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CRUSTACEANA

ON A NEW SPECIES OF *LYSMATA* RISSO, 1816 (DECAPODA, CARIDEA, LYSMATIDAE) FROM THE TROPICAL EASTERN ATLANTIC

BY

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ABSTRACT

During fieldwork on Tenerife (Canary Islands) and São Tomé in the eastern Atlantic, three specimens belonging to the genus *Lysmata* were collected in an underwater cave and tunnel. The specimens are similar to a species known from a single specimen collected in Guam in the tropical western Pacific: *Lysmata guamensis* Anker & Cox, 2011. With this species it shares many morphological characteristics, in special the rostral dentition of only two dorsal teeth, of which one situated post-orbital and the other one on the rostrum proper, which is unique in the genus. Its phylogenetic position in the genus *Lysmata* is reconstructed on the basis of the mitochondrial 16S RNA marker. The specimens are here described and figured as a species new to science.

Key words. — Decapoda, Caridea, East Atlantic, Lysmatidae, new species

INTRODUCTION

The shrimp genus *Lysmata* Risso, 1816 presently comprises 50 species (De Grave & Fransen, 2011; DecaNet, 2025; Guéron et al., 2025) distributed in tropical and temperate waters around the globe from the intertidal to 360 m depth for *L. olavoi* (see Fransen, 1991). Most species in this genus are protandric simultaneous hermaphrodites: shrimps first mature and reproduce solely as males before later becoming functional simultaneous hermaphrodites (Bauer, 2000; Baeza, 2006, 2007a, b, 2009, 2010, 2013).

Bauer (2000) recognized a "cleaner" group comprised of pair-living species with brilliant red and yellow/white colourations that present cleaning fish

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Published with license by Koninklijke Brill BV | DOI: 10.1163/15685403-bja10491

behaviour and a "peppermint" group of species mostly living in aggregates with longitudinal and transverse reddish bands on the body. Molecular analyses suggested three subclades within *Lysmata*, characterized by differences in the morphology of the accessory branch in the dorsolateral antennular flagellum being: (1) short, (2) long, or (3) short/unguiform/absent (i.e., variable in shape) (Baeza, 2010; Fiedler et al., 2010), as summarized by Ashrafi et al. (2021), Aguilar et al. (2022) and Guéron et al. (2023, 2025). The clade with species with a long accessory ramous is well supported and monophyletic in all analyses published. The other clades are less supported and sometimes come out paraphyletic (Baeza, 2010; Fiedler et al., 2010; Ashrafi et al., 2021; Aguilar et al., 2022; Guéron et al., 2023), in part caused by incongruent terminology and interpretation of the morphology of the accessory ramous (Aguilar et al., 2022).

In 2003, while diving in the 'Cueva Marina de San Juan' on the southwestern coast of Tenerife, two specimens of a yet unknown species of *Lysmata* were collected. A single specimen, belonging to the same species, was collected in an underwater tunnel through Santana Islet on São Tomé Island during fieldwork in 2023 carried out by Peter Wirtz.

These specimens are herein described as new to science and compared with the holotype of the closely related *L. guamensis* Anker & Cox, 2011 deposited in the Florida Museum of Natural History at the University of Florida (FLMNH UF). A molecular analysis based on sequences of the 16S mitochondrial gene was carried out to determine its phylogenetic position within the genus *Lysmata*.

MATERIAL AND METHODS

Taxon sampling

In 2003, two specimens of *Lysmata* were collected by Rogelio Herrera while diving in the 'Cueva de San Juan' on the southwestern coast of Tenerife. In 2023, during fieldwork by Peter Wirtz on São Tomé Island, a single specimen was collected in an underwater tunnel through Santana Islet.

Morphological analysis

The specimens were studied using a dissecting stereomicroscope (Zeiss Discovery.V8) and a compound microscope (Olympus BX53), both provided with a drawing tube. Drawings were scanned (Canon Canoscan 9000F) with a resolution of 600 dpi and subsequently mounted into plates using Adobe Photoshop software (Adobe Systems). Post-orbital carapace length (pocl.) was measured from the posterior margin of the orbit to the posterior margin of the carapace along the dorsal midline; rostral characters (R) are formulated as R = number of post-orbital dorsal teeth + number of dorsal teeth on rostrum proper/number of ventral teeth. Field collection number is abbreviated as fcn. The specimens were deposited in Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, RMNH), Leiden, The Netherlands.

DNA analyses

Total genomic DNA was extracted from a pleopod using the DNeasy Blood and Tissue Kit or Qiamp DNA Micro Kit (Qiagen) following the manufacturer's protocols.

For resolving phylogenetic relationships, partial mitochondrial 16S ribosomal RNA (16S), was sequenced and amplified by polymerase chain reaction (PCR) using primer pair 16Sar/16Sbr (Palumbi et al., 1991) following the protocols used by Brinkmann & Fransen (2016). PCR products were submitted to Macrogen for sequencing using the Sanger sequencing reaction with an ABI3730XL DNA Sequencer. Sequence data from prior studies on the genus *Lysmata* were used to construct a phylogenetic tree (table I).

The alignment was carried out using the software MUSCLE (Edgar, 2004), with default setting, as implemented in MEGA-X (Kumar et al., 2018). Highly variable and divergent positions as well as poorly aligned ones were detected and eliminated from the alignment using Gblocks v0.91b (Castresana, 2000) with default parameters except for allowing gap positions: This resulted in 404 nucleotides determined to be suitable for phylogenetic analysis.

The best-fit model for the nucleotide substitution (i.e., HKY + G + I) was selected based on BIC (Bayesian Information Criterion) implemented in MEGA-X (Kumar et al., 2018). The Maximum Likelihood (ML) analysis was conducted in MEGA-X (Kumar et al., 2018) using default settings, except for the number of bootstrap replicates, which was set to 1000.

The final tree was displayed using FigTree v1.4.4 software (Rambaut, 2018).

RESULTS

TAXONOMY

Family LYSMATIDAE Dana, 1852

Genus *Lysmata* Risso, 1816

Lysmata wirtzi spec. nov.

(figs. 1-13)

Lysmata spec. nov. — González, 2018: 412; 2024: 3.

Material examined. — Holotype ovigerous specimen (possibly hermaphrodite), pocl. 3.9 mm (RMNH.CRUS.D.59490): tunnel through Santana Islet, São Tomé, 0°14′28.14″N 6°45′33.23″E, 29

TABLE I

Lysmata species and other selected lysmatid, barbouriid and merguiid species used in the phylogenetic analysis, new sequence underlined

Species	Museum voucher	Locality	Reference	GenBank accession
Lysmata cf. *acicula* (Rathbun, 1906)	Not indicated	Lahi lahi Point, Oahu, Hawaii, U.S.A.	Fiedler et al. (2010)	HQ315575
Lysmata amboinensis De Man, 1888	Not indicated	Bali, Indonesia	Fiedler et al. (2010)	HQ315589
Lysmata cf. *anchisteus* Chace, 1972	Not indicated	Kapapa Island, Oahu, Hawaii, U.S.A.	Fiedler et al. (2010)	HQ315606
Lysmata ankeri Rhyne & Lin, 2006	Not indicated	Haiti	Fiedler et al. (2010)	HQ315597
Lysmata argentopunctata Wicksten, 2000	CNCR 20998	Cabo San Lucas, Mexico	Baeza (2010)	GQ227814
Lysmata bahia Rhyne & Lin, 2006	UMML 32.9453	Panama	Baeza et al. (2009)	EU861503
Lysmata boggessi Rhyne & Lin, 2006	Not indicated	Hernando Beach, Florida, U.S.A.	Fiedler et al. (2010)	HQ315603
Lysmata californica (Stimpson, 1866)	Not indicated	La Jolla, California, U.S.A.	Fiedler et al. (2010)	HQ315596
Lysmata dispar Hayashi, 2008	NTM Cr019377	Heron Island, Queensland, Australia	Aguilar et al. (2022)	OL664575
Lysmata dispar Hayashi, 2008 (as *L. lipkei* Okuno & Fiedler, 2010)	Not vouchered	Okinawa, Japan	Fiedler et al. (2010)	HQ315574
Lysmata debelius Bruce, 1983	Not indicated	Indo-Pacific	Fiedler et al. (2010)	HQ315594
Lysmata elisa Guéron, Baeza, Bochini, Terossi & Almeida, 2023	MOUFPE 21022	Pernambuco, Brazil	Guéron et al. (2023)	OQ382885
Lysmata galapagensis Schmitt, 1924	Not indicated	Nicaragua	Fiedler et al. (2010)	HQ315577
Lysmata grabhami (Gordon, 1935)	Not indicated	Florida, U.S.A.	Fiedler et al. (2010)	HQ315590
Lysmata gracilirostris Wicksten, 2000	UMML 32.9458	Panama	Baeza et al. (2009)	EU861502
Lysmata hochi Baeza & Anker, 2008	UMML 32.9460	U.S.A.	Baeza et al. (2009)	EU861507
Lysmata holthuisi Anker, Baeza & De Grave, 2009 (as *L.* cf. *trisetacea*)	UMML 32.9466	Panama	Baeza et al. (2009)	EU861483
Lysmata intermedia (Kingsley, 1879)	Not indicated	Sebastian Inlet, Florida, U.S.A.	Fiedler et al. (2010)	HQ315579
Lysmata jundalini Rhyne, Calado & dos Santos, 2012	Not indicated	Puerto Rico	Fiedler et al. (2010)	HQ315582
Lysmata kuekenthali (De Man, 1902)	UMML 32.9467	St Petersburg, Florida, U.S.A.	Baeza & Fuentes (2023)	KC962216
Lysmata malagasy Ashrafi, Baeza & Duris, 2021	MNHN-IU-2010-4890	Madagascar	Ashrafi et al. (2021)	MW798244

