

Research article

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Abstract. Three leptostracan species (Crustacea: Phyllocarida) are reported from mud volcanoes at the Moroccan margin of the Gulf of Cadiz (NE Atlantic). *Nebalia strausi* Risso, 1826 and *N. abyssicola* Fage, 1929 were found in experimentally deployed organic substrates in Mercator, Meknès and Darwin mud volcanoes; *N. abyssicola* was also found among bathymodiolin bivalves and is recorded for the first time in the Atlantic Ocean. The third species was collected from the Gemini mud volcanoes and is described herein as *Sarsinebalia ledoyeri* sp. nov. The new species is characterised by having the eyes provided with ommatidia and lacking pigment, the ventral margin of the eye is concave along distal half, the antennular scale is more than twice as long as wide, the second article of the mandibular palp bears one seta on lateral surface about 0.5 times as long as the article and one subterminal seta longer than the third article, the distal article of the maxilla II endopod is about 1.8 times as long as the proximal article, the maxilla II exopod is clearly longer than the endopod proximal article, the lateral margin of the pleopod I exopod lacks setae and the posterodorsal border of pleonites VI–VII is provided with rounded to pointed denticles.

Keywords. Crustacea, Leptostraca, new species, NE Atlantic, mud volcanoes.

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Introduction

The number of known species of extant leptostracans (Crustacea: Phyllocarida) has been substantially expanded in the last decades, with descriptions of new taxa from many areas around the globe, including North and Central America (Modlin 1991; Escobar-Briones & Villalobos-Hiriart 1995; Martin *et al.* 1996; Vetter 1996b; Haney & Martin 2000, 2004, 2005; Haney *et al.* 2001; Ortiz *et al.* 2011), eastern and southeast Asia (Lee & Bamber 2011; Song *et al.* 2012b, 2013, 2017; Song & Min 2017), southwest Africa (Bochert & Zettler 2012), western Pacific Ocean (Ledoyer 2000) and Australia (Walker-Smith 1998, 2000). In the northeast Atlantic, following the review of European leptostracans by Dahl (1985), new taxa have been described and new records reported from across the Atlantic coasts (Ledoyer 1998; Moreira *et al.* 2003a, 2003b, 2009a; McCormack *et al.* 2016) and the Mediterranean Sea (Ledoyer 1997; Koçak & Katagan 2006; Koçak & Moreira 2015; Moreira *et al.* 2007, 2012; Moreira & Junoy 2017). Most of the extant leptostracan species belong to the genus *Nebalia* Leach, 1814, for a total of 11 species in European latitudes and the Mediterranean Sea (Dahl 1985; Ledoyer 1997; Moreira *et al.* 2009a; Koçak *et al.* 2011; McCormack *et al.* 2016; Latry & Droual 2020). The genera *Nebaliella* Thiele, 1904, *Sarsinebalia* Dahl, 1985 and the pelagic *Nebaliopsis* Sars, 1887 and *Pseudonebaliopsis* Petryashov, 1996 have also been recorded from the NE Atlantic (Mauchline & Gage 1983; Dahl 1985) while *Paranebalia* Claus, 1880 has been recently reported from the Mediterranean Sea (Moreira & Junoy 2017).

Regarding the genus *Sarsinebalia*, four species have been described from NE Atlantic (Sars 1870; Ledoyer 1998; Moreira *et al.* 2003b) for a total of six worldwide (Dahl 1985; Ledoyer 2000; Petryashov 2016). The validity of the genus was challenged by the phylogenetic analyses of Walker-Smith & Poore (2001) and later discussed by Moreira *et al.* (2003b) and McCormack *et al.* (2016). The type species of the genus, *S. typhlops* (G.O. Sars, 1870), was considered as having a large distribution across the North Atlantic and the Mediterranean, including the subspecies *S. typhlops occidentalis* (Hessler & Sanders, 1965) from the NW Atlantic; the latter, however, has been suggested to be a different species that might deserve revision and eventually raised to the species rank (Dahl 1985). There are three other species described from European temperate latitudes: *S. biscayensis* Ledoyer, 1998 from deep-sea waters at the Bay of Biscay, and *S. cristoboi* Moreira *et al.*, 2003 and *S. urgorrhii* Moreira *et al.*, 2003, both from shallow coarse and medium sand at the western Iberian Peninsula (Moreira *et al.* 2003b; Sampaio *et al.* 2016); *S. urgorrhii* has also been reported from around the British Isles (McCormack *et al.* 2016) and French Atlantic and Mediterranean waters (Latry & Droual 2020). Species mostly differ in the presence of ommatidia and pigment (both absent in *S. typhlops*, *S. biscayensis* and *S. pseudotyphlops* Petryashov, 2016) and the shape of eye.

Most leptostracans are epifaunal and present in a variety of hard and soft substrata, mainly in shallow waters (< 100 m depth) (Haney & Martin 2016). However, some species are present at greater depths (Mauchline & Gage 1983; Hessler 1984; Haney *et al.* 2001), even reaching the abyssal realm (> 5000 m depth; Petryashov 2016), but the knowledge about the actual diversity and ecology of deep-sea leptostracans is still incomplete and many areas still remain unexplored.

Mud volcanoes (MVs hereafter) are cold-seep related structures formed by the extrusion of sediments with venting of hydrocarbon-rich fluids (mostly methane) that allows for the presence of chemosymbiotic species (Levin 2005; Cunha *et al.* 2013b; Rodrigues *et al.* 2013) and a diverse associated benthic assemblage in comparison to other cold-seep formations (e.g., Cunha *et al.* 2013b; González-García *et al.* 2020). MVs are frequent (ca 40) in the Gulf of Cadiz (southern Iberian margin, NE Atlantic) and located at depths of between 200 and 4000 m (Cunha *et al.* 2013b). Several studies conducted in MVs at the Moroccan margin of the Gulf of Cadiz yielded a number of leptostracan specimens corresponding to three species, namely *Nebalia strausi* Risso, 1826, *Nebalia abyssicola* Fage, 1929 and a new species of *Sarsinebalia* that is described herein as *Sarsinebalia ledoyeri* sp. nov. To our knowledge, these findings constitute the first reports of leptostracans identified to the species level for MVs and the first record of *N. abyssicola* in the Atlantic Ocean.

Material and methods

Specimens of *N. strausi* and *N. abyssicola* were retrieved in the framework of the CHEMECO project (European Science Foundation, EuroDEEP programme) aiming to study the colonization process in organic substrata experimentally deployed in several MVs at the Gulf of Cadiz within the Moroccan EEZ (Fig. 1). The colonization experiment consisted in the deployment of sets of three standardized units (i.e., CHEMECOLI, see Gaudron *et al.* 2010 for details), each including a different substrate treatment: dried alfalfa grass (organic), Douglas fir wood cubes (organic) and carbonate cubes (inorganic/control) enclosed by a 2 mm mesh net. The sets of colonization units were deployed with a ROV in 2007 during the RRS James Cook Cruise 10 (JC10) and in 2008 during the RV Pelagia Cruise 284 (64PE284) along a depth gradient across the continental slope on the crater of the following MVs: Mercator MV in the El Arraiche Field (350 m depth); Meknès and Darwin MVs in the Carbonate Province (700 and 1100 m depth, respectively). One set from Mercator MV was recovered also using a ROV in 2008 (cruise 64PE284) and the others in 2009 during the RV Belgica Cruise B09-14b; the metadata of the experiments, including the duration of the deployments are listed in Table 1. Description of experimental procedures and treatment of samples can be found in Cunha *et al.* (2013a). Samples were not sieved and sub-samples of the substrates enclosed by the net were directly fixed in a solution of 95% ethanol or in 10% formalin. External components of the CHEMECOLI units were washed and all fauna present was fixed and kept separately for further examination. Specimens of *N. abyssicola* were also retrieved from three ROV suction samples (250 µm mesh) carried out at the experimental site on the crater of Darwin MV from aggregations of the chemosymbiotic bivalve *Gigantidas mauritanicus* (Cosel, 2002)

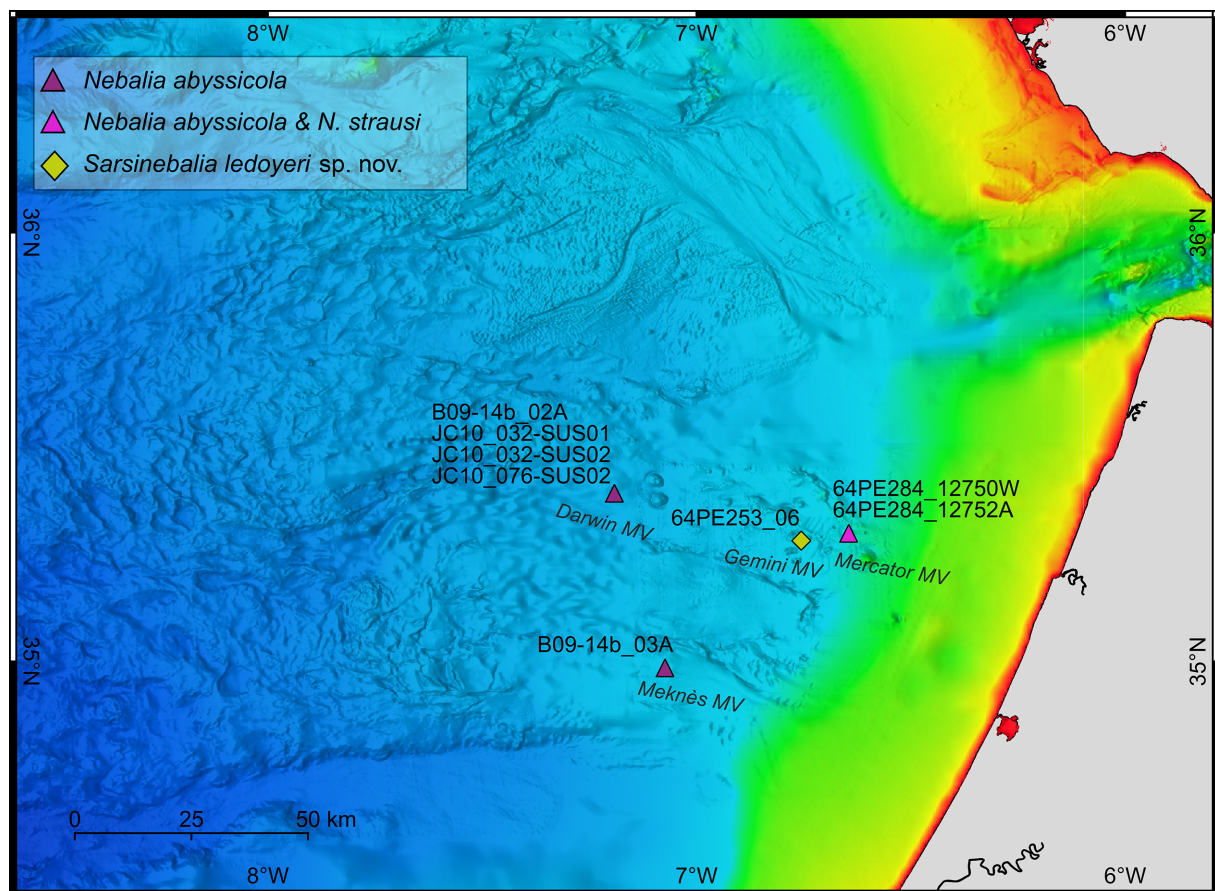


Fig. 1. Location of sampling sites in the mud volcanoes (Darwin, Gemini, Meknès, Mercator) at the Gulf of Cadiz within the Moroccan EEZ. Codes refer to samples obtained at each site.

Table 1. Metadata of the deployment and recovery of the colonization experiments in the Gulf of Cadiz. Abbreviations: DD = deployment duration; MV = mud volcano.

Site	Site coordinates			Deployment		Recovery		Sample	DD (days)
	Latitude	Longitude	Depth	Cruise	Date	Cruise	Date		
Mercator MV	35°17.916' N	06°38.709' W	354 m	JC10	19 May 2007	64PE284 64PE284	2 Mar. 2008 3 Mar. 2008	64PE284_12750W 64PE284_12752A	290 291
Meknès MV	34°59.091' N	07°04.424' W	698 m	64PE284	1 Mar. 2008	B09-14b	20 May 2009	B09-14b_03A	446
Darwin MV	35°23.523' N	07°11.513' W	1100 m	JC10	21 May 2007	B09-14b	19 May 2009	B09-14b_02A	629

(previously referred to as “*Bathymodiolus*” *mauritanicus*; see Génio *et al.* 2008). Two of these samples were obtained just after the deployment of the colonization units.

Specimens of *Sarsinebalia ledoyeri* sp. nov. were collected in 2006 in the Gemini MV by means of a NIOZ box corer (see de Haas & Shipboard Scientific Party 2006 for details; Fig. 1). Sediment samples were layered (0–2 cm, 2–5 cm, 5–10 cm, 10–20 cm), washed through a sieve column (2, 1, 0.5 mm) and the fauna preserved in 96% ethanol.

Line drawings of specimens, dissected parts and appendages were done with the aid of a camera lucida connected to a compound microscope. Drawings of *Sarsinebalia ledoyeri* sp. nov. correspond to several dissected postovigerous and preovigerous females and males (specimens were particularly brittle); the drawing of the lateral view of a full specimen corresponds to the holotype. Measurements were made with an ocular micrometer. The following measurements were considered: Total Length (TL): distance from the articulation between the rostrum and carapace to the posterior end of the uropods excluding setation; Dorsal Carapace Length (DCL): distance between the articulation of the rostrum and the margin of the posterodorsal cleft; Lateral Carapace Length (LCL): distance along lateral surface between the anterior-most and posterior-most margin; Carapace Height (CH): distance between the dorsal and ventral margin; Rostrum Length (RL): distance along the midline. Descriptions are based on females; complementary data for males are also given. Descriptions of *N. strausi* and *N. abyssicola* are limited to relevant diagnostic characters; the new species *Sarsinebalia ledoyeri* sp. nov. is fully described. Terminology for setae follows Watling (1989) and Walker-Smith (2000). Specimens of *N. strausi* and *N. abyssicola* are deposited in the Biological Research Collection (Marine Invertebrates) of the Department of Biology of the University of Aveiro (COBI-DBUA; Portugal); the holotype and some paratypes of *Sarsinebalia ledoyeri* sp. nov. in the Museo Nacional de Ciencias Naturales (MNCN, Madrid) and remaining paratypes in COBI-DBUA.

Abbreviations

- ae = aesthetasc
- asb = short seta with blunt teeth, antennular scale
- ast = long seta with thin teeth, antennular scale
- d = dorsal
- la = lateral
- ld = laterodorsal
- pas = pappose setae, maxilla I endite
- ps = plumose seta(e)
- sps = spatulate seta(e), maxilla I endite
- tcs = thick seta with teeth, maxilla I endite
- tns = thin seta with teeth, maxilla I endite

Results

Order Leptostraca Claus, 1880
Suborder Nebaliacea Calman, 1904
Family Nebaliidae Samouelle, 1819
Genus *Nebalia* Leach, 1814

Nebalia strausi Risso, 1826
Figs 1–5

Nebalia straus Risso, 1826: 84, pl. V, fig. 20.

Nebalia straus – Koçak & Katagan 2006: 321, figs 1–3. — Koçak *et al.* 2007: 449, figs 1–3.

Nebalia strausi – Dahl 1985: 155, figs 63–79. — Ledoyer 1997: 34, fig. 4. — Moreira *et al.* 2004: 84, figs 1–7; 2009b: 101, lam. 1, figs 1–3.

Material examined

MOROCCO • 1 preovigerous ♀, 4 ♂♂, 3 juveniles; Gulf of Cadiz, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; St 64PE284_12750W, experimentally deployed wood substrate; DBUA0001677.01.W • 3 preovigerous ♀♀, 8 ♂♂, 4 juveniles; same locality and coordinates as for preceding; 3 Mar. 2008; St 64PE284_12752A, experimentally deployed alfalfa substrate; DBUA0001677.02.A.

