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A new polymorphic species of *Leptochelia* (Crustacea: Tanaidacea) from Guinea Bissau, West Africa, with comments on genetic variation within *Leptochelia*

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ABSTRACT

A new species of *Leptochelia*, namely *L. africana*, is described from Guinea Bissau, West Africa, following the collection of specimens during the Laboratory of Marine Community Ecology and Evolution's sampling expedition to Macaronesia and Portugal's former colonies. Genetic and morphological analysis separates this species from the other east-Atlantic species of *Leptochelia*, a genus known for its combination of many cryptic species, considerable intra-specific variation, and multiple morphological forms. The diagnostic characters of the female are: antennule proximal article more than 3 times as long as wide, article 2 not longer than article 3; dorsodistal spiniform seta on antennal article 2 weaker than ventrodistal; setae not arising from a process; maxilliped basis with three distal setae longer than endites, palp article 2 with outer spiniform seta arising from a process; uropod exopod biarticulated, longer than proximal endopod article; and endopod terminal article longer than other articles. The males are structurally more complicated and cannot be assigned diagnostic characters based on morphology alone. The primary males have an uniarticulated uropod exopod, whereas that of the secondary males is biarticulated.

KEY WORDS: Crustacea, Tanaidacea, Tanaidomorpha, Leptocheliidae, *Leptochelia africana*, West Africa, Guinea Bissau, new species.

INTRODUCTION

For the size of the continent, spanning over 70° of latitude and 65° of longitude, and with a coastline of about 26 000 km, Africa's shallow-water and littoral tanaidacean fauna is poorly known; most recorded species are from locations other than West Africa. The Mediterranean coast of North Africa is the best studied region (Kossmann 1880; Dollfus 1898; Stebbing 1904, 1910*a*; Monod 1925, 1933; Larwood 1940, 1954; Băcescu 1977; Guţu 2002; Bamber *et al.* 2009), followed by East Africa (Stebbing 1910*b*, *c*; Băcescu 1976*a*–*c*, 1987; Guţu 1991, 1996, 1998), South Africa (Stebbing 1904, 1910*a*; Barnard 1914*a*, *b*, 1920, 1935, 1940, 1955; Brown 1954, 1956*a*, *b*, 1957*a*, *b*, 1958; Boltt 1969), Cape Verde (Bamber 2012; Larsen *et al.* 2012), the Red Sea (Stebbing 1910*c*; Guţu 1987), and Madagascar (Băcescu 1987). Very little has been recorded from the entire West African coast (Monod 1923; Tattersall 1925; Lang 1955). Furthermore, most descriptions of species from the African continent are over 50 years old and of little relevance to modern taxonomic studies.

The species encountered in Guinea Bissau belong to the genus *Apseudes* from the family Apseudidae (Apseudomorpha), and the genus *Leptochelia* from the family Leptocheliidae (Tanaidomorpha). The apseudomorphan species is not treated in this paper as only one specimen was obtained, while *Leptochelia* was collected by the hundreds and was the dominant taxon at the sampling sites. Other species of *Leptochelia* recorded from Africa are listed in Table 1.

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TABLE 1

Species of *Leptochelia* recorded from Africa. *Leptochelia barnardi* and *L. timida* were transferred to Paratanaidae by Lang (1973) but still present on the WoRMS database.

Species	**Authority**	**Locality**
L. savignyi	(Krøyer, 1842)	Gran Canarias
L. barnardi	Brown, 1957	South Africa
L. erythraea	(Kossmann, 1880)	South Africa
L. tanykeraia	Bamber *et al.*, 2009	Israel
L. timida	Brown, 1958	South Africa
L. parasavignyi	Larsen *et al.*, 2012	Cape Verde
L. durbanensis	Brown, 1957	South Africa
L. caldera	Bamber & Costa, 2009	Gran Canarias

To distinguish between species of *Leptochelia* is notoriously difficult, and at the same time it is probably the most common and widely distributed of all shallow-water tanaidacean taxa (Larsen & Rayment 2002). Polymorphic males and ontogenetic variation present the most serious problems as regards intra-specific variation, while females display a cryptic nature in almost all species. Thus, genetic analysis represents a valuable additional tool for separating species in this genus. The male polymorphism is the consequence of a distinctive reproductive strategy involving protogynous hermaphroditism in some if not all species (Lang 1973; Sieg 1983; Ishimaru, 1985; Larsen 2005). Adult males are devoted exclusively to reproduction and do not have functional mouthparts. Where known, the females construct tubes or galleries by secreting sticky mucus from the tip of the dactylus of the first pereopods, which glues sediment particles together (Krasnow & Taghon 1997). The female spends most if not all her lifespan inside the tube and does not leave it unless required by environmental factors. In contrast, the males locate females via pheromones and actively roam the substratum. Such activity, combined with a non-feeding lifestyle and a presumed high predation pressure, results in a short male lifespan; and males rarely constitute more than a few percent of the population (Larsen 2005). In the few detailed studies that have been carried out on this family (Buckle-Ramirez 1965; Ishimaru 1985), it was demonstrated that when the male to female ratio falls, females may molt into males of different morphological forms, depending on the life stage of the female. Males of some species have been recorded as having up to four different morphs (Buckle-Ramirez 1965; Lang 1973; Sieg 1978, 1983; Highsmith 1982, 1983; Ishimaru 1985; Stoner 1986; Modlin & Harris 1989). Apart from sexual polymorphism, ontogenetic variation amongst species in the genus complicates identification. Characters such as uropod articulation and relative pereonite length have been shown to vary considerably according to developmental stage (Larwood 1940; Masunari 1983; Larsen 2005; Bamber 2010), in this genus as well as amongst other tanaids (Larwood 1954; Bird 2008). While there are few demonstrated examples of hermaphroditism in Leptocheliidae, there are many examples of polymorphic males, indicating that hermaphroditism is widespread in this family, if not universal.

A molecular approach to facilitate identification of species in this genus thus seems appropriate (Larsen *et al.* 2012), but presents its own problems. Because of the small size of the animals and chemical properties of the cuticle, it is often difficult to extract sufficient DNA from a specimen and multiple repetitions are frequently necessary. This

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is expensive and time consuming, and precludes the use of taxa that are rare (Larsen & Froufe 2010). Fortunately, the species that is the subject of this paper is very abundant, and molecular techniques could thus be applied. The advantage of employing a molecular approach is that it can both determine conspecificity of dramatically different morphological forms, and separate morphologically similar cryptic species (Larsen 2001; Larsen *et al.* 2012). Once this procedure of combining morphological and genetic evidence becomes more widespread, it will allow us to demonstrate the genetic distance between geographically distant species so as to perhaps provide clues regarding their areas of origin. Considering that morphologically similar species of *Leptochelia* occur globally, the conservative morphological approach gives rise to problems that puzzle many scientists. Therefore, further genetic studies are strongly indicated (Larsen *et al.*, in prep.).

MATERIAL AND METHODS

The material is in the Museum Municipal do Funchal (História Natural; MMF), Madeira, and was collected via snorkeling by K. Larsen during a LMCEE (Laboratory of Marine Community Ecology and Evolution) sampling expedition (2–11 December 2011) at one location on Acunda and one on Orango Island, Bijagos Archipelago, Guinea Bissau. The material was passed through a 0.5 mm sieve and immediately fixed in 96% ethanol. The DNA extraction procedure and the subsequent amplification method and sequencing of the mitochondrial COI gene followed Larsen and Froufe (2010). Estimates of the average evolutionary divergence over sequence pairs (unc. *p*-distances) between species were calculated using MEGA5 (Tamura *et al.* 2011). Standard error estimates were obtained by means of a bootstrap procedure (1,000 replicates).

Dissections were carried out in glycerin using chemically sharpened tungsten wire needles. Body length was measured from the tip of the cephalothorax to the apex of the pleotelson.

The morphological terminology is based on Larsen (2003). Adjectives such as *long* and *short* are used as relative qualifiers in respect of the appendage being described.

TAXONOMY

Order Tanaidacea Dana, 1849
Suborder Tanaidomorpha Sieg, 1980
Superfamily Paratanoidea Lang, 1949
Family Leptocheliidae Lang, 1973
Genus *Leptochelia* Dana, 1849

Leptochelia africana sp. n.

Figs 1–7

Etymology: Named after the African continent.