TABLE I
(Continued)

Species	Museum voucher	Locality	Reference	GenBank accession
Lysmata moorei (Rathbun, 1901)	Not indicated	Bahia, Brazil	Fiedler et al. (2010)	HQ315578
Lysmata nayaritensis Wicksten, 2000	UMML 32.9463	Panama	Baeza et al. (2009)	EU861506
Lysmata nilita Dohrn & Holthuis, 1950	SMF 32005	Italy	Baeza et al. (2009)	EU861482
Lysmata olavoi Fransen, 1991	SMF 32006	Portugal	Baeza et al. (2009)	EU861494
Lysmata pederseni Rhyne & Lin, 2006	Not indicated	Florida Keys, Florida, U.S.A.	Fiedler et al. (2010)	HQ315601
Lysmata rafa Rhyne & Anker, 2007	Not indicated	Florida Keys, Florida, U.S.A.	Fiedler et al. (2010)	HQ315604
Lysmata rauli Laubenheimer & Rhyne, 2010	UF 047210	Port Island, Mirs Bay, Hong Kong	Aguilar et al. (2022)	OL690313
Lysmata seticaudata (Risso, 1816)	UMML 32.9614	Cabo Raso, Cascais, Portugal	Fiedler et al. (2010)	HQ315583
Lysmata ternatensis De Man, 1902	Not indicated	Akajima, Keramas, Japan	Fiedler et al. (2010)	HQ315584
Lysmata cf. *trisetacea* (Heller, 1861)	Not indicated	Kapapa Island, Oahu, Hawaii, U.S.A.	Fiedler et al. (2010)	HQ315576
Lysmata udoi Baeza, Bolaños, Hernandez & López, 2009 (as *L.* cf. *boggessi*)	UMML 32.9603	Venezuela	Baeza (2010)	GQ227815
Lysmata uncicornis Holthuis & Maurin, 1952 (as *L. arvoredensis* Giraldes et al., 2018)	MNRJ 27976	Santa Catarina, Brazil	Giraldes et al., 2018	MH142085
Lysmata vittata (Stimpson, 1860)	RMNH.CRUS.D.35616	Thailand	Baeza (2010)	GQ227829
Lysmata wirtz sp. nov.	RMNH.CRUS.D.59490	São Tomé	Present study	PV918497
Lysmata wurdemanni (Gibbes, 1850)	Not indicated	Florida Keys, Florida, U.S.A.	Fiedler et al. (2010)	HQ315605
Exhippolysmata ensirostris (Kemp, 1914)	UMML 32.9602	Quindao, China	Baeza (2010)	GQ227819
Exhippolysmata oplophoroides (Holthuis, 1948)	UMML 32.9469	Ubatuba, Brazil	Baeza et al. (2009)	EU861510
Barbouria cubensis (von Martens, 1872)	Not indicated	San Salvador, Bahamas	Fiedler et al. (2010)	HQ315565

TABLE I
(Continued)

Species	Museum voucher	Locality	Reference	GenBank accession
Lysmatella prima Borradaile, 1915	Not indicated	Sulawesi, Indonesia	Fiedler et al. (2010)	HQ315569
Merguia oligodon (De Man, 1888)	Not indicated	Iriomote Island, Japan	Fiedler et al. (2010)	HQ315570
Merguia rhizophorae (Rathbun, 1900)	MZUSP 37510	Sergipe, Brazil	Giraldes et al. (2018)	MH102013
Parhippolyte mystica (Clark, 1989)	Not indicated	Odo Point, Okinawa, Japan	Fiedler et al. (2010)	HQ315560
Synalpheus brevicarpus (Herrick, 1891)	Not indicated	Puerto Rico	Fiedler et al. (2010)	HQ315564

Catalogue numbers, Museum or collection: CNCR, Colección de Crustáceos, Instituto de Biología, Departamento de Zoología, Universidad Nacional Autónoma de México, México; MOUFPE, Museu de Oceanografia Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco, Recife, Brazil; MNHN, Museum National d′Histoire Naturelle, Paris, France; MNRJ, National Museum of Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP, Museum of Zoology of the University of São Paulo, São Paulo, Brazil; NTM, Museum and Art Gallery Northern Territory (MAGNT), Darwin, Australia; RMNH, Naturalis Biodiversity Center, Leiden, Netherlands; SMF, Senckenberg Museum, Frankfurt, Germany; UF, Florida Museum of Natural History, Gainesville, FL, U.S.A.; UMML, University of Miami Marine Laboratories, Renstiel School of Marine Science, University of Miami, Miami, FL, U.S.A.

January 2023, below a stone, depth 15 m, scuba diving, collected by P. Wirtz (fcn. 13). Paratypes: 2 non-ovigerous specimens, pocl. 5.7 mm (RMNH.CRUS.D.59491): in 'Cueva Marina de San Juan' (part of the ZEC ES7020117 habitat), just south of the port of San Juan, in front of the mouth of the Chabugo ravine, approximately at 28°10′N 16°4′W, between the headlands of El Roque de Mataoveja and La Tisera, in the municipality of Guía de Isora, south-western coast of Tenerife, Canary Islands, Spain, 2003, from the cracked walls of the cave covered with brain sponges (*Neophrissospongia nolitangere* (Schmidt, 1870)), depth 3-8 m, scuba diving, collected by Rogelio Herrera.

Material for comparison of *Lysmata guamensis* Anker & Cox, 2011. — Holotype ovigerous specimen (possibly euhermaphrodite) (carapace length 6.30 mm, pocl. 4.15 mm, total length 19.80 mm), FLMNH UF Arthropoda 1229, Mariana Archipelago, Guam, Glass Breakwater near mouth of Apra Harbor, "among rocks", 3-6 m, collected by H.T. Conley, 17 October 2001.

Description. — Medium-sized species of *Lysmata* (fig. 1A). Carapace relatively high, covered with tegumental scales (figs. 1B-D, 2A, B, 13). Rostrum (figs. 1B-D, 2B) with two teeth on mid-dorsal line with one simple seta in front of each tooth; first tooth situated on carapace, distinctly posterior to level of post-orbital margin, second situated on rostrum, at about 3/5 of rostrum length. Rostrum about half as long as carapace, almost reaching distal margin of second segment of antennular peduncle; tip acute; lateral carina developed; ventral margin with 2-4 well-developed teeth; deep notch in proximal part of ventral margin. Total carapace teeth formula: 1 + 1/2-4. Antennal tooth strong, reaching beyond base of cornea. Intraorbital process of carapace not protruding (fig. 1C, D). Pterygostomial angle broadly rounded, without tooth.

Abdominal somites with tegumental scales. First to third abdominal pleura rounded ventrally (fig. 1A); fourth and fifth with subacute or acute posteroventral tooth (fig. 2E); sixth pleura with sharp posteroventral tooth (fig. 2E).

Telson (fig. 2F) slender, about three times as long as wide proximally, tapering posteriorly. Dorsal surface covered with tegumental scales; with two pairs of spines at about 0.5-0.6 and 0.8 of telson length, respectively; with six long simple setae proximally on midline. Lateroventral margins with row of long plumose setae in distal half. Posterior margin (fig. 3A) produced centrally, with two long, robust plumose setae flanked on each side by two spines, mesial spine at least four times as long as lateral spine.

