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Research article

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Three new species of *Spongiopsyllus* Johnsson, 2000 (Copepoda: Siphonostomatoida: Entomolepididae) associated with *Aplysina cauliformis* (Carter, 1882) (Porifera: Demospongiae) from Todos-os-Santos Bay, Northeastern Brazil

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Abstract. Entomolepididae is a small siphonostomatoid family with a distinct shield-like body morphology, comprising 9 genera and 20 species. These genera are divided into two subfamilies, mostly based on their body segmentation, the genera with fused pedigerous somites 2 and 3 are included in the Parmulodinae subfamily, and the genera with free pedigerous somites 2 and 3 are included in the Entomolepinae subfamily. *Spongiopsyllus* is an endemic Entomolepinae genus, and its four known species are known only of Northeastern Brazil. This study reports three new species of this genus, all found associated with the sponge *Aplysina cauliformis*. The three new species share 16-segmented antennules, the position of the aesthetasc on the 14th segment, a 2-segmented antennal endopod and 4 setae on the outer lobe of the maxillule. *Spongiopsyllus athosi* sp. nov. has the maxillule with 3 setae on the inner lobe, and maxilliped endopod 3-segmented with setal formula (2,1,1+claw); *S. porthosi* sp. nov. has the maxilliped endopod 3-segmented with setal formula (2,2,0+claw); and *S. aramisi* sp. nov. differs from its congeners by having the antennal exopod with 6 spinules, plus the maxilliped endopod 3-segmented with seta formula (2,1,1+claw). An updated key to the species of the family is provided.

Keywords. Associated copepod, symbiotic fauna, marine invertebrate parasite, sponges.

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Demospongiae) from Todos-os-Santos Bay, Northeastern Brazil. *European Journal of Taxonomy* 968: 37–59. https://doi.org/10.5852/ejt.2024.968.2715

Introduction

Entomolepididae Brady, 1899 is a small siphonostomatoid family with a distinct body morphology (Boxshall & Halsey 2004). Its species are characterized by a flattened and oval aspect of the body shield, covering almost the entire body, suggesting a life style attached to its hosts (Borges *et al.* 2021). According to Boxshall & Halsey (2004), sponges are the most common hosts for these animals. Nevertheless, other marine invertebrates, such as scleractinian corals, octocorals, anemones, and tunicates are known associates (Borges *et al.* 2021).

Entomolepidids are a cosmopolitan family, comprising 9 genera and 20 species (Walter & Boxshall 2024). The occurrence of five genera is reported from the Atlantic Ocean: *Parmulodes* C.B. Wilson, 1944, *Parmulella* Stock, 1992, *Spongiopsyllus* Johnsson, 2000, *Neoparmulella* Farias, Neves & Johnsson, 2020, and *Parmulopsyllus* Borges, Farias, Mácola, Neves & Johnsson, 2021. Among them, *Spongiopsyllus* is the most diverse, with four described species (Borges *et al.* 2021).

Spongiopsyllus is an endemic genus recorded only from Northeastern Brazil (Borges *et al.* 2021) – the ecoregions Northeastern Brazil and Eastern Brazil (Tropical Southwestern Atlantic Province) (Spalding *et al.* 2007). These animals are placed within the subfamily Entomolepinae Eiselt, 1959 by showing two free pedigerous somites (McKinnon 1988; Johnsson 2000). *Spongiopsyllus* differs from *Entomolepis* Brady, 1899, *Entomopsyllus* McKinnon, 1988, and *Lepeopsyllus* Thompson & Scott, 1903, other Entomolepinae genera, by showing 3 and 4 postgenital urosomites in female and male respectively, plus the fourth leg with a 3-segmented exopod as well as endopod absent (Johnsson 2000).

Currently, *Spongiopsyllus* comprises four species – *S. adventicius* Johnsson, 2000, *S. redactus* Canário, Neves & Johnsson, 2012, *S. atypicus* Canário, Hurbath, Rocha, Neves & Johnsson, 2019 and *S. intermedius* Borges, Farias, Mácola, Neves & Johnsson, 2021 (Johnsson 2000; Canário *et al.* 2012, 2019; Borges *et al.* 2021).

The present study describes three new species from *Spongiopsyllus* in Todos-os-Santos Bay, Northeastern Brazil; all of them were found associated with the sponge *Aplysina cauliformis* (Carter, 1882). An updated key to the species of Entomolepididae is also provided.

Material and methods

Samples of *Aplysina cauliformis* were hand-collected at a depth of 12 m at Pedra Cardinal, Todos-os-Santos Bay, Bahia, Brazil (12°50′15″ S, 38°32′49″ W). The sponges were placed in plastic bags filled with seawater and then transported to the laboratory. The samples were washed in 5% alcohol and filtered through a 106 µm plankton net. The washing was transferred to a petri dish and sorted under a dissecting microscope.

Selected specimens were cleared in lactic acid, measured from the anterior margin of the cephalosome to the end of the furcal rami, and their bodies drawn before being stained with Chlorazol Black E, dissected, and mounted permanently in CMC-9® (Masters Chemical Company, Inc.) mounting medium. Specimen examination, measurements, hand-made drawings, and photos were done using a Zeiss Axio Lab A1 microscope equipped with a digital camera AxioCam ERc 5S connected to an iPad (7th generation) with Zeiss Labscope Software (ver. 4.0.2). The hand-drawn illustrations were scanned and vectorized with CorelDRAW 2021 software (ver. 23.1.0.389). The length of the antennulary segments was measured along the posterior, non-setiferous margin. For the antennule formula, Roman numerals

indicate the ancestral copepod segments followed by the number of setae in Arabic numerals (Huys & Boxshall 1991). For the armature formula of legs 1–4, Roman numerals represent spines, and Arabic numerals indicate setae. The abbreviations P1–P5 refer to legs 1–5.

The studied specimens were deposited in the Museu de História Natural da Bahia of the Universidade Federal da Bahia (UFBA).

Results

Taxonomy

Class Maxillipoda Dahl, 1956
Subclass Copepoda Milne Edwards, 1830
Order Siphonostomatoida Burmeister, 1835
Family Entomolepididae Brady, 1899

Genus ***Spongiopsyllus*** Johnsson, 2000

Type species

Spongiopsyllus adventicius Johnsson, 2000.

Revised diagnosis

Entomolepididae Brady, 1899
Circular body, shield-shaped, composed of cephalosome and pedigerous somites. Pedigerous somites 2 and 3 free. Pedigerous somite 4 expanded posteriorly, covering urosome, except for tip of caudal rami. Three postgenital urosomites in females, four in males. Antennule 14- to 17-segmented. Antennary endopod 2- or 3-segmented; exopod 1-segmented, as long as first endopodal segment. Legs 1 to 3 biramous, 3-segmented. Leg 3 endopod with reduced armature formula. Leg 4 uniramous, 3-segmented exopod.

Remarks

The original diagnosis of the genus was restricted to the body shape and segmentation, and did not deal with the antennule and antenna segmentation, leg morphology or setal formula (Johnsson 2000). The free pedigerous somites 2 and 3 characterize the Entomolepinae which differ from Parmulodinae, (*Parmulodes*, *Paralepeopsyllus*, *Parmulella*, *Neoparmulella* and *Parmulopsyllus*), that exhibit pedigerous somites 2 and 3 fused (Wilson 1944; Ummerkutty 1960; Stock 1992; Canário *et al.* 2019; Farias *et al.* 2020; Borges *et al.* 2021). In Entomolepinae, leg 4 is absent in *Entomolepis* (Brady, 1899), and *Lepeopsyllus* shows a reduced endopod (Thompson & Scott 1903). The uniramous and 3-segmented leg 4 of *Spongiopsyllus* is shared with *Entomopsyllus* (McKinnon 1988), but the later exhibits 2 postgenital segments, instead of 3 exhibited by *Spongiopsyllus* (Johnsson 2000).