Diagnosis: ♀. Antennule proximal article more than 3× as long as wide, article 2 not longer than article 3. Antennal article 2 dorsodistal spiniform seta weaker than ventrodistal; not arising from process. Maxilliped base with 3 distal setae longer than endites. Palp article 2 with outer spiniform seta arising from a process. Cheliped basis with small inner dorsodistal process; carpus about twice as long as wide. Pereopod 4–6 carpus with 2 dorsodistal simple and 3 distal spiniform setae. Uropod exopod biarticulated, longer than proximal endopod article; endopod terminal article longer than other articles.

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Primary ♂. Body about half the size of adult female. Pereonite 6 longer than pereonite 2. Antennule with 8 articles (flagellum with only 5 articles). Antennal spiniform setae thinner than those of female. Cheliped slender, about ¼ the length of body; basis with small inner dorsodistal process; pereopods much thinner than in female. Pereopod 1 dactylus and unguis much shorter than in female. Pereopod 6 base without dorsal ridge. Uropod exopod uniarticulated.

Secondary ♂. Body as large as that of adult female. Cheliped basis with large inner dorsodistal process. Fixed finger with 2 pointed processes. Pereopods as wide as in female. Pereopod 6 basis with dorsal ridge. Uropod exopod biarticulated.

Pereopod 4–6 carpal spiniform setae number consistent in both females and primary/secondary males.

Description:

Female (Figs 1–3; body from non-ovigerous holotype, appendages from dissected ovigerous paratype).

Body (Fig. 1A, B). Elongate, slender, 8.5× as long as wide. *Cephalothorax* nearly oval, almost twice as long as wide, longer than pereonites 1 and 2 combined. *Pereonites* 1 and 4–6 bearing short, simple dorsal setae. Pereonite 1 shortest, pereonites 2, 3, 4 and 5 progressively longer; pereonite 6 marginally longer than pereonite 2. *Pleon* slightly wider than pereon, about ¼ of total length. *Pleonites* approx. 3× as wide as long; with paired, simple dorsal and mediolateral setae. *Pleotelson* only marginally longer than pleonite 5, with 1 simple lateral seta and 2 pairs of simple terminal setae.

Antennule (Fig. 1C) with 4 articles. Article 1 longer than rest of antennule, l/w ratio 3.5, with 1 dorsomedial and 1 simple ventro-subdistal seta. Article 2 as long as article 3, with 2 distal setae. Article 3 less than half as long as article 1, with 1 distal seta simple and the other short and setulose. Article 4 minute and only attached to dorsal portion of article 3, with 4 simple distal setae and 1 aesthetasc.

Antenna (Fig. 1D) with 6 articles. Article 1 bare. Article 2 longer than article 3, with a conspicuous ventrodistal seta and a less conspicuous dorsodistal spiniform one. Article 3 shorter than half of article 4, with a dorsodistal spiniform seta. Article 4 longest, with 1 mid-length setulose seta and 3 simple setae distally. Article 5 half as long as article 4, with 2 distal setae. Article 6 minute, with 1 setulose, 1 short, and 4 long distal setae.

Mouthparts. Labrum (Fig. 2A, B) setulose, apically rounded and laterally expanded in dorsal view; bent ventrally beyond clypeus. *Mandibles* (Fig. 2C, D). Molar robust with rugose distal ridges and serrated denticles; left incisor wide, simple and almost smooth, *lacinia mobilis* with crenulated apex; right incisor with weakly bifurcate apex and crenulated outer margin. *Labium* (Fig. 2E) with 2 pairs of lobes, outer larger than inner, distal margin densely setulose. *Maxillule* (Fig. 2F) apex with 8 relatively short distal spiniform and several simple dorsodistal setae; palp slender, with 2 long distal setae. *Maxilla* (Fig. 2G) ovoid and featureless. *Maxilliped* (Fig. 2H) bases unfused, each with 3 distal setae longer than endites. Endites with single outer seta distally and 3 flat spiniform inner setae, inner being shorter than the outer. Palp article 1 bare; article 2 with outer spiniform seta on apophysis/process, 4 inner distal setae only, and proxi- to medial setulation; article 3 with 6 inner setae; article 4 with 1 outer subdistal seta and 7 inner setae. *Epignath* (Fig. 2I) long (as long as maxilliped basis/endite) and slender, with dense distal setulation.

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Cheliped (Fig. 3A) about ¼ as long as body. Basis longer than propodus including fixed finger, divided unequally by triangular sclerite, with 1 dorsodistal seta and a small, inner dorsodistal process extending beyond carpus. Merus triangular, with 3 ventral setae.

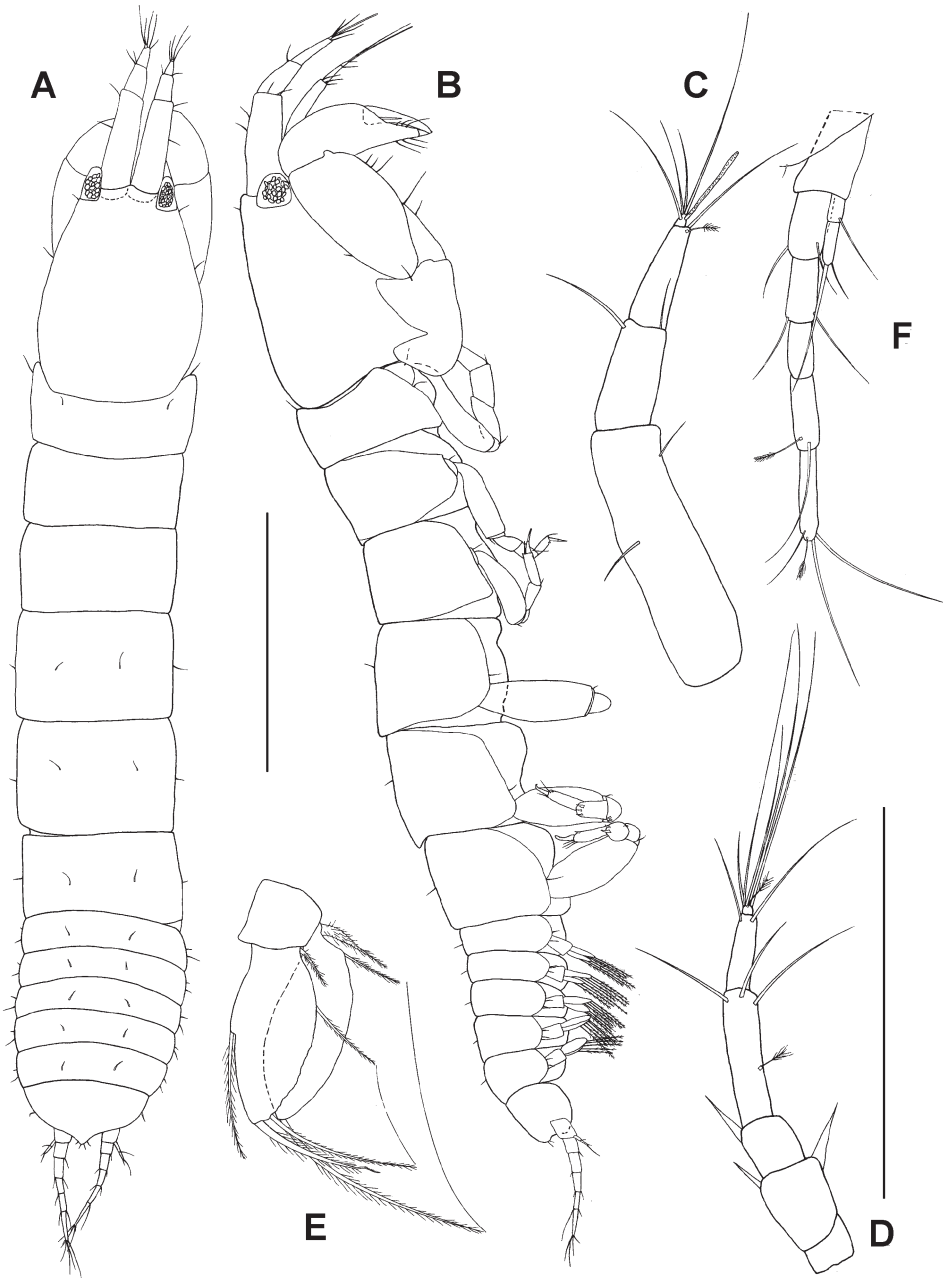


Fig. 1. *Leptochelia africana* sp. n., female: (A, B) holotype: (A) dorsal view, (B) lateral view; (C–F) paratype: (C) antennule, (D) antenna, (E) pleopod, (F) uropod. Scale bars = 1.0 mm (A, B) and 0.5 mm (C–F).