Description of female

MEASUREMENTS. Preovigerous females measuring TL 5.275–5.8 mm, RL 0.925–1.025 mm, DCL 2.15–2.25 mm, LCL 2.675–3.0 mm, CH 1.825–1.95 mm.

CARAPACE, ROSTRUM AND EYE. Carapace covering at least lateral sides of pleonites 1–4; LCL about 1.5 times CH. Rostrum long, with parallel margins, length about 2.3 times width, 0.45 times DCL (Fig. 2A, C). Eye about 0.65 times as long as rostrum; ommatidia numerous, distributed about 5/6 of eye (Fig. 2B); dark pigment in most ommatidia.

ANTENNAE. Antennule peduncle fourth article with anterior row of 5–6 simple setae and two distal robust setae, proximal one shorter (Fig. 2D), juveniles (< 4 mm TL) with one robust seta; antennular scale length 2.25–2.4 times width; flagellum with up to 11–13 articles. Antenna peduncle third article lateral margin with three proximal plumose setae on proximal half and three distal spine-like setae (Fig. 2E–F); flagellum with up to 11–14 articles (Fig. 2E).

MOUTHPARTS. Mandibular palp second article with two subequal setae: one seta setulose along distal half on lateral margin at mid-length and one simple seta on distal third; third article slightly longer than second (Fig. 3A). Maxilla I palp well-developed, about 4.5 times as long as protopod (Fig. 3B). Maxilla II endopod proximal article about 1.5–1.6 times as long as distal article; exopod longer than endopod first article (Fig. 3C).

THORACOPODS. Endopod slightly longer than exopod (Fig. 3D–E); endopod distal article slightly enlarged, with several (ca 10) setae; endopod segmentation weak. Thoracopod VIII epipod smaller than in other thoracopods and lacking setae (Fig. 3F).

PLEONITES AND PLEOPODS. Pleonite IV epimeron posterolateral corner slightly pointed (Fig. 4C). Pleonites VI–VII posterodorsal border bearing denticles acutely pointed (Fig. 4G–H). Pleopod I exopod about 0.72 times as long as protopod and endopod; lateral border with ‘comb-row’ of ca 30 bi-pectinate setae

(sensu Walker-Smith 2000) (Fig. 4A); protopod with long seta near base of exopod, hardly reaching middle of ‘comb-row’. Pleopods II–IV exopod with row of 5–7 pairs of smooth setae (‘spine pairs’) (Fig. 4B). Pleopod IV protopod posterior border with four serrations. Pleopod V distal article 3.4 times as long as wide, with five simple setae along distolateral and terminal margins, proximal-most the shortest

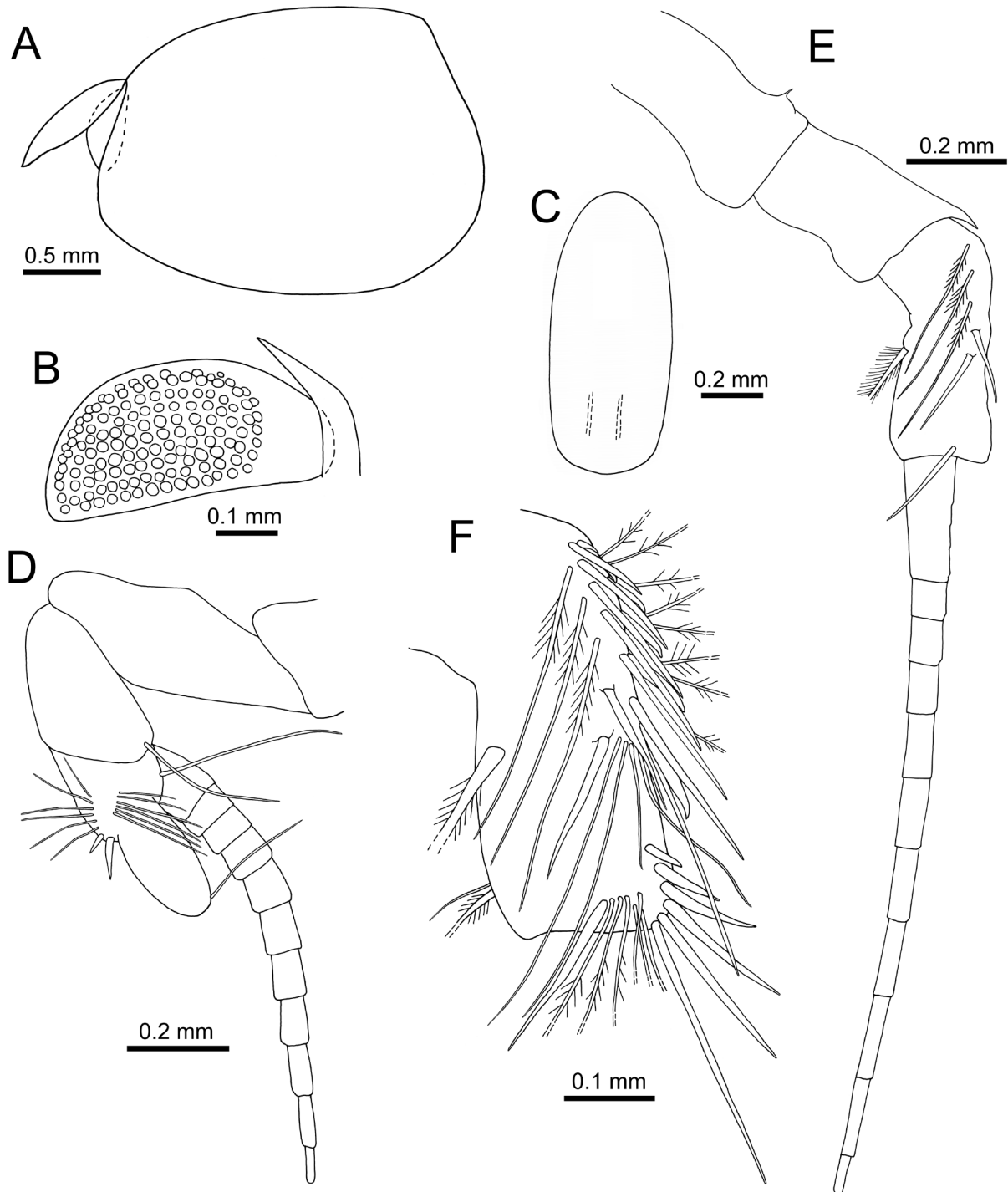


Fig. 2. *Nebalia trausi* Risso, 1826. Preovigerous female (DBUA0001677.01.W). **A.** Rostrum, eye and carapace outline, lateral view. **B.** Eye and supra-orbital plate, lateral view. **C.** Rostrum, dorsal view. **D.** Antennule, lateral view. **E.** Antenna, lateral view. **F.** Antenna, peduncle third article, lateral view. D–E: only selected setae illustrated.

(Fig. 4D). Pleopod VI 2.0 times as long as wide, with five simple setae along lateral and terminal margins, distal-most the longest (Fig. 4E). Pleopod V–VI pairs with acute triangular process between rami bases.

ANAL SOMITE, ANAL PLATES AND UROPODS. Anal somite 0.8–0.95 times as long as pleonite VII. Anal plates acutely tapering distally, ‘shoulder’ well-defined (Fig. 4F, I). Uropods 0.8–0.92 times as long as pleonite VII+anal somite; terminal seta 1.7 times as long as ramus.

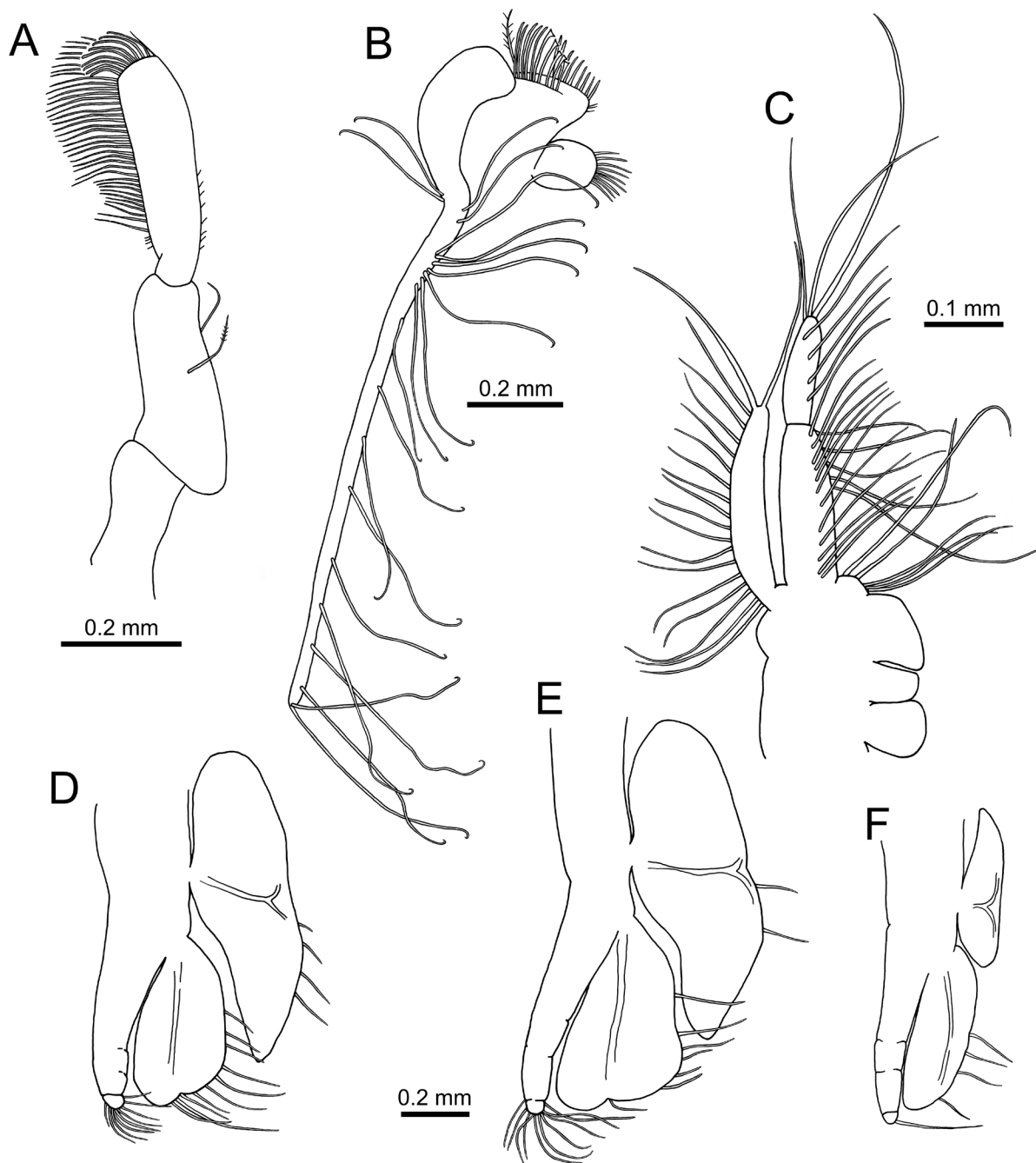


Fig. 3. *Nebalia strausi* Risso, 1826. Preovigerous female (DBUA0001677.01.W). **A.** Mandibular palp. **B.** Maxilla I. **C.** Maxilla II. **D.** Thoracopod II. **E.** Thoracopod V. **F.** Thoracopod VIII. D–F: same scale bar; C: setules and endites' setae not illustrated; D–F: only selected setae illustrated.

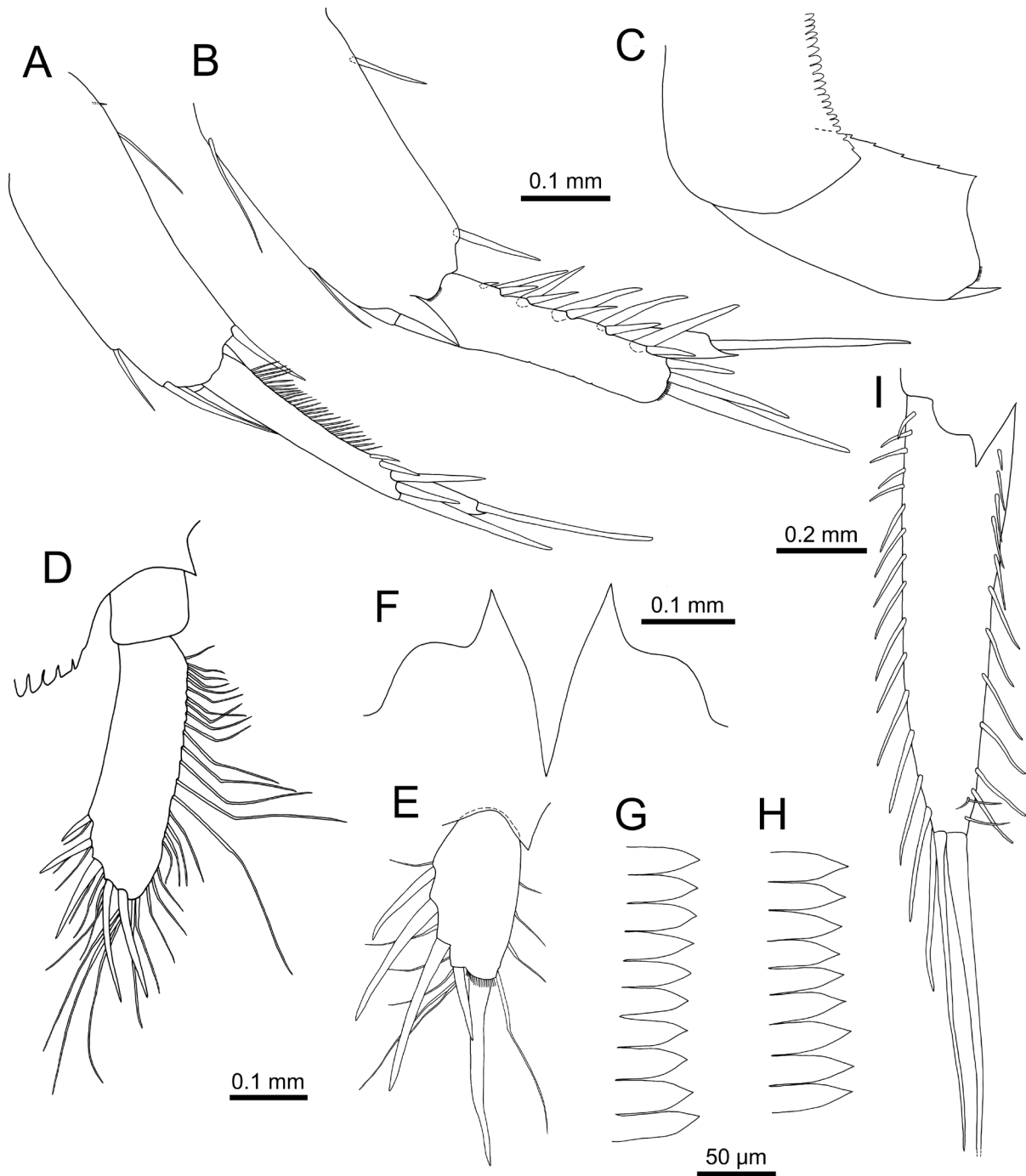


Fig. 4. *Nebalia strausi* Risso, 1826. Preovigerous female (DBUA0001677.01.W). **A.** Pleopod I, lateral view. **B.** Pleopod II, lateral view. **C.** Pleonite IV, epimeron and pleopod IV protopod, lateral view. **D.** Pleopod V, ventral view. **E.** Pleopod VI, ventral view. **F.** Anal plates, ventral view. **G.** Pleonite VI, posterior dorsal and laterodorsal border, denticles. **H.** Pleonite VII, posterior dorsal and laterodorsal border, denticles. **I.** Right uropod and anal plate, ventral view. A–C, D–E, G–H: same scale bars; A–B, I: plumose setae not illustrated.

