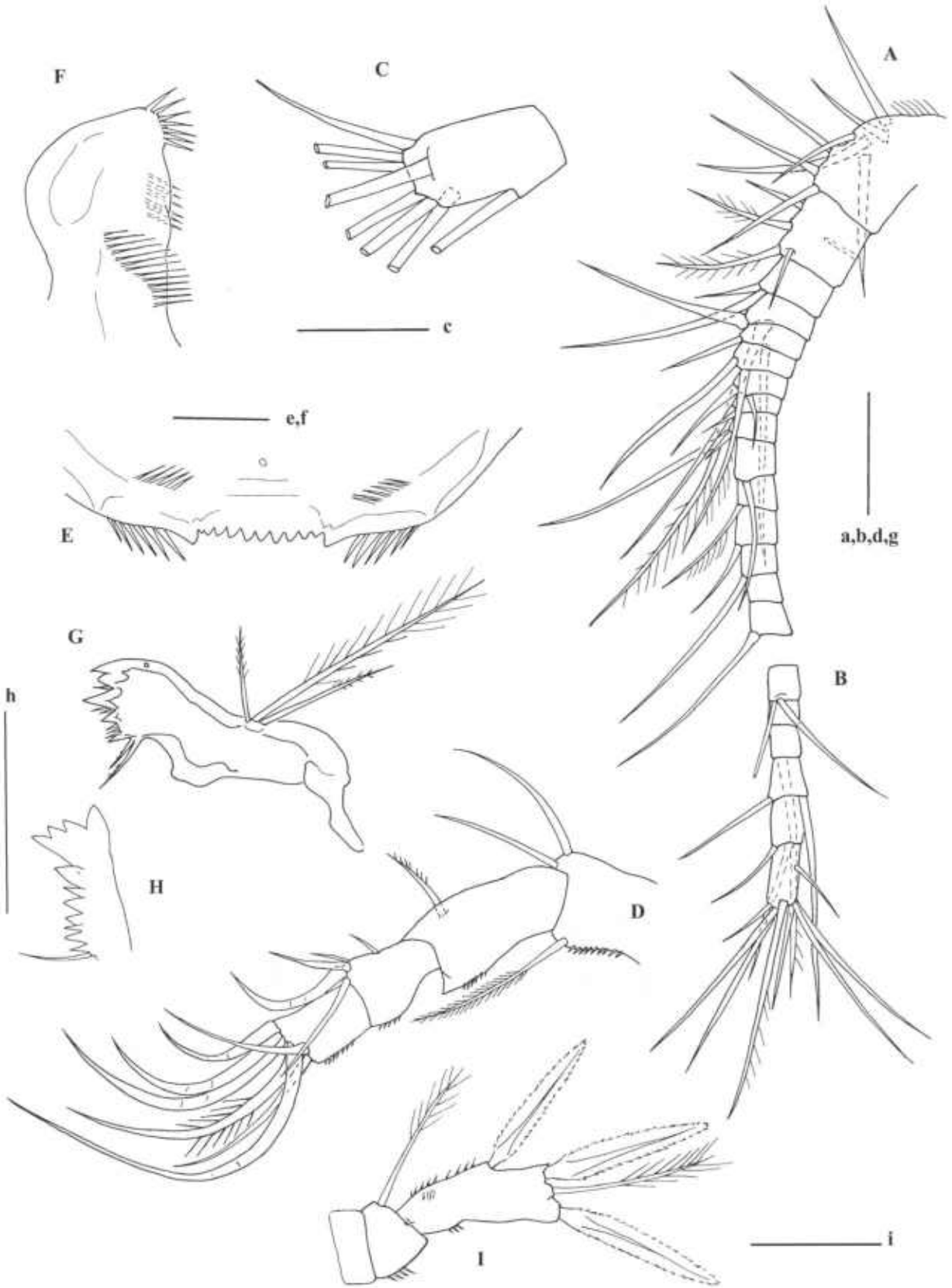

Fig. 2. *Euryte longicauda* Philippi, 1843, CVI Female: A, antennule, segments 1–15; B, antennule, segments 16–21; C, antennule, segment 21; D, antenna; E, labrum, distal part; F, paragnath; G, mandible; H, mandibular gnathobase, ventral-lateral; I, P5. Scale line "a, b, d, g" is 0.05 mm for A, B, D, G; line "e, f" is 0.025 mm for E, F; line "c" is 0.025 mm for C; line "h" is 0.025 mm for H.

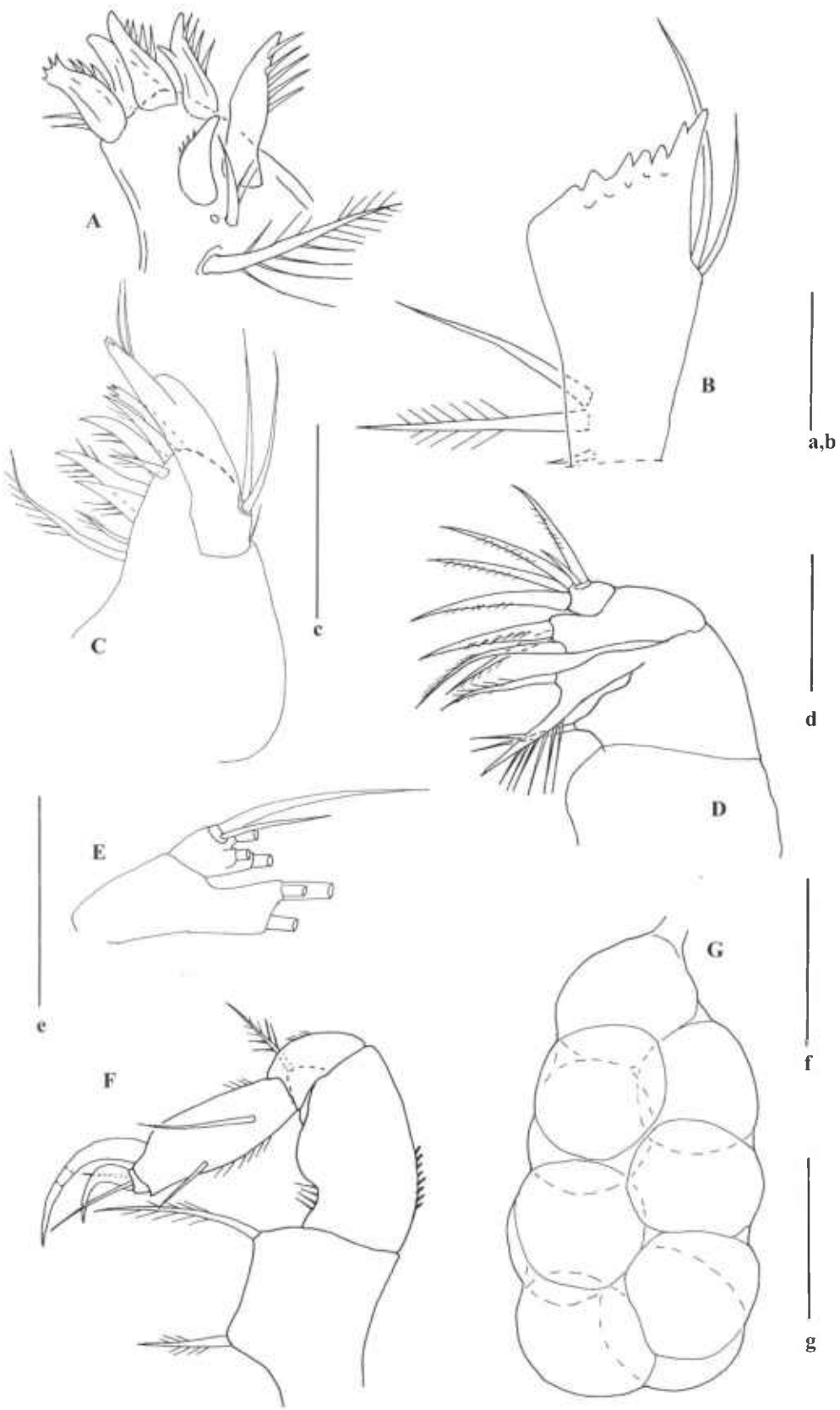

Fig. 3. *Euryte longicauda* Philippi, 1843, CVI Female: A, maxillule, praecoxa; B, maxillule, coxa and palp; C, maxillule; D, maxilla; E, maxilla, ramus; F, maxilliped; G, egg sac. Scale line "a, b" is 0.025 mm for A, B; line "c" is 0.025 mm for C; line "d" is 0.05 mm for D; line "e" is 0.05 mm for E; lines "f", "g" are 0.1 mm for F, G.