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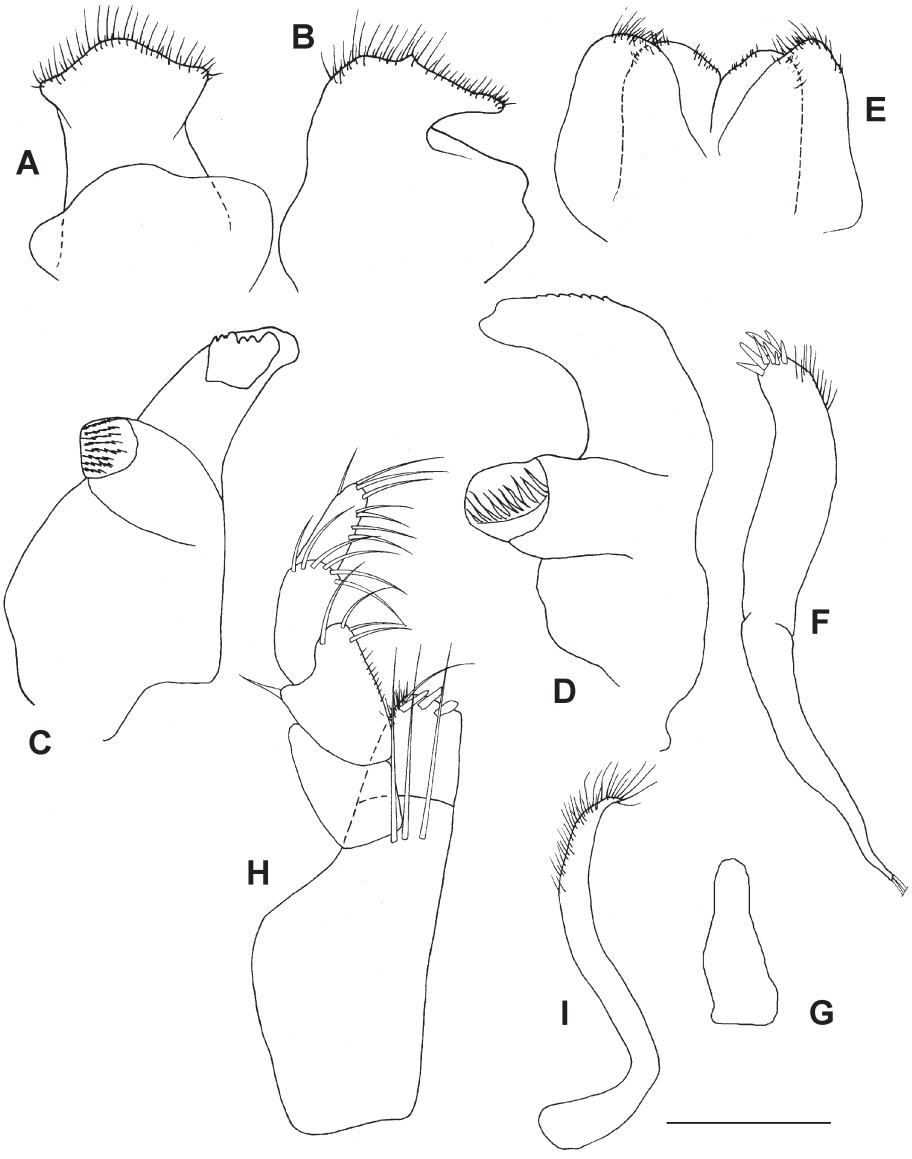


Fig. 2. *Leptochelia africana* sp. n., female, paratype: (A) labrum, dorsal view; (B) same, lateral view; (C) left mandible; (D) right mandible; (E) labium; (F) maxillule; (G) maxilla; (H) maxilliped; (I) epignath. Scale bar = 0.1 mm.

Carpus 1.3× longer than basis, l/w ratio 2.1, with dorsoproximal setulation, 1 dorsoproximal and 1 dorsodistal seta, and 3 ventral subdistal setae. Ventral margin of propodus including fixed finger, shorter than merus, with 1 spiniform seta at dactylus insertion. Fixed finger with 3 ventral setae and 3 on cutting edge; cutting edge with weak undulations. Dactylus with 1 dorsoproximal seta, inner margin smooth.

Pereopod 1 (Fig. 3B) 1.25× as long as other pereopods. Coxa with 1 simple seta. Basis shorter than carpus and propodus combined, l/w ratio 4.6, with 1 dorsoproximal simple

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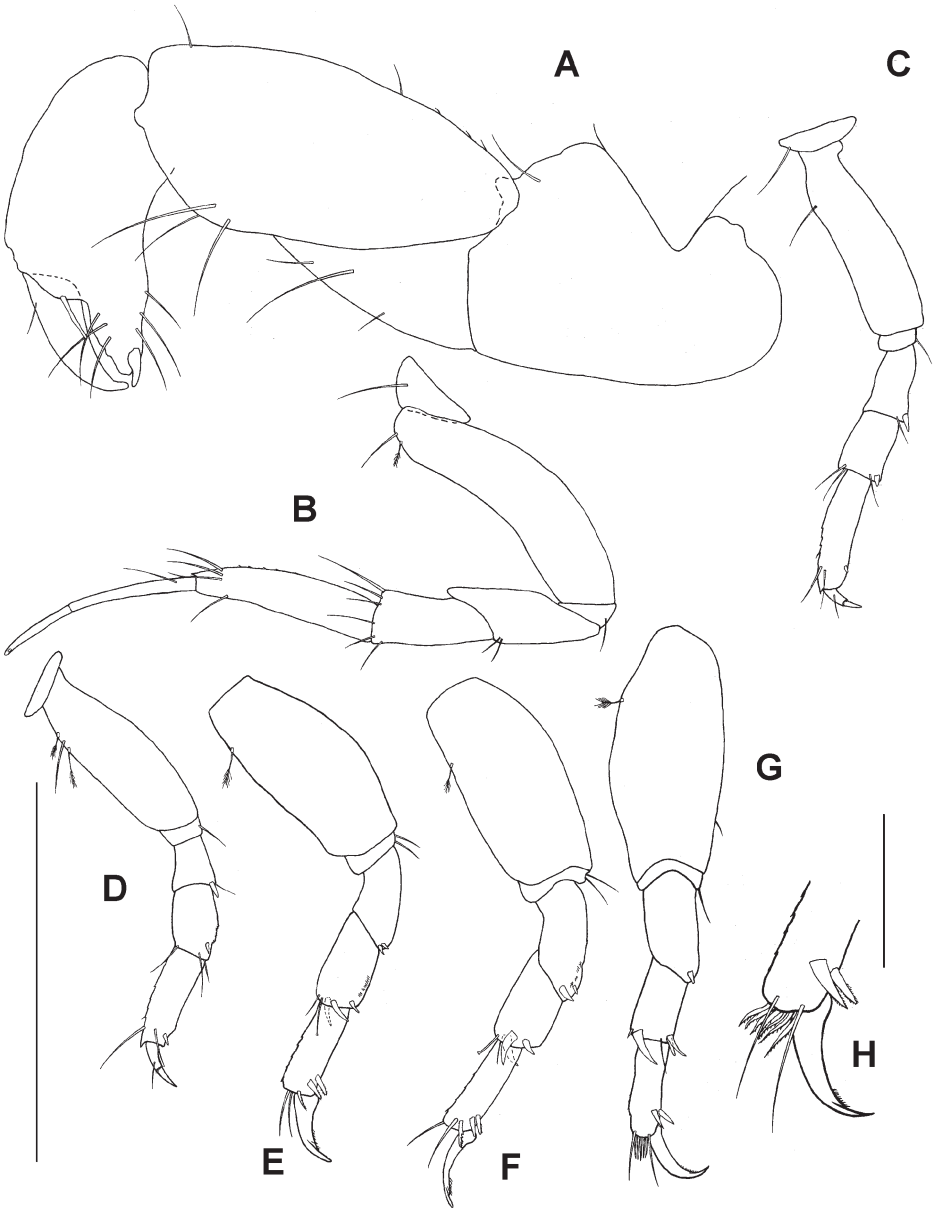


Fig. 3. *Leptochelia africana* sp. n., female, paratype: (A) cheliped; (B) pereopod 1; (C) pereopod 2; (D) pereopod 3; (E) pereopod 4; (F) pereopod 5; (G) pereopod 6; (H) pereopod 6, propodus/dactylus. Scale bars = 0.5 mm (A–G) and 0.1 mm (H).

and 1 setulated seta. Ischium with 1 ventral seta. Merus as long as carpus, with 2 simple setae. Carpus shorter than half of basis, with 6 distal setae. Propodus 0.9× as long as carpus and merus combined, with 1 ventro-subdistal seta, 3 dorso-subdistal setae, and small dorsomedial spines. Dactylus and unguis combined 1.1× as long as propodus. Dactylus with dorsoproximal seta, 1.1× as long as unguis.