Eyestalk with well-developed cornea (figs. 1A, 2B), its dorsal margin not reaching dorsal margin of rostrum.

Antennular peduncle (fig. 3B, C) moderately robust, with tegumental scales on dorsal surface of peduncle and posterior part on lateral flagellum; first segment longest, with stylocerite reaching to distal margin, with two or three short spines on dorsal anterior margin, with small forward directed tooth at about 3/5th of ventromesial surface; second segment slightly longer than wide, longer than third

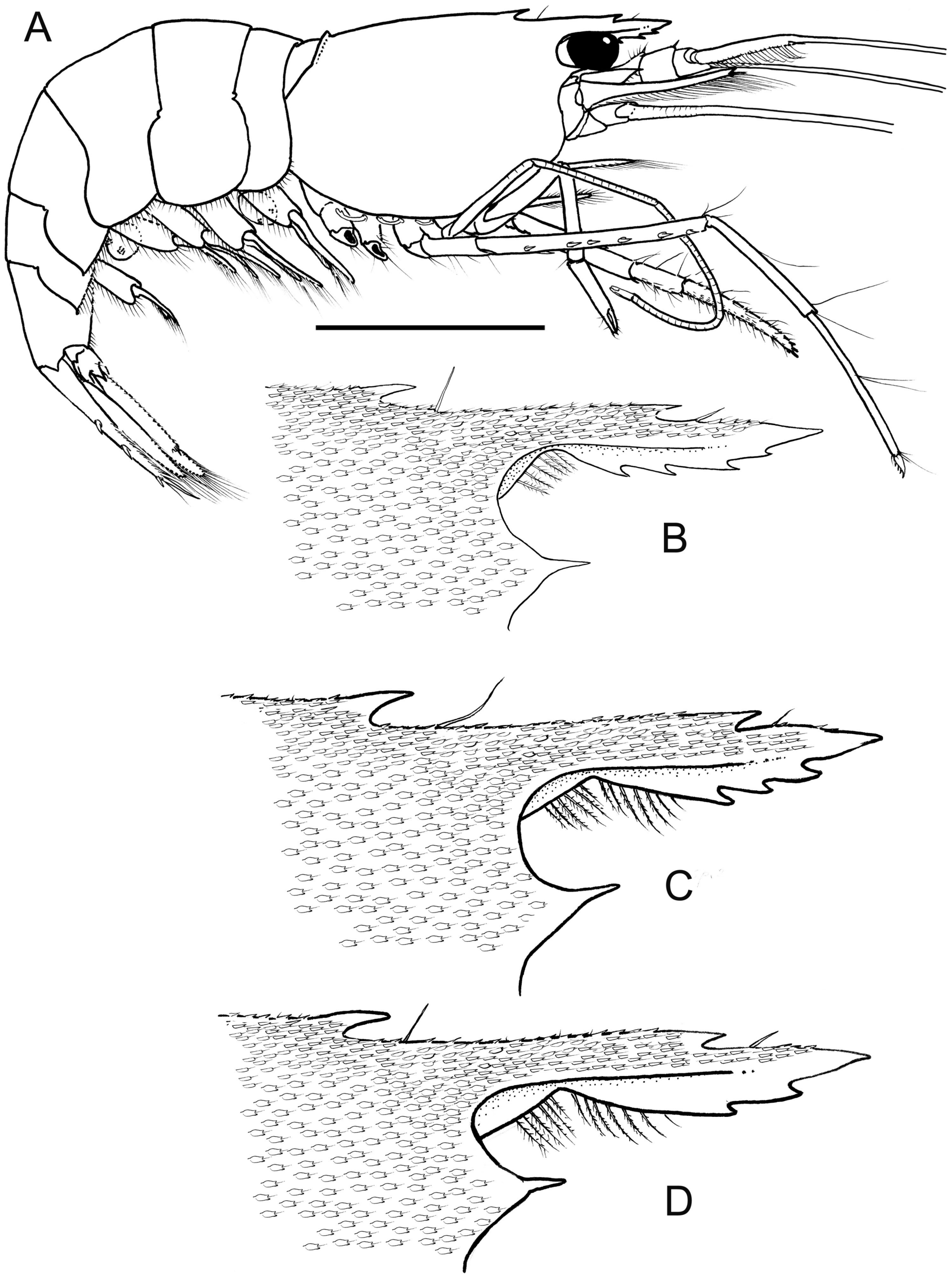

Fig. 1. *Lysmata wirtzi* spec. nov. A-B, ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490; C-D, non-ovigerous specimen, pocl. 5.7 mm, Tenerife, RMNH.CRUS.D.59491. A, habitus; B-D, rostrum, lateral view. Scale A = 4 mm; B-D = 1 mm.

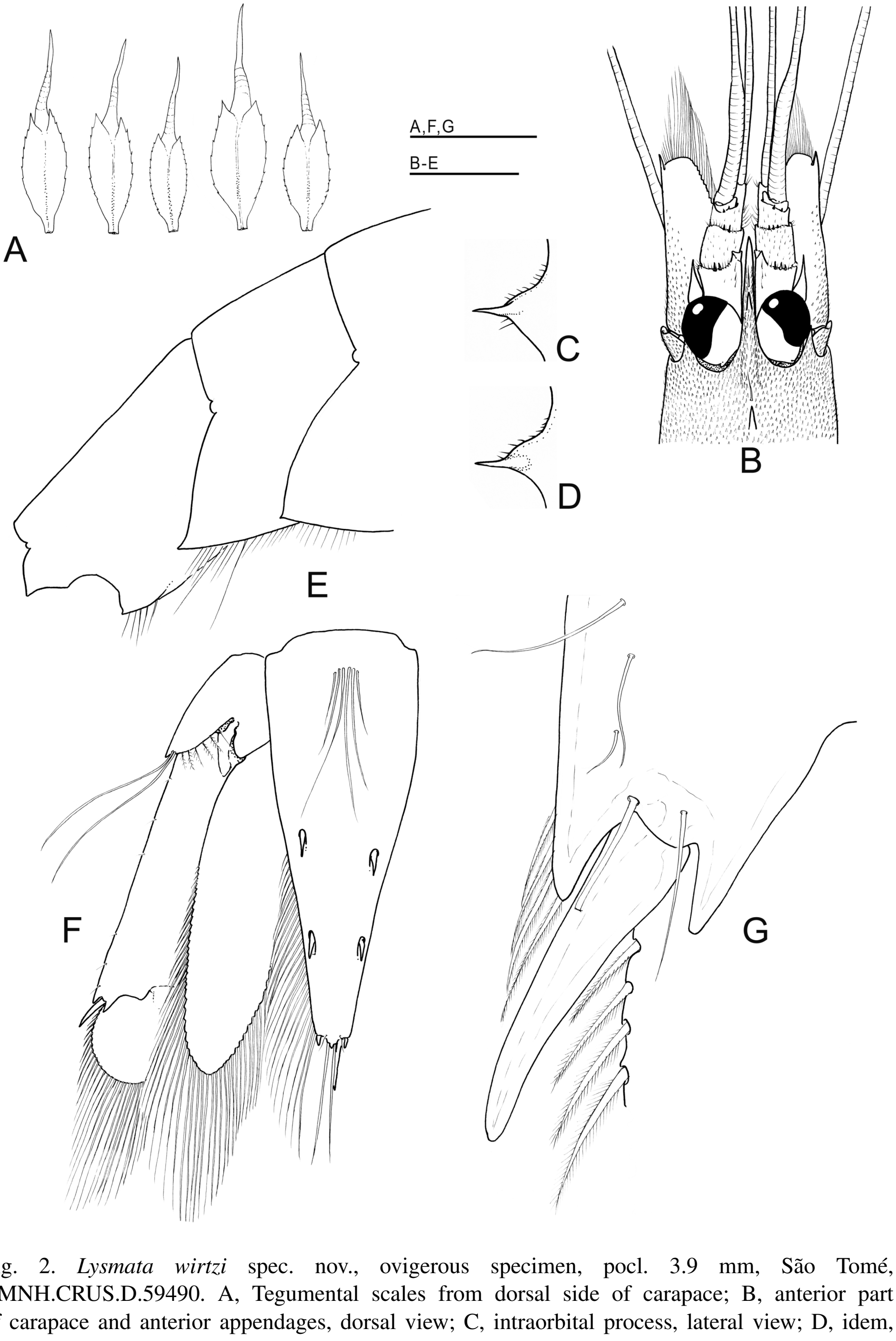

Fig. 2. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Tegumental scales from dorsal side of carapace; B, anterior part of carapace and anterior appendages, dorsal view; C, intraorbital process, lateral view; D, idem, dorsolateral view; E, abdominal pleura 3-6, lateral view; F, caudal fan, dorsal view, right uropod omitted;. Scale: A, G = 0.125 mm; B = 2 mm; C-E = 1 mm; F = 1.25 mm.