Description of male

TL 3.95–5.375 mm, RL 0.825–1.05 mm, DCL 1.575–2.125 mm, LCL 2.2–3.0 mm, CH 1.625–1.925 mm. Carapace proportions (LCL:CH) similar to females (Fig. 5A). Ommatidia and dark pigment covering $\frac{5}{6}$ of eye (Fig. 5B). Antennule peduncle fourth article with 1–2 distal robust setae; antennular scale proportions similar to females (2.25–2.30 times as long as wide) (Fig. 5D); flagellum with up to 10–12 articles, thicker than in females. Antenna peduncle third article lateral margin with similar setation as in females; flagellum with many articles (> 30) but not surpassing TL (Fig. 5C). Pleonites VI–VII denticles acutely pointed. Pleopod IV protopod posterior border with four serrations. Uropods length similar to females.

Remarks

Nebalia strausi is a well-known species that is characterized by having ommatidia and dark pigment extending through most of the eye; the antennular scale is more than twice as long as wide; the fourth article of antennule peduncle bears two distal robust setae of different length; the exopod of maxilla II surpasses the level of articulation of endopod articles, and the endopod proximal article is clearly longer than the distal one; the posterolateral corner of the pleonite IV epimeron is not acutely produced; the posterior margin of pleopod IV protopod bears four serrations; and the posterodorsal denticles of pleonites VI–VII are acutely pointed (Dahl 1985; Ledoyer 1997; Moreira *et al.* 2004). Furthermore, the terminal simple seta of the pleopod I protopod barely reaches half-length of the ‘comb-row’ and

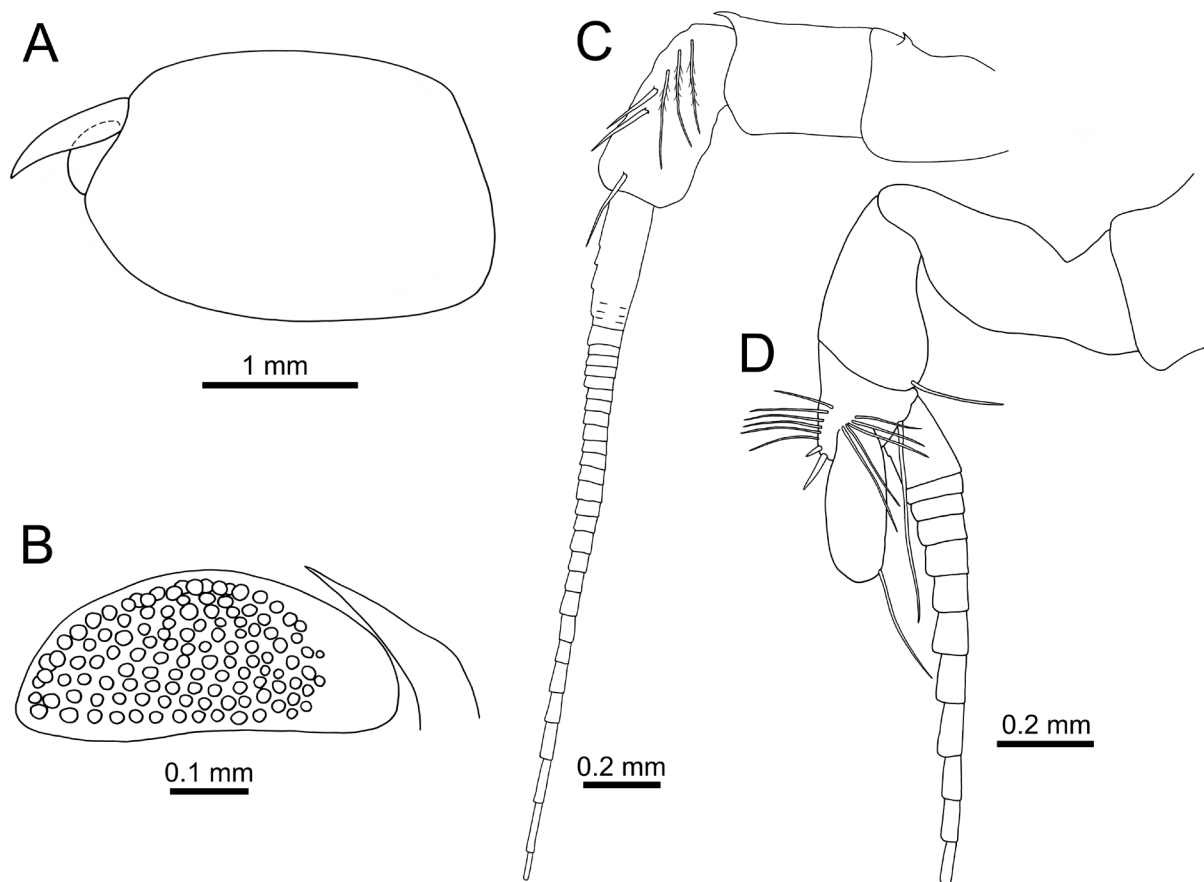


Fig. 5. *Nebalia strausi* Risso, 1826. Male (DBUA0001677.01.W). **A.** Rostrum, eye and carapace outline, lateral view. **B.** Eye and supra-orbital plate, lateral view. **C.** Antenna, lateral view. **D.** Antennule, lateral view. C–D: only selected setae illustrated.

the uropods are at least as long as pleonite VII and anal somite combined, and slightly longer in mature specimens (Dahl 1985).

Specimens from Mercator MV mostly agree with the diagnosis of the species. The only minor difference is that the uropods are slightly shorter, but this may be due to the state of development, i.e., no specimen was fully mature. Note that the organic substrates where the specimens were found were enclosed by a 2 mm mesh size net, and it is likely that the specimens settled on the substrates as juveniles just released from the brood pouch. The anal plates have an even more prominent shoulder than in the Mediterranean specimens described by Dahl (1985); those reported by Ledoyer (1997) bear, in turn, a gently sloping 'shoulder', whereas there is almost no 'shoulder' at all in those described by Moreira *et al.* (2004) from the NW Iberian Peninsula. Most specimens bear two robust setae on the fourth article of antennule peduncle but small males and juveniles bear instead only one. Moreira *et al.* (2004) reported similar observations in immature females whereas ovigerous and postovigerous females always had two robust setae of different length. Number of setae is known to vary during ontogeny (Dahl 1985) and therefore this character should be considered with care for identification unless fully-grown specimens are available; this also applies for the number of articles in the antennae flagella that are fewer on juveniles. On the other hand, some minor variations have also been reported for specimens from the eastern Mediterranean (Koçak *et al.* 2010) and therefore the possibility of a complex of species across its wide distribution range has been suggested (Koçak *et al.* 2011).

Ecology

Recorded from the intertidal to depths of 140 m, in rocky substrates and sandy and muddy soft bottoms, and among the seagrasses *Zostera marina* L., 1753, *Z. noltii* Hornem., 1832, *Cymodocea* sp. and *Posidonia oceanica* (L.) Delile, 1813 (Dahl 1985; Ledoyer 1997; Moreira *et al.* 2004, 2009a, 2009b; Koçak *et al.* 2007; Latry & Droual 2020). The present findings of the species from experimentally deployed wood and alfalfa substrates at the Mercator MV extend its known bathymetric range to depths of 354 m.

Distribution

SW European Atlantic from north western Ireland to NW Iberian Peninsula (Dahl 1985; Moreira *et al.* 2004, 2009a, 2009b; McCormack *et al.* 2016; Latry & Droual 2020); Mediterranean Sea (Dahl 1985; Ledoyer 1997; Koçak & Katagan 2006; Koçak *et al.* 2011; Latry & Droual 2020); Canary Islands (Dahl 1985; Moreira *et al.* 2009b), Madeira and St Helena (Dahl 1985); Moroccan margin of the Gulf of Cadiz (this study; Fig. 1).

Nebalia abyssicola Fage, 1929

Figs 1, 6–9

Nebalia bipes abyssicola Fage, 1929: 41, pl. III, figs 88–89.

Nebalia abyssicola – Ledoyer 1997: 29, fig. 1. — Moreira *et al.* 2012: 352, figs 1–5.

Material examined

MOROCCO • 1 preovigerous ♀, 6 ♂♂, 1 juvenile; Gulf of Cadiz, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; St 64PE284_12750W, experimentally deployed wood substrate; DBUA0001676.01.W • 4 preovigerous ♀♀, 5 ♂♂, 3 juveniles; same locality and coordinates as for preceding; 3 Mar. 2008; St 64PE284_12752A, experimentally deployed alfalfa substrate; DBUA0001676.02.A • 1 ♂, 3 juveniles; Gulf of Cadiz, Meknès MV; 34°59.091' N, 07°04.424' W; 698 m depth; 20 May 2009; St B09-14b_03A, experimentally deployed alfalfa substrate; DBUA0002350.02.A •

3 ovigerous ♀♀, 1 ♂, 1 juvenile; Gulf of Cadiz, Darwin MV; 35°23.523' N, 07°11.513' W; 1100 m depth; 19 May 2009; St B09-14b_02A, experimentally deployed alfalfa substrate; DBUA0002350.01.A • 2 ♀♀, 2 ♂♂, 25 juveniles; same locality and coordinates as for preceding; 1109 m depth; 21 May 2007; St JC10_032-SUS01, suction sample from Bathymodiolinae bed; DBUA0002392.01 • 2 ♀♀, 8 ♂♂, 11 juveniles; same locality and coordinates as for preceding; 1110 m depth; 22 May 2007; St JC10_032-SUS02, suction sample from Bathymodiolinae bed; DBUA0002392.02 • 3 juveniles; same locality and coordinates as for preceding; 1110 m depth; 1 Jun. 2007; St JC10_076-SUS01, suction sample from Bathymodiolinae bed; DBUA0002392.03.

Description of female

MEASUREMENTS. Ovigerous ♀♀: TL 6.0–6.625 mm, RL 1.05–1.125 mm, DCL 2.375–2.5 mm, LCL 3.0–3.125 mm, CH 2.125–2.25 mm; preovigerous ♀♀: TL 4.6–6.5 mm, RL 0.75–0.925 mm, DCL 1.75–2.25 mm, LCL 2.125–2.875 mm, CH 1.5–1.925 mm.

CARAPACE, ROSTRUM AND EYE. Carapace covering at least lateral sides of pleonites 1–4 (Fig. 6A); LCL about 1.4 times CH. Rostrum long, with parallel margins, length about 2.5 times width, 0.45 times DCL (Fig. 6B–C). Eye about 0.4–0.5 times as long as rostrum; some ommatidia irregularly distributed on distal half or second third (Fig. 6C); inferior distal border slightly produced downwards.

ANTENNAE. Antennule peduncle fourth article with anterior row of 9–10 simple setae and one distal robust seta (one preovigerous female with two) (Fig. 6D); antennular scale length 2.15–2.5 times width; flagellum with up to 10–11 articles. Antenna peduncle third article lateral margin with 4–5 proximal plumose setae and three distal thin long spine-like setae (Fig. 6E–F); flagellum with up to 12–14 articles (Fig. 6E).

MOUTHPARTS. Mandibular palp second article with two simple setae: one simple seta on distal third and one simple slightly longer seta on lateral margin at mid-length; third article 1.15 times as long as second (Fig. 7A). Maxilla I palp well-developed, about six times as long as protopod (Fig. 7B). Maxilla II endopod proximal article about 1.6 times as long as distal; exopod as long as endopod first article (Fig. 7C).

THORACOPODS. Endopod longer than exopod (Fig. 7D–E); endopod distal article slightly enlarged, with several (> 10) long setae; endopod segmentation weak. Thoracopod 8 epipod smaller than in other thoracopods and lacking setae (Fig. 7F).

PLEONITES AND PLEOPODS. Pleonite IV epimeron posterolateral corner forming triangular process acutely pointed (Fig. 8C). Pleonites VI–VII posterodorsal border bearing distally rounded to slightly pointed denticles (Fig. 8F–G). Pleopod I protopod with long seta near base of exopod, reaching first half of exopod ‘comb-row’; exopod about 0.7 times as long as protopod and endopod; lateral margin with ‘comb-row’ of about 25–30 bi-pectinate setae (Fig. 8A). Pleopods II–IV exopod with row of 4–6 smooth setae (‘spine pairs’) (Figs 6A, 8B). Pleopod IV protopod posterior border with 3(4?) serrations. Pleopod V distal article 4.0 times as long as wide, with five simple setae along distolateral and terminal margins, proximal-most the shortest (Fig. 8D). Pleopod VI 2.7 times as long as wide, with five simple setae along lateral and terminal margins, distal-most the longest (Fig. 8E). Pleopod V–VI pairs with acute triangular process between rami bases.

ANAL SOMITE, ANAL PLATES AND UROPODS. Anal somite 1.15–1.4 times as long as pleonite VII. Anal plates acutely tapering distally, lacking distinct ‘shoulder’ (Fig. 8H). Uropods 1.15–1.28 times as long as pleonite VII+anal somite (Fig. 6A); terminal seta two times as long as ramus.

Description of male

TL 3.5–6.25 mm, RL 0.675–1.075 mm, DCL 1.375–2.425 mm, LCL 1.875–3.25 mm, CH 1.375–1.875 mm. Carapace slightly longer than in females (Fig. 9A), LCL about 1.7 times CH. Ommatidia irregularly distributed along distal $\frac{2}{3}$ of eye (Fig. 9B). Antennular scale proportionally longer than in females (2.7–2.75 times as long as wide) (Fig. 9C); flagellum with up to 9–12 articles, thicker than in females. Antenna peduncle third article lateral margin with similar setation as in females; flagellum with