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Pereopod 2 (Fig. 3C) coxa with 1 simple seta. Basis longer than carpus and propodus combined, with 1 dorsoproximal simple seta. Ischium with 1 ventral seta. Merus as long as carpus, with 1 simple and 1 spiniform ventrodistal seta. Carpus l/w ratio 1.5, half as long as propodus, with 3 simple setae and 1 small spiniform ventrodistal seta. Propodus 1.8× as long as carpus, with 1 small ventro-subdistal spiniform seta, 2 dorso-subdistal setae, small dorsomedial and strong dorsodistal spines. Dactylus and unguis short, combined being ⅓ of the length of propodus. Dactylus with dorsoproximal seta, longer than unguis.

Pereopod 3 (Fig. 3D) similar to pereopod 2, except basis has 2 setulose setae and 1 simple dorsoproximal seta.

Pereopod 4 (Fig. 3E) coxa fused with body. Basis wider than that of pereopods 1–2, l/w ratio 2.0, longer than the 3 succeeding articles combined, with a dorsoproximal setulose seta. Ischium with 2 ventral setae. Merus as long as carpus, with 2 ventrodistal spiniform setae. Carpus with 2 dorsodistal simple and 3 distal spiniform setae. Propodus as long as carpus, dorsal margin with small spines, with 2 spiniform ventro-subdistal setae, 2 dorsodistal simple setae, and 1 small spiniform distal comb-seta. Dactylus incompletely fused with unguis, with fine ventral setules, combined being shorter than propodus.

Pereopod 5 (Fig. 3F) similar to pereopod 4.

Pereopod 6 (Fig. 3G, H) as pereopod 4, except: basis with dorsoproximal setulose and ventro-subdistal simple setae. Ischium apparently has only 1 seta (possible aberration). Carpus with 1 simple seta, 3 large setae and 1 minute spiniform seta. Propodus (Fig. 3H) with 2 ventro-subdistal spiniform setae, 2 longer simple ones, and 7 serrated, robust dorsodistal setae.

Pleopods (Fig. 1E) all similar. Basal article bare. Endopod with single inner plumose seta, distal seta shorter than adjacent setae and with curved serrated tip (for enlarged illustration, see primary male: Fig. 4J), outer margin with 13 outer plumose setae, and proximal stout circumplumose seta separated from remaining setae by large gap. Exopod with 21 outer plumose setae, and 1 proximal stout circumplumose seta separated by small gap.

Uropod (Fig. 1F) basal article naked. Exopod biarticulated, marginally longer than proximal endopod article, proximal article slightly shorter than distal, with a distal seta; distal article with 1 long and wide and 1 simple distal seta. Endopod with 5 articles, article 5 longest, most articles having either simple or setulated setae.

Primary male (Figs 4, 5).

Body (Fig. 4B, C) only half as long as that of adult female and secondary male. *Cephalothorax* subrectangular, 1.4× as long as wide, almost as long as pereonites 1–3 combined, eyes larger than those of female, with visual elements. *Pereonites* bear short, simple dorsal setae. Pereonite 1 marginally shorter than pereonite 2. Pereonites 2, 3, and 6 subequal. Pereonites 4 and 5 longest, almost twice as long as pereonite 1. *Pleon* wider than pereon; proportionally only marginally longer than in female; bearing paired lateral and dorsal setae. *Pleotelson* (Fig. 5H) short, 1.2× as long as pleonite 5, twice as wide as long, with a mediolateral simple seta, 1 subapical pair of setae on each side, and 2 pairs of apical simple setae.

Antennule (Fig. 4D) of 9 articles. Article 1 only about 3× as long as wide, with 1 dorsodistal simple seta. Article 2 0.6× as long as article 1, with 1 ventrodistal setulated seta

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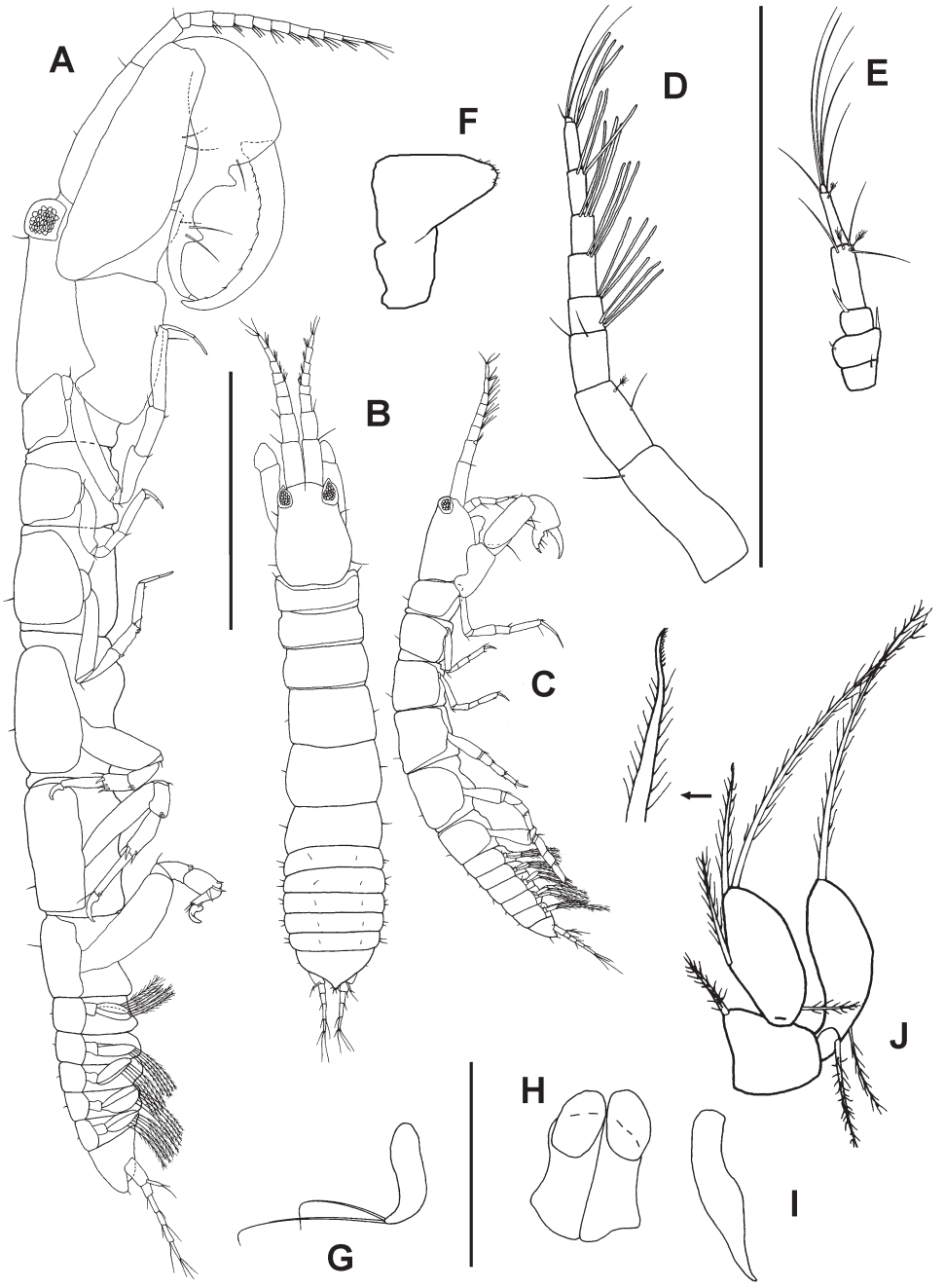


Fig. 4. *Leptochelia africana* sp. n., male paratypes: (A) secondary male, lateral view; (B–J) primary male: (B) dorsal view, (C) lateral view, (D) antennule, (E) antenna, (F) labrum, (G) maxillule palp, (H) maxilliped, (I) epignath, (J) pleopod. Scale bars = 1.0 mm (A–C), 0.5 mm (D, E, J) and 0.1 mm (F–H).