Spongiopsyllus athosi sp. nov.
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Figs 1–2, Tables 1, 4

Diagnosis

Body shield-form dorso-ventrally flattened, pedigerous somite three and four not fused. Antennule 16-segmented, presenting fusions of segments (III–VI, IX–XIII, XXIII–XXVIII), and with aesthetasc on segment 14. Antenna with 4 spinules on outer, and 1 spinule on inner margins of exopod segment, and endopod 2-segmented with 2 long and 2 short apical setae. Maxillule with 3 setae on inner lobe,

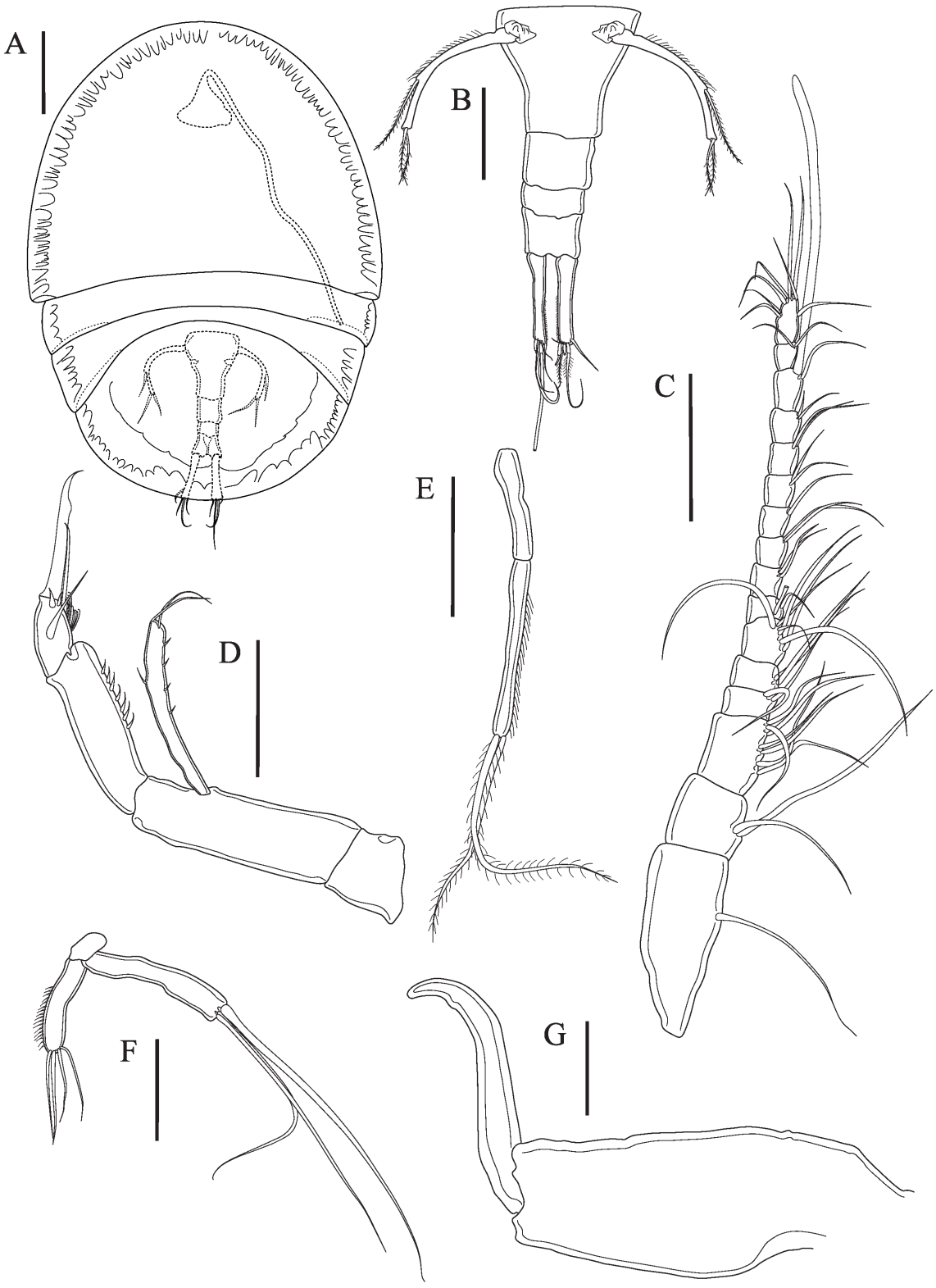

Fig. 1. *Spongiopsyllus athosi* sp. nov., ♀, holotype (UFBA 3291). **A**. Habitus, dorsal view. **B**. Urosome. **C**. Antennule. **D**. Antenna. **E**. Mandibular palp. **F**. Maxillule. **G**. Maxilla. Scale bars: A = 200 µm; B–G = 50 µm.

and 4 setae on outer lobe. Maxilliped with endopod 3-segmented, showing 2 setae on first segment, 1 on second and three on third; setal formula (2,1,1+claw).

Etymology

The tapered morphology of leg 1 third endopodal segments, showing sharpened processes, inspired the species name referring to the swordsman 'Athos', one of Alexandre Dumas' characters from '*The Three Musketeers*', a historical adventure novel written in 1844.

Material examined

Holotype

BRAZIL • ♀; Bahia, Todos-os-Santos Bay, Pedra Cardinal; 12°50′15″ S, 38°32′58″ W; 20 May 2017; L.C.C. Silvany leg.; manually collected, associated with the sponge *Aplysina cauliformis* (Carter, 1882); UFBA 3291.

Description

Female

Body length (from cephalosome to the furcal rami) 1170 µm and greatest body width (cephalosome) 850 µm. Prosomal shield flattened (Fig. 1A), with radiating bands along outer margin. Pedigerous somites 2–4 free. Urosome (Fig. 1B) 4-segmented. Genital double-somite fused with fifth pedigerous somite, 150 µm long, and with length:width ratio 1.3:1. Three postgenital somites present, all wider than long, 80 × 67, 75 × 47, 65 × 32 µm, respectively. Prosome:urosome length ratio 1.5:1. Caudal rami elongate, 107 µm long, with setules along medial-distal inner margin, and armed with 6 setae distally.

Antennule (Fig. 1C) slender, 251 µm long (not including setae), and 16-segmented. Length of segments: 62, 22, 24, 10, 9, 13, 7, 10, 10, 12, 11, 11, 12, 14, 8 and 16 µm, respectively. Segmental homologies and setation as follows: I-1; II-2; III–VI-7; VII-2; VIII-2; IX–XIII-6; XIV-2; XV-2; XVI-2; XVII-1; XVIII-2; XIX-2; XX-2; XXI-1+ae; XXII-2; XXIII–XXVIII-8. All setae naked. Aesthetasc 102 µm long.

Antenna (Fig. 1D) 224 µm long (including distal claw); coxa 24 µm long; basis 76 µm long. Exopod 1-segmented, 65 µm long, with 2 long slender distal setae, and 5 small spinules along margins. Endopod 2-segmented; first segment 53 µm long, unarmed, with 7 spinules on outer margin; second segment 22 µm long, ornamented with row of setules along outer margin, and armed with 2 long and 2 short naked setae; distally curved claw (49 µm) with bump-like projection subdistally.

Oral cone 210 µm long, reaching first postgenital somite (Fig. 1A). Mandible comprising stylet and slender 2-segmented palp (Fig. 1E) measuring 40 and 62 µm long, respectively. Palp with second segment armed with 2 apical, plumose setae and ornamented with setules along outer margin. Stylet slender and pointed, 142 µm long.

Maxillule (Fig. 1F) bilobed; inner lobe 68 µm long, armed with 3 long apical setae. Outer lobe 49 µm long, armed with 4 short setae and ornamented with setules along outer margin; all setae naked.

Maxilla (Fig. 1G) with syncoxa and curved claw measuring 217 and 134 µm long, respectively; claw with soft bump-like projection subdistally.

Maxilliped (Fig. 2A) 5-segmented, 298 µm long (excluding claw); syncoxa 84 µm long, with inner seta and 3 setules on distal inner margin; basis 138 µm long, unarmed. Endopod 3-segmented, 22, 23, and 31 µm long, respectively; first segment with 2 naked unequal setae; second segment with distal small seta; third segment with small distal seta and curved claw measuring 56 µm long.