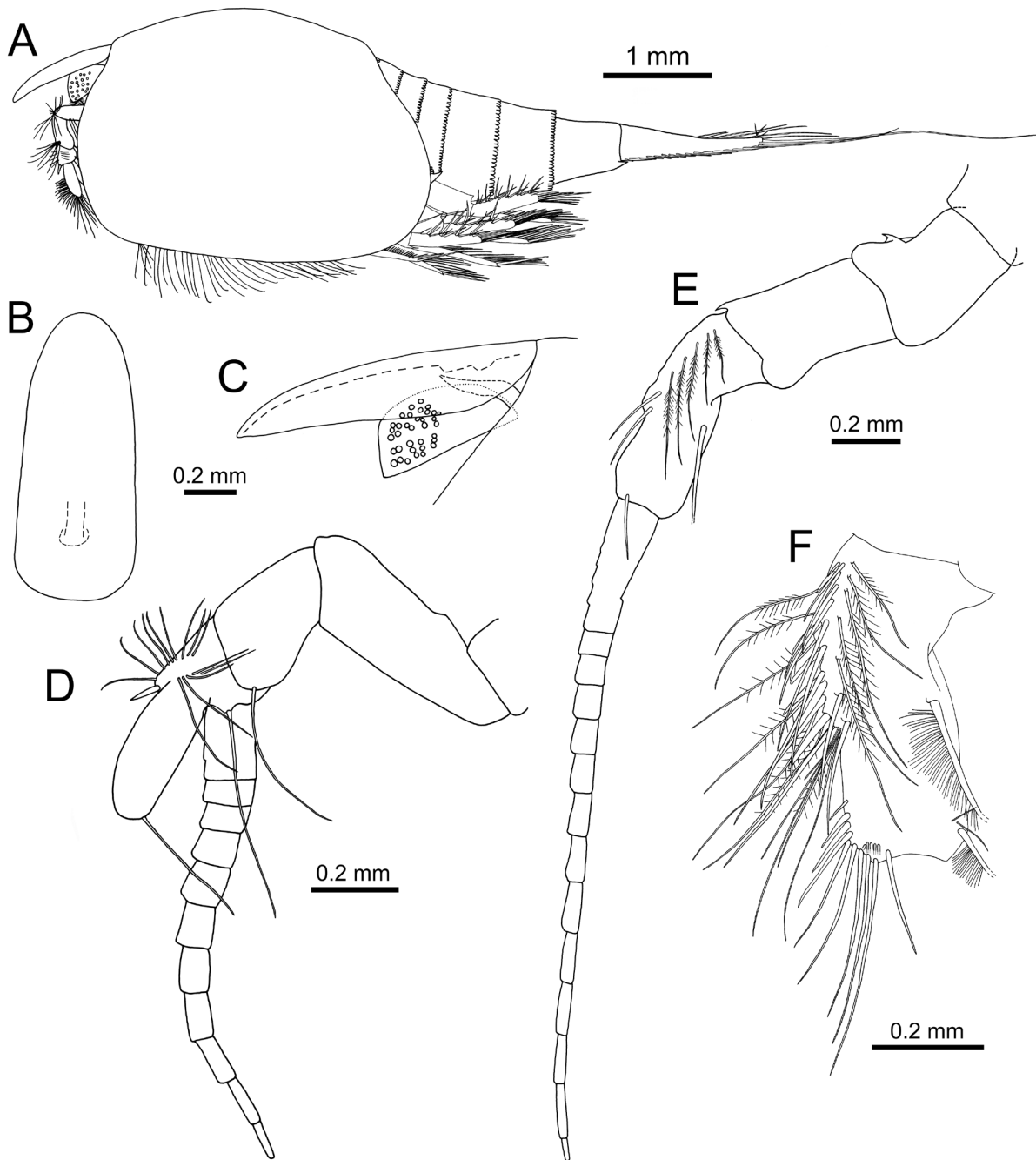


Fig. 6. *Nebalia abyssicola* Fage, 1929. Ovigerous female (DBUA0002350.01.A). **A.** Complete specimen, lateral view. **B.** Rostrum, dorsal view. **C.** Rostrum and eye, lateral view. **D.** Antennule, lateral view. **E.** Antenna, lateral view. **F.** Antenna, third article, lateral view. B–C: same scale bar; D–E: only selected setae illustrated.

many articles (> 40) but not surpassing TL (Fig. 9D). Pleonites VI–VII denticles more pointed distally than in females. Pleopod IV protopod posterior border with four serrations. Small males (< 4.8 mm TL) with uropods about as long as pleonite VII+anal somite; proportions in larger males (1.14–1.23) similar to females.

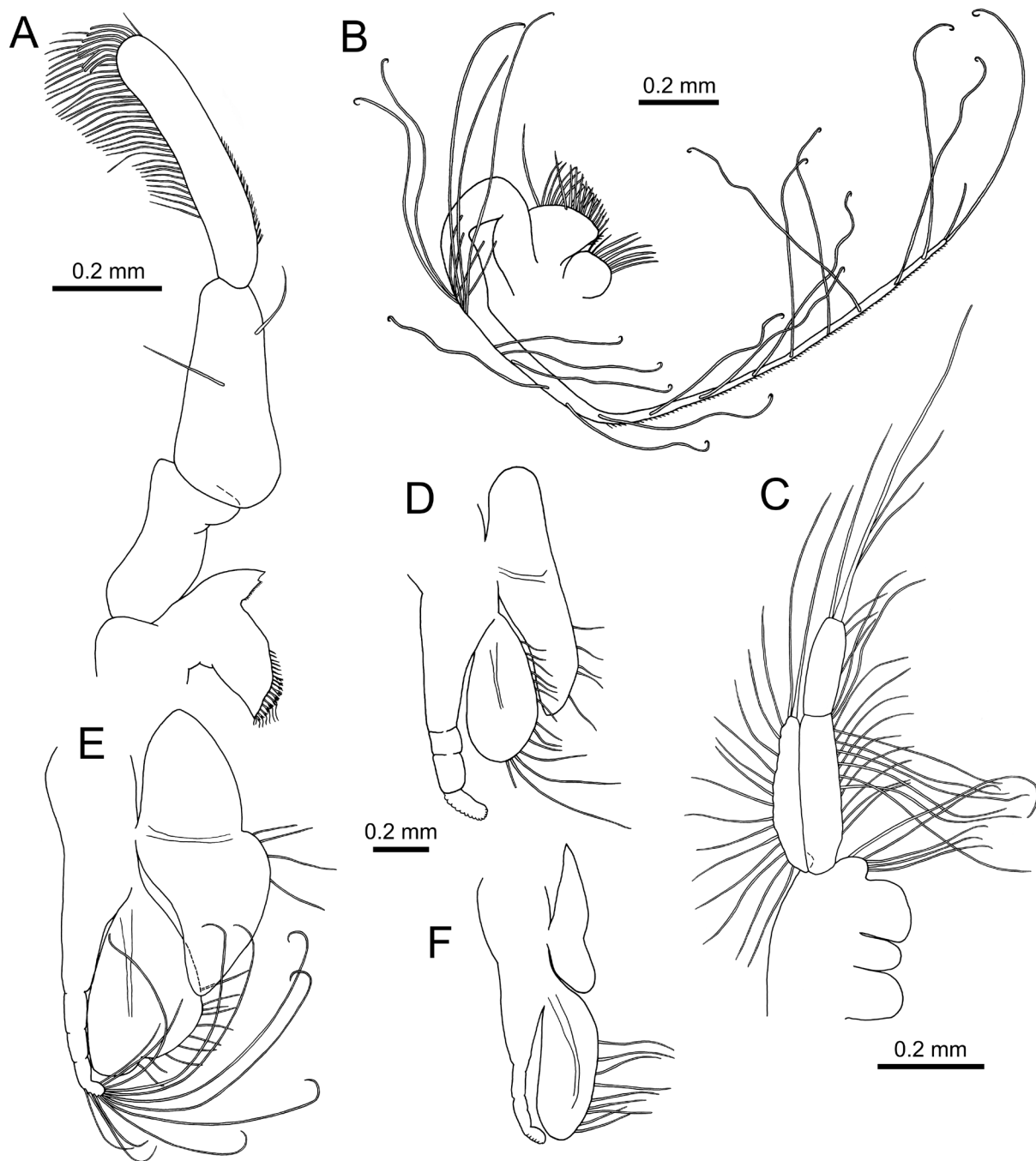


Fig. 7. *Nebalia abyssicola* Fage, 1929. Ovigerous female (DBUA0002350.01.A). **A.** Mandible. **B.** Maxilla I. **C.** Maxilla II. **D.** Thoracopod II. **E.** Thoracopod VII. **F.** Thoracopod VIII. C: setules and endites' setae not illustrated; D, F: endopod distal setae not illustrated; D–F: same scale bar.

Remarks

Nebalia abyssicola is mostly characterized by the shape of the eye and the number and distribution of ommatidia, as discussed by Fage (1929), Ledoyer (1997) and Moreira *et al.* (2012). Fage (1929) also highlights the differences in setal armature of the fourth article of antennule, that includes one distal robust seta and a larger number of medial simple setae (up to 10) in comparison to other species of

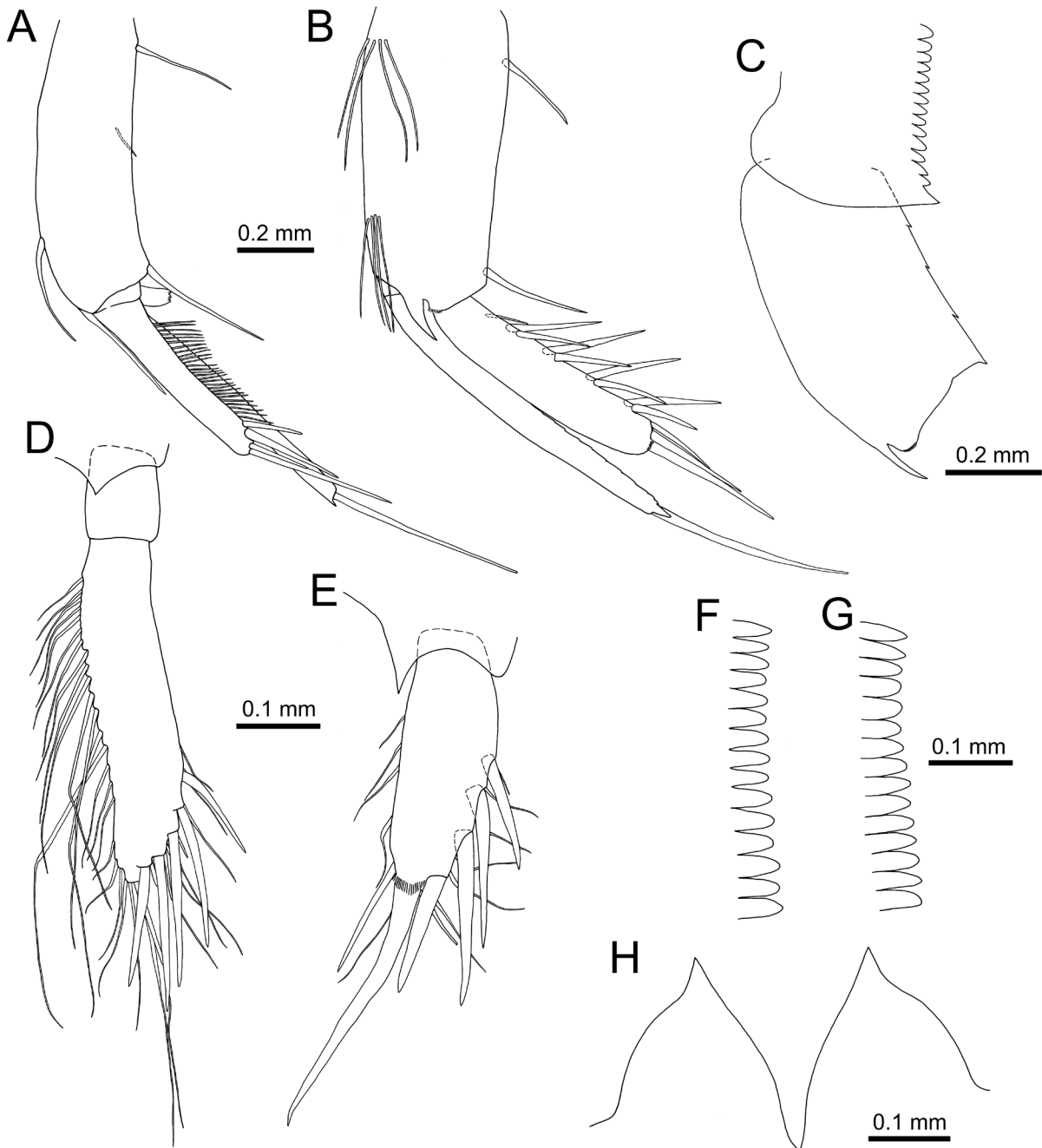


Fig. 8. *Nebalia abyssicola* Fage, 1929. Ovigerous female (DBUA0002350.01.A). **A.** Pleopod I, lateral view. **B.** Pleopod II, lateral view. **C.** Pleonite IV, epimeron and pleopod IV, protopod, lateral view. **D.** Pleopod V, ventral view. **E.** Pleopod VI, ventral view. **F.** Pleonite VI, dorsal and laterodorsal posterior border, denticles. **G.** Pleonite VII, dorsal and laterodorsal posterior border, denticles. **H.** Anal plates, ventral view. A–B, D–E, F–G: same scale bars; A–B: plumose setae not illustrated.

similar body length, such as *N. herbstii* Leach, 1814, *N. strausi* and *N. mediterranea* Koçak & Moreira, 2015, that bear 5–7 simple setae.

The specimens from the Gulf of Cadiz agree well with the full description of the species by Ledoyer (1997), including diagnostic characters such as eye features, antennular scale proportions, setae of the fourth article of antennule peduncle (one distal robust seta and row of 9–10 setae on anterior margin), proportions of the articles of the maxilla 2 endopod and exopod, and shape of pleonites 6–7 denticles. The second article of the mandibular palp is provided with two setae whereas Ledoyer (1997: fig. 1) only illustrates one; two setae are present as well in specimens from the Aegean Sea but the proximal seta is provided with short setules instead of being naked (Moreira *et al.* 2012: fig. 3A). Furthermore, one specimen had two robust setae on the fourth article of antennule peduncle instead of one as found in all other specimens and those reported elsewhere; such variation may occur, however, in other species as discussed above for *N. strausi*.

Ecology

This species has been reported at depths between 410 and 2368 m; specimens from the Aegean Sea have been found in mud-clay sediments (Moreira *et al.* 2012). Specimens from MVs were found at depths of 354 to 1100 m in experimentally deployed wood and alfalfa substrata and associated with *Gigantidas mauritanicus* aggregations in cracks between large carbonate slabs at Darwin MV (1100 m depth).

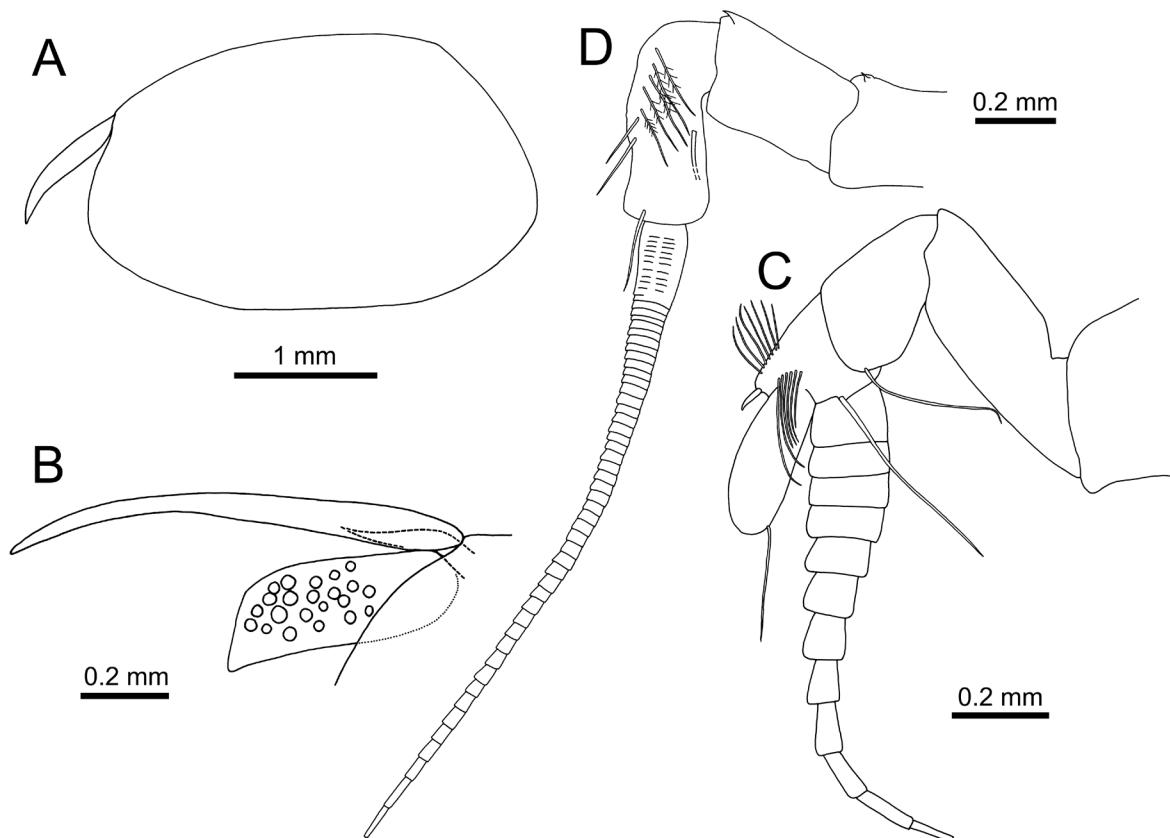


Fig. 9. *Nebalia abyssicola* Fage, 1929. Male (DBUA0001676.02.A). **A.** Rostrum and carapace, lateral view. **B.** Rostrum and eye, lateral view. **C.** Antennule, lateral view. **D.** Antenna, lateral view. C–D: only selected setae illustrated.