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and a single ventromedial simple seta. Article 3 about half as long as article 2, with 2 simple distal setae. Articles 4–8 serially repeating, all with aesthestascs (many more than illustrated). Article 9 minute, with 3 long setae and 1 tiny, simple distal seta.
Antenna (Fig. 4E). Article 1 square and with 1 simple seta. Article 2 marginally longer than but 1.6× as wide as article 1, with ventro- and dorsodistal spiniform setae (thinner than in female). Article 3 about 0.8× as long as article 2, with a dorsodistal spiniform seta. Article 4 twice as long as article 2, with 3 long simple and 2 setulose distal setae. Article 5 slender and shorter than article 4, with 2 long simple setae and 1 short setulose distal seta. Article 6 minute, with 4 long simple distal setae.
Mouthparts reduced. *Labrum* and particularly clypeus (Fig. 4F) prominent, with very weak setulation. *Mandibles* absent. *Maxillule* (Fig. 4G) endite absent, palp slender, with 2 long distal setae. *Maxilliped* (Fig. 4H) basis bare, endite absent, palp uniarticulated. *Epignath* (Fig. 4I) fully developed but without distal setulation.
Cheliped (Fig. 5A) slender, about ¼ the length of body, attached to body via triangular sclerite bearing a dorsal seta. Basis l/w ratio 1.8, with single, outer sub-dorsodistal seta and inner dorsodistal process. Merus triangular, with 3 ventral setae. Carpus l/w ratio 1.8, being1.2× as long as propodus including fixed finger, with 1 dorsoproximal and 1 simple dorsodistal seta, and with 2 simple ventromedial setae. Propodus as long as basis, with 1 robust seta at dactylus insertion and vertically orientated, row of about 14 inner distal setae. Fixed finger with 2 small bifurcate projections on cutting edge, not overlapping unguis, with 3 setae on cutting edge and 3 ventral setae. Dactylus with dorsoproximal seta and inner row of small spiniform setae.
Pereopod 1 (Fig. 5B) coxa with seta. Basis slender and bare, l/w ratio 4.8. Ischium with 1 ventral seta. Merus about as long as carpus, with 1 small ventral seta. Carpus about half as long as propodus, with 1 longer dorso-subdistal seta and 3 shorter distal setae. Propodus marginally longer than combined length of dactylus/unguis, with 3 dorsal subdistal setae and spine proximal to setae, and with 1 ventro-subdistal seta. Dactylus 1.4× as long as unguis, with proximal fine seta.
Pereopod 2 (Fig. 5C) coxa with 1 simple seta. Basis shorter and wider than pereopod 1, l/w ratio 4.0, as long as carpus and propodus combined, with 1 dorsoproximal simple seta and 2 shorter setulose setae. Ischium with 1 ventral seta. Merus as long as carpus, with 1 ventrodistal spiniform seta. Carpus 0.6× as long as propodus, with 1 simple dorsodistal seta and 2 minute spiniform distal setae. Propodus about half as long as basis, with 1 ventro-subdistal spiniform seta, 2 dorso-subdistal setae, small dorsomedial seta and spine proximal to dorsal setae. Dactylus and unguis combined less than half as long as propodus, thicker and shorter than in pereopod 1, dactylus twice as long as unguis, with proximal seta.
Pereopod 3 (Fig. 5D) similar to pereopod 2, except basis with 2 setulose dorsoproximal setae. Ischium with 2 ventral setae. Carpus with an additional simple seta.
Pereopod 4 (Fig. 5E) coxa fused with body. Basis only marginally wider than on pereopod 3, l/w ratio 2.3, and 1.2× as long as 3 succeeding articles combined, bare. Ischium with 2 ventral setae. Merus 0.7× as long as carpus, with 2 ventrodistal spiniform setae. Carpus with 2 dorsodistal simple and 3 distal spiniform setae. Propodus 1.3× as long as carpus, dorsal margin undulating with a distal spine, with 2 spiniform ventro-subdistal setae and 3 dorsodistal simple setae. Dactylus incompletely fused with unguis, with fine ventral setules, combined length 0.6× as long as propodus.

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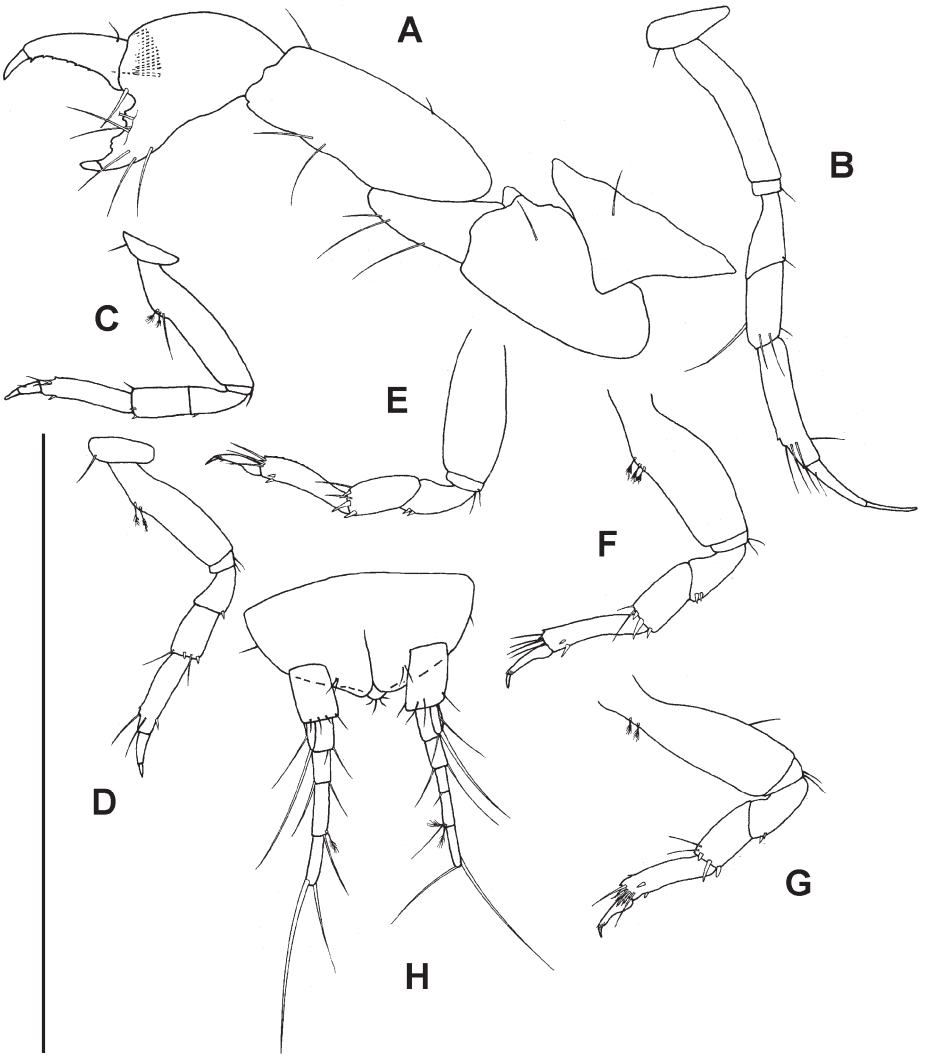


Fig. 5. *Leptochelia africana* sp. n., primary male, paratype: (A) cheliped; (B) pereopod 1; (C) pereopod 2; (D) pereopod 3; (E) pereopod 4; (F) pereopod 5; (G) pereopod 6; (H) uropod. Scale bar = 0.5 mm.

Pereopod 5 (Fig. 5F) similar to pereopod 4, except basis with 3 dorsoproximal setulose setae. Propodus with 2 spiniform ventro-subdistal setae and 4 dorsodistal simple setae. *Pereopod 6* (Fig. 5G) as pereopod 5, except basis with 2 dorsoproximal setulose setae and 1 ventro-subdistal simple seta. Propodus with 2 ventro-subdistal spiniform setae, 2 longer simple setae, and 4 serrated robust dorsodistal setae.

Pleopods (Fig. 4J) all similar. Basal article with proximal circumplumose setae. Endopod with single inner plumose seta, distal seta shorter than adjacent setae and with curved serrated tip, outer margin with 10 additional outer plumose setae. Exopod with 9 outer plumose setae, and 1 proximal stout circumplumose seta separated by small gap and arising from outer process.

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Uropod (Fig. 5H) basal article with 4 distal setae. Endopod with 4 or 5 articles (variation in number between left and right uropod), all with simple or setulose setae, terminal setae longer than on other articles. Exopod uniarticulated, almost as long as first endopod article, with 1 medial and 1 long (as long as endopod) distal seta.