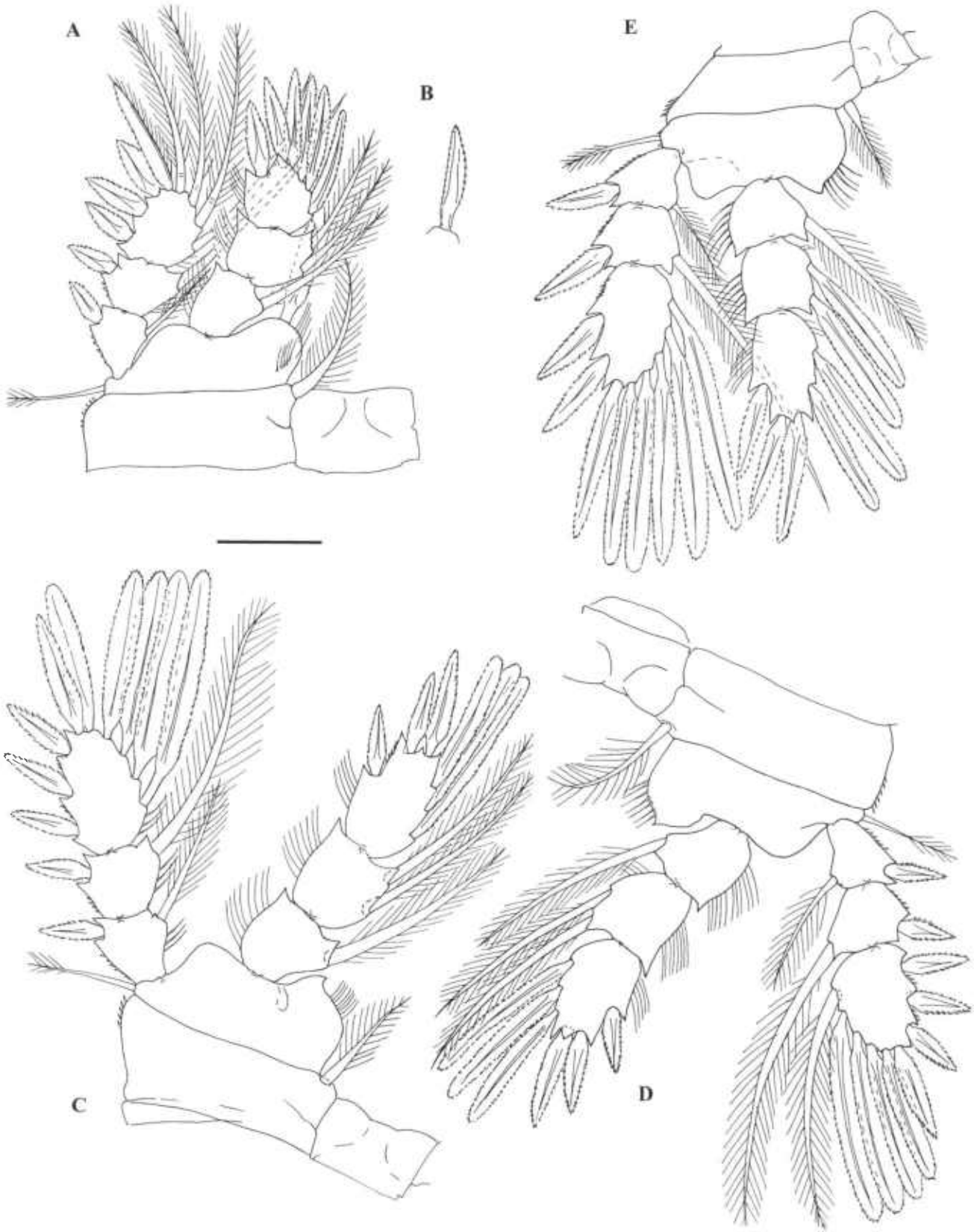

Fig. 4. *Euryte longicauda* Philippi, 1843, CVI Female: A, swimming leg 1, anterior; B, leg 1, inner spine of basis, anterior; C, swimming leg 3, anterior; D, swimming leg 2, anterior; E, swimming leg 4, anterior. Scale line is 0.05 mm for A–E.

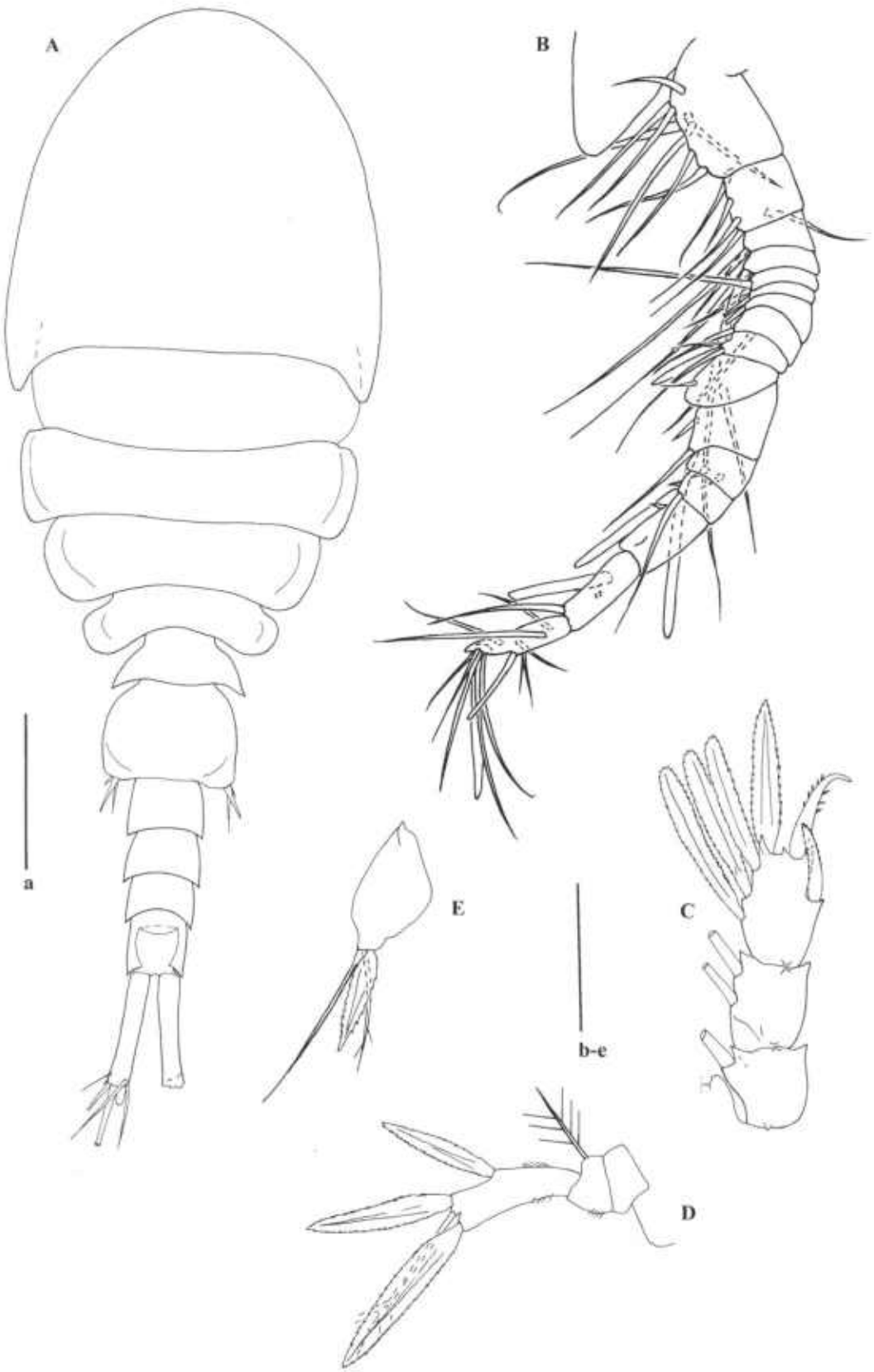

Fig. 5. *Euryte longicauda* Philippi, 1843, CVI Male: A, habitus, dorsal; B, rostrum and antennule; C, leg 3, endopod; D, leg 5; E, leg 6. Scale line "a" is 0.1 mm for A, line "b–e" is 0.05 mm for B–E.

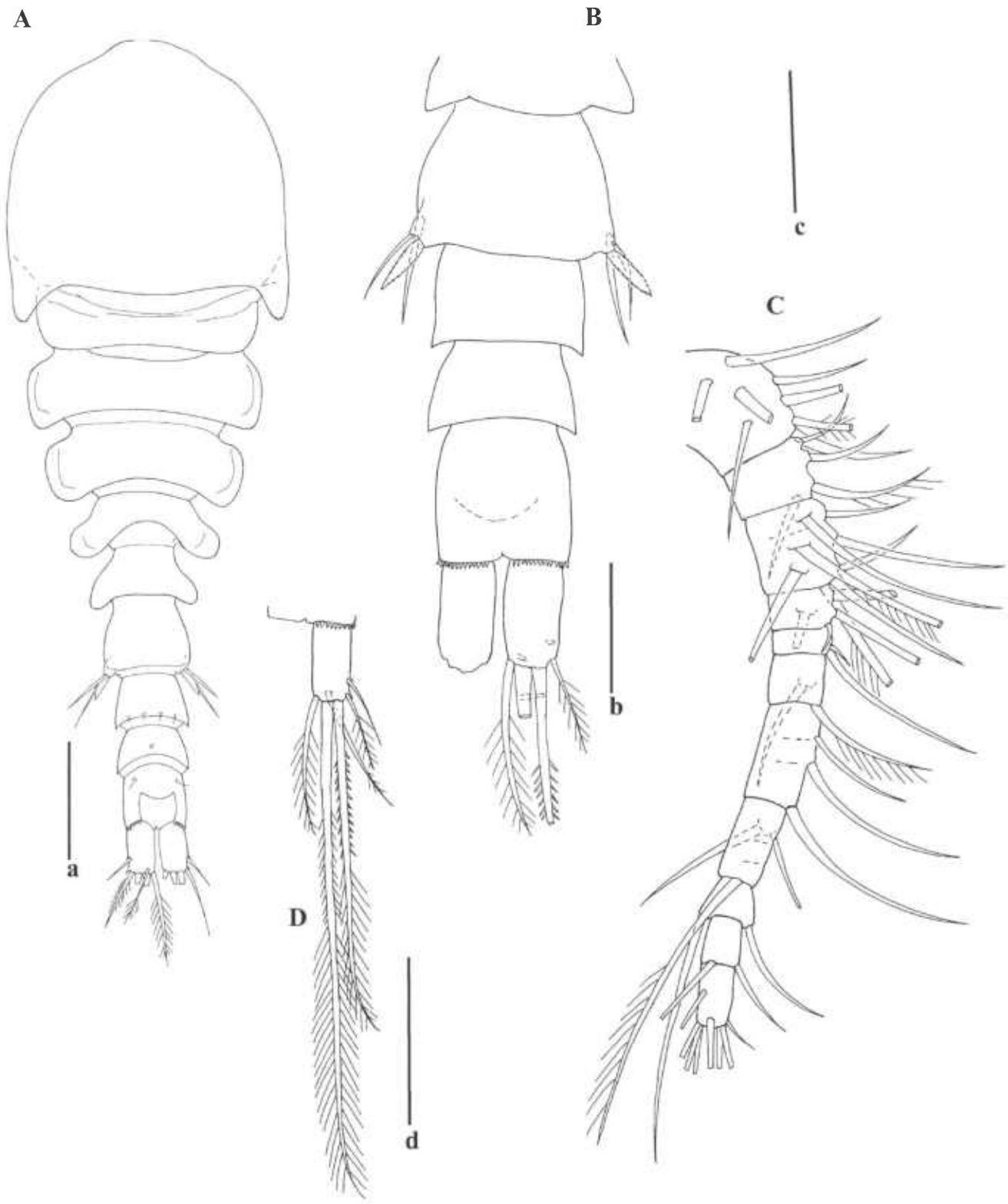

Fig. 6. *Euryte longicauda* Philippi, 1843, CV: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, caudal ramus, ventral. Scale line "a" is 0.1 mm for A, line "b" is 0.05 mm for B, line "c" is 0.05 mm for C, line "d" is 0.1 mm for D.