Distribution

There are few records of this species; its known distribution ranges from the western Mediterranean (Monaco: Fage 1929; Corsica and Provence, France: Ledoyer 1997) and the Ionian Sea (Froglia 2010) to the Aegean Sea (Moreira *et al.* 2012). Darwin, Meknès and Mercator MVs, Moroccan continental slope, Gulf of Cadiz (Fig. 1); this is the first record for the Atlantic Ocean.

Genus *Sarsinebalia* Dahl, 1985

Sarsinebalia ledoyeri sp. nov.

[urn:lsid:zoobank.org:act:6203DB5B-D428-494D-AE12-96671063F37A](https://zoobank.org/act:6203DB5B-D428-494D-AE12-96671063F37A)

Figs 1, 10–16, Table 2

Diagnosis

Rostrum length 2.4–2.5 times width. Compound eye provided with 10–20 spaced ommatidia along distal half; pigment not observed; eye distal half with concave ventral margin; distal third gradually compressed laterally. Antennular scale length about 2.2 times width. Antennule peduncle fourth article with one distal robust seta. Antenna peduncle third article with 2–3 slightly plumose setae and three similar spine-like setae on lateral margin. Mandibular palp second article with two setae: 1) proximal seta on lateral surface, setulose along distal half inferior margin, about 0.5 times as long as article; 2) subdistal simple seta, longer than third article. Maxilla II endopod weakly segmented, distal article 1.8 times as long as proximal article; exopod 1.4 times as long as endopod proximal article. Pleonite IV epimeron posterolateral corner as triangular acute process. Pleonite IV posterolateral border with denticles distally acute; pleonites V–VII posterodorsal border with denticles distally rounded to pointed, never acutely produced. Pleopod I exopod lateral margin lacking setae. Pleopod IV protopod posterior border with three serrations; posterolateral corner acutely pointed. Uropods 0.7–0.85 times as long as pleonite VII+anal somite.

Etymology

The new species is named after the French carcinologist Michel Ledoyer because of his many contributions to leptostracan taxonomy.

Type material

Holotype

MOROCCO • postovigerous ♀, TL 4.0 mm, RL 0.675 mm, DCL 1.65 mm, LCL 2.15 mm, CH 1.4 mm; Gulf of Cadiz, Gemini MV; 35°16.88' N, 06°45.35' W; 418 m depth; 6 Oct. 2006; St 64PE253_06, MV crater, mud breccia; MNCN 20.04/13706.

Allotype

MOROCCO • ♂, TL 3.9 mm, RL 0.625 mm, DCL 1.6 mm, LCL 1.975 mm, CH 1.3 mm; same locality and station as for holotype; MNCN 20.04/13707.

Paratypes

MOROCCO • 4 postovigerous ♀♀; same locality and station as for holotype; MNCN 20.04/13708 to 20.04/13711 • 10 preovigerous ♀♀; same locality and station as for holotype; MNCN 20.04/13712 to 20.04/13721 • 6 ♂♂; same locality and station as for holotype; MNCN 20.04/13722 to 20.04/13727 • 3 juveniles; same locality and station as for holotype; MNCN 20.04/13728 to 20.04/13730 • 4 postovigerous ♀♀, 10 preovigerous ♀♀, 5 ♂♂, 3 juveniles; same locality and station as for holotype; DBUA0002351.01.

Description of female

MEASUREMENTS. Postovigerous ♀♀: TL 3.625–4.0 mm, RL 0.575–0.70 mm, DCL 1.50–1.75 mm, LCL 1.90–2.375 mm, CH 1.325–1.50 mm; preovigerous ♀♀: TL 3.375–3.85 mm, RL 0.575–0.625 mm, DCL 1.125–1.60 mm, LCL 1.625–2.075 mm, CH 1.125–1.40 mm.

CARAPACE, ROSTRUM AND EYE. Carapace roughly oval, margins convex or rounded, covering laterally most of pleonites III–IV (Fig. 10A); LCL about 1.5–1.6 times CH. Rostrum long, extending well beyond eyestalk, length 2.4–2.5 times width, 0.4–0.45 times DCL (Fig. 10A, D); tapering gradually on distal half and turning downwards (Fig. 10B); paired ventral keels present; tip of rostrum provided with terminal spine, segmented proximally. Compound eye slightly longer than high, distal third becoming gradually compressed laterally (Fig. 10C); dorsal and distal margins almost straight, ventral margin straight proximally and concave on distal half (Fig. 10B); 10–20 spaced ommatidia, present mostly along distal half; pigmentation not observed in fixed specimens; supra-orbital plate with acute tip, reaching at least end of distal half of eye dorsal surface.

ANTENNULE. Peduncle composed of four articles (Fig. 11A). First article shorter than second, naked. Second article widest at midpoint, length almost 3.0 times width, with (1) one plumose seta on anterior margin at mid-length, (2) cluster of about 12 smooth and plumose setae arising from posterolateral distal third surface, (3) cluster of about 10 short and long simple setae and one plumose seta on anterodistal

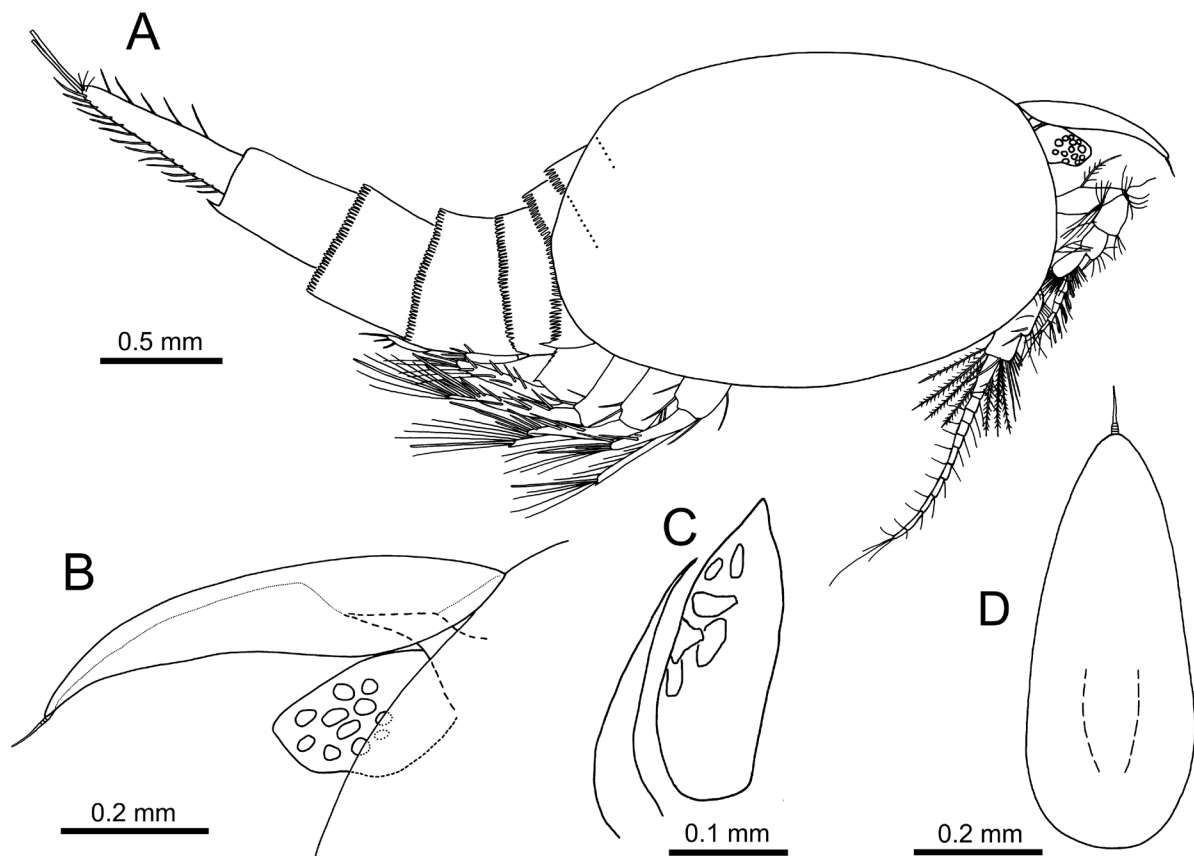


Fig. 10. *Sarsinebalia ledoyeri* sp. nov. Postovigerous females. **A.** Holotype (MNCN 20.04/13706). **B–D.** Paratypes (MNCN 20.04/13708, MNCN 20.04/13709). **A.** Complete specimen, lateral view. **B.** Rostrum and eye, lateral view. **C.** Eye and supra-orbital plate, ventral view. **D.** Rostrum, dorsal view. A: dashed lines marking distribution of denticles on posterior borders of pleonites II and III.

margin. Third article 0.5 times as long as second, wider distally, with terminal cluster of about 12 simple setae on anterodistal and posterodistal margins, one long simple seta on external surface and two shorter setae on inner surface. Fourth article shorter than third, with (1) anterior row of 5–6 simple setae, (2) one distal robust seta, (3) lateral row of 2–3 simple setae on external surface, distal-most the longest,

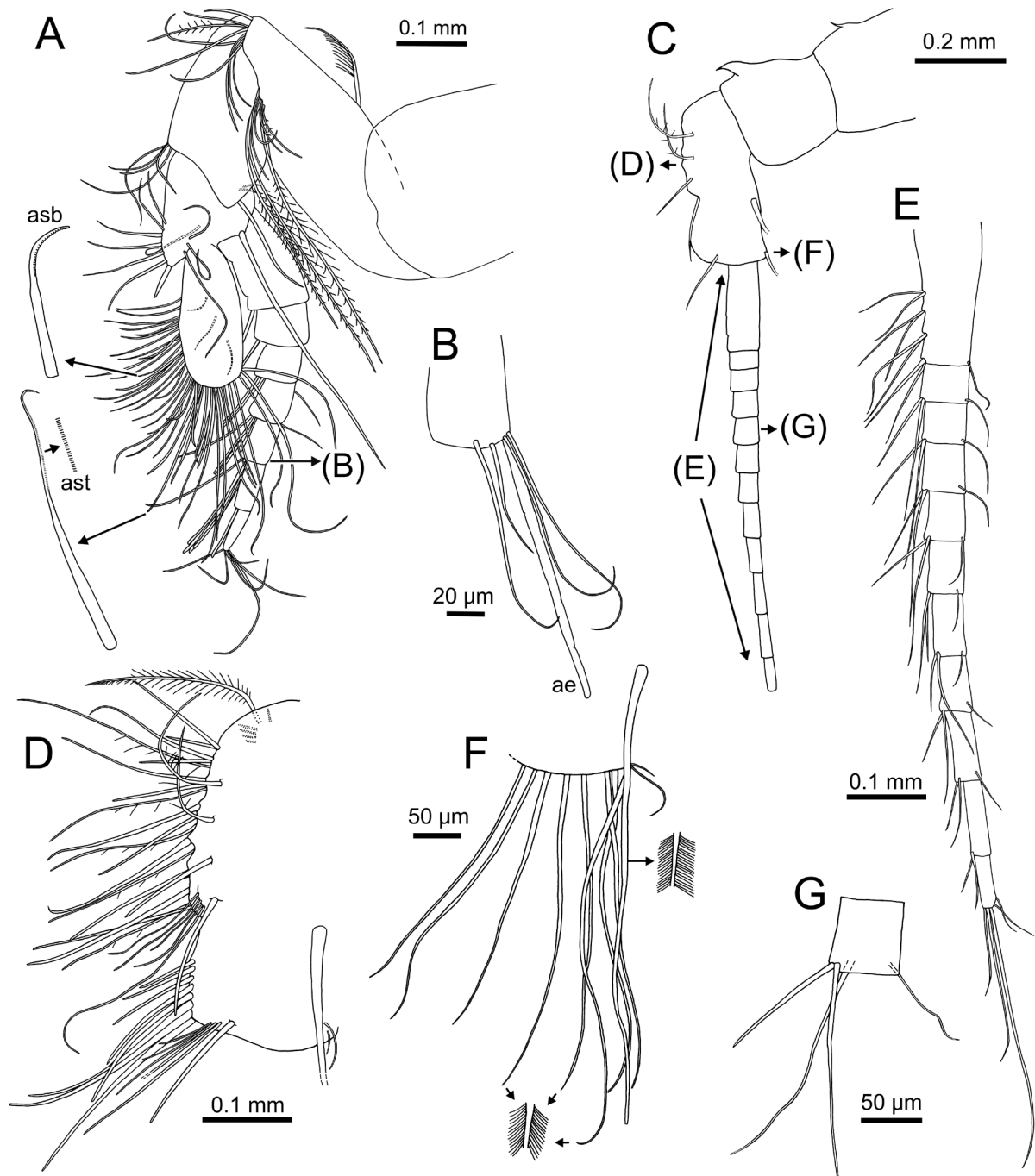


Fig. 11. *Sarsinebalia ledoyeri* sp. nov. Postovigerous female, paratype (MNCN 20.04/13708). A. Antennule, lateral view. B. Antennule, flagellum, fifth article. C. Antenna, lateral view, outline. D. Antenna, peduncle, third article, lateral view. E. Antenna, flagellum. F. Antenna, peduncle, third article, distal margin plumose setae. G. Antenna, flagellum, fifth article. A, C: letters in brackets refer to parts detailed in other drawings with same letters; B: only one aesthethasc out of five figured.