Notes: The primary male antennules have only one, partly-fused minute terminal article (while the secondary have two unfused minute terminal articles). The pleopods have fewer but longer setae than the female. The uropodal endopod in the dissected specimen displays variation in article number between left and right uropod. This form of variation within a specimen, while certainly not a normal condition, has been observed in other species of the genus, as well as in other Tanaidacea (Larsen, unpubl. data). It is well known that in many tanaids like *Leptochelia* (Masunari 1983), *Heterotanais* (Bückle-Ramirez 1965), and *Zeuxoides* (Bird 2008), the uropodal article number increases with size. A specimen having different article numbers in the left and right uropod could thus reflect an incomplete ecdysis. However, the males of *Leptochelia* are terminal, and therefore do not increase in size or go through ecdysis.

Secondary male (Figs 4A, 6, 7).

Body (Fig. 4A) elongate 3.9 mm, 8.5× as long as wide. *Cephalothorax* almost oval, nearly twice as long as wide, longer than pereonites 1 and 2 combined, bare; eyes present with visual elements. *Pereonites* bearing short, simple dorsal setae. Pereonite 1 shortest, pereonites 2, 3, 4, and 5 progressively longer; pereonite 6 as long as pereonite 2. *Pleon* slightly wider than pereon, about ¼ of total length. *Pleonites* about 3× as wide as long; anterior 3 pleonites with 1 seta and posterior 2 pleonites with 3 short, simple mediolateral setae. *Pleotelson* (Fig. 6I) only marginally longer than pleonite 5, with 2 simple lateral and 2 pairs of simple terminal setae.

Antennule (Fig. 6A, B) consists of 12 articles. Article 1 5.5× as long as wide, with 1 dorsodistal simple seta. Article 2 0.4× as long as article 1, with 1 ventrodistal simple seta. Article 3 0.5× as long as article 2, with 1 simple dorsodistal seta. Articles 4–10 serially repeating, all with aesthestascs (many more than illustrated). Articles 11 and 12 minute (Fig. 6B), with several long and short simple distal setae.

Antenna (Fig. 6C). Article 1 square and with 1 simple seta. Article 2 square, with single dorsodistal spiniform (thinner than in female) and a ventrodistal simple seta. Article 3 l/w ratio 1.2, shorter and thinner than article 2, with dorsodistal spiniform seta. Article 4 is 3.6× as long as article 2, with 3 simple distal setae. Article 5 slender, only marginally shorter than article 4, with 1 long simple distal seta. Article 6 minute, with 4 long setae and 1 short simple distal seta.

Mouthparts. *Labrum* (Fig. 6D), *maxillule* (Fig. 6E), *maxilliped* (Fig. 6F), and *epignath* (Fig. 6G) as in primary male.

Cheliped (Fig. 7A). Longer than half of total body length. Sclerite with simple medial seta. Basis divided unequally by sclerite, l/w ratio 1.7, and 0.6× as long as carpus, having dorso-subdistal seta, and with large inner dorsodistal process extending beyond carpus. Merus triangular, with 3 ventral setae. Carpus as long as propodus including fixed finger, l/w ratio 2.5, with 1 dorsoproximal and 1 dorsomedial seta, ventral margin with 3 medial setae. Propodus longer than cephalothorax, with 1 seta at dactylus insertion and inner row of at least 14 short setae and 1 longer seta. Fixed finger inner margin with 3 setae and 2 processes, ventral margin with 3 simple setae. Dactylus as long as

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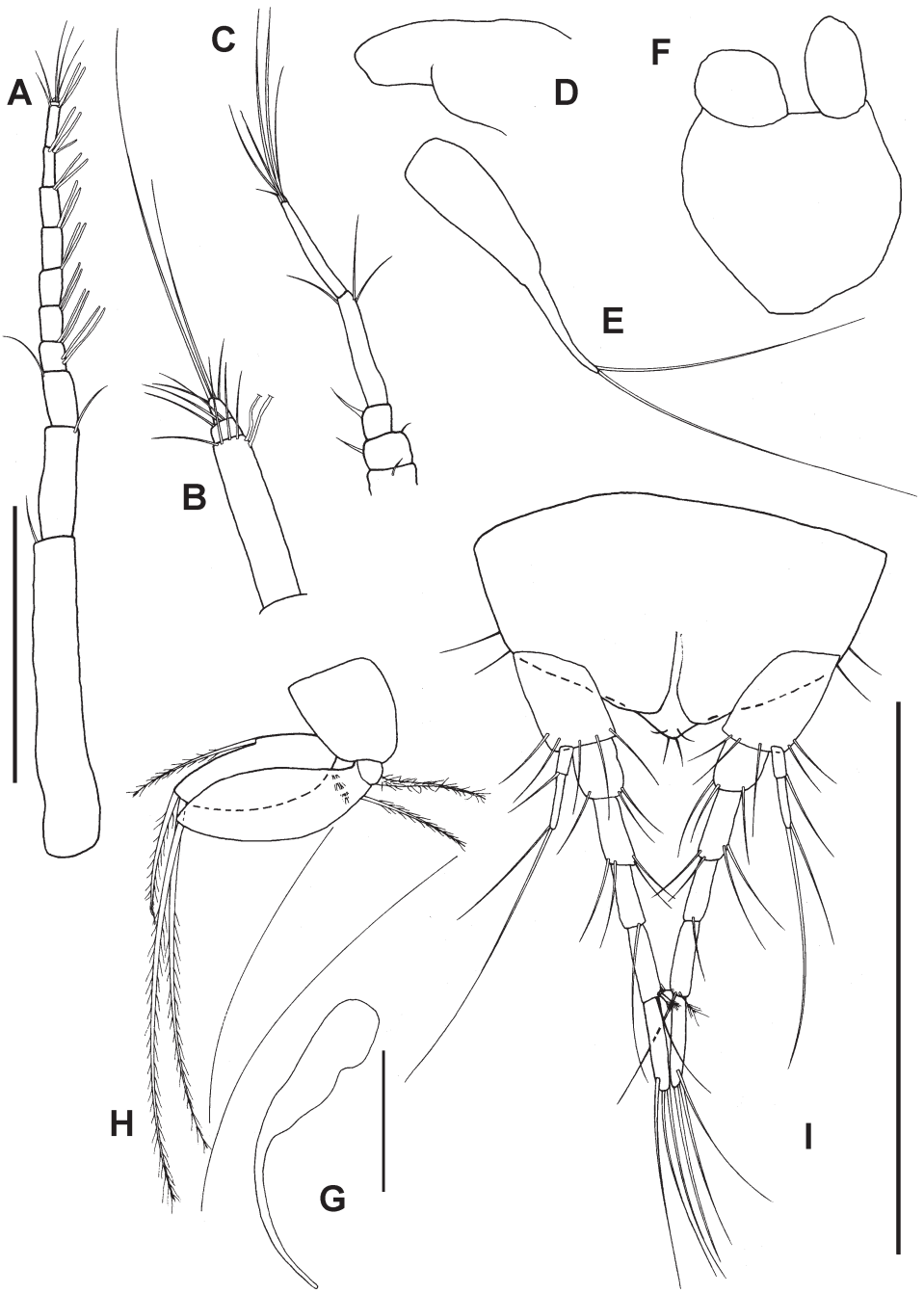


Fig. 6. *Leptochelia africana* sp. n., secondary male, paratype: (A) antennule; (B) same, apex; (C) antenna; (D) labrum; (E) maxillule palp; (F) maxilliped; (G) epignath; (H) pleopod; (I) pleotelson/uropods. Scale bars = 0.5 mm (A, C, H, I) and 0.1 mm (B, D–G).

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fixed finger, with small dorsoproximal seta and a row of small, evenly spaced setae on inner margin.