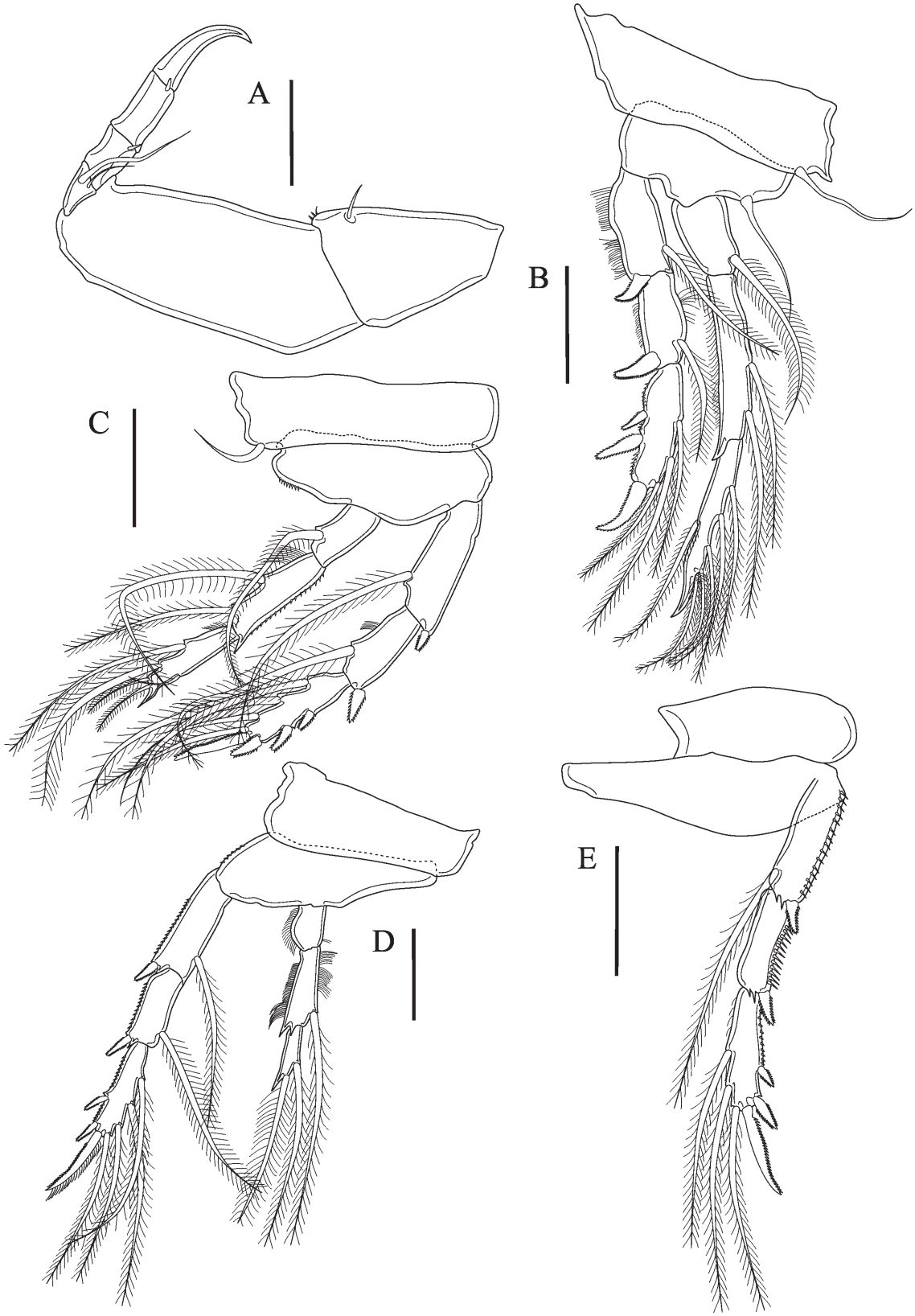

Fig. 2. *Spongiopsyllus athosi* sp. nov., ♀, holotype (UFBA 3291). **A**. Maxilliped. **B**. L1. **C**. L2. **D**. L3. **E**. L4. Scale bars = 50 µm.

Table 1. *Spongiopsyllus athosi* sp.nov., armature formula of L1–L4.

	coxa	basis	exopod	endopod
L1	0-1	0-1	I-1; I-1; III,3	0-1; 0-2; 1,5
L2	0-1	0-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
L3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,1,1
L4	0-0	0-0	I-1; I-0; II,I,3	absent

P1–P3 (Fig. 2B–D) biramous, with 3-segmented rami. P4 (Fig. 2E) with 3-segmented exopod and endopod absent. Armature formula reported in Table 1.

First and second exopodal segments of P1 (Fig. 2B) with setules on outer margins; second segment with setules on inner margin; outer margin of third segment with spinules, inner margin naked. Second endopodal segment of P1 (Fig. 2B) with setules on outer margin and moderate sharpened process on distal margin. Third endopodal segment of P1 (Fig. 2B) prolonged distally into sharpened process, therefore distal setae located sub-distally on inner margin.

First and second exopodal segments of P2 (Fig. 2C) with outer margins naked, second exopodal segment of P2 with few setules on medial inner margin. Second endopodal segment of P2 (Fig. 2C) with spinules on outer margin and setules on inner margin; third endopodal segment with setules on proximal inner margin.

Basis of P2 and P3 with spinules on inner and outer margins, respectively.

P3 exopodal outer margins with spinules (Fig. 2D); first and second endopodal segments with setules on both margins; second endopodal segments with one small and one tiny sharpened process on distal margin; third endopodal segment with small sharpened process on distal margin.

P4 exopodal outer margin with spinules (Fig. 2E,), which are larger on second segment than on other segments; medial distal margins of first and second segments with two tiny, sharpened processes on medial distal margin.

Free exopodal segment of P5 (Fig. 1B) elongate, curved, 207 μm long, longer than genital double-somite, and armed with 2 distal and one outer medial plumose seta.

Male

Unknown.

Spongiopsyllus porthosi sp. nov.

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Figs 3–5, Tables 2, 4

Diagnosis

Body shield dorso-ventrally flattened, pedigerous somite 3 and 4 not fused. Antennule 16-segmented, showing fusion of segments (III–VI, IX–XIII, XXIII–XXVIII), and aesthetasc on segment 14. Antenna with 2 spinules on outer, and 3 spinules on inner margins of exopod segment, and endopod 2-segmented with 2 long and 2 short apical setae. Maxillule with 4 setae on inner lobe, and 4 setae on outer lobe. Maxilliped with endopod 3-segmented, showing 2 setae on first segment, 2 on second and unarmed third segment, setal formula (2,2,0+claw).

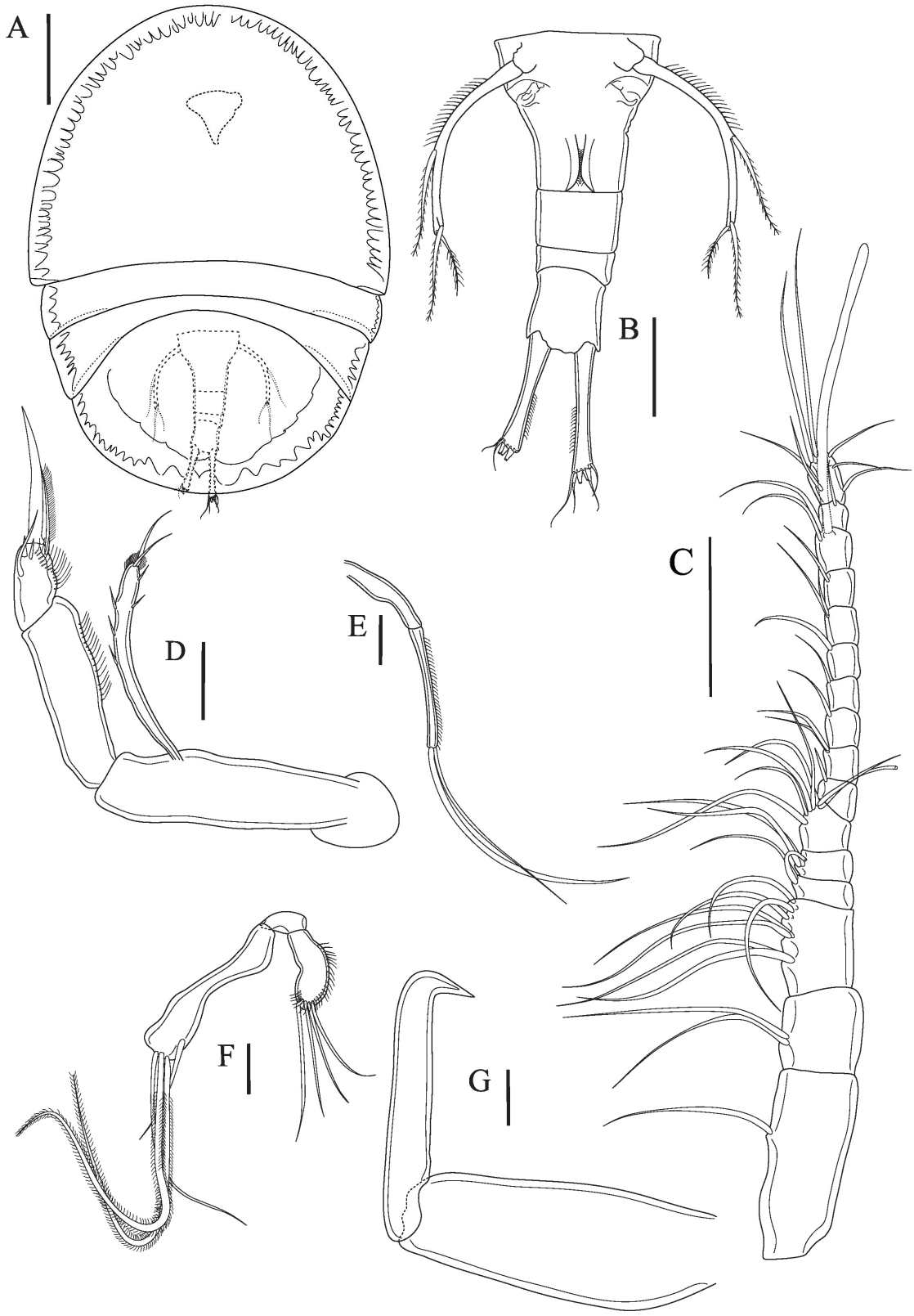

Fig. 3. *Spongiopsyllus porthosi* sp. nov., ♀, holotype (UFBA 3292). **A**. Habitus, dorsal view. **B**. Urosome. **C**. Antennule. **D**. Antenna. **E**. Mandibular palp. **F**. Maxillule. **G**. Maxilla. Scale bars: A = 200 µm; B = 50 µm; C–F = 25 µm; G = 50 µm.

Etymology

The tapered morphology of leg 1 endopodal segments, showing sharpened processes, inspired the species name referring to the swordsman 'Porthos', one of Alexandre Dumas' characters from '*The Three Musketeers*', a historical adventure novel written in 1844.