Urosome (Fig. 5A): 6 parts; Th6, 7, Abd2, 3, 4, 1 articulating; genital pore ventrolateral on Th7.

Antennule (Fig. 5B): 16 articulating segments with 9, 4, 2, 2, 2, 2, 2, 2+1, 2, 2, 2, 2, 1, 1+1, 11+2 setae + aesthetase.

Leg 3 endopod (Fig. 5C): tip of outer terminal seta of distal segment complex curved outward.

Leg 6 (Fig. 5E): unilobe bud with 3 terminal setae.

CR (Fig. 5A): length to width ratio 4.8:1

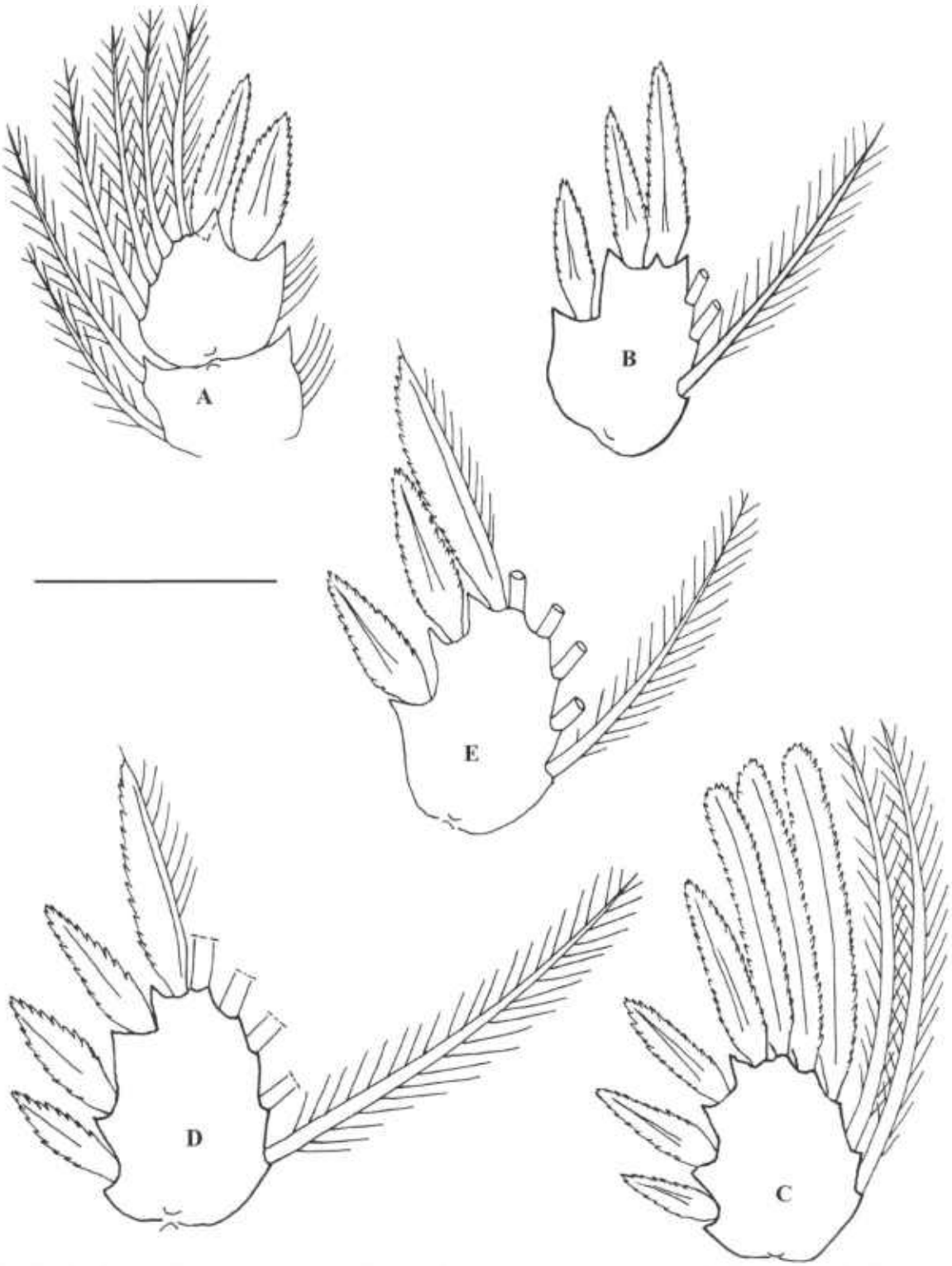

Fig. 7. *Euryte longicauda* Philippi, 1843, CV: A, swimming leg 1, two distal segments of endopod, anterior; B, swimming leg 2, distal segment of endopod, anterior; C, swimming leg 2, distal segment of exopod, anterior; D, swimming leg 3, distal segment of exopod, anterior; E, swimming leg 4, distal segment of exopod, anterior. Scale line is 0.05 mm.

CV.—Differs from CVI female as follows: Body length range 0.65–0.76 mm; ratio of length of prosome to length of urosome 1.6:1 (based on 7 specimens).

Urosome (Fig. 6B): 5 parts; Th6, 7, Abd2, 3, 1 articulating. Th7 without copulatory pores or oviducal openings.

Antennule (Fig. 6C): 11 articulating segments with 3, 4, 6, 4, 2, 4, 2, 2, 2, 2, 4, 2, 3, 9+1 setae + aesthetasc.

Swimming legs 1–4 (Fig. 7B–F): medial seta with setules in proximal position on distal segmental complex of both rami; more distal setae fluted. Spine and setal formula as in Table 3.

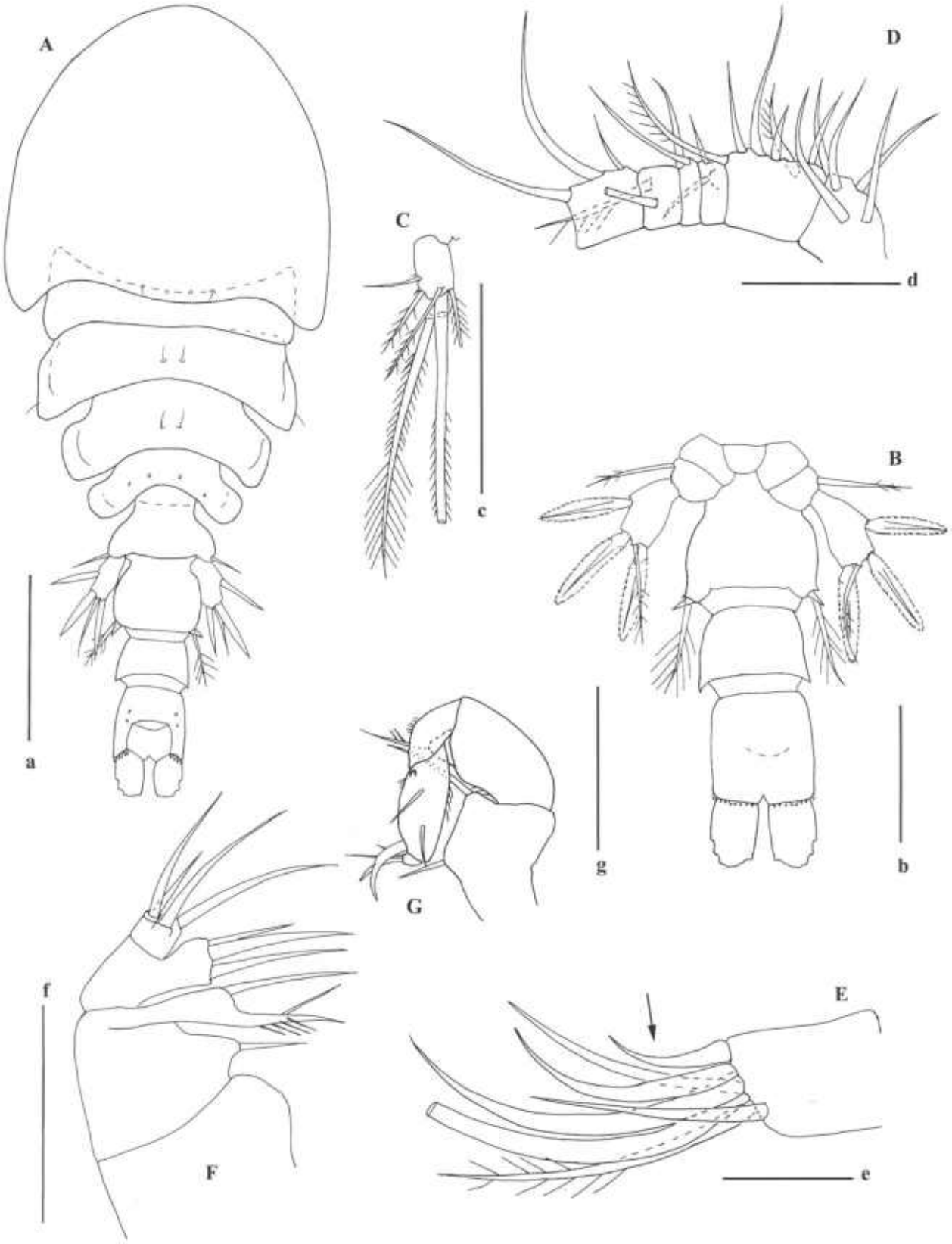

Fig. 8. *Euryte longicauda* Philippi, 1843, CIV: A, habitus, dorsal; B, urosome, ventral; C, caudal ramus, dorsal; D, antennule, segments 1–6, distal 4 segments not shown and as in female; E, antenna, distal segment; F, maxilla; G, maxilliped. Scale line "a" is 0.1 mm for A, line "b" is 0.05 mm for B, line "c" is 0.1 mm for C, line "d" is 0.05 mm for D, line "e" is 0.025 mm for E, line "f" is 0.025 mm for F, line "g" is 0.05 mm for G.