Pereopod 1 (Fig. 7B) 1.25× as long as other pereopods. Coxa with 1 simple seta. Basis as long as carpus and propodus combined, l/w ratio 7.4, with 1 dorsoproximal simple and 1

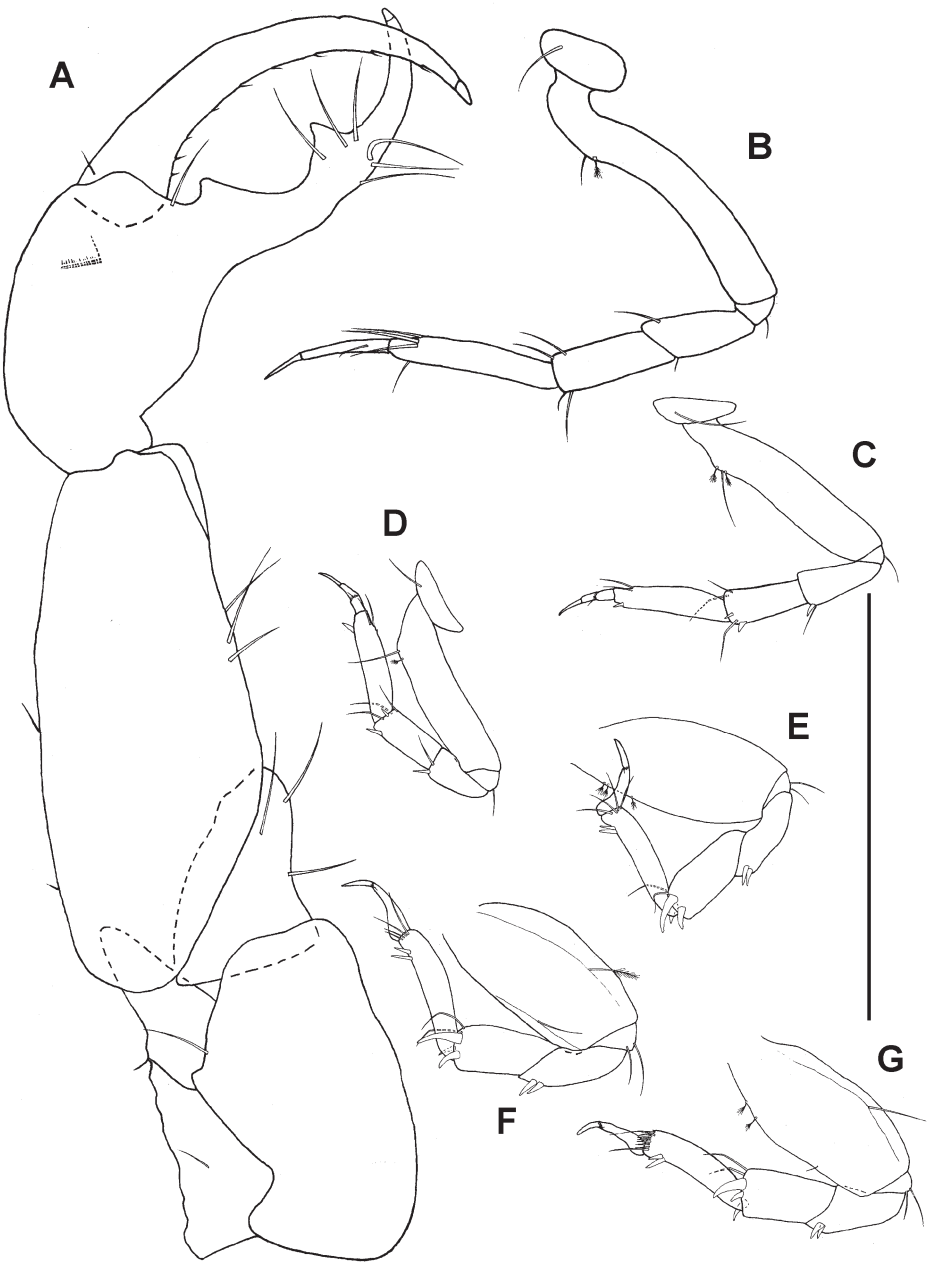


Fig. 7. *Leptochelia africana* sp. n., secondary male, paratype: (A) cheliped; (B) pereopod 1; (C) pereopod 2; (D) pereopod 3; (E) pereopod 4; (F) pereopod 5; (G) pereopod 6. Scale bar = 1.0 mm.

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setulated seta. Ischium with 1 ventral seta. Merus as long as carpus, with 1 simple distal seta on each margin. Carpus 0.4× as long as basis, with 4 distal setae. Propodus 1.6× as long as carpus, with 1 ventro-subdistal seta, and 3 dorso-subdistal setae. Dactylus and unguis combined 0.8× as long as propodus. Dactylus longer than unguis, with dorsoproximal seta.

Pereopod 2 (Fig. 7C) coxa with one simple seta. Basis longer than carpus and propodus combined, l/w ratio 4.8, with 2 dorsoproximal setulose setae and 1 simple seta. Ischium with 1 ventral seta. Merus as long as carpus, with 1 simple and 1 spiniform ventrodistal seta. Carpus 0.7× as long as propodus, with 1 simple seta and 2 small spiniform ventrodistal setae, and 2 simple dorsodistal setae. Propodus 0.7× as long as basis, with 1 ventro-subdistal spiniform seta and 2 dorso-subdistal setae. Dactylus and unguis combined 0.5× as long as propodus. Dactylus 1.1× as long as unguis, with dorsomedial seta and setules.

Pereopod 3 (Fig. 7D) similar to pereopod 2, except basis with only 1 setulose and 1 simple dorsoproximal seta.

Pereopod 4 (Fig. 7E) coxa fused with body. Basis stout (much more so than in primary male), l/w ratio 4.3, and 1.4× as long as 3 succeeding articles combined, with 3 dorsoproximal setulose setae. Ischium with 2 ventral setae. Merus 0.8× as long as carpus, with 2 ventrodistal spiniform setae. Carpus with 2 dorsodistal simple and 3 spiniform distal setae. Propodus 1.6× as long as carpus, with 2 spiniform ventro-subdistal setae and 3 distal simple setae. Dactylus incompletely fused with unguis, with fine ventral setules, combined being 0.2× as long as propodus.

Pereopod 5 (Fig. 7F) similar to pereopod 4, except basis with dorsal and ventral ridge, the dorsal bearing a setulose seta whereas the ventral has a simple seta. Propodus with 2 spiniform ventro-subdistal setae and 4 distal simple setae.

Pereopod 6 (Fig. 7G) as pereopod 4 except: basis with 2 dorsoproximal setulose setae and dorsal margin bearing 1 simple seta. Ischium with 2 setae. Propodus with 2 ventro-subdistal spiniform setae, 2 longer simple setae, and 7 serrated dorsodistal setae.

Pleopods (Fig. 6H) all similar. Basal article naked. Endopod with single inner plumose seta, distal seta shorter than adjacent setae and with curved serrated tip, outer margin with 14 additional outer plumose setae, and 1 additional, proximal stout circumplumose seta, separated from remaining setae by a gap. Exopod with 23 outer plumose setae, and 1 proximal stout circumplumose seta separated by a gap and arising from a process.

Uropod (Fig. 6I) basal article with 5 terminal setae. Exopod biarticulated, 1.7× as long as proximal endopod article, proximal article much shorter than distal, with distal seta, distal article with 1 long and wide and 1 simple distal seta. Endopod with 5 articles, all articles with either simple or setulated setae.

Holotype: Non-ovigerous ♀ GUINEA BISSAU: Bijagos Archipelago, Acunda I., 13°43'N 15°50'W, -0.5 m (body length 3.8 mm; MMF 42314).

Paratypes: 1 primary ♂ (MMF 42363), 1 secondary ♂ (MMF 42364), same locality; >100 specimens of both genders and all developmental stages, same locality (MMF 42315; ♀ T313: GenBank JX316006 & ♂ T312: GenBank JX316005); 3♀ 2 mancae, Orango I., Bijagos Archipelago, 13°53'N 16°01'W, -0.5 m.

Remarks: The secondary male differs substantially from the primary male, not just in respect of the typical characters of size and cheliped development, but also as regards the antennule structure, and pleopod setal number (higher in secondary male). It is clear that secondary (or later) males develop more antennule articles, and the number is probably dependent on the developmental stage of the female when it changed sex, as seen in *Heterotanais* (vide Bückle-Ramirez 1965).

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DISCUSSION

Leptochelia africana sp. n. belongs to the '*dubia*' group, which is separated from the '*minuta*' group by the relatively short male chelipeds (being shorter than the total body length). *L. africana* differs in the female from *L. savignyi* (Krøyer, 1842) and *L. caldera* Bamber & Costa, 2009, by having only three maxilliped basis setae and a biarticulated uropodal exopod that is longer than the first endopod article.