(4) one simple seta on inner surface, (5) one simple seta arising from posterodistal margin, longer than article and antennular scale combined. Antennular scale roughly oval, length 2.2 times width; anterior margin slightly convex; anterior and terminal margins with (1) row of shorter setae recurved distally and provided with blunt teeth along distal half (asb in Fig. 11A), (2) numerous simple setae of different lengths with thinner teeth, setae arising from posteroterminal margin the longest (ast in Fig. 11A); row of three spaced simple setae on inner surface. Flagellum long, well-developed, shorter than peduncle, with 7 articles (6–7 in previgorous females), proximal article as long as following three combined; each

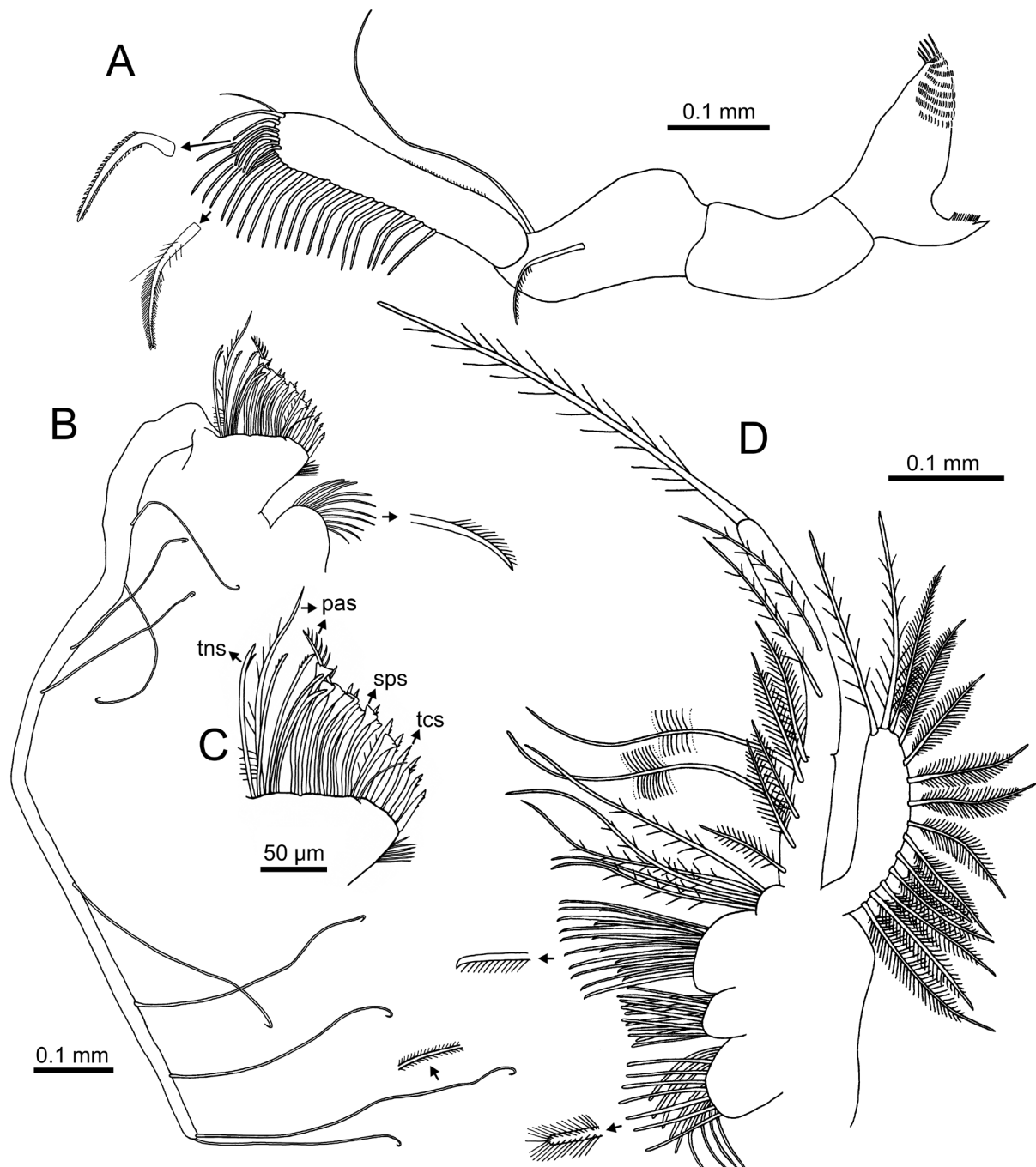


Fig. 12. *Sarsinebalia ledoyeri* sp. nov. Postovigorous female, paratype (MNCN 20.04/13708). A. Mandible. B. Maxilla I. C. Maxilla I, endites, detail. D. Maxilla II.

article with (1) cluster of 2–8 aesthetascs and (2) 2–4 simple setae on distal margin (Fig. 11B), distal article with 5–6 setae and lacking aesthetascs.

ANTENNA. Peduncle composed of three articles (Fig. 11C). First article anterior margin with process ending in small acute spine. Second article about as long as first, anterior margin with subdistal acutely pointed process. Third article about 2.0 times as long as second; plumose seta arising proximally from inner surface, associated to four simple short setae; medial and lateral anterior margins with several rows of setae (Fig. 11D): (1) five sparsely plumose setae, (2) two rows of simple thin spine-like setae, of 5–6 setae each (most arranged in pairs), (3) five simple, thin setae, (4) terminal row of eight simple setae, increasing in length distally, (5) 2–3 slightly plumose setae and three spine-like similar setae along lateral margin, distal-most seta associated to 5–7 simple setae; posterior margin with long, densely plumose seta (Fig. 11F); cluster of 8–9 plumose setae along distal margin inner surface; posterodistal margin with two short simple setae of different length. Flagellum well-developed, composed of 11 articles (12 in one postovigerous female) (Fig. 11E); each article with four terminal setae, one shorter than others (Fig. 11G).

MANDIBLE (Fig. 12A). Molar process well-developed, about as long as first palp article, with several rows of teeth on distal third and several distal simple setae; incisor process smaller, broadest basally, with row of acute teeth on medial margin and acute terminal process. Mandible palp composed of three articles; second article slightly longer than first, widest on proximal third; two setae: one at mid-length on lateral surface, setulose on inferior margin of distal half, about 0.5 times as long as article, and one subterminal simple seta, longer than third article. Third article 1.3 times as long as second, with almost parallel sides, slightly tapering distally; inferior margin with (1) a row of plumose setae extending from ending of proximal third to distal end, first four setae increasing gradually in length, (2) a row of six subdistal dentate setae, (3) two terminal setae, one as long as those of (1); superior margin proximal half with a row of minute setae.

MAXILLA I. First endite (proximal) with rounded medial margin bearing row of plumose setae (Fig. 12B). Second endite (distal) larger than first; inner margin with several distal simple setae; medial margin with several types of setae arranged in two rows: first row with (1) about 9 setae of increasing size with several teeth along distal half and one large tooth on distal superior margin (tcs in Fig. 12C) and (2) two pappose setae (pas in Fig. 12C); second row with (3) about ten spatulate setae (sps in Fig. 12C) and (4) six setae with several teeth (2–4) along distal superior margin, thinner than those of type (1) (tns in Fig. 12C); setae of types (1), (3) and (4) with one margin provided with long, spaced setules (Fig. 12C). Palp well-developed, about 4.0 times as long as protopod, with about 7–9 long setae along its entire length; setae provided with minute setules along distal third and with apex recurved distally (Fig. 12B).

MAXILLA II (Fig. 12D). Protopod with four endites; first (proximal) and third endite the largest, fourth endite much shorter; first to third endites bearing numerous plumose setae arranged in two rows; fourth endite with five longer plumose setae. Endopod weakly segmented, longer than exopod, distal article 1.8 times as long as proximal; medial margin of both articles with one row of spaced plumose setae, proximal with two additional longer setae with long setules along distal half; distal article with one plumose seta, longer than endopod. Exopod 1.4 times as long as endopod proximal article; lateral margin with plumose setae, two distal-most setae as long as exopod.

THORACOPODS. Endopod longer than exopod, segmentation weak; with numerous plumose setae along anterior margin arranged in two rows and one long sparsely plumose seta (Fig. 13A); distal article expanded, in postovigerous females lacking long setae, in preovigerous females with several setae shorter than exopod (Fig. 13B–C). Exopod posterior margin with 6–9 plumose setae, 1–2 distal-most the longest (Fig. 13A). Epipod posterior margin with two plumose setae. Thoracopod VIII shorter than

others, with epipod comparatively reduced and lacking setae (Fig. 13D); exopod posterior margin with about 5 plumose setae comparatively longer than those of other thoracopods.

PLEONITES. Pleonite I posterior border lacking denticles. Pleonites II–VII bearing denticles along posterior border, at least dorsally and laterodorsally (Fig. 10A). Pleonite II with denticles along dorsal border and extending to dorsolateral border (Fig. 14A); denticles thin, distally acute. Pleonite III with denticles along dorsal border extending well into lateral border, ending at mid-length (Fig. 14B); denticles distally pointed with more or less parallel sides (dorsal) to triangular (laterodorsal). Pleonites IV–VII with posterior border fully provided with denticles. Pleonite IV with dorsal and dorsolateral denticles pointed to rounded becoming distally acute and triangular in shape along lateral border (Fig. 14C); epimeron posterolateral corner forming large tooth with triangular distal end, acutely pointed. Pleonites V–VII

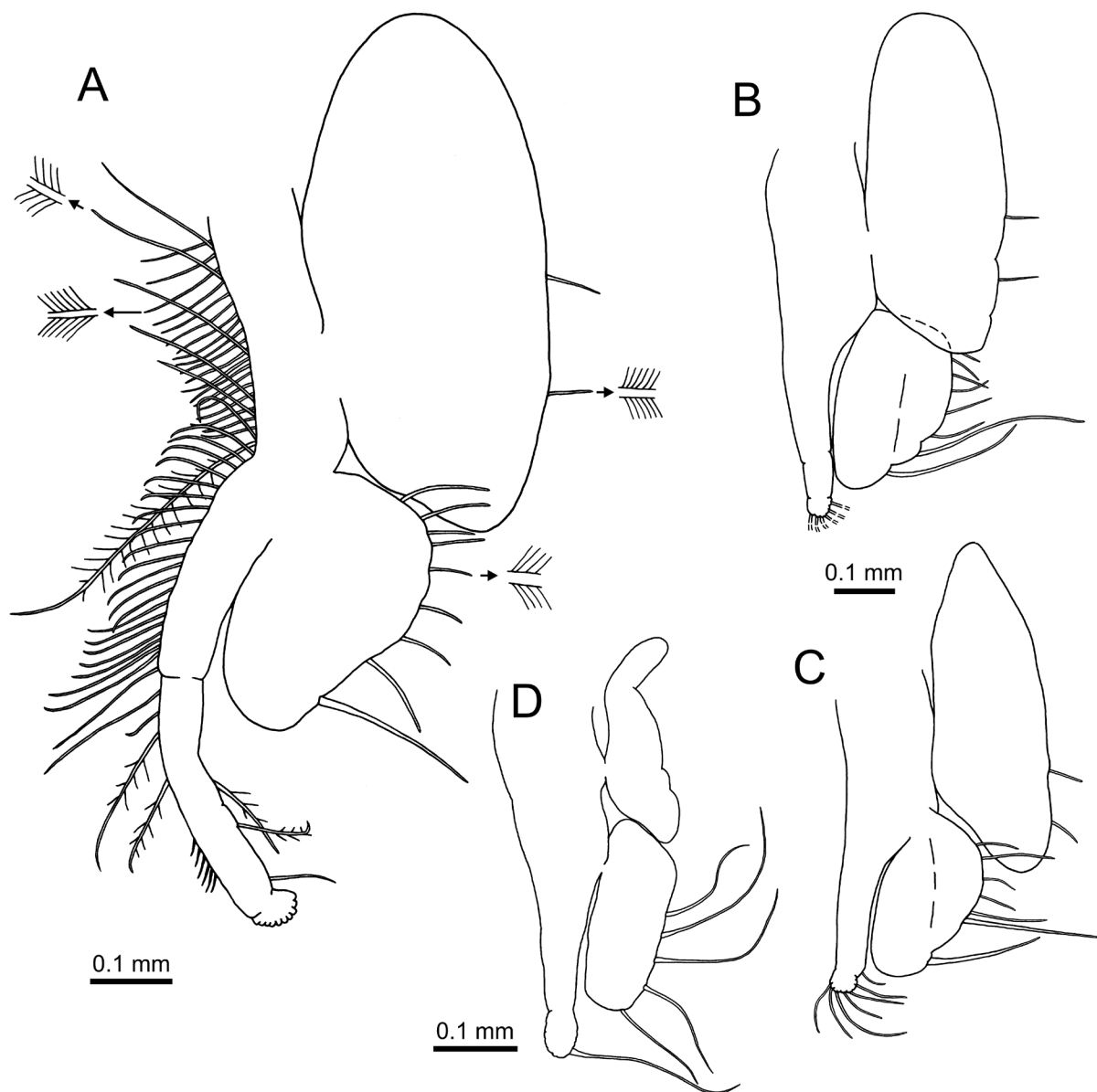


Fig. 13. *Sarsinebalia ledoyeri* sp. nov. Female, paratypes (MNCN 20.04/13708). **A.** Thoracopod III, showing setation. **B.** Thoracopod V. **C.** Thoracopod VII. **D.** Thoracopod VIII. A, D: postovigerous female; B–C: preovigerous female, same scale bar; B–D: only selected setae illustrated.

dorsal and dorsolateral denticles similar in shape to those of pleonite III, distal end roughly pointed to rounded but never acutely produced (Fig. 14D–F); some denticles on ventrolateral border distally acute (Fig. 14D).

PLEOPODS 1–4. Pleopod 1 protopod with posterior margin even (Fig. 15A); with one short simple seta proximally on posterior margin and four distal simple setae: one seta on anterior margin arising subdistally and one seta between rami, posterior margin with long seta near exopod base and hardly reaching exopod distal half plus one shorter subdistal seta. Exopod about 0.6 times as long as protopod; lateral margin lacking ‘comb-row’; distolateral margin with one short simple seta and four stout simple setae, distal-most the longest; long plumose setae (> 15) along medial margin. Endopod of two articles, 1.25 times as long as exopod; proximal article shorter, with *appendix interna* provided with three short recurved hooks; lateral and medial margins of distal article each with one row of > 10 plumose setae, distal margin with acute process at apex and long, robust terminal seta.

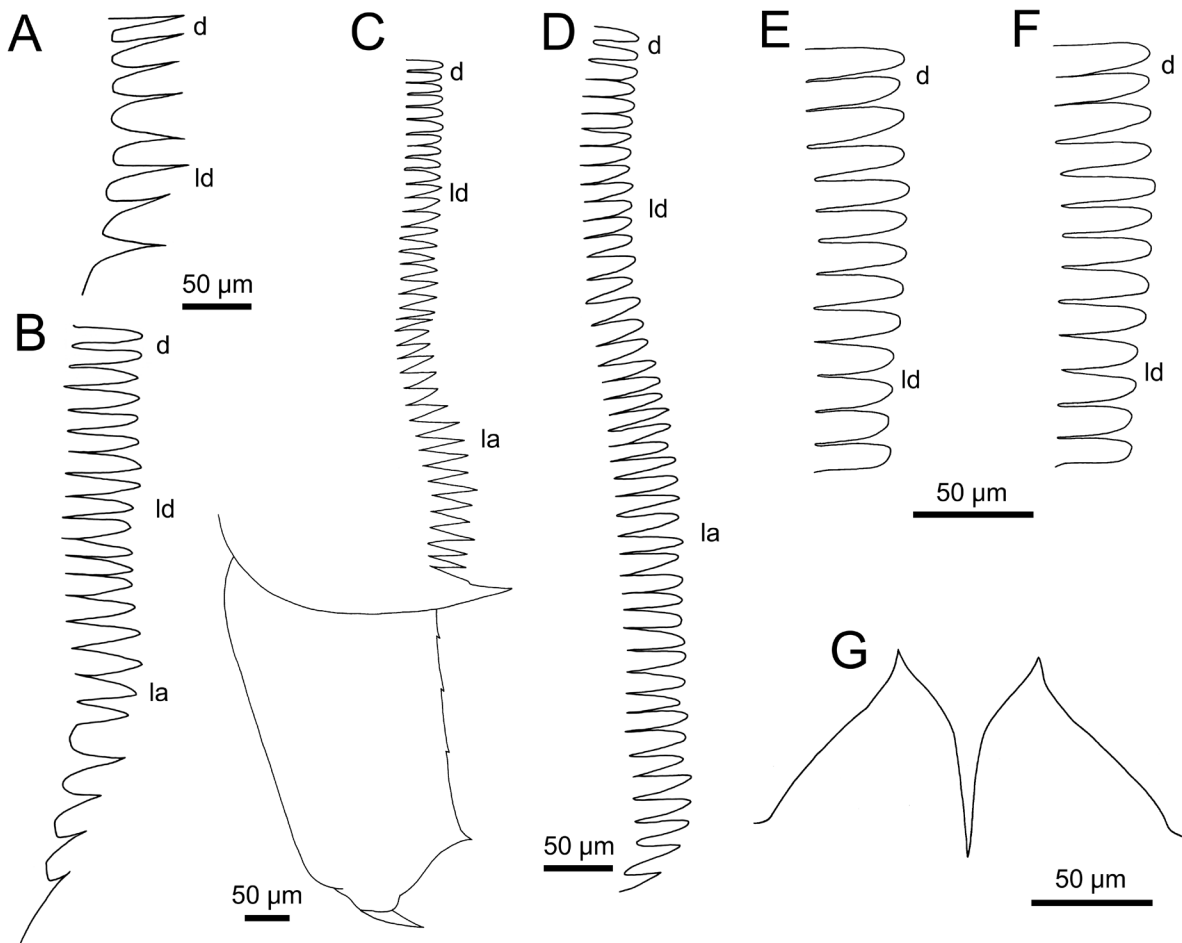


Fig. 14. *Sarsinebalia ledoyeri* sp. nov. Postovigerous female, paratype (MNCN 20.04/13708). **A.** Pleonite II, dorsal and laterodorsal posterior border, denticles. **B.** Pleonite III, dorsal and lateral posterior border, denticles. **C.** Pleonite IV (posterior border, denticles and epimeron) and pleopod IV (protopod), lateral view. **D.** Pleonite V, dorsal and lateral posterior border, denticles. **E.** Pleonite VI, dorsal and laterodorsal border, denticles. **F.** Pleonite VII, dorsal and laterodorsal border, denticles. **G.** Anal plates. A–B, E–F: same scale bars.