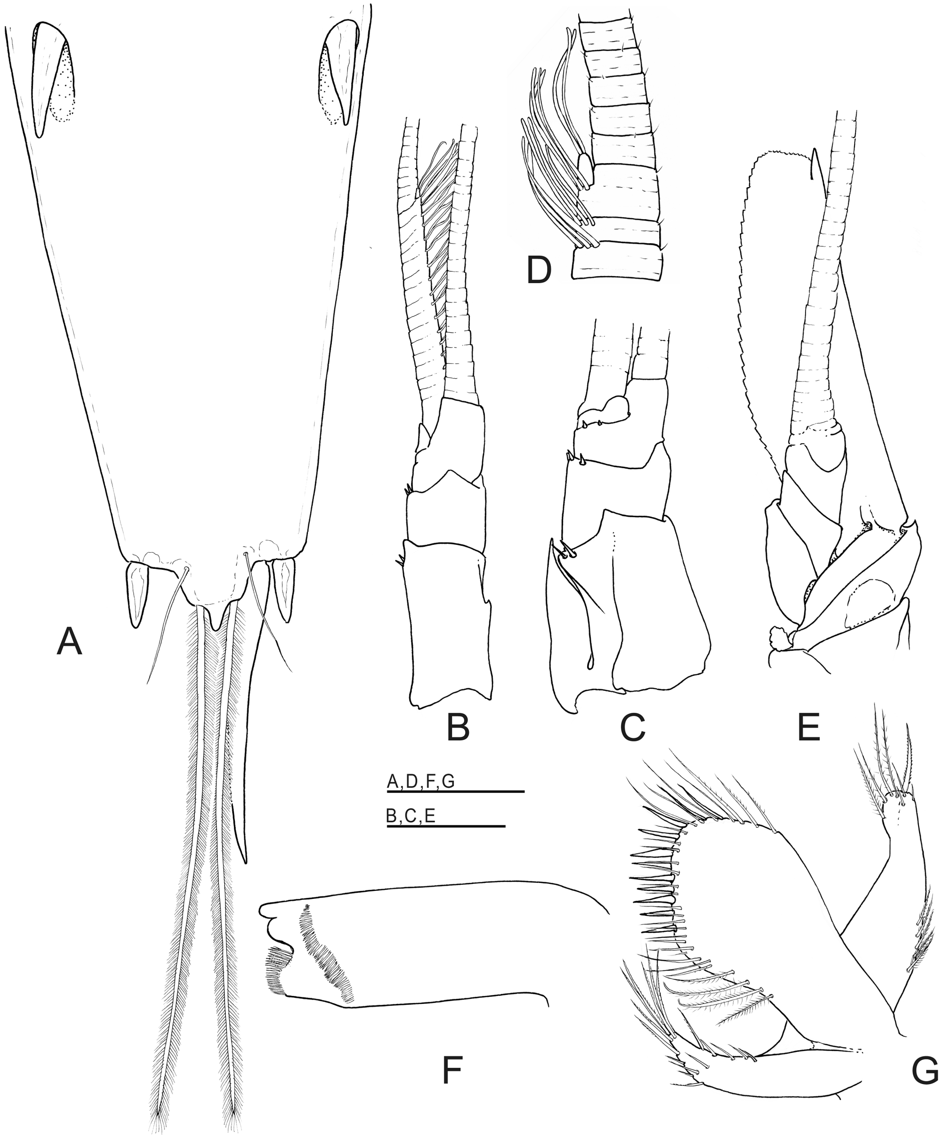

Fig. 3. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Telson, tip, dorsal view; B, antennular peduncle and basal part flagella, mesial view; C, antennular peduncle, dorsal view; D, lateral antennular flagellum, detail accessory branch, mesial view; E, antenna, ventral view; F, left mandible, ventral view; F, left maxillula, ventral view. Scale: A = 0.25 mm; B, C, E = 1 mm; D, F, G = 0.5 mm.

segment, with two or three short spines on dorsal anterior margin; third segment shortest, also with two or three small spines along dorsal anterior margin; flagella at least five times as long as post-orbital carapace length; lateral flagellum with groups of aesthetascs starting from second segment; accessory branch very short, stump-like, situated at 16th or 17th segment (fig. 3B, D); mesial flagellum distinctly thinner than lateral.

Antenna (fig. 3D) with short basicerite bearing small subacute tooth distoventrally. Carpocerite very short, not exceeding level of anterior margin of first segment of antennular peduncle. Scaphocerite subrectangular, elongate, reaching far beyond distal margin of antennular peduncle, with tegumental scales on dorsal surface; with strong distolateral tooth; blade narrow, broadly rounded distally, not reaching tip of distolateral tooth.

Left mandible (fig. 3E) simple. Incisor process not developed. Molar process with three blunt lobes and area of short serrulate setae.

Maxillula (fig. 3F) with broad rectangular upper endite with rows of stout and slender setae along mesial margin. Lower endite slender, with slender, finely serrulate setae in distal part. Palp distally bilobed with one robust serrulate and several more slender serrulate setae distally.

Maxilla (fig. 4A) with lower endite reduced, separated from upper endite by deep notch, with few long setae along mesial margin. Upper endite bilobed, with upper lobe broader than lower lobe, both fringed by long serrulate and simple setae. Palp simple, overreaching upper endite; with few plumose setae along mesial margin; with row of few plumose setae on proximal lateral margin; with one long, finely plumose seta distally. Scaphognathite with squarish anterior lobe and rounded posterior lobe.

First maxilliped (fig. 4B, C) with endites of coxa and basis separated by shallow notch. Coxal endite lost in dissection. Basal endite mesially fringed by rows of long and short serrulate and simple setae. Palp 3-segmented, overreaching basal endite; with rows of plumose setae along mesial margin. Caridean lobe rather small; with long exopodal flagellum with plumose setae in distal half. Epipod bilobed, anterior lobe overreaching caridean lobe.

Second maxilliped (fig. 5A) with coxal endite slightly produced mesially; with triangular epipod with podobranch. Basal and ischial segments partly fused, with deep excavation mesially. Basal segment with long exopod fringed by plumose setae in distal half. Ischial segment with row of long setae along ventromesial margin. Carpal and meral segments short, triangular, without special features. Propodal segment anteriorly produced, rounded, with row of rows of robust and slender long setae. Dactylar segment broad, fringed by short simple and serrulate setae.

Third maxilliped (fig. 5B) long, slender. Antepenultimate segment slightly longer than ultimate segment, with small spines distolaterally. Penultimate segment about half as long as ultimate segment, with one spine distolaterally. Ultimate segment tapering distally, tip (fig. 5C) with circle of six robust, serrulate spines,