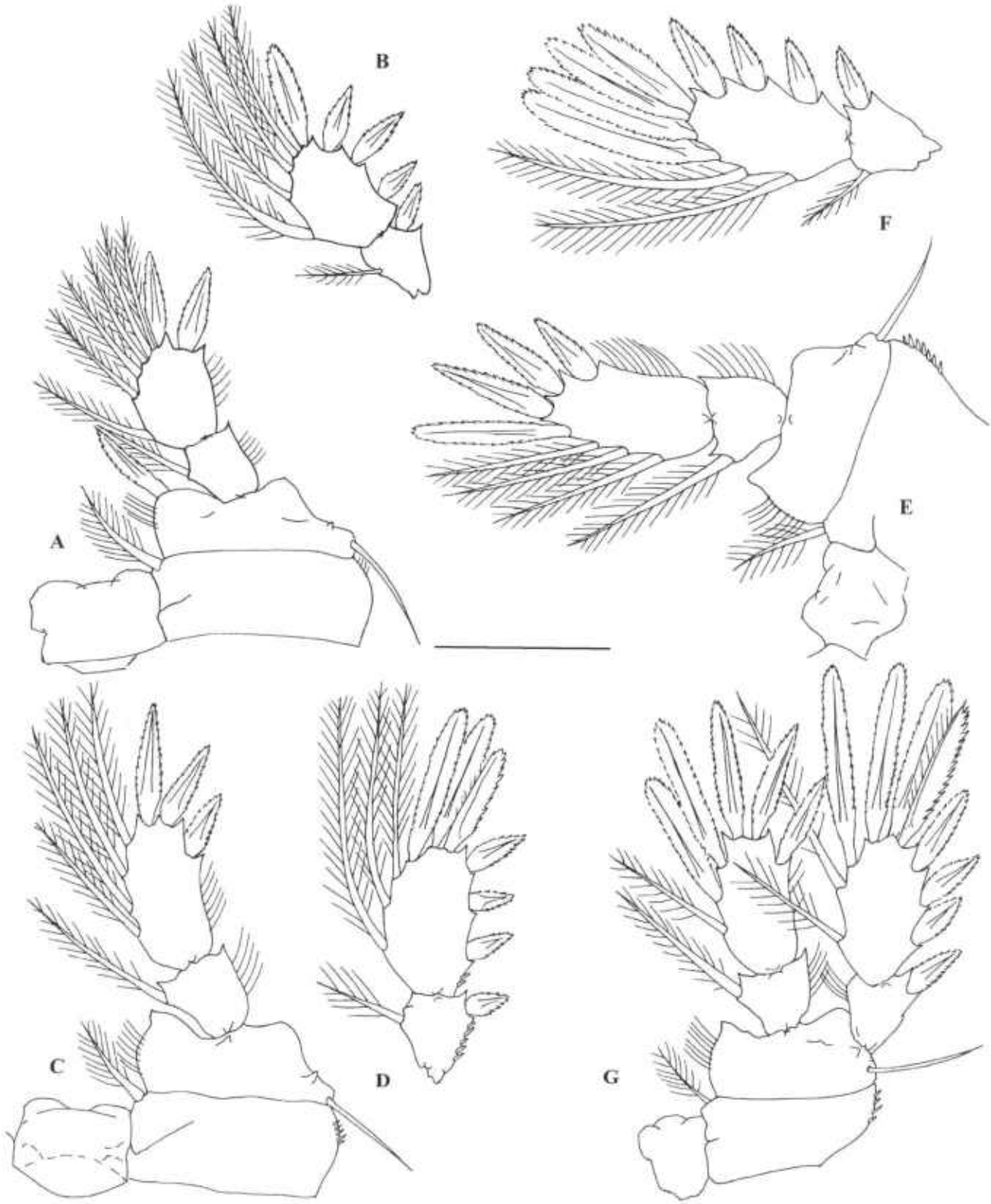

Fig. 9. *Euryte longicauda* Philippi, 1843, CIV: A, swimming leg 1, anterior; B, exopod of leg 1, anterior; C, swimming leg 2, anterior; D, exopod of leg 2, anterior; E, swimming leg 3, anterior; F, exopod of leg 3, anterior; G, swimming leg 4, anterior. Scale line is 0.05 mm.

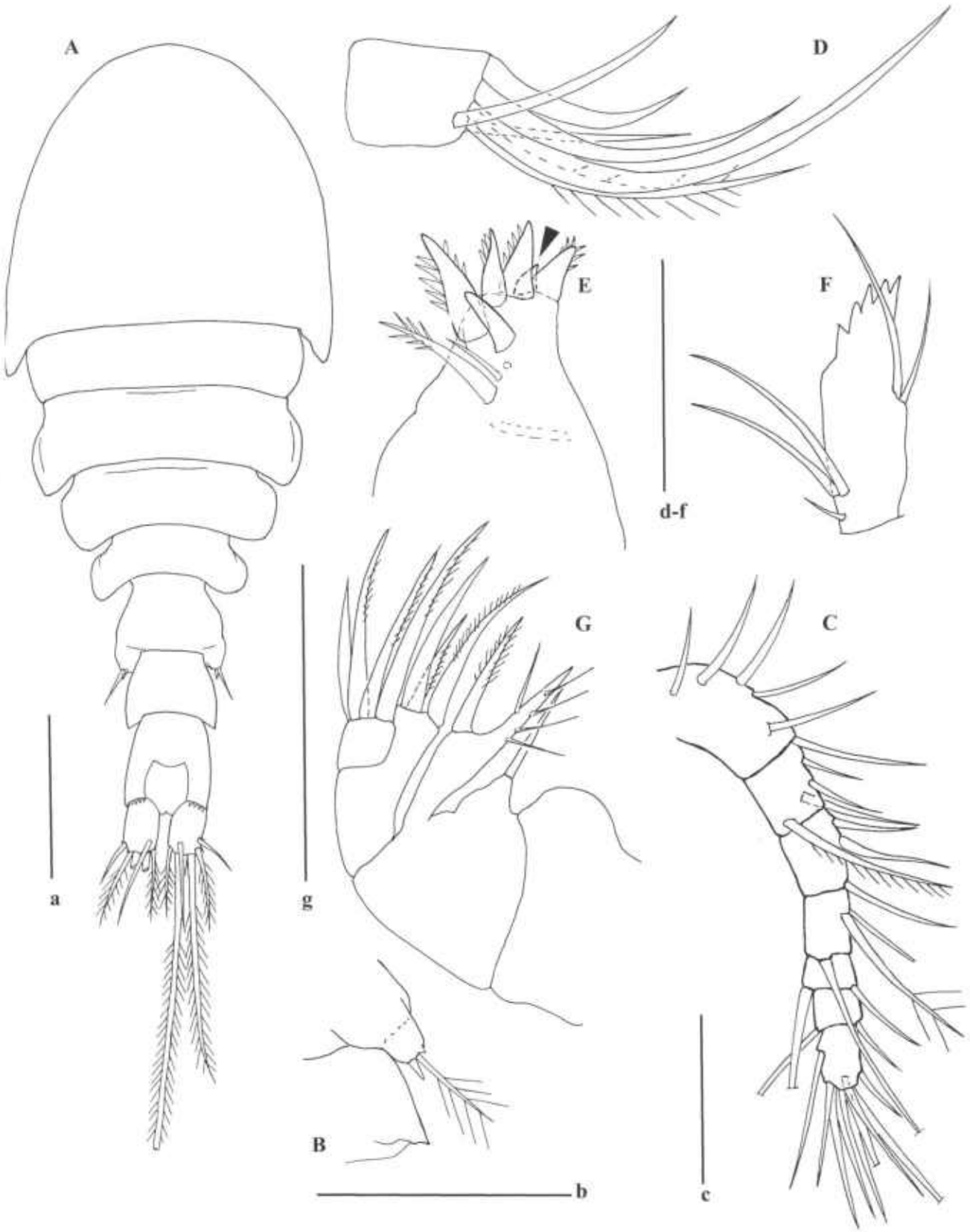

Fig. 10. *Euryte longicauda* Philippi, 1843, CIII: A, habitus, dorsal; B, leg 5, ventral; C, antennule; D, antenna, distal segment; E, maxillula, praecoxa; F, maxillule, coxa; G, maxilla. Scale line "a" is 0.1 mm for A, line "b" is 0.1 mm for B, line "c" is 0.05 mm for C, line "d–f" is 0.05 mm for D–F, line "g" is 0.05 mm for G.