PLEOPODS II–III. Similar in appearance. Protopod inner surface with 1–2 simple setae on proximal third, and cluster of 2–6 long simple setae at mid-length, posterior margin with cluster of three long simple setae on distal third, and two simple setae near rami bases: one near *appendix interna* and one thicker

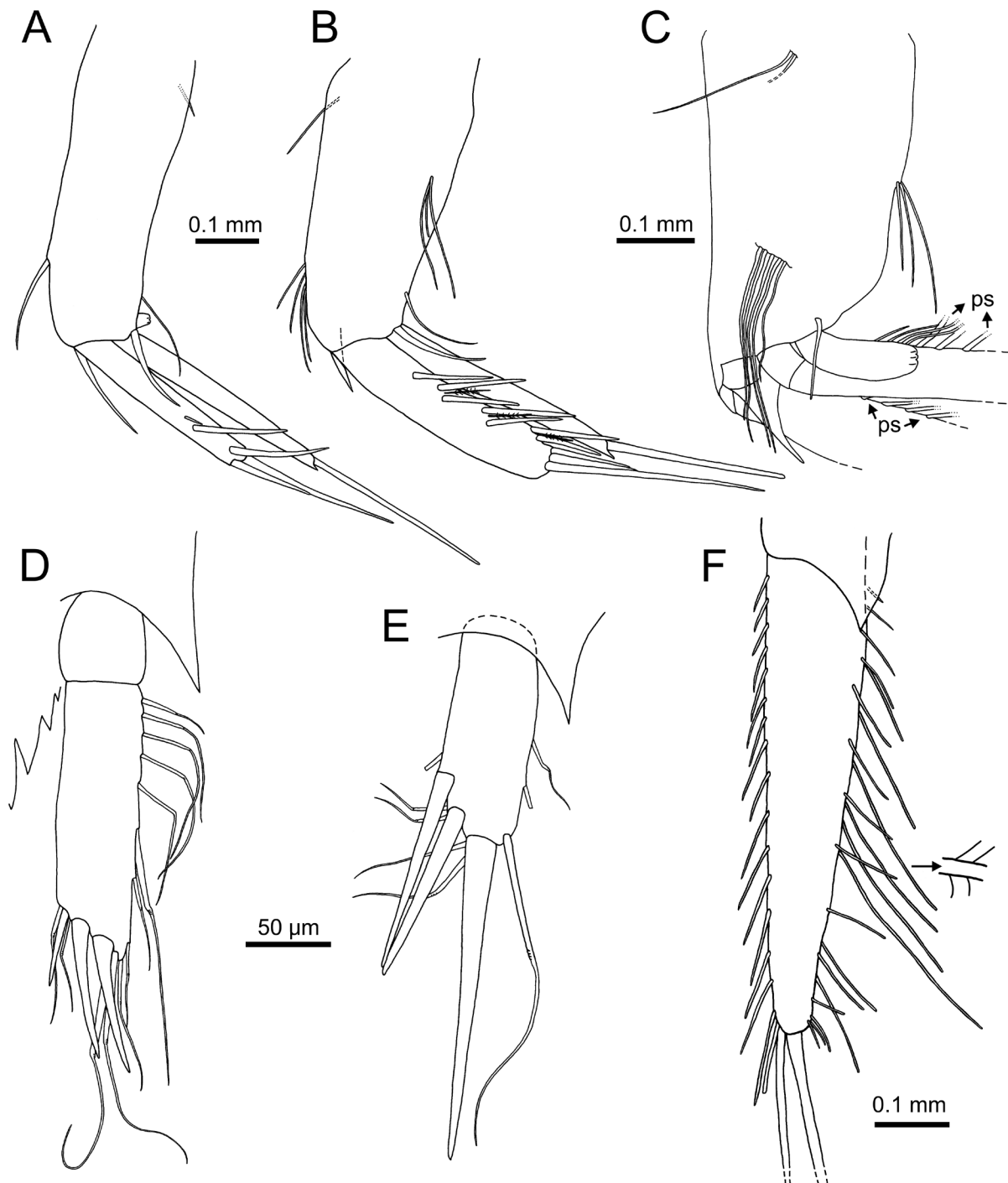


Fig. 15. *Sarsinebalia ledoyeri* sp. nov. Postovigerous female, paratype (MNCN 20.04/13708). **A.** Pleopod I, lateral view. **B.** Pleopod II, lateral view. **C.** Pleopod III, protopod and endopod *appendix interna*, inner side. **D.** Pleopod V, ventral view. **E.** Pleopod VI, ventral view. **F.** Right uropod, ventral view. A–B, D–E: same scale bars; A–B: plumose setae not illustrated; C: exopod and endopod plumose setose: setules not illustrated.

seta close to exopod (Fig. 15B–C); acute triangular process between rami; posterior margin even. Exopod shorter than endopod; lateral margin with row of four smooth setae ('spine pairs'), each pair consisting of two setae subequal or one slightly shorter (sometimes one lacking in proximal pair), with short setulose seta in between; medial margin with about 10 long plumose setae; distal margin with three simple setae, distal-most the longest. Endopod of two articles; proximal article short, provided with *appendix interna*; lateral and medial margins of distal article each with one row of > 15 plumose setae; terminal margin with one long, robust distal seta.

PLEOPOD IV. Protopod posterior margin with three serrations (Fig. 14C); posterolateral corner acutely pointed. Rami similar to pleopods II–III.

PLEOPODS V–VI. Pleopod V–VI pairs with acute triangular process between rami bases. Pleopod V uniramous, length 4.3 times width, with three terminal stout simple setae, proximal-most much shorter (Fig. 15D); approximately 12–13 simple setae of different lengths along medial and terminal margins, appearing jointed at mid-length. Pleopod VI uniramous, length 3.0 times width (Fig. 15E); with three terminal simple setae, one longer than entire ramus; medial, distolateral and terminal margins with about eight 'jointed' setae of different lengths.

ANAL SOMITE, ANAL PLATES AND UROPODS. Anal somite 1.15–1.35 times as long as pleonite VII (Fig. 10A). Anal plates with broad bases and acutely tapering distally (Fig. 14G); medial margins convex defining a Y-shaped invagination between plates; lateral margins gently sloping, lacking 'shoulder'. Uropods tapering distally, 0.7–0.85 times as long as pleonite VII+anal somite (Fig. 10A); lateral margin with 15–18 simple setae gradually increasing in length towards distal end; terminal margin with two longer robust setae, broken in all specimens but distal-most at least as long as uropods (Fig. 15F); medial margin with one row of simple setae similar to those on lateral margin but fewer and thinner plus one row of long plumose setae; distomedial margin with cluster of three short simple setae.

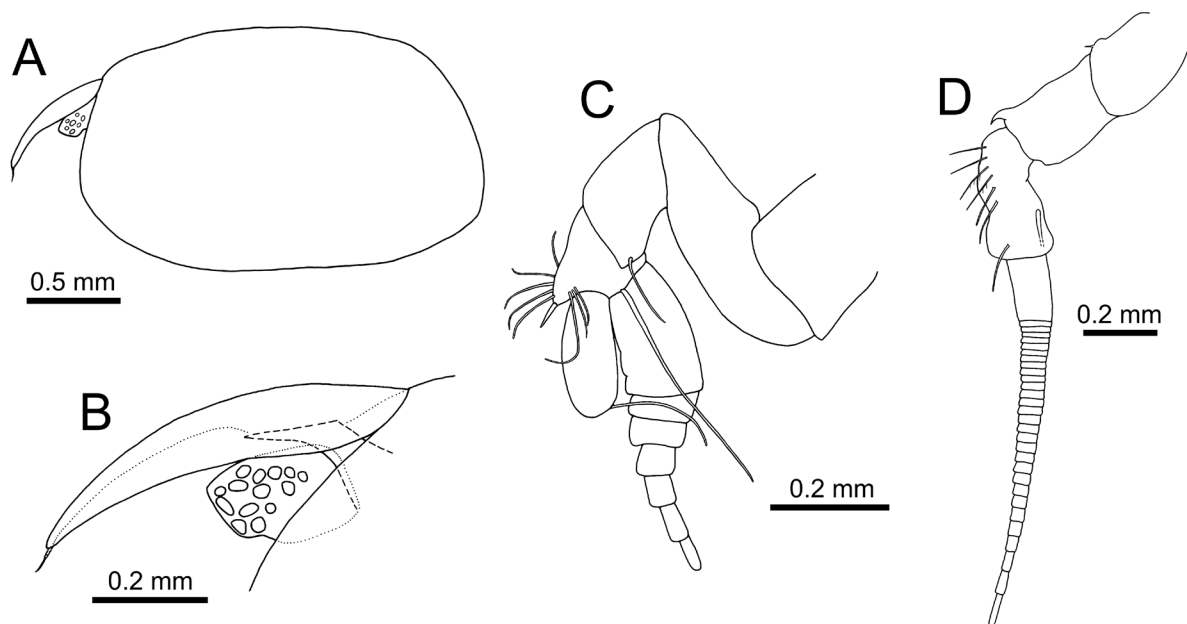


Fig. 16. *Sarsinebalia ledoyeri* sp. nov. Male. **A.** Allotype (MNCN 20.04/13707). **B–D.** Paratype (MNCN 20.04/13722). **A.** Rostrum, eye and carapace outline, lateral view. **B.** Rostrum and eye, lateral view. **C.** Antennule, lateral view. **D.** Antenna, lateral view. C–D: only selected setae illustrated.

Table 2. Comparison of selected diagnostic characters for all known species of *Sarsinebalia* Dahl, 1985.

Species	Ommatidia	Eye pigment	Eye shape	Antennular scale: length/width	Antennule peduncle 4 th article: distal spine	Mandibular palp 2 nd article: setae	Mandibular palp: 2 nd article vs proximal seta ³	Maxilla II: endopod articles	Maxilla II: exopod length	Pleonites VI–VII: posterodorsal border, denticles	Pleopod I: exopod lateral margin	Pleonite IV: epimeron posterior corner + posterolateral border, denticles	Source
<i>S. typhlops</i> (G.O. Sars, 1870)	No	No	Almost rectangular, longer than high; proximal half higher than distal	> 2:1	1	Distal longer than proximal ¹ ; setae smooth (?) ²	Seta > half length of article	Limit between articles hard to distinguish; articles subequal	Exopod slightly shorter than endopod first article	Length about 2 times width; distal third: slightly triangular, distally rounded to slightly pointed	Smooth	Corner acute+ denticles triangular, distally acute	Sars (1896), Dahl (1985)
<i>S. biscoyensis</i> Ledoyer, 1998	No	No	Elongated, inferior margin distal half convex	> 2:1	0	Distal slightly longer than proximal; setae plumose	Seta > half length of article	Limit between articles not defined	Exopod < half length of endopod	Triangular; distally acute	12 setae (proximal half) + 12 spines (distal half)	Corner acute+ denticles triangular, distally acute	Ledoyer (1998)
<i>S. kunyensis</i> Ledoyer, 2000	Yes	No	Oval, elongated	~ 2:1	1	Two setae at distal end of second third, one slightly longer; setae smooth (?) ²	Both setae > half length of article	Limit between articles hard to distinguish; articles subequal	Exopod > endopod first article	Elongated (> 2 times longer than wide); distally rounded	Smooth (mostly along distal half)	Corner acute+ denticles distally rounded	Ledoyer (2000)
<i>S. cristoboi</i> Moreira <i>et al.</i> , 2003	Numerous, extending orange for most of eye	Yes (red-orange)	Slightly longer than high; dorsal and ventral margins convex	2.3:1	1	Distal > 2 times length of proximal; setae setulose on distal half	Seta < half length of article	Limit between articles well-defined; proximal longer than distal	Exopod > endopod first article	Length 2 times width or less, parallel sides; distal end bluntly rounded	Smooth	Corner acute+ acute spine-like denticles	Moreira <i>et al.</i> (2003b)
<i>S. argorrii</i> Moreira <i>et al.</i> , 2003	Numerous, at least along distal 2/3 of eye	Yes (red, orange, dark)	Longer than high; dorsal and ventral margins running almost parallel	1.8:1	1	Distal > 2 times length of proximal; distal: setulose on distal half; proximal: setulose along full length	Seta 1/3 length of article	Limit between articles well-defined; distal slightly longer than proximal	Exopod > endopod first article	Length 2 times width, parallel sides; distal end bluntly rounded	Smooth	Corner ending in large triangular process, tooth-shaped+ denticles triangular, distally rounded to slightly pointed	Moreira <i>et al.</i> (2003b); McCormack <i>et al.</i> (2016)
<i>S. pseudo-typhlops</i> Petyashov, 2016	No	No	Oblong, length 1.4 times height	2.5:1	0?	Distal slightly longer than proximal; setae smooth (?) ²	Seta > half length of article	Limit between articles well-defined; proximal longer than distal	Exopod < endopod first article	Proximal 2/3 with parallel sides; distal third triangular, acute	7+2 spines (distal half)	Corner acute+ denticles with parallel sides and distal third triangular, acute	Petyashov (2016)
<i>S. ledoyeri</i> sp. nov.	10–20, mostly along eye distal half	No (at least in fixed specimens)	Slightly longer than high; distal third becoming gradually compressed laterally; ventral margin concave on distal half	2.2:1	1	Distal > 2 times length of proximal; distal: smooth; proximal: setulose on distal half	Seta about half length of article	Limit between articles weakly defined; distal longer than proximal	Exopod > endopod first article; < half length of endopod	Elongated; distal third: slightly triangular, distally rounded to pointed	Smooth	Corner acute+ denticles triangular, distally acute	This work

¹ Sars (1896) only mentions and illustrates one distal seta that is longer than article; Dahl (1985) illustrates two setae, distal seta seems broken but it might be longer than proximal one (cf. Sars 1896: table IV, fig. 12). ² Drawings included in original description illustrate setae with smooth borders; description does not state whether they are smooth or setulose/plumose.

³ The mandibular palp second article of *S. kunyensis* bears two setae located at the same level; remaining species bear one distal and one proximal seta.

Description of male

TL 3.3–3.925 mm, RL 0.525–0.675 mm, DCL 1.275–1.675 mm, LCL 1.6–2.05 mm, CH 1–1.3 mm. Carapace proportions similar to females (Fig. 16A), LCL about 1.5–1.6 times CH. Ommatidia irregularly distributed along distal half or $\frac{2}{3}$ of eye (Fig. 16B). Antennular scale proportionally longer than in females (2.2–2.45 times as long as wide) (Fig. 16C); flagellum with up to 6–7 articles, thicker than in females. Antenna peduncle third article lateral margin with similar setation as in females; flagellum with many articles (> 30) but not surpassing TL (Fig. 16D). Pleopod IV protopod posterior margin with three serrations. Pleonites VI–VII denticles elongated, more pointed than in females.