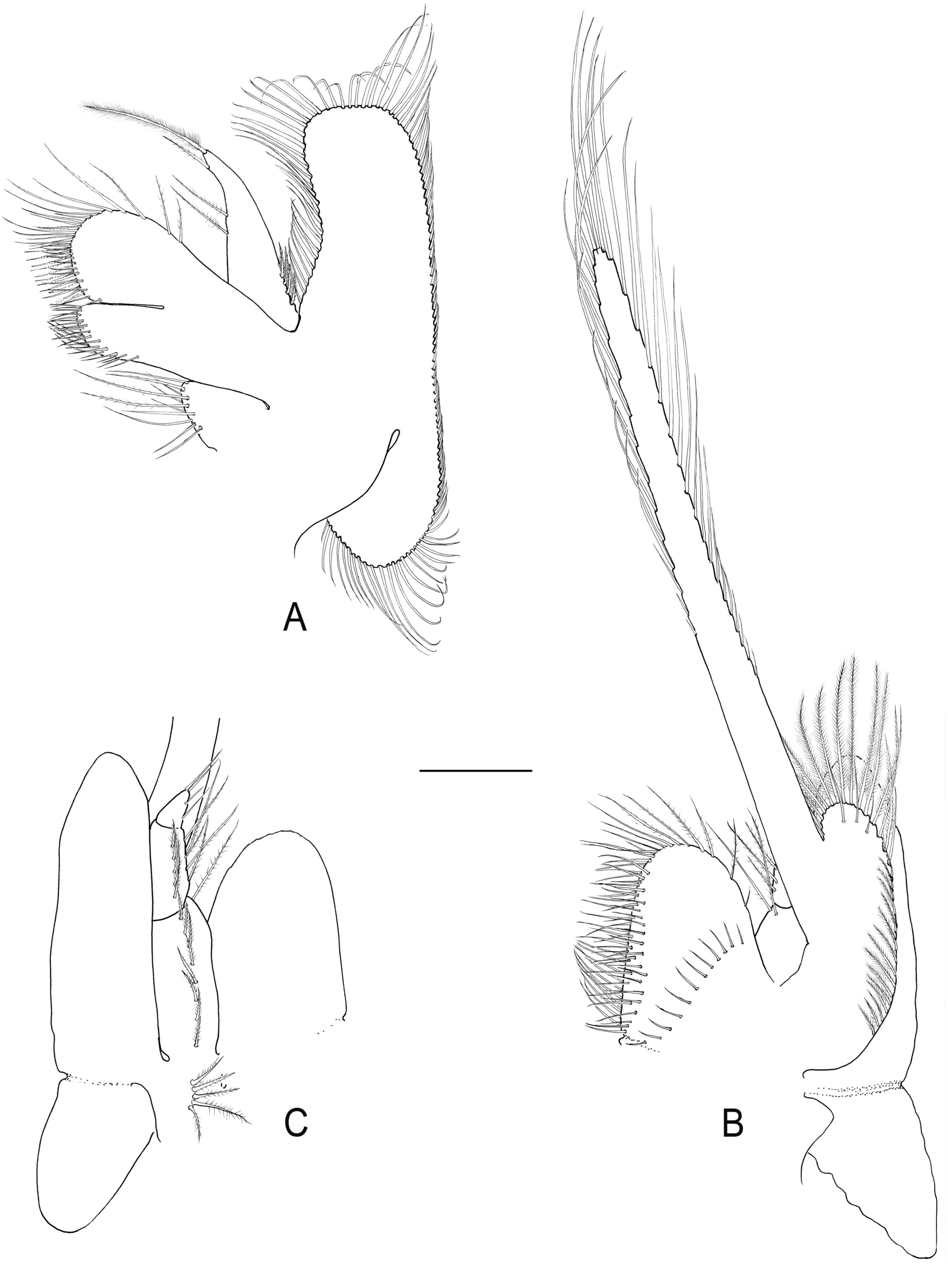

Fig. 4. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Left maxilla, ventral view; B, left first maxilliped, ventral view; C, idem, dorsal view. Scale = 0.5 mm.

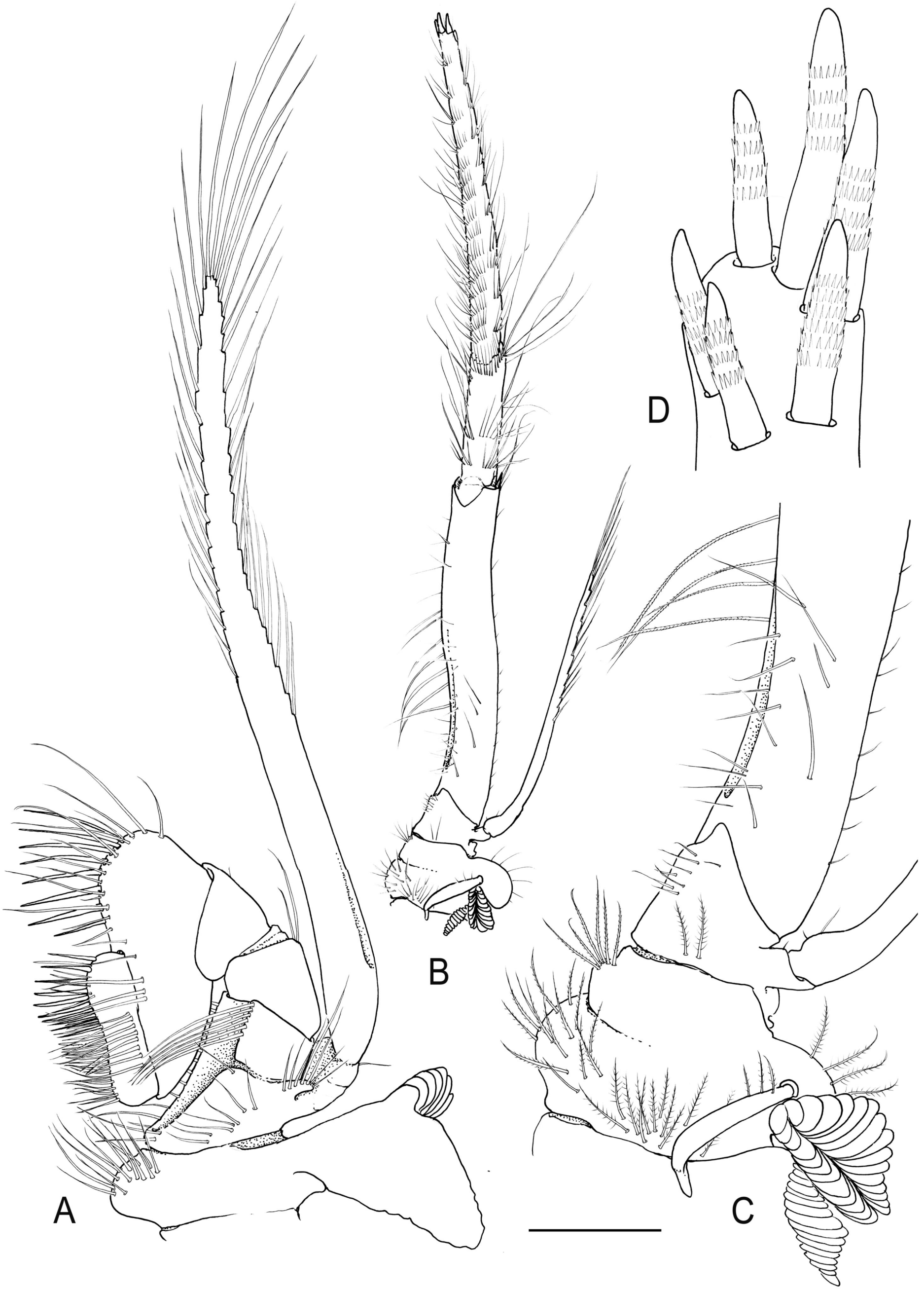

Fig. 5. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Left second maxilliped, ventral view; B, left third maxilliped, ventral view; C, idem, coxa and basis, lateral view; D, idem, tip, dorsal view. Scale A, C = 0.5 mm; B = 1.25 mm; D = 0.125 mm.

with many rows of serrulate setae on dorsal surface. Basal segment (fig. 5D) short, with short exopod, reaching to 2/3rd of antepenultimate segment; fringed by long plumose setae in distal half. Coxal segment (fig. 5D) mesially slightly produced; with lateral plate well-developed, rounded; arthrobranch and strap-like epipod present.

First pereiopod (cheliped) (fig. 6A) fairly slender, with not particularly enlarged chela. Coxa (fig. 6B) with strap-like epipod and setobranch. Basis (fig. 6B) short, without armature. Ischium (fig. 6B) slightly longer than basis, with row of six to eight short robust spines (fig. 6B, C) on ventral margin, with tips of these spines slender, thread-like. Merus longer than ischium, slightly shorter than carpus, without armature (fig. 6A). Carpus cylindrical, elongate, around six times as long as wide, with rows of grooming setae (fig. 6D) ventrolaterally. Chela (fig. 6D, E) simple, smooth, slender, with fingers about half as long as palm; cutting edges of fingers unarmed, distally biunguiculate.

Second pereiopod (fig. 7A) slender. Coxa (fig. 7B) with strap-like epipod and setobranch. Basis (fig. 7B) short, with two flattened, curved setae along mesial margin. Ischium with 3-5 barely visible subdivisions distally and row of flattened, curved setae in proximal part of mesial margin. Carpus of holotype with about 24 (right) and 27 (left) articles. Merus of holotype with about 15 (right) and 21 (left) articles. Articulation difficult to observe in proximal part of merus and carpus. One paratype with only the left second pereiopod present with the carpus with 33 articles and the merus with 23 articles. Chela small, simple, with fingers as long as palm.