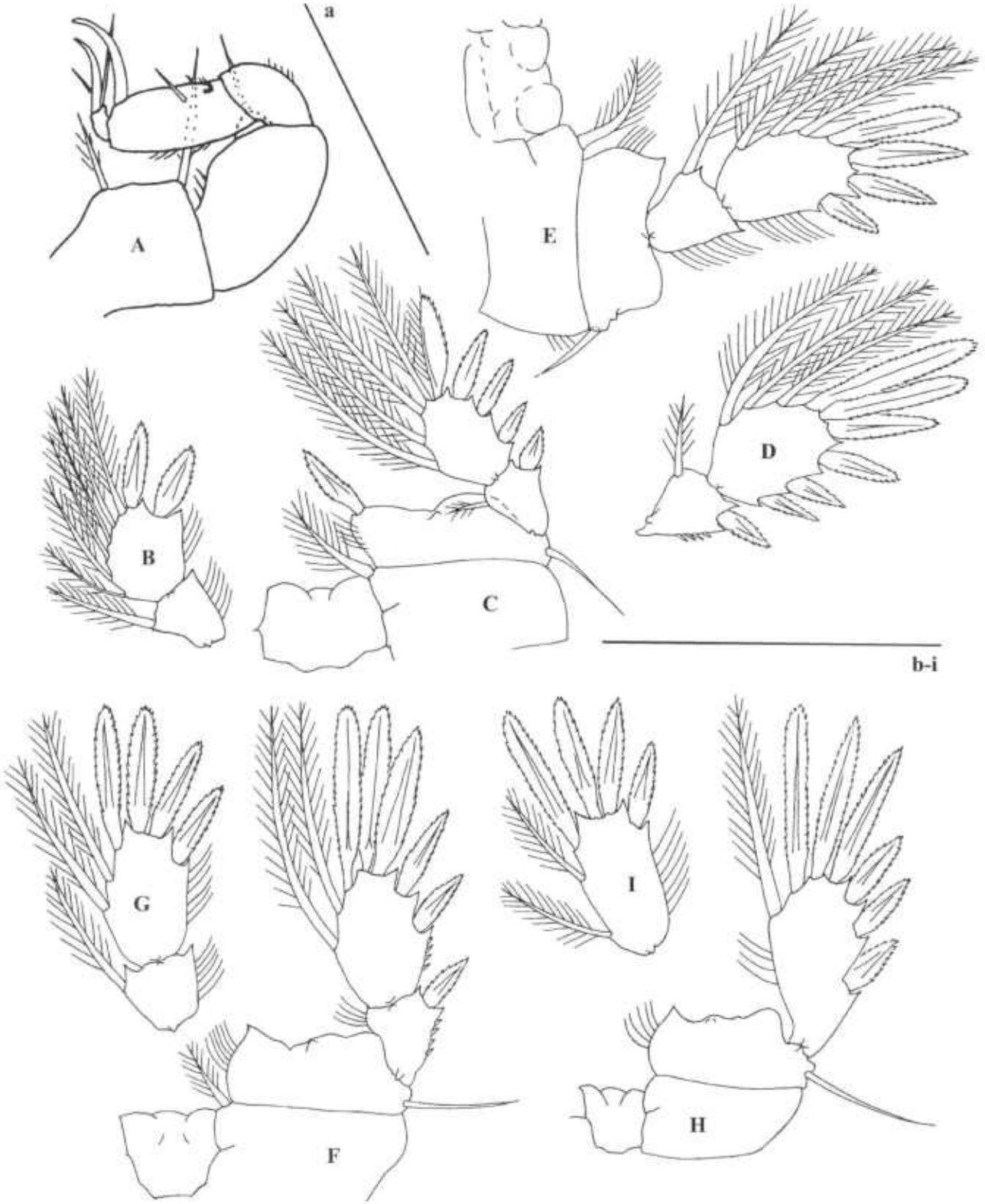

Fig. 11. *Eurvte longicauda* Philippi, 1843, CIII: A, maxilliped; B, endopod of swimming leg 1, anterior; C, swimming leg 1, anterior; D, exopod of swimming leg 2, anterior; E, swimming leg 2, anterior; F, swimming leg 3, anterior; G, endopod of swimming leg 3, anterior; H, swimming leg 4, anterior; I, endopod of swimming leg 3, anterior. Scale line "a" is 0.05 mm for A, line "b–i" is 0.1 mm for B–I.

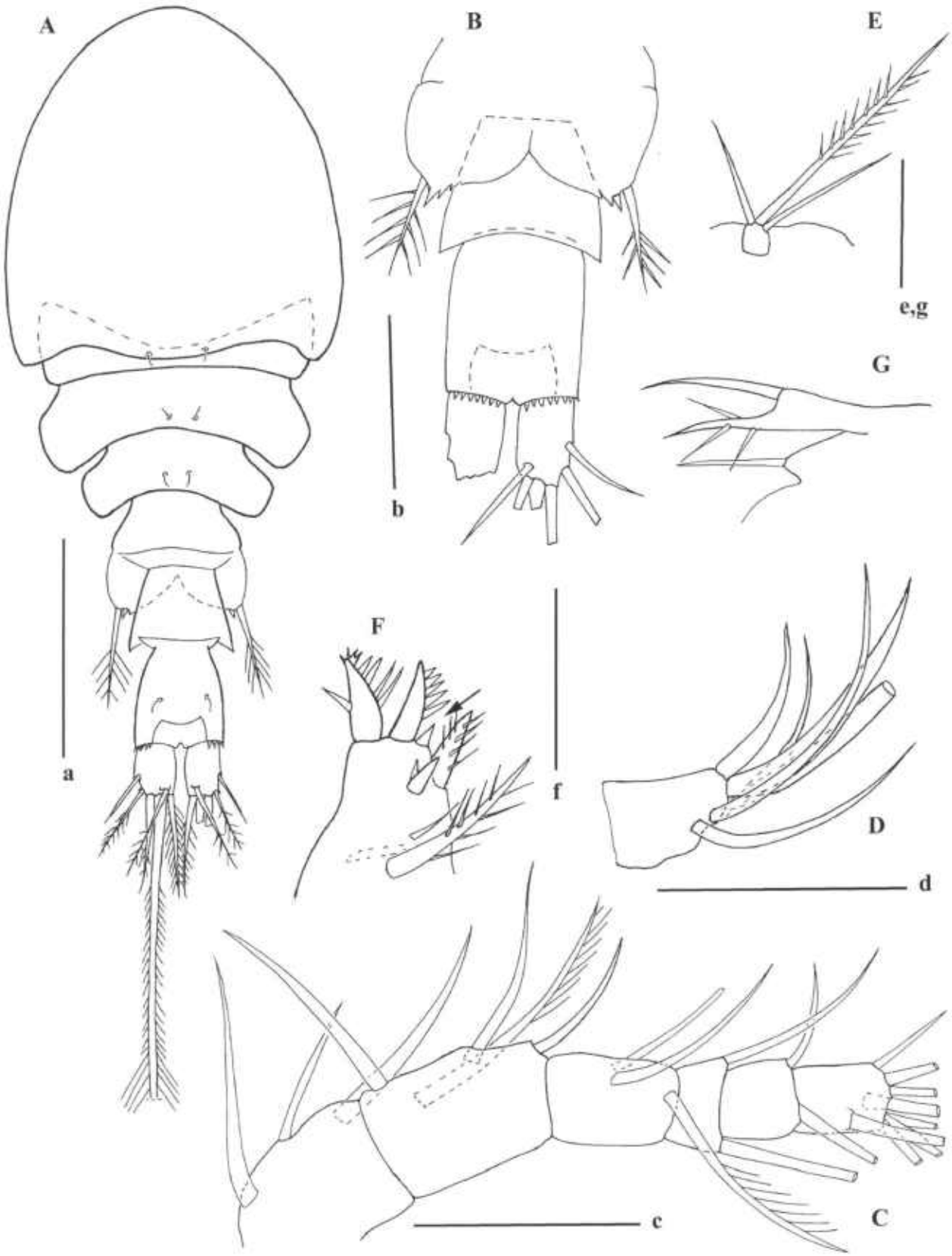

Fig. 12. *Euryte longicauda* Philippi, 1843, CII: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna, distal segment; E, mandible, palp; F, maxillula, praecoxa; G, maxilla, endites of basis. Scale line "a" is 0.1 mm for A, line "b" is 0.05 mm for B, line "c" is 0.05 mm for C, line "d" is 0.05 mm for D, line "e,g" is 0.025 mm for E,G; line "f" is 0.025 mm for F.

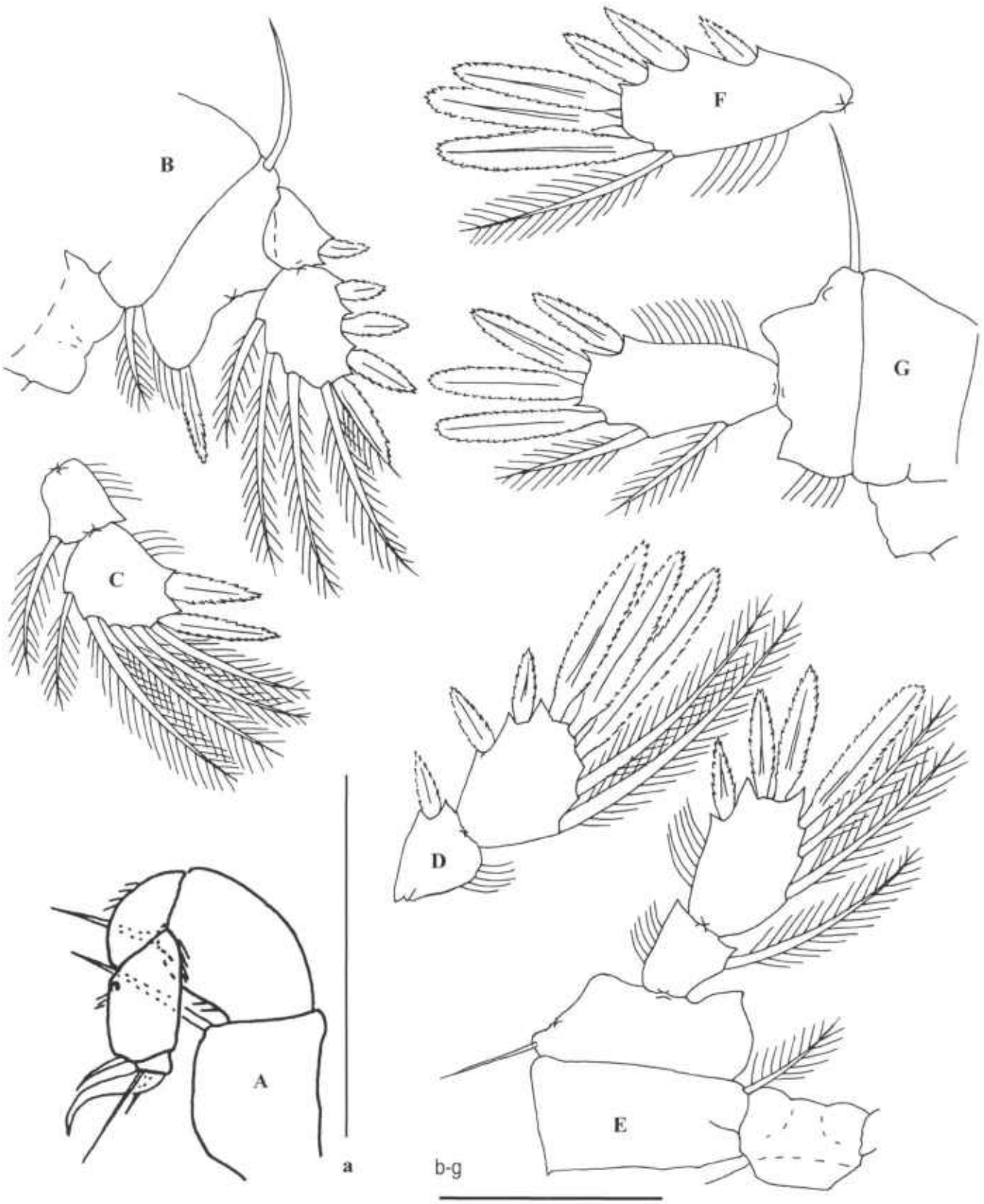

Fig. 13. *Euryte longicauda* Philippi, 1843, CII: A, maxilliped; B, swimming leg 1, anterior; C, endopod of swimming leg 1, anterior; D, exopod of swimming leg 2, anterior; E, swimming leg 2, anterior; F, exopod of swimming leg 3, anterior; G, swimming leg 3, anterior. Scale line "a" is 0.05 mm for A, line "b–g" is 0.05 mm for B–G.