Material examined

Holotype

BRAZIL • ♀; Bahia, Todos-os-Santos Bay, Pedra Cardinal; 12°50′15″ S, 38°32′58″ W; 20 May 2017; L.C.C. Silvany leg.; manually collected, associated with the sponge *Aplysina cauliformis* (Carter, 1882); UFBA 3292.

Allotype

BRAZIL • ♂; same data as for holotype; UFBA 3293.

Paratype

BRAZIL • 1 ♀; same data as for holotype; UFBA 3297.

Description

Female

Body length (from cephalosome to the furcal rami) 1220 µm and body greatest width (cephalosome) 870 µm. Prosomal shield flattened (Fig. 3A), with radiating bands along outer margin. Pedigerous somites 2–4 free. Urosome (Fig. 3B) 4-segmented. Genital double-somite fused with fifth pedigerous somite, 160 µm long, and with length:width ratio 0.9:1. Three postgenital somites present, first and second wider than long, 58 × 84, 20 × 78 µm, respectively; anal somite longer than wide, 130 × 70. Prosome:urosome length ratio 2.7:1. Caudal rami elongate, 130 µm long, with setules along medial-distal inner margin, and armed with 6 setae distally.

Antennule (Fig. 3C) slender, 241 µm long (not including setae), and 16-segmented. Length of segments: 58, 25, 27, 7, 9, 13, 10, 10, 12, 9, 11, 12, 12, 14, 7 and 7 µm, respectively. Segmental homologies and setation as follows: I-1; II-2; III–VI-7; VII-2; VIII-2; IX–XIII-7; XIV-1; XV-2; XVI-1; XVII-1; XVIII-1; XIX-2; XX-1; XXI-2+ae; XXII-1; XXIII–XXVIII-7. All setae are naked. Aesthetasc 100 µm long.

Antenna (Fig. 3D) 222 µm long (including distal claw); coxa 37 µm long; basis 80 µm long. Exopod 1-segmented, 67 µm long, and with 2 long subequal distal setae and 5 spinules along margins; ornated with setules on distal margin. Endopod 2-segmented; first segment 57 µm long, unarmed, with spinules on outer margin; second segment 27 µm long, ornamented with row of setules along outer margin, and armed with 2 long setae on outer margin, one of them covered with setules, and 2 short naked setae; distal claw slightly curved, 58 µm long.

Oral cone broken (Fig. 3A). Mandible comprising stylet and slender 2-segmented palp (Fig. 3E) measuring 52 and 64 µm long, respectively. Palp with second segment armed with 2 apical, smooth setae and ornamented with setules along outer margin.

Maxillule (Fig. 3F) bilobed; inner lobe 86 µm long, armed with 4 setae, 2 plumose and longer than the others. Outer lobe 40 µm long, armed with 4 setae and ornamented with setules along outer margin; all setae naked.

Maxilla (Fig. 3G) with syncoxa and curved claw measuring 143 and 147 µm long, respectively; distal claw tip abruptly curved.

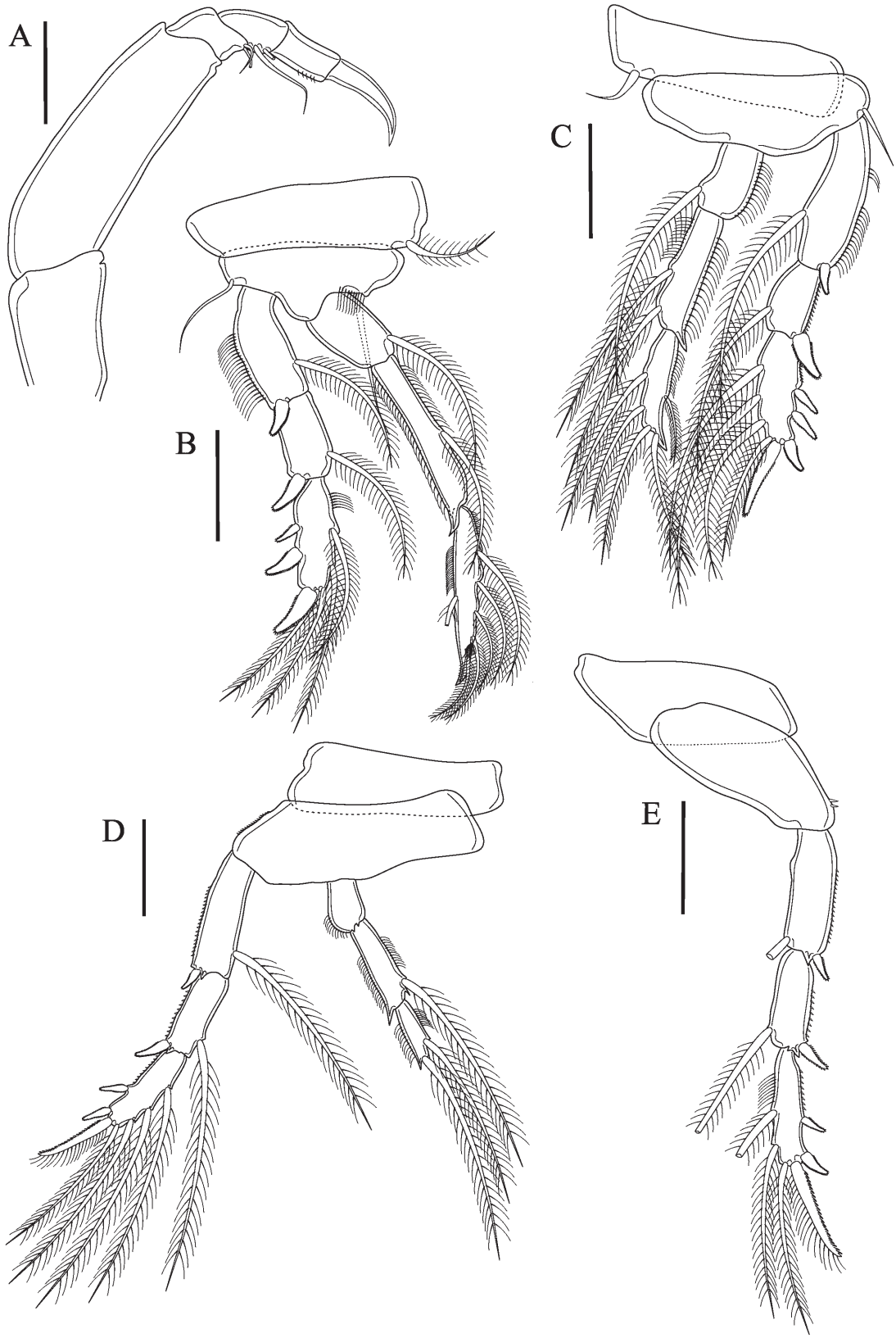

Fig. 4. *Spongiopsyllus porthosi* sp. nov., ♀, holotype (UFBA 3292). **A**. Maxilliped. **B**. L1. **C**. L2. **D**. L3. **E**. L4. Scale bars = 50 µm.

Table 2. *Spongiopsyllus porthosi* sp.nov., armature formula of L1–L4.

	coxa	basis	exopod	endopod
L1	0-1	1-1	I-1; I-1; III,4	0-1; 0-1; 1,5
L2	0-1	1-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
L3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,1,1
L4	0-0	0-0	I-1; I-1; II,I,3	absent

Maxilliped (Fig. 4A) 5-segmented, 298 µm long (excluding claw); syncoxa 84 µm long, unarmed; basis 138 µm long, unarmed. Endopod 3-segmented, 22, 23, and 31 µm long, respectively; first and second segment each with 2 naked setae; third segment with curved claw measuring 56 µm long and few setules on outer margin.

P1–P3 (Fig. 4B–D) biramous, with 3-segmented rami. P4 (Fig. 4E) with 3-segmented exopod and endopod absent. Armature formula below (Table 2).