Third to fifth pereiopods slender, elongate, similar in shape and length, but different in article proportions and armature. Coxa of third to fifth pereiopods with setobranchs. Coxa of third and fourth pereiopod with strap-like epipod. Ischia unarmed. Merus of third pereiopod (fig. 8A) around 13 times as long as wide, armed with 6-8 articulating spines of which 2 proximoventral, the rest lateral. Carpus around 0.6 times as long as merus, 0.85 times as long as propodus, 8.5 times as long as wide, with 2-3 spinules on ventral surface. Propodus slightly longer than carpus, 13 times as long as wide, with 5-8 spinules on ventral margin, including one distal spinule adjacent to dactylus. Dactylus (fig. 8B) fairly slender, biunguiculate distally, ventral (flexor) margin with 2 or 3, additional spines.

Fourth pereiopod (fig. 9A) generally similar to third. Merus slightly shorter than in third pereiopod, 12 times as long as wide, armed with 5-7 articulating spines of which 2 proximoventral, the rest lateral. Carpus distinctly shorter than in third pereiopod, 0.68 times as long as merus, 0.82 times as long as propodus, 8.2 times as long as wide, without or with 2-3 spinules. Propodus distinctly longer than carpus, 15 times as long as wide, with 5-8 spinules on ventral margin, including one

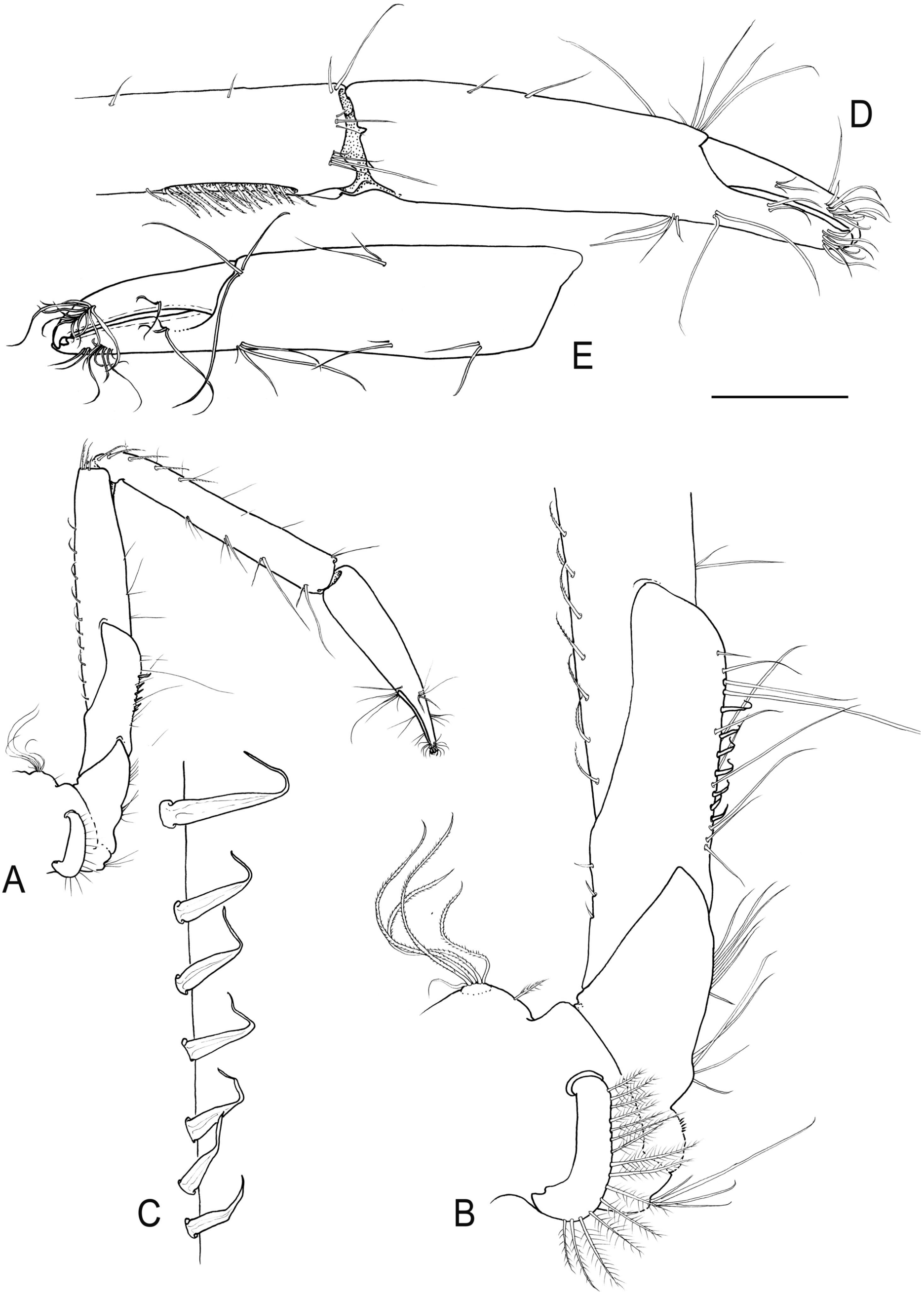

Fig. 6. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Left first pereiopod (cheliped), ventrolateral view; B, idem, coxa, basis and ischium; C, idem, lateral spines on ischium; D, idem, distal part carpus and chela, lateral view; E, chela, mesial view. Scale A = 1.25 mm, B, D, E = 0.5 mm; C = 0.125 mm.

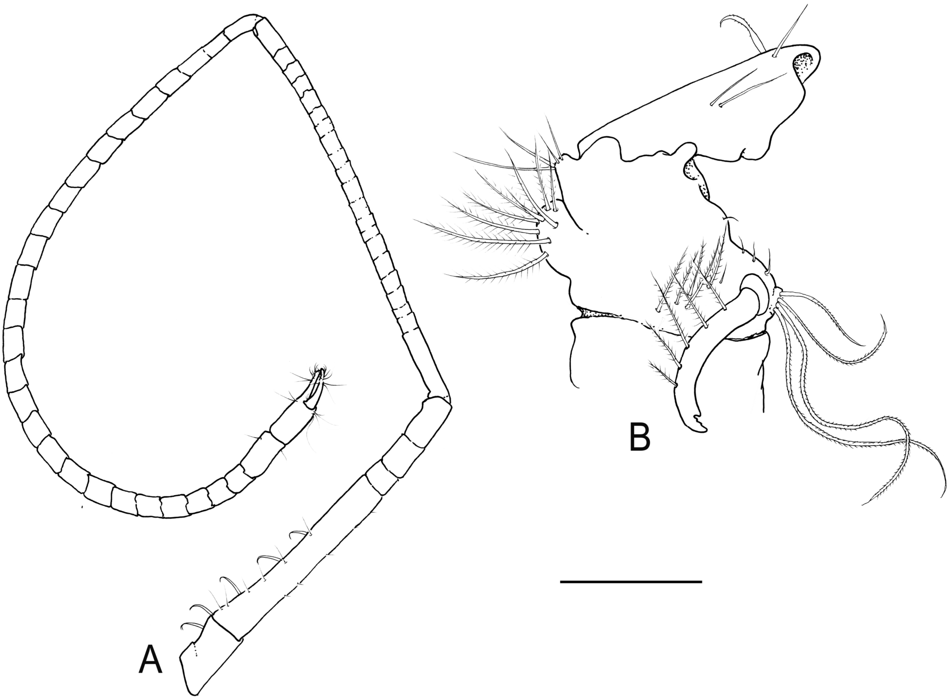

Fig. 7. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Left second pereiopod, lateral view; B, idem, coxa and basis. Scale A = 1.25 mm; B = 0.5 mm.

distal spinule adjacent to dactylus. Dactylus (fig. 9B) fairly slender, biunguiculate distally, ventral (flexor) margin with 2, additional spines.

Fifth pereiopod (fig. 10A) with merus shorter than in third and fourth pereiopods, 11 times as long as wide, armed with 1-2 articulating spines in distal part of lateral surface. Carpus 0.8 times as long as merus, 0.74 times as long as propodus, 10 times as long as wide, unarmed or with 2 ventral spinules. Propodus longer than in third and fourth pereiopods, 16.5 times as long as wide, slender, with 3-7 spinules on ventral margin, including one distal spinule adjacent to dactylus. Dactylus (fig. 10B) as in fourth pereiopod.