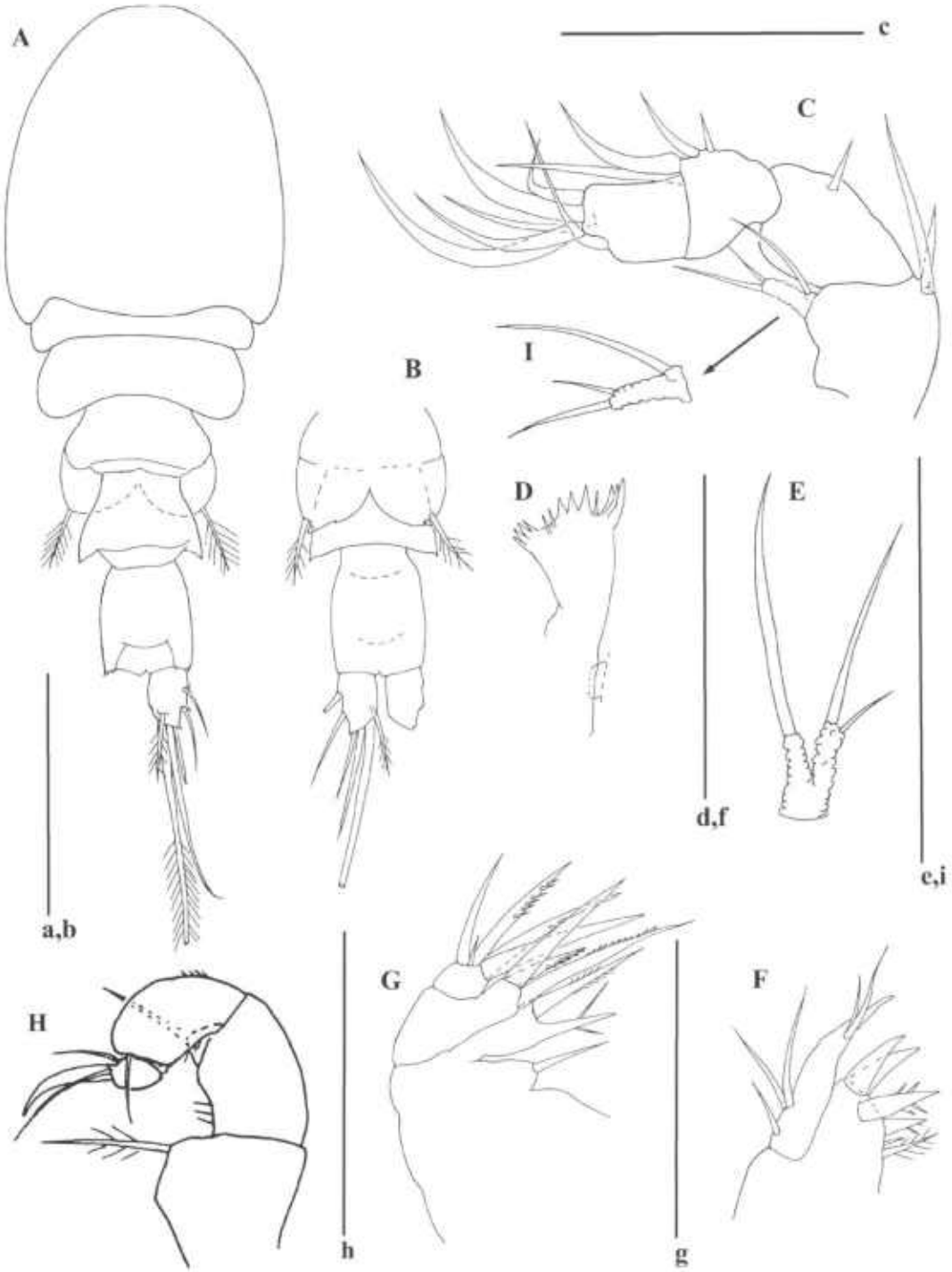

Fig. 14. *Euryte longicauda* Philippi, 1843, CI: A, habitus, dorsal; B, urosome, ventral; C, antenna; D, mandible, gnathobase; E, mandible, palp; F, maxillula; G, maxilla; H, maxilliped; I, exopod of antenna. Scale line "a,b" is 0.1 mm for A, B; line "c" is 0.05 mm for C; line "d,f" is 0.05 mm for D, F; line "e, i" is 0.05 mm for E, I; line "g" is 0.05 mm for G; line "h" is 0.05 mm for H.

Leg 6 (Fig. 6B): unilobe bud with 3 distal-lateral setae.
CR (Fig. 6B, D): ratio of length to width 2.0:1.

CIV.—Differs from CV as follows: Body length range 0.50–0.60 mm; ratio of length of prosome to that of urosome 1.6–1.7:1 (based on 5 specimens).

Urosome (Fig. 8A, B): 4 parts; Th6, 7, Abd2, 1 articulating.

Antennule (Fig. 8D): 10 articulating segments with 5, 6, 2, 2, 2, 3, 2+1, 2, 2, 6+1 setae + aesthetase.

Maxilla (Fig. 8F): fourth segment with 2 setae, each on a small lobe.

Maxilliped (Fig. 8G): curved seta of distal segment thinner.

Swimming legs 1–4 (Fig. 9A–G): with 2-segmented rami. Setal and spine formula as in Table 4.

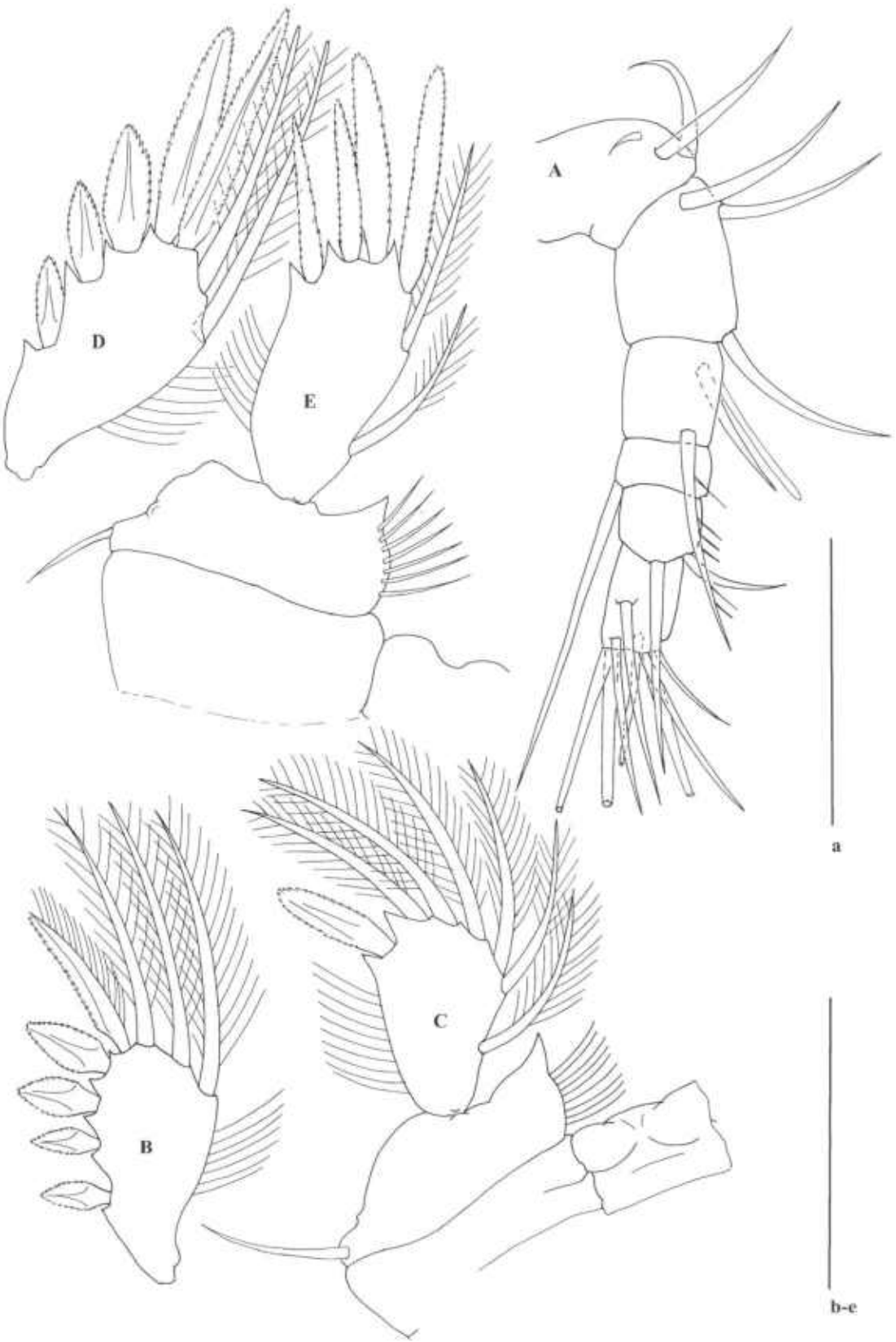

Fig. 15. *Euryte longicauda* Philippi, 1843, Cl: A, antennule; B, exopod of swimming leg 1, anterior; C, swimming leg 1, anterior; D, exopod of swimming leg 2, anterior; E, leg 2, anterior. Scale line "a" is 0.05 mm for A, line "b–e" is 0.05 mm for B–E.

Table 2. Spines and setae on swimming legs 1–4 of *Euryte longicauda* CVI female.

			Exopod			Endopod		
	Coxa	Basis	2nd	3rd	1st	2nd	3rd	1st
Leg 1	0–I	I–I	I–I;	I–I;	III, I, 4	0–1;	0–2;	I, II, III
Leg 2	0–I	I–0	I–I;	I–I;	III, I, IV+1	0–1;	0–2;	I, II, III
Leg 3	0–1	I–0	I–I;	I–I;	III, I, V	0–1;	0–2;	I, II, III
Leg 4	0–I	I–0	I–I;	I–I;	II, I, V	0–I;	0–II;	I, II, II

Leg 6 (Fig. 8B): 2 distal-lateral setae.