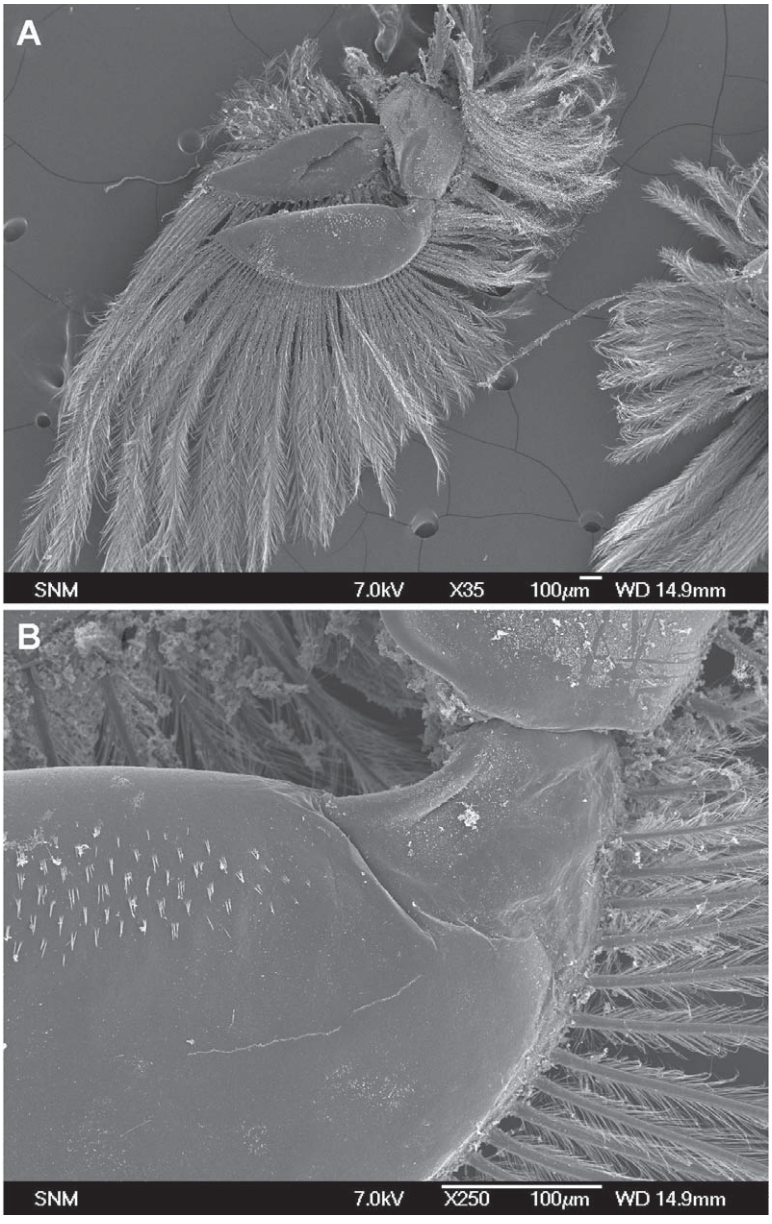


Fig. 8. *Protanais ligniamator* Larsen, 2006, SEM: (A) pleopod 1; (B) same, exopod, higher magnification.

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TABLE 2

Estimates of evolutionary divergence over sequence pairs between species of *Leptochelia* (unc. *p*) for COI sequences (418 bp). Standard error estimates are shown above the diagonal. Abbreviations: CV – Cape Verde; FL – Florida, USA; FR – France; GB – Guinea Bissau; GC – Gran Canaries.

	savignyi (FR)	*savignyi* (GC)	*para-savignyi* (CV)	*dubia* (FL)	*forresti* (FL)	*rapax* (FL)	*longiche-lipedes* (FL)	*africana* (GB)
savignyi (FR)[1]		0.007	0.019	0.020	0.019	0.020	0.020	0.020
savignyi (GC)[1]	0.020		0.019	0.020	0.020	0.019	0.021	0.020
parasavignyi (CV)[1]	0.190	0.188		0.021	0.018	0.019	0.021	0.013
dubia (FL)[2]	0.249	0.237	0.232		0.021	0.021	0.022	0.021
forresti (FL)[2]	0.205	0.210	0.188	0.254		0.021	0.020	0.020
rapax (FL)[2]	0.227	0.225	0.195	0.264	0.257		0.020	0.020
longicheli-pedes (FL)[2]	0.262	0.264	0.259	0.291	0.240	0.259		0.021
africana (GB)[3]	0.215	0.215	0.074	0.249	0.225	0.220	0.279	

[1]Larsen *et al.* (2012); [2]Drumm (2010); [3]this study.

Genetic distance between *L. africana* and the two other African species that have been sequenced: *L. savignyi* recently collected by LMCEE from Gran Canarias and the Atlantic coast of France and *L. parasavignyi* recently obtained by LMCEE from Cape Verde (Larsen *et al.* 2012), differ in the COI gene by about 20 %. A similar genetic distance was reported between other species of *Leptochelia* (Table 2), while the intraspecific distance between remote populations of the same species (*L. savignyi*) was as low as 2 %. A larger molecular phylogeny of the family is currently being constructed (Araújo-Silva *et al.*, in prep.), and we therefore refrain from inferring phylogenetic conclusions in this study.

There are currently only six other species described that have (like *L. africana*) only three setae on the maxilliped basis (*L. itoi* Ishimaru, 1985, *L. lusei* Bamber & Bird, 1997, *L. nobbi* Bamber, 2005, *L. karragarra* Bamber, 2008, *L. tanykeraia* Bamber *et al.*, 2009, and *L. caldera*), but only *L. tanykeraia* and *L. caldera* have been recorded from Africa (the others are Pacific or Indopacific species). *Leptochelia africana* (females) can be separated from all of these species by the presence of a biarticulated uropodal exopod.

Variation within a specimen in the uropodal endopod article number (Fig. 5H) is also observed within *Zeuxoides* (Larsen, unpubl. data) and *Hexapleomera* (Larwood 1954), and leads us to recommend much caution as regards use of this character for species identification, as otherwise suggested by Bamber (2012). It is therefore not impossible that our species is conspecific with *L. affinis* Hansen, 1895, collected from Cape Verde, but both the original description and the supplementary one by Vanhöffen (1914) are useless for modern-day taxonomy. Moreover, the type material is in a very bad condition (Bamber 2012: 17). Male antennule and uropodal article numbers are not suitable as diagnostic characters, and the articles also display other variations. We therefore cannot completely agree with Edgar's (2012: 2) philosophy that it is better to describe and diagnose species of this genus on the basis of male characters rather than features in females. However, we do agree with Edgar that the males display more

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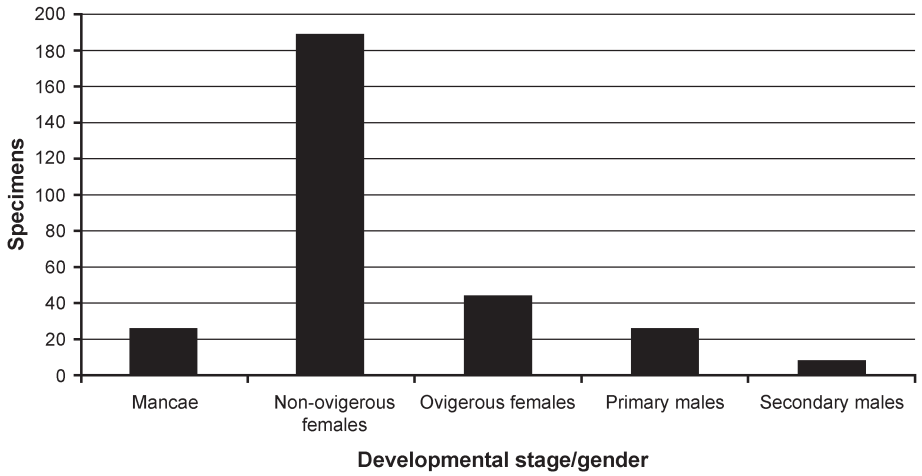


Fig. 9. Population structure.

characters; but until the matter of the extent and significance of intra-specific variation in this taxon is resolved, males are, in our view, not suitable as holotypes (unless females are not available).

The pleopod exopod proximal circumplumose seta arises from an outer process that is perhaps a rudiment of the first exopod article, as seen in some members of Apseudomorpha, Neotanaidomorpha (Lang 1968), and even in plesiomorphic taxa of Tanaidomorpha (Fig. 8A, B). This feature thus represents support for the suggestion of Bird and Larsen (2009) that the Leptocheliidae should be considered among the most basal (plesiomorphic) families within the superfamily Paratanaoidea.

The population structure (Fig. 9) shows, as have other studies (Ishimaru 1985; Bird & Bamber 2000; Bamber 2005), a strong bias towards females (mancae excluded), with less than 12% males present. However, even this low number is relatively high compared with the findings in the previous studies mentioned above. It is interesting that the ratio of secondary males only constitutes less than 20% of all males. This lends support to the hermaphroditic theory of Buckle-Ramirez (1965), as there would be little reason for females to change into (secondary) males since the population is not depleted of (primary) males.

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