Pleopods with exopods slightly longer than endopods. First pleopod of ovigerous specimen (fig. 11A) with endopod about 2/3rd of exopod length, tapering towards tip. First pleopod of non-ovigerous specimens (fig. 11C) with endopod about half length of exopod, slender, tapering towards tip. Second pleopod of non-ovigerous specimens (fig. 11D, E) with endopod about 3/4th length of exopod, with slender appendix interior and slightly shorter, robust appendix masculina with many serrulate setae.

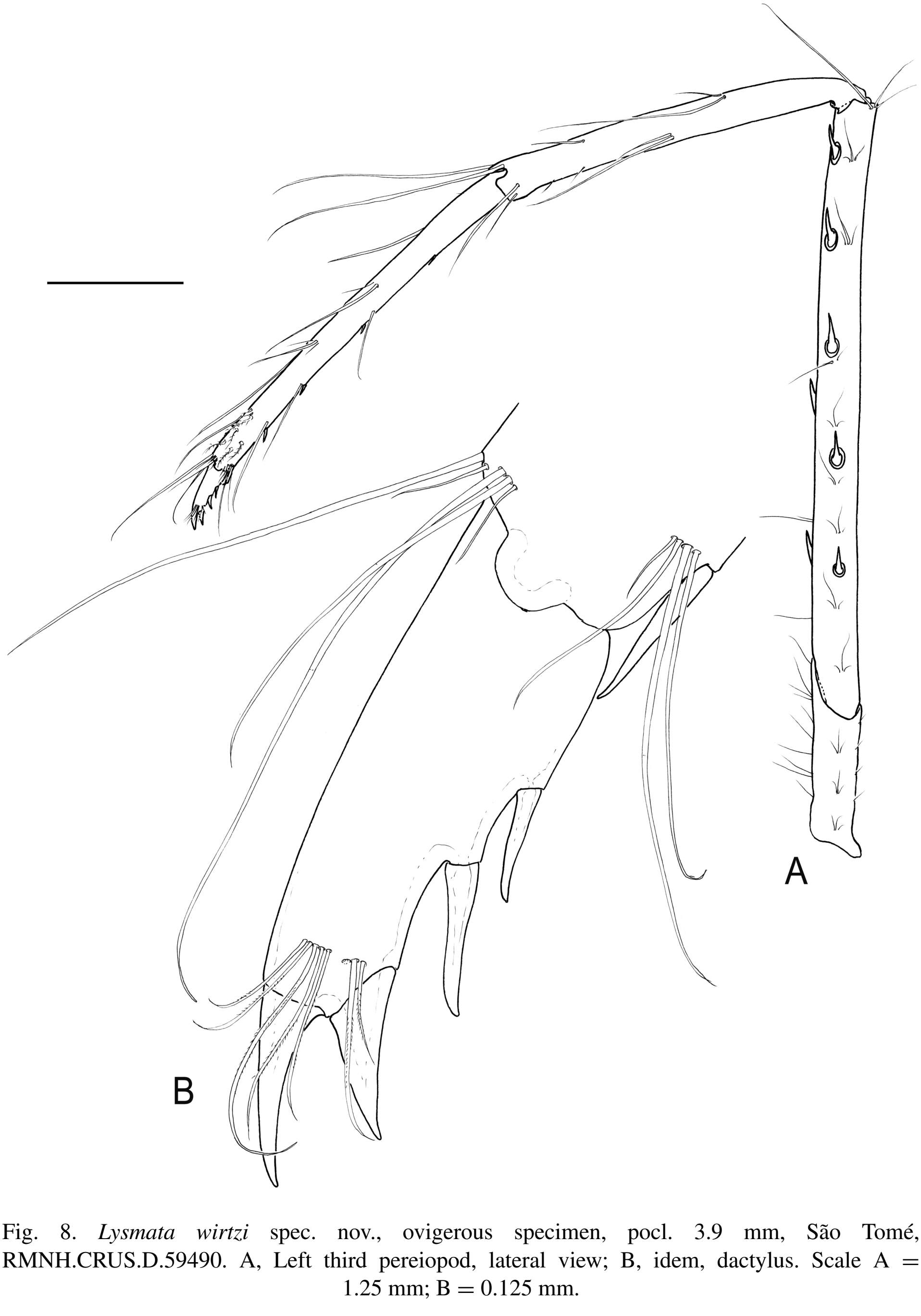

Fig. 8. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Left third pereiopod, lateral view; B, idem, dactylus. Scale A = 1.25 mm; B = 0.125 mm.

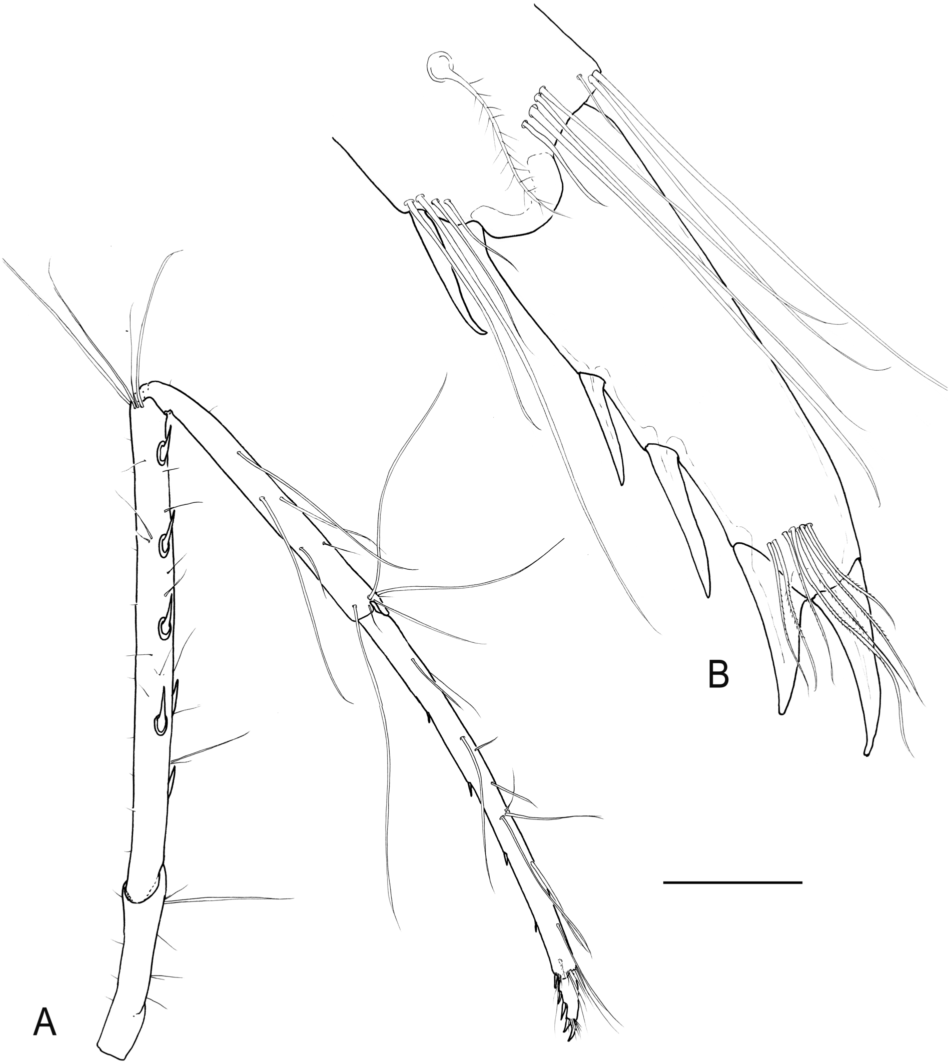

Fig. 9. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Right fourth pereiopod, lateral view; B, idem, dactylus. Scale A = 1.25 mm; B = 0.125 mm.

Uropod (fig. 2C) with protopod distally acute, with few, long, slender, simple setae. Protopod, endopod and exopod with tegumental scales dorsally. Endopod and exopod slender, exopod slightly longer than endopod. Exopod with distolateral margin (fig. 2G) with two fixed teeth flanking long movable spine.

Gill/exopod formula typical for genus.