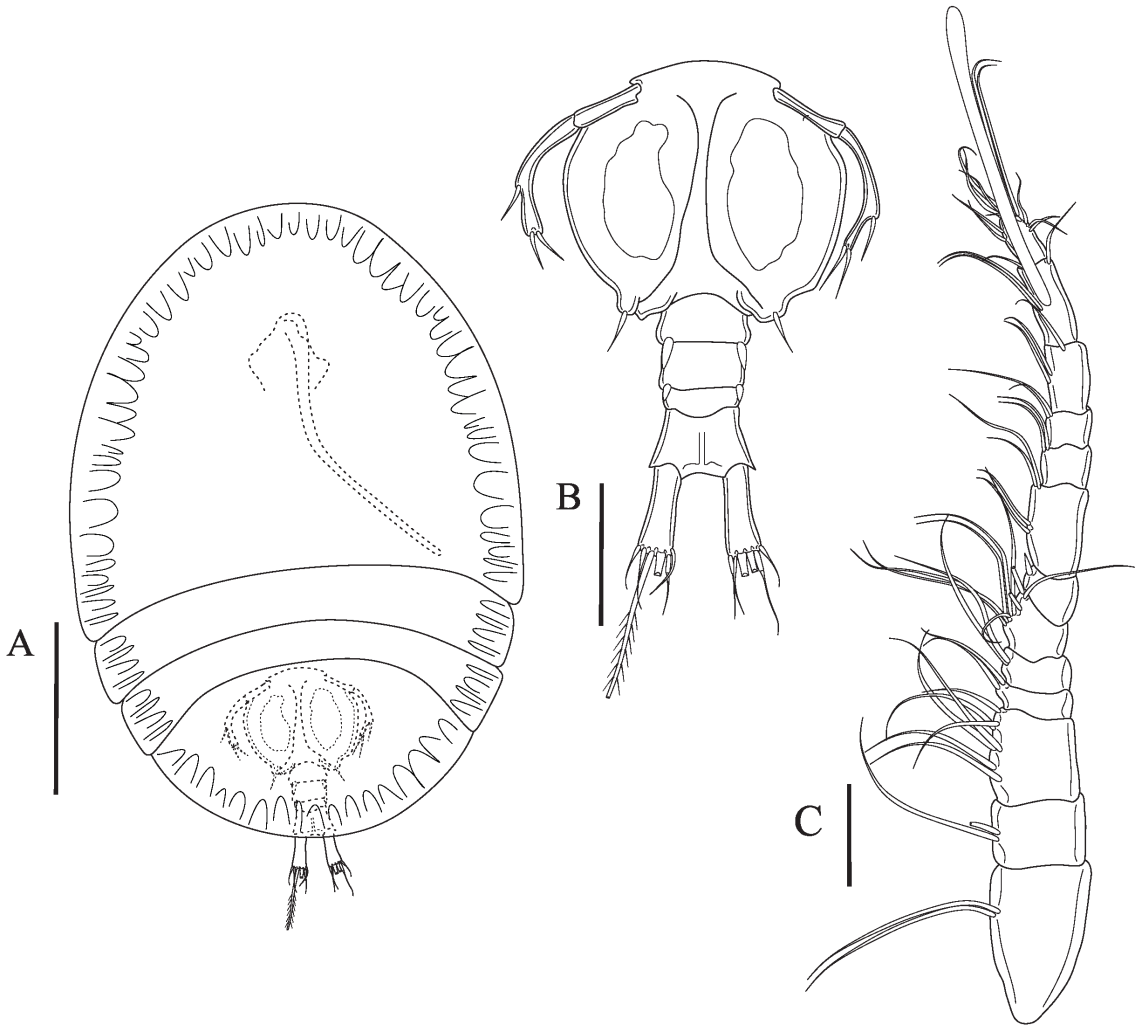

Fig. 5. *Spongiopsyllus porthosi* sp. nov., ♂, allotype (UFBA 3293). **A**. Habitus, dorsal view. **B**. Urosome. **C**. Antennule. Scale bars: A = 100 µm; B–C = 25 µm.

First exopodal segments of P1 (Fig. 4B) with setules on outer margins; second endopodal segments with setules on both margins, third endopodal segment with setules on outer margin.

First exopodal segments of P2 (Fig. 4C) with setules on outer margins, second and third with spinules on outer margins; second endopodal segments with setules on both margins, third endopodal segment with setules on outer margin.

P3 (Fig. 3D) basis with spinules on outer margin; distal spines of exopod with long setules on inner margin; endopodal segments with setules on outer margin on first segment, and both margins on second and third segments.

P4 (Fig. 4E) with two spinules on outer margin of basis; second and third exopodal segments with spinules on outer margins; third exopodal segment setules on inner margin; distal spines of exopod with long setules on inner margin.

Free exopodal segment of P5 (Fig. 3A) elongate, curved, 212 µm long, reaching distal margin of genital double-somite, and armed with 2 distal and an outer plumose medial seta.

Male

Body (Fig. 5A) similar but smaller than female. Body length (excluding caudal setae) 740 µm and body width 510 µm. Prosomal shield flattened with radiation bands along outer margin. Pedigerous somites 2–4 free. Pedigerous somite 4 expanded, covering urosome except for caudal rami. Urosome 5-segmented (Fig. 5B). Genital somite fused with fifth pedigerous somite, 118 µm long, and length:width ratio 0.8:1. Four postgenital somites; all wider than long (48 × 25, 42 × 25, 38 × 12, 42 × 28 µm, respectively. First and second postgenital somites with spine on each distal lateral margin. Prosome:urosome length ratio 2.9:1. Caudal rami elongate, 48 µm long, armed with six setae.

Antennule (Fig. 5C) slender, 223 µm long (not including setae), 13 segmented. Length of segments measured along anterior to posterior margins: 42, 17, 22, 6, 8, 12, 11, 25, 11, 9, 18, 23 and 19 µm, respectively. Segmental homologies and setation as follows: I-2; II-2; III–VI-7; VII-2; VIII-2; IX–XIII-9; XIV-1; XV–XVI-4; XVII-2; XVIII-2; XIX–XX-3; XXI–XXIII-4+ae; XXIV–XXVIII-11; all setae smooth. Aesthetasc 86 µm long. Oral cone (Fig. 5A) 350 µm long, reaching genital somite.

All other appendages as in female.

Spongiopsyllus aramisi sp. nov.

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Figs 6–8, Tables 3–4

Diagnosis

Body shield-form dorso-ventrally flattened, pedigerous somites three and four not fused. Antennule 16-segmented, presenting the fusions of the segments (III–VI, IX–XIII, XXIII–XXVIII), and aesthetasc on segment 14. Antenna with 4 spinules on outer, and 2 spinules on inner margins of the exopod segment, and endopod 2-segmented with 1 long and 1 short apical setae. Maxillule with 4 setae on inner lobe, and 4 setae on outer lobe. Maxilliped with endopod 3-segmented, showing 2 seta on first, one seta on second and one seta on third segment, with setal formula (2,1,1+claw).

Etymology

The tapered morphology of leg 1 endopodal segments, showing sharpened processes, inspired the species name referring to the swordsman 'Aramis', one of Alexandre Dumas' characters from '*The Three Musketeers*', a historical adventure novel written in 1844.

Type material

Holotype

BRAZIL • ♀; Bahia, Todos-os-Santos Bay, Pedra Cardinal; 12°50′15″ S, 38°32′58″ W; 20 May 2017; L.C.C. Silvany leg.; manually collected, associated with the sponge *Aplysina cauliformis* (Carter, 1882); UFBA 3298.

Paratypes

BRAZIL • 3 ♀♀; same data as for holotype; UFBA 3299 to 3301.

Description

Female

Body length (from cephalosome to the furcal rami) 1190 µm and body greatest width (cephalosome) 840 µm. Prosomal shield flattened (Fig. 6A), with radiating bands along outer margin. Pedigerous somites 2–4 free. Urosome (Fig. 6B) 4-segmented. Genital double-somite fused with fifth pedigerous somite, 175 µm long, with length:width ratio 1.2:1. Three postgenital somites present, all wider than

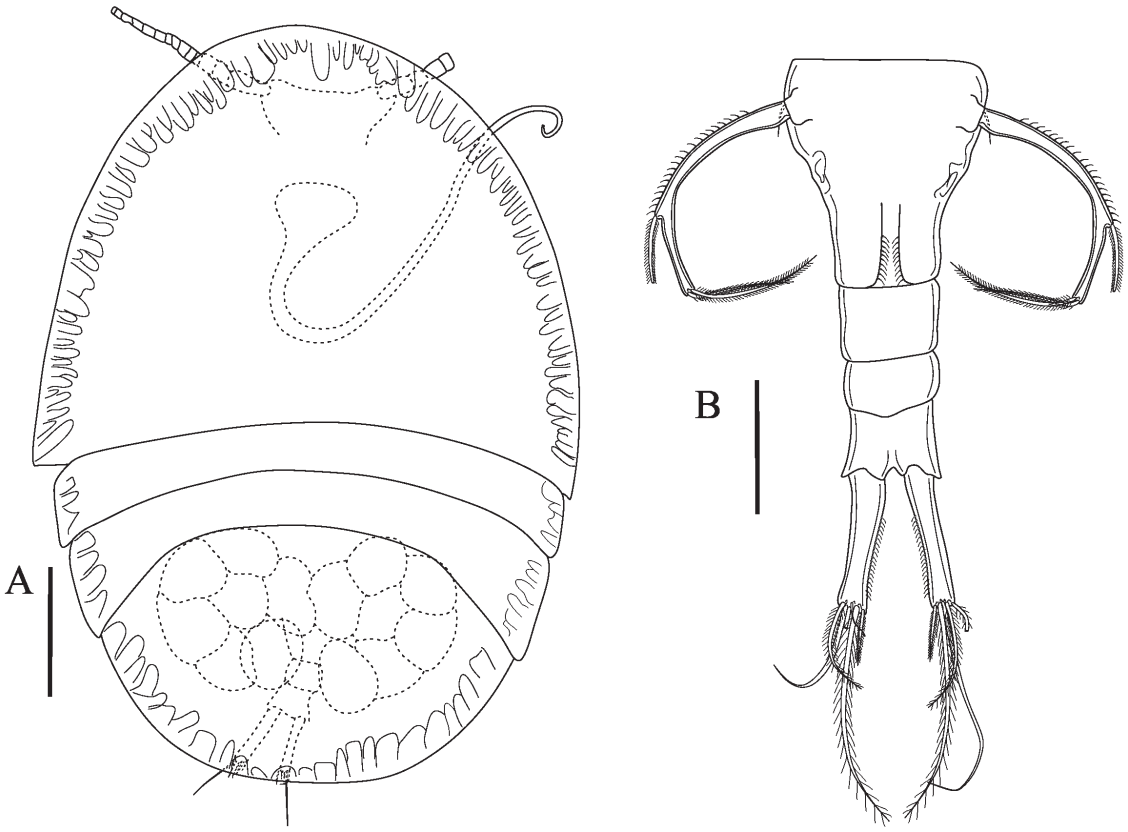

Fig. 6. *Spongiopsyllus aramisi* sp. nov., ♀, paratype (UFBA 3299). **A**. Habitus, dorsal view. **B**. Urosome. Scale bars: A = 200 µm; B = 100 µm.