CR (Fig. 8C): ratio of length to width 1.4:1.

CIII.—Differs from CIV as follows: Body length 0.35–0.40 mm; ratio of length of prosome to that of urosome 1.9:1 (based on 6 specimens).

Urosome (Fig. 10A): 3 parts; Th6, 7 and Abd1 articulating.

Antennule (Fig. 10C): 7 articulating segments with 6, 4, 3, 3, 2, 2, 8 + 1 setae + aesthetasc.

Antenna (Fig. 10D): 6 setae on terminal segment.

Maxilliped (Fig. 10A): middle endopodal segmental complex with 2 setae; middle seta missing.

Swimming legs 1–4 (Fig. 11B–I): swimming legs 1–3 with 2-segmented rami, swimming leg 4 with 1-segmented rami. Setal and spine formula as in Table 5.

Leg 5 (Fig. 10B): lateral, unilobe bud with 1 short, distal spine and 1 distal seta with setules.

Leg 6: absent

CII.—Differs from CIII as follows: Body length range 0.31–0.36 mm; ratio of length of prosome to that of urosome 1.5:1(based on 7 specimens).

Prosome (Fig. 12A): 3 parts; first a complex of 5 cephalic somites plus Th1&2; Th3, 4 articulating.

Urosome (Fig. 12B): 3 parts; Th5, 6, Abd1 articulating.

Antennule (Fig. 12C): 6 articulating segments with 3, 4, 2+1, 2, 2, 6+1 setae + aesthetasc.

Maxilliped (Fig. 13A): syncoxa with 1 distal seta; middle endopodal segment complex with 1 lateral seta thin and slightly curved at tip, proximal seta missing.

Swimming Legs 1–3 (Fig. 13B–G): swimming legs 1, 2 with 2-segmented rami, swimming leg 3 with 1-segmented rami. Spine and setal formula as in Table 6.

Swimming Leg 4 (Fig. 12B): bilobe bud; lateral lobe with 1 distal spine and 1 distal seta; medial lobe unarmed.

Leg 5: absent.

CI.—Differs from copepodid stage II as follows: Body length range 0.28–0.34 mm; ratio of length of prosome to that of urosome 1.3:1 (based on 5 specimens).

Table 3. Spines and setae on swimming legs 1–4 of *Euryte longicauda* CV.

			Exopod			Endopod		
	Coxa	Basis	2nd	3rd	1st	2nd	3rd	1st
Leg 1	0–1	I–I	I–I;	I–1;	III, I, 4	0–1;	0–2;	I, I+1, 3
Leg 2	0–1	I–0	I–I;	I–1;	III, I, III+2	0–1;	0–2;	I, II, II+1
Leg 3	0–1	I–0	I–I;	I–1;	III, I, IV+1	0–1;	0–2;	I, II, III
Leg 4	0–1	I–0	I–I;	I–I;	II, I, IV+1	0–1;	0–II;	I, II, II

Table 4. Spines and setae on swimming legs 1–4 of *Euryte longicauda* CIV.

			Exopod			Endopod		
	Coxa	Basis	2nd	3rd	1st	2nd	3rd	1st
Leg 1	0–1	I–I	I–1;	* ;	III, I, 4	0–1;	* ;	I, I+1, 5
Leg 2	0–1	I–0	I–1;	* ;	III, I, III+2	0–1;	* ;	I, II, I+4
Leg 3	0–1	I–0	I–1;	* ;	III, I, II+3	0–1;	* ;	I, II, I+3
Leg 4	0–1	I–0	I–0;	* ;	III, I, III+2	0–1;	* ;	I, II, II+1

Prosome (Fig. 14A): 2 articulating parts; first a complex of 5 cephalic somites plus Th1&2; Th 3 articulating.

Urosome (Fig. 14B): 3 parts; Th4–5, Abd1 articulating.

Antennule (Fig. 15A): 6 articulating segments with 3, 3, 2+1, 1, 2, 6 + 1 setae + aesthetasc.

Antenna (Fig. 14C) with short, wrinkled and poorly-sclerotized exopod with 1 proximal and 2 distal setae.

Mandible (Fig. 14D, E): with wrinkled, poorly-sclerotized bilobe palp; lobes with 1 and 2 setae.

Maxilliped (Fig. 14H): 4 segmented armed with 1, 1, 1, 3 setae.

Swimming legs 1–2 (Fig. 15B–E): with 1-segmented rami. Spine and setal formula as in Table 7.

Swimming leg 3 (Fig. 14B): a bilobe bud; lateral lobe with 1 distal spine and 1 distal seta; medial lobe unarmed.

Swimming leg 4: absent.

CR (Fig. 14B): inner seta is longest, terminal seta.

Remarks.—Holthuis (1954: 5–7) published a translation of a classification of crustaceans by Rafinesque (1815: 94–101). It seems clear from this translation that Rafinesque intended to establish the family Cyclopia (by the category Famille), and he provided a short diagnosis. A recent opinion by L. B. Holthuis and J. C. von Vaupel Klein in Karanovic (2004: vi) on behalf of the editorial committee of Crustaceana states that Rafinesque should be the author and 1815 the date of publication of the family name Cyclopidae and the ordinal name Cyclopoida. We concur with the opinion about the author of the family Cyclopidae because the intent of the author is clear.

Many of the species (Table 2) of *Euryte* require redescription. For example, originally leg 5 of *E. bellatula* Humes, 1991, and of *E. verecunda* Humes, 1992, was described as having a 1-segmented protopod. Jaume and Boxshall (1996) then suggested that the two species should be placed in *Ancheuryte* Herbst, 1989. We re-examined type specimens of *E. bellatula* and *E. verecunda* on slides from Humes' personal collection [uncatalogued at the USNM], and found that the protopod of leg 5 of both species is 2-segmented (Fig. 16A, B). These species should remain in

Table 5. Spines and setae on swimming legs 1–4 of *Euryte longicauda* CIII.

			Exopod			Endopod		
	Coxa	Basis	2nd	3rd	1st	2nd	3rd	1st
Leg 1	0–1	I–I	I–1;	* ;	III, I, 4	0–1;	* ;	I, I+1, 5
Leg 2	0–1	I–0	I–1;	* ;	III, I, II+3	0–1;	* ;	I, II, I+3
Leg 3	0–1	I–0	I–0;	* ;	III, I, I+2	0–1;	* ;	I, II, I+2
Leg 4	0–0	I–0	* ;	* ;	III, I, II+1	* ;	* ;	I, II, I+2

Table 6. Spines and setae on swimming legs 1–3 of *Euryte longicauda* CII.

			Exopod			Endopod		
	Coxa	Basis	2nd	3rd	1st	2nd	3rd	1st
Leg 1	0–1	1–1	1–0;	* ;	III, I, 4	0–1;	* ;	I, I, 5
Leg 2	0–1	1–0	1–0;	* ;	II, I, II+2	0–1;	* ;	I, II, I+2
Leg 3	0–0	1–0	* ;	* ;	III, I, II+I	* ;	* ;	I, II, I+2

Table 7. Spines and setae on swimming legs 1–2 of *Euryte longicauda* CI.

			Exopod			Endopod		
	Coxa	Basis	2nd	3rd	1st	2nd	3rd	1st
Leg 1	0–0	1–0	* ;	* ;	IV, I, 3	* ;	* ;	I, 2, 4
Leg 2	0–0	1–0	* ;	* ;	III, I, I+2	* ;	* ;	I, II, I+2

Euryte. We have followed Sewell (1949) in synonymizing *E. propinqua* Brady, 1910, and *E. similis* Scott, 1912, with *E. robusta* and not with *E. longicauda* as was proposed by Kiefer (1929). Sewell (1949) indicated a relatively short caudal ramus (length to width ratio if 4:1) for the three species and that this is the state of *E. robusta*.

Thomas Scott (1905) and Sars (1913, 1919) stated that *E. longicauda* was a common species in shallow waters of Scotland and Norway. More recently Jaume and Boxshall (1996) consider it rare in the Mediterranean Sea. The fact that all copepodid stages were collected from samples of animals associated with the bryozoan *Flustra foliacea* in the White Sea suggests that it may be more easily collected from larger benthic invertebrates and that this association may alter our understanding of its abundance.

Euryte longicauda is the type species of the genus and differs from its congeners by the relatively longer caudal ramus (Giesbrecht, 1900; Sars, 1913). Illustrations by Giesbrecht (1900) and Sars (1913) show features of the caudal ramus and other appendages similar to specimens from the White Sea. Sars describes and illustrates the proximal inner seta on the distal segment complex of the exopod of leg 2 as a fluted seta. On our specimens this is a seta with setules, and this is the case for specimens from Norway examined Jaume and Boxshall (1996) who suggest an error by Sars. Our specimens also differ from Sars' description in a number of attributes of the mouthparts: one seta more on the terminal segment of the antenna; a seta on the exite of the maxillule; five setae, rather than four, on the ultimate and penultimate segments of maxilla; and six setae, rather than four, on the ultimate and penultimate segments of maxilliped. The second segment of the antennule of *E. longicauda* from the White Sea is subdivided in some females and this variation was noted by Sars (1913) for *E. longicauda* from Norway.