Remarks

Known species of *Sarsinebalia* can be distinguished by whether or not eyes are provided with ommatidia/pigment and lateral margin of pleopod I exopod is provided with setae, as well as by the eye shape, features of maxilla II exopod and endopod and pleonites denticles (Table 2). *Sarsinebalia ledoyeri* sp. nov. is characterised by the following combination of characters: the rostrum is about 2.4–2.5 times as long as wide, the eye is provided with ommatidia (10–20) and lacks pigment, the eye is gradually compressed laterally along distal third and towards anterior margin, the eye ventral margin is concave along distal half, the antennular scale is about 2.2 times as long as wide, the second article of the mandibular palp bears one seta on lateral surface about 0.5 times as long as article and one subterminal seta longer than the third article, the distal article of the endopod of the maxilla II is about 1.8 times as long as the proximal article, the exopod of the maxilla II is clearly longer than the proximal article of the endopod, the posterodorsal border of pleonites VI–VII are provided with distally rounded to pointed denticles, the protopod of pleopod IV has three serrations along the posterior border and the posterolateral corner is acutely pointed, and the uropods are shorter than the pleonite VII and anal somite combined.

Sarsinebalia ledoyeri sp. nov. mainly differs from *S. typhlops*, *S. biscayensis* and *S. pseudotyphlops* in having eyes provided with ommatidia. Furthermore, *S. typhlops* also differs in that the two articles of the maxilla II endopod are subequal (Sars 1896: fig. 14), the proximal seta of the mandibular palp second article is more than two thirds of the length of the article whereas in *S. ledoyeri* sp. nov. is only half the length of the article, and the pleopod V–VI have more stout distal/distolateral setae according to Sars (1896) (V: 5, VI: 5 vs 3/3); *S. typhlops* also seems a larger species, reaching 9 mm in length (Sars 1896) whereas the largest mature specimens of *S. ledoyeri* sp. nov. only reach 4 mm. In turn, *S. biscayensis* has elongated eyes, the fourth article of the antennule peduncle lacks the distal robust seta bearing instead one long simple seta similar to those along the medial margin, the pleopod I exopod is provided with ‘spines’ along the lateral border (as it happens in *S. kunyensis* Ledoyer, 2000 and *S. pseudotyphlops*) and the pleopod I protopod bears a row of simple, long setae along the proximal half of the posterior border instead of only one shorter seta (cf. Ledoyer 1998: fig. 2 vs Fig. 15A); *S. pseudotyphlops* has a comparatively longer antennular scale, the proximal article of the maxilla II endopod is longer than the distal one, the pleopod IV protopod has an even posterior margin and the posterodorsal denticles of pleonites VI–VII are acute distally. On the other hand, *S. kunyensis* is also provided with ommatidia but differs from *S. ledoyeri* sp. nov. in having oval elongated eyes, the two articles of the maxilla II endopod are subequal, the proximal seta of the mandibular palp second article is comparatively longer and the denticles along the lateral border of the pleonite IV epimeron are distally rounded instead of being acute. *Sarsinebalia ledoyeri* sp. nov. differs from the shallow-water species, *S. cristoboi* and *S. urgorrii*, in lacking eye pigment and in the shape of the eyes, that has distal and ventral margins parallel in *S. urgorrii* and convex in *S. cristoboi*; the aforementioned species also bear proportionally shorter denticles along posterodorsal borders of pleonites VI–VII that are always distally rounded, the distal long seta of the mandibular palp second article bears short setules along distal half instead of being naked, and the proximal article of the maxilla II endopod is longer than the distal one in *S. cristoboi* while the distal

article is, in turn, only slightly longer in *S. urgorrhii*. Finally, the description of *S. typhlops occidentalis* is brief but it shows that the rostrum is wider basally than that of *S. ledoyeri* sp. nov. and the furca is about as long as the pleonite VII and the anal somite combined instead of the former being clearly shorter; Hessler & Sanders (1965) also mention that the mandible is provided with “two large setae on second segment of palp” whereas in *Sarsinebalia ledoyeri* sp. nov. the length of the proximal seta is about one third of the distal one.

On the other hand, *S. typhlops* has been previously recorded in the Mediterranean at deep-sea depths (Lo Bianco 1903). Ledoyer (1997) also reports *S. typhlops* from southern France in *Posidonia* beds at a shallow depth (11 m); the only examined specimen corresponded to one ovigerous female but this mostly differs from the description by Dahl (1985) in having eyes that are provided with many ommatidia (ca 40 each), the maxilla II has an endopod with the two articles clearly defined, the distal one being slightly longer than the proximal, and the maxilla II exopod is clearly longer than the proximal article of the endopod. In fact, this description fits better with that of *S. urgorrhii*, that is mostly present in shallow waters as well; the shape of the eyes and the denticulation of pleonite IV epimeron, as illustrated by Ledoyer (1997) is also very similar to that of *S. urgorrhii* (cf. Ledoyer 1997: fig. 5 and Moreira *et al.* 2003b: figs 8f and 14g). Therefore, previous records of *S. typhlops* in shallow waters and into the Mediterranean might correspond to other taxa and deserve further revision (McCormack *et al.* 2016; Latry & Droual 2020).

Ecology

This species was collected from the crater of the Gemini MV and was the most abundant species in a box core sample. The sediments (mud breccia) yielded a highly diverse macrofaunal assemblage (ca 50 species) characterized by the presence of mega-epifauna (Pennatulacea, Hydrozoans, Crinoids), the chemosymbiotic species *Siboglinum* spIb (as in Hilário *et al.* 2010), and numerous species of peracarid crustaceans.

Distribution

Only known from the type locality, Gemini MV (418 m depth), in the Moroccan margin of the Gulf of Cadiz (this study; Fig. 1).

Discussion

Taxonomy of *Sarsinebalia* Dahl, 1985

McCormack *et al.* (2016) recently reviewed the characters considered diagnostic for *Sarsinebalia* and concluded that further work is needed to assess the validity of the genus, including a molecular approach. Nevertheless, the new species described here was tentatively included in *Sarsinebalia* mostly because it has a rostrum with subterminal spine and it lacks a ‘comb-row’ of bi-pectinate setae on the lateral margin of the pleopod I exopod (sensu Walker-Smith 2000); such setae are present instead in *Nebalia*, *Dahlella* Hessler, 1984, *Paranebalia* and *Levinebalia* Walker-Smith, 2000 (Haney & Martin 2004). However, some species of *Sarsinebalia* bear a pleopod I exopod that is provided with setae along lateral margin (Table 2); furthermore, some are simple while other setae are provided with lateral ornamentation as in *S. biscayensis* and *S. kunyensis* (“finement ciliées”, cf. Ledoyer 2000: 66) but with simple distal tip (“les épines sont apparemment simples et non barbelées et trifides”, cf. Ledoyer 1998: 32). On the contrary, bi-pectinate setae of pleopod I ‘comb-row’ in species of *Nebalia* are usually described as laterally serrated and ending in a tridentate tip, composed by a bifid, stout apex flanked by two distally-acute sinuous processes (e.g., Dahl 1985; Martin *et al.* 1996; Olesen 1999; Moreira *et al.* 2003b, 2007, 2009a; Haney & Martin 2005; Koçak & Moreira 2015; Othman *et al.* 2016). Therefore, as stated by McCormack *et al.* (2016), species of *Sarsinebalia* nowadays seem only united by bearing a rostrum with subterminal spine, a character that is also shared with other genera, and this lack of synapomorphies challenges

the validity of the genus (see Walker-Smith & Poore 2001). However, the possibility of sharing other diagnostic characters that have not yet been fully evaluated cannot be ruled out (McCormack *et al.* 2016). For example, species of *Sarsinebalia* seem to differ from *Nebalia* in the appearance of the setae on the mandibular palp although there is a lack of accurate descriptions for some species of each genus. Thus, the second article is provided in *Sarsinebalia* with two setae: one can be much longer than the other and the article as well (*S. typhlops* – but see also Table 2 –, *S. cristoboi*, *S. urgorrii*, *Sarsinebalia ledoyeri* sp. nov.) or, alternatively, both are similar in length but if so, they are at least longer than half the length of the article (*S. biscayensis*, *S. kunyensis*, *S. pseudotyphlops*). Species of *Nebalia* usually bear two setae, one shorter than the other or as long as each other, being both shorter than half the length of the article (e.g., *N. strausi*, *N. brucei* Olesen, 1999, *N. gerkenae* Haney & Martin, 2000, *N. kocatasi* Moreira, Koçak & Katagan, 2007, *N. deborahae* Bochert & Zettler, 2012, *N. terazakii* Othman, Toda & Kikuchi, 2016); some species bear instead one seta (*N. lagartensis* Escobar-Briones & Villalobos-Hiriart, 1995, *N. hessleri* Martin, Vetter & Cash-Clark, 1996) or three setae (*N. marerubri* Wägele, 1983, *N. cannoni* Dahl, 1990) but in any case not longer than the second article. The exception to this apparent pattern are those species of *Nebalia* with eyes provided with distal lobes namely *N. daytoni* Vetter, 1996, *N. daytoni brevicaudata* Ledoyer, 2000 and *N. schizophthalma* Haney, Hessler & Martin, 2001, that show a similar pattern to that of *Sarsinebalia*. Regarding the third mandibular palp article, there is one row of setae along the inferior margin that might subtly differ between *Sarsinebalia* and *Nebalia*; thus, the first few proximal setae in *Nebalia* seem much shorter than the others (Figs 3A, 7A) while in *Sarsinebalia* there seems to be a gradual increase in length (*S. cristoboi*, *S. urgorrii*) or no difference at all (Fig. 12A); again, the lack of accurate or explicit descriptions in many taxa prevents at the moment further generalization.

In any case, it seems that detailed studies of patterns of setation in antennae and mouthparts of leptostracans might eventually reveal whether they may have a taxonomic value or, alternatively, being related to trophic strategy. In fact, SEM examination of such appendages has shown a high variety of setal ornamentation (e.g., Martin *et al.* 1996) and, for instance, Moreira *et al.* (2009a: fig. 1C, F) showed that the denticulation of some equivalent setae in the third peduncle article of the antenna differ between the sympatric *S. cristoboi* and *S. urgorrii* that, in turn, seem to show a spatial segregation related to sedimentary features.

Bathymetric distribution and mud volcanoes

Most of the extant leptostracans are known from depths usually shallower than 100 m (Haney & Martin 2016), including members of *Nebalia*, *Nebaliella*, *Dahlrella*, *Sarsinebalia* and *Levinebalia*; the three known species of *Paranebalia* and the only representant of *Saronebalia* Haney & Martin, 2004 are apparently restricted to shallow waters, including soft-bottoms colonised by seagrasses and macroalgae (e.g., Modlin 1991; Ledoyer 2000; Haney & Martin 2004; Roccatagliata *et al.* 2010; Song *et al.* 2012a). Some leptostracans have been reported from bathyal depths down to 3000 m, such as *Dahlrella caldariensis* Hessler, 1984 (2490–2620 m depth), *Nebaliella caboti* Clark, 1932 (378–2900 m depth), *Nebaliella declivatas* Walker-Smith, 1998 (down to 1840 m), *Nebalia abyssicola* (410–2368 m depth), *Nebalia schizophthalma* (2886 m depth) and *S. biscayensis* (2100–2167 m depth) (Hessler 1984; Ledoyer 1998; Walker-Smith 1998; Haney *et al.* 2001). At the moment, the only two known species reaching greater depths are *Nebaliella kurila* Petryashov, 2016 and *S. pseudotyphlops* that were described from specimens collected at depths well below 5000 m near the Kuril-Kamchatka Trench (Petryashov 2016). On the other hand, *S. typhlops* has been reported from a wide depth range, with records from the continental shelf (90–250 m depth: Vader 1973; Dahl 1985) to depths of ca 2000 m (Mauchline & Gage 1983). However, as mentioned above, it is likely that some records of this species might refer to other species described after Dahl's review of European leptostracans (Dahl 1985); a review of past records would therefore be desirable to assess the actual geographic and bathymetric distribution of *S. typhlops* (Koçak *et al.* 2011; McCormack *et al.* 2016; Latry & Droual 2020).

To our knowledge, leptostracans were previously reported from mud volcanoes only by Ritt *et al.* (2012) who mentions the occurrence of undetermined Leptostraca in reduced sediments from Amon and Cheops MVs (1000 and 3007 m depth, respectively; Nile Deep-sea Fan, Eastern Mediterranean Sea). The three species reported here from MVs at the Moroccan margin of the Gulf of Cadiz constitute the first record of leptostracans at species level in this kind of environment, also showing apparent differences in their bathymetric distribution. *Sarsinebalia ledoyeri* sp. nov. was collected only from mud volcano sediments at 418 m depth in the Gemini MV in 2006, while the two species of *Nebalia* were collected in association with experimentally deployed organic substrates. Thus, *N. abyssicola* was present in all three MVs where colonization experiments were deployed (Darwin, Meknès and Mercator). It was found both inside and outside the net enclosing the organic substrates and showed the widest range in depth as expected (354–1100 m). The presence of *N. strausi* in a deep-sea MV was, however, unexpected. Although this species has been recorded at depths of 140 m (Moreira *et al.* 2009b), it is usually reported from the shallow subtidal (Dahl 1985; McCormack *et al.* 2016) reaching high abundances in *Zostera* meadows (Moreira *et al.* 2004). The presence of this species at greater depths (Mercator MV, 354 m) may be explained by the attraction of specimens from shallower bottoms to eventual accumulation of organic matter at the top of the MV; this would allow for specimens to colonise the CHEMECOLI units filled with organic substrates deployed in the experiment developed in 2007–2009. In fact, the units deployed in the shallower and closer to coast Mercator MV showed higher rates of colonization by typical organic-fall species (e.g., opportunist scavengers feeding on phytodetritus) than the ones deployed at deeper MVs (Cunha *et al.* 2013a). Some leptostracans are known to reach high abundances in areas where dead macroalgae are deposited (Martin *et al.* 1996) and are also attracted to baited traps (Lee & Morton 2004; Morton & Lee 2012) while other species do not respond to organic enrichment (Vetter 1996a). Indeed, *N. strausi* may feed on accumulations of dead leaves of *P. oceanica* (François *et al.* 2018) and is considered to behave as an opportunistic species responding positively to organically-enriched sediments below cages for fish farming (Tomassetti *et al.* 2016). On the other hand, specimens of *N. strausi* found on the MV corresponded only to immature males and preovigerous females. Lee & Morton (2005) highlighted that specimens of *Nebalia mortoni* Lee & Bamber, 2011 (as *Nebalia* sp.) were differently attracted to baited traps depending of the life-cycle stage; for instance, mature males were never found in traps while immature specimens (non-ovigerous females) constituted about 80% of the leptostracan catch being ovigerous and post-ovigerous females collected in fewer numbers. Finally, *N. strausi* was only found in the first sampling, that occurred after 290 days of units deployment but not in a second sampling of the colonization sets at Mercator MV that was carried out after almost two years. Except for one juvenile (washed from the net) the specimens were all found inside the net enclosing the organic substrates; this would suggest that *N. strausi* was present in the experimental units as long as the organic substrate (alfalfa) remained or that the juveniles that settled on the decaying organic substrates could not survive to maturity inside the net (2 mm mesh size) that enclosed the deployed substrates. In fact, the scavenging lysianasid *Orchomene grimaldii* Chevreux, 1890 was also found on such units after one year but not in samples collected after two years when most of the alfalfa had disappeared or been consumed (Cunha *et al.* 2013a). On the contrary, *N. abyssicola* was found at the three MVs in samples recovered both after 1 and 2 years. Ovigerous females (with small juveniles in their brood pouches) were only found in Darwin MV and were all collected from the external components of the colonization unit; inside the net enclosing the organic substrates only smaller specimens (juveniles, preovigerous females and males) were found. Furthermore, *N. abyssicola* was also collected from *Gigantidas mauritanicus* aggregations at the experimental site in Darwin MV just after the deployment of the CHEMECOLI units, and a couple of weeks after that; this suggests that the species is usually present in this habitat and might rely on other food sources as well.

In any case, more sampling in MVs is needed to test whether there is a regular presence in MVs of the deep-sea species *N. abyssicola*, if *N. strausi* is an occasional visitor of shallow MVs when attracted by organic accumulations, and to assess what is the actual pattern of geographic and bathymetric distribution of *Sarsinebalia ledoyeri* sp. nov.

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