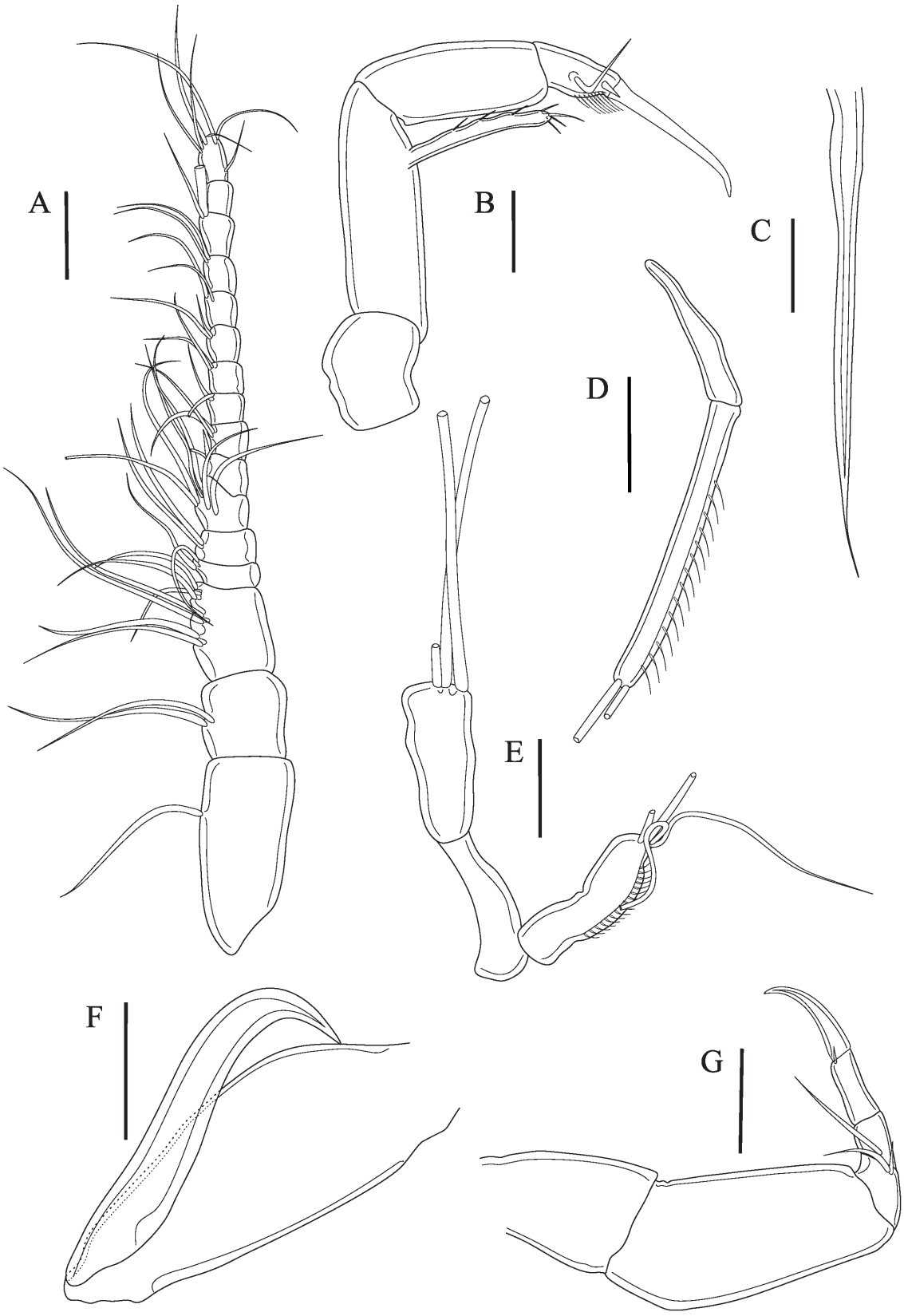

Fig. 7. *Spongiopsyllus aramisi* sp. nov., ♀, paratype (UFBA 3299). **A**. Antennule. **B**. Antenna. **C**. Stylet. **D**. Mandibular palp. **E**. Maxillule. **F**. Maxilla. **G**. Maxilliped. Scale bars: A–E = 25 µm; F–G = 50 µm.

Table 3. *Spongiopsyllus aramisi* sp.nov., armature formula of L1–L4.

	coxa	basis	exopod	endopod
L1	0-0	1-1	I-1; I-1; II,I,4	0-1; 0-2; 1,5
L2	0-1	1-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
L3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,1,1
L4		0-0	I-0; I-1; II,I,3	absent

long, 72 × 55, 70 × 30, 55 × 32 µm, respectively. Prosome:urosome length ratio 3:1. Caudal rami elongate, 108 µm long, with setules along medial-distal inner margin, and armed with 6 setae distally.

Antennule (Fig. 7A) slender, 220 µm long (not including setae), and 16 segmented. Length of segments: 54, 20, 25, 7, 9, 13, 9, 10, 9, 9, 11, 10, 11, 12, 9 and 13 µm, respectively. Segmental homologies and setation as follows: I-1; II-2; III–VI-7; VII-2; VIII-2; IX–XIII-7; XIV-1; XV-2; XVI-2; XVII-2; XVIII-2; XIX-2; XX-2; XXI-1+ae; XXII-1; XXIII–XXVIII-7. All setae naked.

Antenna (Fig. 7B) 226 µm long (including distal claw); coxa 36 µm long; basis 62 µm long. Exopod 1-segmented, 45 um long, with 1 small delgate distal seta, 2 distal spinules, and 4 on lateral margin. Endopod 2-segmented; first segment 54 µm long, unarmed; second segment 23 µm long, ornamented with row of setules along outer margin, and armed with 1 long seta and 1 small robust spine; distally slightly curved claw, 51 µm long.

Oral cone 800 µm long, reaching prosomal distal margin (Fig. 6A). Mandible comprising stylet (Fig. 7C) and slender 2-segmented palp (Fig. 7D) measuring 36 and 67 µm long, respectively. Palp with second segment armed with 2 apical, smooth setae and ornamented with setules along outer margin.

Maxillule (Fig. 7E) bilobed; inner lobe 80 µm long, armed with 3 setae, 2 longer and plumose. Outer lobe 42 µm long, armed with 4 setae and ornamented with setules along outer margin; all setae naked.

Maxilla (Fig. 7F) with syncoxa and curved claw measuring both 152 µm long, respectively; distal claw tip perpendicularly curved.

Maxilliped (Fig. 7G) 5-segmented, 326 µm long (excluding claw); syncoxa 80 µm long, unarmed; basis 122 µm long, unarmed. Endopod 3-segmented, 18, 20, and 32 µm long, respectively; first segment with 2, and second with 1 naked seta; third segment with seta and curved claw measuring 53 µm.

P1–P3 (Fig. 8A–C) biramous, with 3-segmented rami. P4 (Fig. 7D) with 3-segmented exopod and endopod absent. Armature formula below (Table 3).

First exopodal segment of P1 (Fig. 7A) with setules on outer margin, second and third segments with outer margins ornamented with spinules on exopod, and setules on endopod.

First exopodal segment of P2 (Fig. 7B) also ornamented with setules on outer margin, outer margins ornamented with spinules on second exopodal segment, and with setules on endopodal segment, distal spines of third exopodal segment with long setules on inner margin.

Exopodal segments of P3 (Fig. 7D) with spinules on outer margins, second segment with setules on inner margin.