Specimens of *E. longicauda* from Cova de na Mitjana, Capdepera, Mallorca [1313–1322, CR04/43T, collected 01.04.1995 by D. Jaume + G. Boxshall] differ from those from the White Sea in the following: female ratio of length

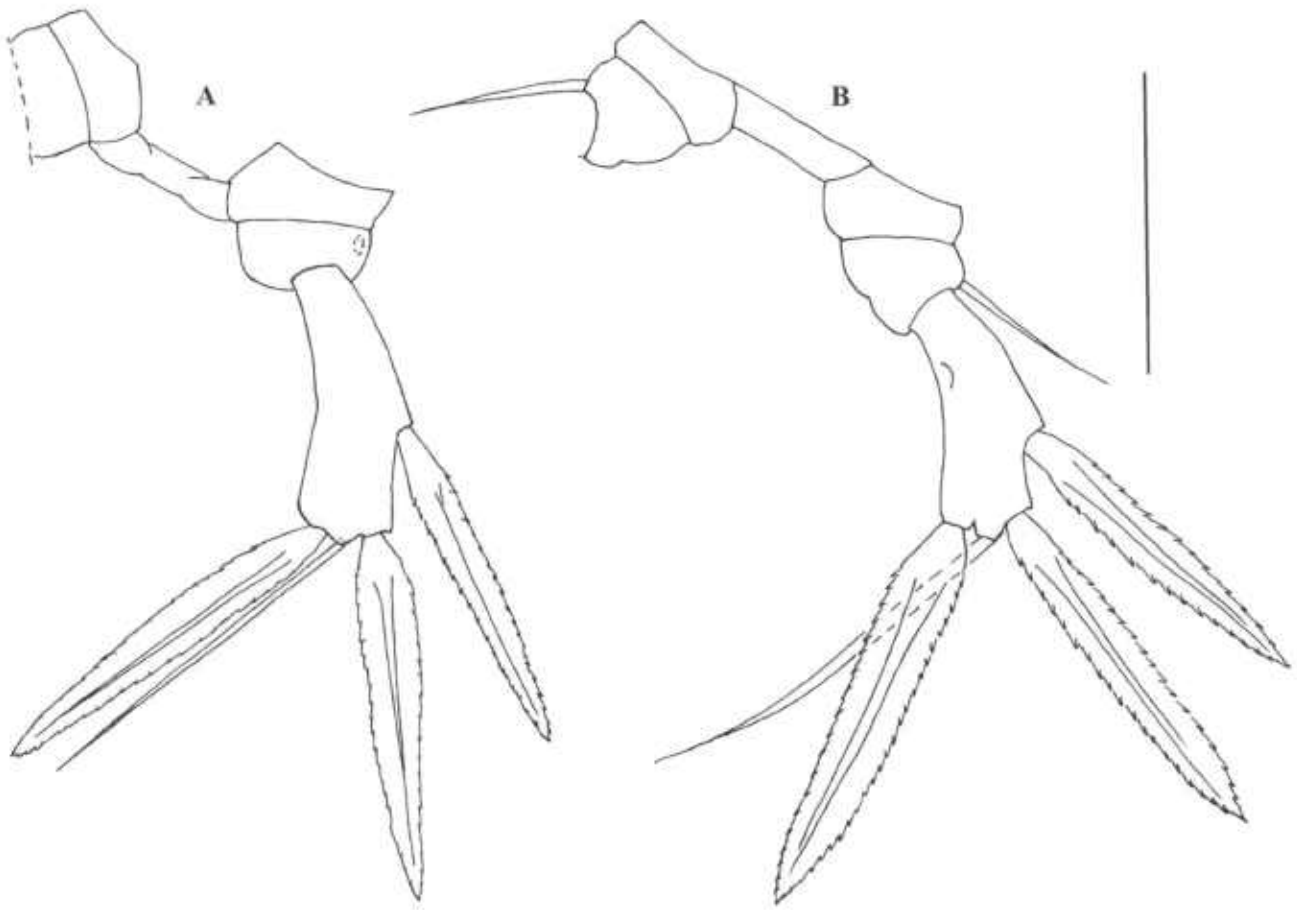

Fig. 16. *Euryte bellatula* Humes, 1991, Female: A, leg 5; *Euryte verecunda* Humes, 1992, Female: B, leg 5. Scale line is 0.05 mm.

to width of caudal ramus is about 6.0:1; the posterior-lateral corners of thoracomere 6 are not as well developed; the lateral process of the genital complex is more closely appressed to the genital complex. Males from Mallorca have more aesthetases on antenna 1 (Jaume and Boxshall, 1996: fig. 8G), the aesthetases are much longer, and each is distinctively constricted toward its tip; the lateral and terminal setae on the endopod of leg 3 of these males are not modified. Specimens from Mallorca agree with those from the White Sea in: setation of the antennules; degree of denticulation on the antenna; number of setae on palp of maxillule; origin of a seta attributed here to the exite of the maxillule; segmentation of maxilla; number, origin of setae and degree of denticulation on the maxilliped.

Grandori (1926) described the antennule, leg 5, and caudal ramus of the male of *E. lougiseta* from Laguna Veneta in the Mediterranean Sea. The species later was placed in synonymy with *E. lougicauda* by Kiefer (1929). *Euryte longiseta* is remarkably similar to the description of *E. longicauda* by Jaume and Boxshall (1996). *Euryte lougiseta* also bears an elongate medial seta on middle segment of endopod of leg 4 which does not occur on *E. lougicauda*.

Euryte lougicauda has been reported as free living from sublittoral habitats close to the benthos or associated with algae, or from caves (Sars, 1913; Jaume and Boxshall, 1996). In the White Sea the copepod is associated with the common sublittoral bryozoan *Flustra foliacea*, indicating a symbiotic mode of life (Ivanenko and Smurov, 1997).

Development and Relationships

A recent analysis of antennule development of species of Cyclopidae (Schutze *et al.*, 2000) used a series of marker setae to identify homologous segments from six copepodid stages among 35 species in 29 genera. We are unable to locate the following marker setae an the antennule of *E. lougicauda*: a proximal conical seta, a distal bithek [seta plus aesthetasc] on the penultimate segment, or the distinctive bifurcate seta/aesthetasc on the distal segment. Two adjacent setae found on the fifth from distal segment of copepodid VI and third from distal segment of copepodids V–I appear to correspond to the proximal bithek found on the same stages and segments by Schutze *et al.* (2000). Proximal to this marker, the number of articulating antennular segments, two, does not change between copepodids I and II of *E. lougicauda*, agreeing with species of *Ancheuryte*, *Paracyclops*, *Eucyclops*, *Neocyclops*, *Halicyclops* and *Ectocyclops* (Schutze *et al.*, 2000: table 1). However, the number of setae on these segments of *E. lougicauda* [3 and 3 at copepodid I; 3 and 4 at copepodid II] appears to be unique among species of Cylopidae.

The palp of the mandible of *E. lougicauda* is reduced from a wrinkled, poorly-sclerotized, bilobe-like structure with a seta on one lobe and two setae on the other lobe at copepodid I to three setae originating in the middle of the distal boundary of the gnathobase at copepodids II–VI. The palp of the maxillule is not presented as a wrinkled structure at CI and remains unchanged, as two setae on the distal face of the coxa, throughout copepodid development. The absence of a wrinkled stage may be explained because the maxillule never develops beyond a bud in nauplii of species of Cyclopoida (see Ferrari and Ambler, 1992) in contradistinction to the mandible which is a biramal limb during the naupliar phase of development. The coxa of the maxillule appears as a gnathobase perpendicular to the proximal/distal axis of the limb, with two medial setae. This perpendicular orientation is echoed in the broad multi-cusp distal seta on the maxillular praecoxa whose tips are perpendicular to the remaining setae of the praecoxa, as well as the distal set of teeth of the mandibular gnathobase which are perpendicular to the proximal set of teeth.

Recent observations (Ferrari and Grygier, 2003) indicate that the crustacean protopod is patterned distally from a point where the limb attaches to the body. If the architecture of the protopod of the maxilla is determined simply by truncation of this patterning and the maxillule, maxilla, and maxilliped are serially homologous limbs with a single coxal lobe, then the proximal articulating segment of the maxilla of *Euryte* is an unarmed syncoxa. In other cyclopoids this syncoxa may bear the coxal lobe distally. In copepods like calanoids, misophrioids, and harpacticoids, the syncoxa also may bear the distal praecoxal lobe, located proximal to the coxal lobe. The next articulating segment of the maxilla of *Euryte* is the basis with two medial lobes, and the remainder of the limb is a 3-segmented ramus. This interpretation agrees with that of Hansen (1925: pl. II, 5a) for the shaft of the protopod of the copepod maxilla, although Hansen did not associate lobes of the maxilla with specific protopodal segments.

Medial fluted setae appear on the distal segment complex of both rami of swimming legs 1–4 and on the middle endopodal segment of swimming leg 4 of both adult genders of *E. lougicauda*. At copepodid V and VI, an identical number of setae is found on the swimming legs but some of the setae, which are simple setae with setules on the immature copepodid V, are fluted setae on adult rami, suggesting fluted setae are not new setae but simple seta with setules which have been transformed during development.

Development of thoracopods (maxilliped, swimming legs, and legs 5 and 6) recently has been used to infer relationships among species of different genera of Cyclopidae (Ferrari, 1998). *Euryte lougicauda* retains the ancestral pattern of swimming leg development because setation and segmentation of both rami of swimming legs 1–4 are complete at copepodid V, and a proximal and middle segment, plus a distal segment complex result from this development. Ancestral states also have been retained during development of legs 5 and 6, although *E. lougicauda* has both a coxa and intercoxal plate, which fail to develop in *Macrocyclops albidus* (Jurine, 1820), the species of Cyclopidae with the fewest number of transformed states analyzed by Ferrari (1998). A subsequent study of maxilliped development of cyclopoid copepods (Ferrari and Ivanenko 2001) shows that *E. lougicauda*, *Troglocyclops jaustocki* Rocha and Iliffe, 1994, and *Neocyclops vicinus* (Herbst, 1955) retain a seta on the presumptive fifth segment of the endopod at copepodid IV. This state also is expressed during development of those older species of the order Cyclopoida with a well-developed mandibular palp, like

Cyclopina caroli Lotufo, 1994. All other species of Cyclopidae that express the ancestral pattern of swimming leg development, as well as species with derived swimming leg development, either truncated or delayed, share a derived state for the maxilliped; development of the endopod is truncated after copepodid I. *Euryte longicauda* and *Troglocyclops janstocki* share two derived states of maxilliped development: absence of an arthrodial membrane between the fourth and fifth endopodal segments; absence of an arthrodial membrane between the fifth and second endopodal segments. Derived states of the maxilliped shared by *E. longicauda*, *E. bellatula*, and *E. verecunda* include: a thick, curved seta on the terminal segment; a thick, curved seta of lateral origin on the penultimate segment; basis with only one seta; distal praecoxal lobe of the syncoxa with only one seta. It appears that the evolution of the Cyclopidae with a reduced mandibular palp of 2–3 setae, without a seta on the proximal maxillipedal endopodal segment, and with only three setae, rather than four, on the terminal endopodal segment has resulted in an older cyclopoid lineage which lost the arthrodial membrane between the fifth and second endopodal segments of the maxilliped. Subsequent truncation of development of the maxillipedal endopod has resulted in the second lineage, which then diversified through the delay or the truncation of swimming leg development (Ferrari, 1998).

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