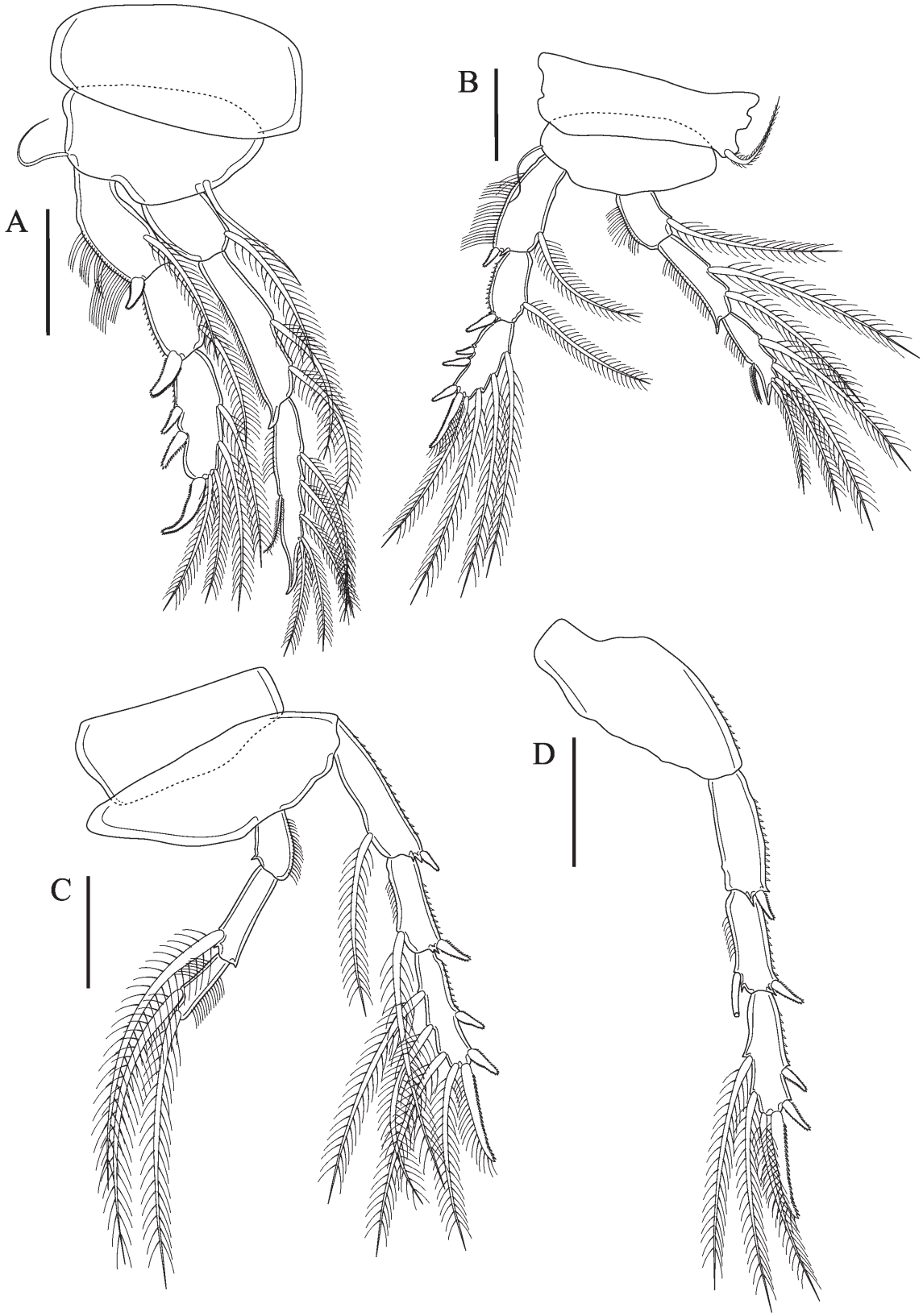

Fig. 8. *Spongiopsyllus aramisi* sp. nov., ♀, paratype (UFBA 3300). **A**. L1. **B**. L2. **C**. L3. **D**. L4. Scale bars = 50 µm.

Table 4. Comparison of species of *Spongiopsyllus* Johnsson, 2000.

	A1	A1	A1	A2	A2	A2	Mxll	Mxll	Mxlp
	nº of segments	aesthetasc segment	fused segments	nº of exopod spinules	nº of segment endopod	nº of setae on 2nd endopod	nº of setae on inner lobe	nº of setae on outer lobe	endopod formula
S. adventicius Johnsson, 2000	17	15	III–V, VII–VIII, IX–XII, XXII–XXIII, XXIV–XXVIII	4	3	1 short	3	3	0,2,1+claw
S. redactus Canário *et al*., 2012	15	14	II–III, IV–VI, IX–XIII, XXII–XX-VIII	3	2	1 long 2 short	3	3	2,1,1+claw
S. atypicus Canário *et al*., 2019	14	12	III–VIII, IX–XIII, XXII–XXIII, XIV–XVIII	7	2	2 long 2 short	4	4	2,0,1+claw
S. intermedius Borges *et al*., 2021	16	14	II–III, IV–VI, IX–XIII, XXIII–XXVIII	5	2	1 long 1 short	2	3	1,1,1+claw
S. athosi sp. nov.	16	14	III–VI, IX–XIII, XXIII–XXVIII	5	2	2 long 2 short	3	4	2,1,1+claw
S. porthosi sp.nov.	16	14	III–VI, IX–XIII, XXIII–XXVIII	5	2	2 long 2 short	4	4	2,2,0+claw
S. aramisi sp. nov.	16	14	III–VI, IX–XIII, XXIII–XXVIII	6	2	1 long 1 short	4	4	2,1,1+claw

Outer margin of P4 basis (Fig. 7E) ornamented with spinules, exopodal segments of P4 also ornamented with spinules on outer margins, second segment with setules on inner margin, distal spines of exopod with long setules on inner margin.

Free exopodal segment of P5 (Fig. 5E) elongate, curved, 207 µm long, reaching first postgenital somite, and armed with 2 distal and one medial outer seta.

Male

Unknown.

Discussion

Species of *Spongiopsyllus* exhibit four different fusion patterns of antennulary segments: *Spongiopsyllus adventicius* has 5 compound segments (III–V, VII–VIII, IX–XII, XXII–XXIII and, XXIV–XXVIII), resulting in a 17-segmented antennule. *Spongiopsyllus redactus* exhibits fewer segments, with 4 compound segments (II–III, IV–VI, IX–XIII and, XXII–XXVIII), resulting in a 15-segmented antennule.

Moreover, *Spongiopsyllus atypicus* exhibits even fewer antennulary segments, with 4 compound segments (III–VIII, IX–XIII, XXII–XXIII and, XXIV–XXVIII) forming a 14-segmented antennule. *Spongiopsyllus intermedius* is the only known species with a 16-segmented antennule, result of the formation of 4 compound segments (II–III, IV–VI, IX–XIII and, XXIII–XXVIII) (Table 4).

The three new species here described exhibit a new fusion pattern not observed in any of the previously described species. The antennule of *S. athosi* sp. nov., *S. porthosi* sp. nov., and *S. aramisi* sp. nov. exhibit only 3 compound segments (III–VI, IX–XIII and, XXIII–XXVIII), resulting in a 16-segmented antennule.

Besides the differences on the antennule, the three new species share a 2-segmented antennal endopod with the congeners *S. redactus*, *S. atypicus* and, *S. intermedius*, except *S adventicius* that shows a 3-segmented endopod.

Spongiopsyllus athosi sp. nov. shares the setal formula (2,2,1+claw) on the endopodal segments of the maxilliped with *S. redactus* and *S. aramisi* sp. nov., but *S. athosi* differs from these species by showing 4 setae on the second endopodal segment of antenna, instead of 3 in *S. redactus* and 2 in *S. aramisi*.

Spongiopsyllus porthosi sp. nov. shares the ornamentation of the antennal exopod with 5 spinules with *S. intermedius* and *S. athosi* sp. nov. The species can be differentiated from *S. intermedius* by showing 4 setae, instead of 2, on the second endopodal segment of the antenna; and from *S. athosi* by showing 4 setae, instead of 2, on the maxillule of the inner lobe. *Spongiopsyllus porthosi* also presents the setal formula (2,2,0+claw) on the endopodal segments of the maxilliped as a unique feature among species of *Spongiopsyllus*.

Spongiopsyllus aramisi sp. nov. shares with *S. porthosi* sp. nov. and *S. atypicus* the setal formula of maxillule lobes but differs from both species by showing the setal formula (2,1,1+claw) on the endopodal segments of the maxilliped, instead of (2,2,0+claw), and (2,0,1+claw), respectively. *Spongiopsyllus aramisi* also exhibits 6 spinules on the antennal exopod as a unique feature among its congeners.

Key to the species of the family Entomolepididae Brady, 1899 (adapted from Borges *et al.* (2021)

1. Pedigerous somite 3 and 4 fused 2
– Pedigerous somites 3 and 4 not fused 8

2. Most of urosome exposed 3
– Most of urosome hidden under body shield 4

3. Antennule 18-segmented with aesthetasc on segment 15, L 4 reduced to a knob ..... ***Parmulella emarginata*** Stock, 1992
– Antennule 17-segmented with aesthetasc on segment 16, L 4 biramous with 3-segmented rami ..... ***Neoparmulella peripheriensis*** Farias *et al.*, 2020

4. P3 biramous 5
– P3 uniramous (*Paralepeopsyllus* Ummerkutty, 1960) 6

5. P4 reduced to a knob and antennule 17-segmented ..... ***Parmulodes verrucosa*** Wilson, 1944
– P4 absent and antennule 16-segmented ..... ***Parmulopsyllus iamarinoi*** Borges *et al.*, 2021

6. Antennule 15-segmented ..... ***Paralepeopsylllus leei*** Lee & Kim, 2017
– Antennule 14-segmented 7

7. Third exopodal segment of P3 with 3 setae ..... ***Paralepeopsyllus mannarensis*** Ummerkutty, 1960
– Third exopodal segment of P3 with 4 spines and 3 setae ..... ***Paralepeopsyllus dambayensis*** Lee & Kim, 2017

8. P4 absent (*Entomolepis* Brady, 1899) 9
– P4 present 10

9. Caudal ramus 5–6 × as long as wide ..... ***Entomolepis ovalis*** Brady, 1899
– Caudal ramus at least 10 × as long as wide ..... ***Entomolepis hamondi*** McKinnon, 1988

10. P4 endopod reduced to a small segment (*Lepeopsyllus* Thompson & Scott, 1903) 11
– P4 endopod absent 12

11. Female antennule 15-segmented ..... ***Lepeopsyllus typicus*** Thompson & Scott, 1903
– Female antennule 13-segmented ..... ***Lepeopsyllus ovalis*** Thompson & Scott, 1903

12. Three postgenital somites in female and four in male (*Spongiopsyllus* Johnsson, 2000) 13
– Two postgenital somites in female and three in male (*Entomopsyllus* McKinnon, 1988) 19

13. Female antennule 14-segmented ..... ***Spongiopsyllus atypicus*** Canário *et al.*, 2019
– Female antennule with 15 or more segments 14

14. Female antennule 15-segmente ..... ***Spongiopsyllus redactus*** Canário *et al.*, 2012
– Female antennule with 16 or more segments 15

15. Female antennule 16-segmented 16
– Female antennule 17-segmented ..... ***Spongiopsyllus adventicius*** Johnsson, 2000

16. Maxillule inner lobe with 4 setae 17
– Maxillule inner lobe with at least 3 setae 18

17. Maxilliped endopod formula (2,1,1+claw) ..... ***Spongiopsyllus aramisi*** sp. nov.
– Maxilliped endopod formula (2,2,0+claw) ..... ***Spongiopsyllus porthosi*** sp. nov.

18. Maxilliped endopod formula (2,1,1+claw), maxillule inner lobe with 3 setae ..... ***Spongiopsyllus athosi*** sp. nov.
– Maxilliped endopod formula (1,1,1+claw), maxillule inner lobe with 2 setae ..... ***Spongiopsyllus intermedius*** Borges *et al.* 2021

19. Endopod of P1 shorter than exopod ..... ***Entomopsyllus nichollsi*** McKinnon, 1988
– Endopod of P1 shorter than exopod 20

20. Female antennule 15-segmented; third exopodal segment of P4 showing 2 setae ..... ***Entomopsyllus stocki*** Kim, 2004
– Female antennule with more than 16-segments; third exopodal segment of P4 showing 3 or more setae 21

21. Female antennule 16-segmented; third exopodal segment of P4 showing 3 setae ..... ***Entomopsyllus adriae*** (Eiselt, 1959)
– Female antennule 17-segmented; third exopodal segment of P4 showing 4 setae ..... ***Entomopsyllus brevicaudatus*** Lee & Kim, 2017

Ecological considerations

Entomolepididae is a cosmopolitan siphonostomatoid family that comprises, to date, 23 species. These copepods are characterized by the flattened and oval aspect of the shield, covering almost the entire

Table 5. Hosts of Entomolepididae Brady, 1899.

Species of Entomolepididae Brady, 1899	Hosts
Entomolepis hamondi McKinnon, 1988	Tunicata Lamarck, 1816 (Chordata Dallas, 1875)
Entomolepis ovalis Brady, 1899	mud
Entomopsyllus adriae (Eiselt, 1959)	*Aplysina aerophoba* (Nardo, 1833) (Porifera Grant, 1836) *Aplysina cavernicola* (Vacelet, 1959) (Porifera)
Entomopsyllus brevicaudatus Lee & Kim 2017	unidentified sponges (Porifera)
Entomopsyllus nichollsi McKinnon, 1988	plankton (unknown)
Entomopsyllus stocki Kim, 2004	*Tubipora musica* Linnaeus, 1758 (Cnidaria Hatschek, 1888)
Entomopsyllus takara Uyeno & Johnsson, 2018	*Heliopora coerulea* (Pallas, 1766) (Cnidaria) *Distichopora violacea* (Pallas, 1766) (Cnidaria)
Lepeopsyllus ovalis Thompson & Scott, 1903	general invertebrates
Lepeopsyllus typicus Thompson & Scott, 1903	oyster washings (Mollusca Cuvier, 1797)
Paralepeopsyllus dambayensis Lee & Kim, 2017	unidentified sponges (Porifera)
Paralepeopsyllus leei Lee & Kim, 2017	unidentified sponges (Porifera)
Paralepeopsyllus mannarensis Ummerkutty, 1960	sponges (Porifera) crinoids (Echinodermata Bruguière, 1791 [ex Klein, 1734])
Parmulella emarginata Stock, 1992	*Chondrilla nucula* Schmidt, 1862 (Porifera)
Parmulodes verrucosa Wilson, 1944	*Chondrilla nucula* Schmidt, 1862 (Porifera)
Parmulopsyllus iamarinoi Borges *et al*., 2021	*Aplysina cauliformis* (Carter, 1882) (Porifera)
Neoparmulella periperiensis Farias *et al*., 2020	*Phyllogorgia dilatata* (Esper, 1806) (Cnidaria)
Spongiopsyllus adventicius Johnsson, 2000	*Aplysina* Nardo, 1834 (Porifera) *Dysidea janiae* (Duchassaing & Michelotti, 1864) (Porifera) *Monanchora* Carter, 1883 (Porifera)
Spongiopsyllus aramisi sp nov.	*Aplysina cauliformis* (Carter, 1882) (Porifera)
Spongiopsyllus athosi sp nov.	*Aplysina cauliformis* (Carter, 1882) (Porifera)
Spongiopsyllus atypicus Canário *et al*., 2019	*Aplysina insularis* (Duchassaing & Michelotti, 1864) (Porifera)
Spongiopsyllus intermedius Borges *et al*., 2021	*Aplysina solangeae* Pinheiro, Hajdu & Custódio, 2007 (Porifera)
Spongiopsyllus porthosi sp nov.	*Aplysina cauliformis* (Carter, 1882) (Porifera)
Sp*ongiopsyllus redactus* Canario *et al*., 2012	*Mussismilia hispida* (Verrill, 1901) (Cnidaria)

body, suggesting a life mode attached to its hosts (Borges *et al.* 2021). Although copepod associations with algae and marine invertebrates such as scleractinian corals, octocorals, anemones, and echinoderms are known, the most common host group for entomolepidids are sponges (Boxshall & Halsey 2004; Johnsson & Neves 2012; Lee & Kim 2017; Borges *et al.* 2021).

Spongiopsyllus is an endemic genus of Entomolepididae, reported only from the northeastern region of Brazil. Its species are characterized by 3 and 4 postgenital urosomites, on female and male respectively, and uniramous fourth leg with 3-segmented exopod (Johnsson 2000).

Sponges are important components of marine ecosystems and can dominate the benthos biomass (Maldonado *et al.* 2017; Chin *et al.* 2020). Due to the diverse shapes and sizes, including encrusting, massive, erect and cup forms, sponge-community associations are essential in marine benthos dynamics (Chin *et al.* 2020; Borges *et al.* 2021). Currently, it is documented that marine invertebrates, such as polychaetes, crustaceans, molluscs, and ophiuroids (Villamizar & Laughlin 1991; Chin *et al.* 2020;

Borges *et al.* 2021) use sponges as a refuge, nursery, and food resource, and besides the external morphology, the skeleton composition and aquiferous system may be influencing these associations and their species richness (Hadju *et al.* 2011; Borges *et al.* 2021).

Aplysina has a circumtropical distribution and the body is composed of skeleton with only spongin fibers and alpha chitin. The genus is characterized by large sponges with many forms and live colors (Pinheiro *et al.* 2007; Borges *et al.* 2021). *Aplysina* presently comprises 44 valid species (Van Soest *et al.* 2021), 14 of them described from the northeastern region of Brazil (Borges *et al.* 2021), and four of them – *Aplysina lacunosa* (Lamarck, 1814), *Aplysina insularis* (Duchassaing & Michelotti, 1864), *Aplysina cauliformis* and *Aplysina solangeae* Pinheiro, Hajdu & Custódio, 2007 – are host to *Spongiopsyllus* (Johnsson 2000; Canário *et al.* 2012, 2019; Borges *et al.* 2021).

At present, there are seven known species of *Spongiopsyllus*, including the three newly described ones – *S. adventicius*, *S. redactus*, *S. atypicus, S. intermedius*, *S. athosi* sp. nov., *S. porthosi* sp. nov., and *S. aramisi* sp. nov. *Spongiopsyllus redactus* has been recorded only from the scleractinian coral *Mussismilia hispida* (Verrill, 1901). In addition to the known host-associate relationships between Entomolepididae and sponges (Table 5), the records of *Spongiopsyllus* and *Aplysina* associations establish evidence of specificity between these two genera. Consequently, sampling efforts on the geographical distribution of species of *Aplysina*, preferential hosts to *Spongiopsyllus*, can reveal new records and new species of this copepod genus.

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