Colour (fig. 12, based on the specimen from São Tomé). — Body and anterior appendages pale red, with somewhat deeper red transverse bands on posterior half

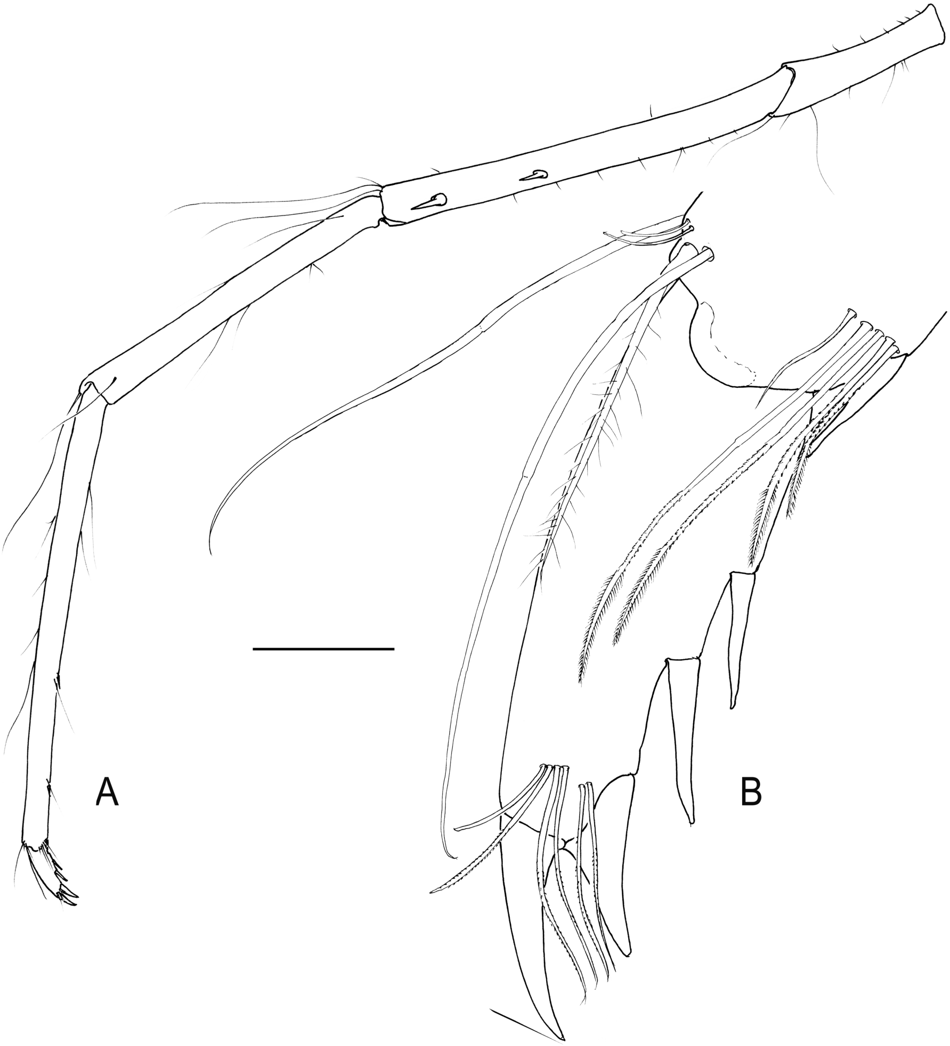

Fig. 10. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490. A, Right fifth pereiopod, lateral view; B, idem, dactylus. Scale A = 1.25 mm; B = 0.125 mm.

of abdominal somites. Scattered bright yellow chromatophores on carapace and abdomen, most dense in proximal part of dorsal part of carapace. Third maxilliped pale red. Ambulatory pereiopods pale red except for propodus and dactylus which are translucent. Hepatopancreas orange.

Etymology. — The species is named in honour of Peter Wirtz, who collected the holotype specimen and whose collecting skills have resulted in the discovery of many rare and new shrimp species.

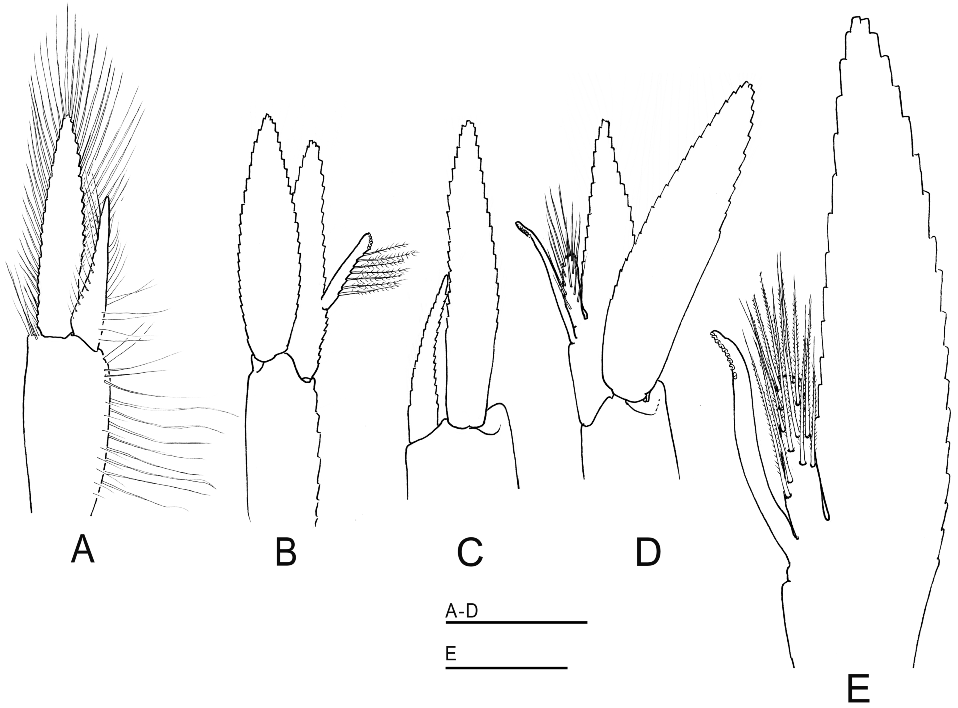

Fig. 11. *Lysmata wirtzi* spec. nov. A-B, ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490; C-E, non-ovigerous specimen, pocl. 5.7 mm, Tenerife, RMNH.CRUS.D.59491. A, Left first pleopod, anterior view; B, left second pleopod, anterior view, setae omitted; C, right first pleopod, anterior view, setae omitted; D, right second pleopod, anterior view, setae omitted; E, idem, detail appendix interna and appendix masculina, setae endopod omitted. Scale A-D = 1 mm, E = 1.25 mm.

Habitat. — ‘Cueva Marina de San Juan’, Tenerife. This habitat is of enormous structural and morphological complexity, consisting of a complex of marine caves with secondary openings and freshwater seepages (filtrations). The lava tube consists of two environments: a submerged part and an emergent or terrestrial part, with both connected by several points (locally known as “jameos”). In the submerged part, the cave presents a central gallery of approximately 40-60 m in length and 15-30 m in width, from which several tubes of various sizes and shapes branch out, with both open and closed “jameos” present. The longest tube is located on the left side of the cave, reaching a length of about 80 m from the entrance. The submarine cave covers an area of 0.78 hectares. The main entrance of the cave is situated at a depth of 8 m, while the submerged space has depths ranging from 3 to 8 m. The entrance and the bottom of the main passages of the cave are covered by medium sandy sediments, while gravel and boulders are found in certain areas of the middle sections (Monterroso et al., 2015; Riera et al., 2016).

Fig. 12. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490, photographed in plastic bag after collecting. Photo credit: Peter Wirtz.

Systematic remarks. — The present specimens are similar to *Lysmata guamensis* Anker & Cox, 2011. *L. guamensis* is only known from a single specimen collected ‘among rocks’ at a depth of 3-6 m in Apra Harbor, Guam, in the Mariana Archipelago, tropical western Pacific. The specimens from Tenerife and São Tomé share a unique character within the genus *Lysmata* with *L. guamensis*: the presence of only two dorsal rostral teeth of which one situated post-orbital and the other one on the rostrum proper. Some features noted for *L. wirtzi* have not been described nor drawn for *L. guamensis*. These have been checked in the holotype of *L. guamensis*: (1) the presence of tegumental scales; re-examination of the holotype of *L. guamensis* revealed that tegumental scales are also present in this species (fig. 14); (2) a deep notch in the proximal part of the ventral margin of the rostrum; this is also present in the holotype of *L. guamensis*; (3) the presence of 6 long simple setae proximally on the dorsal midline of the telson; in the holotype of *L. guamensis* there are 3 long setae in that position; (4) the presence of two or 3 short spines on the dorsal anterior margin of both first and second antennular segments; in the holotype of *L. guamensis* there are 1 (left) and 2 (right) dorsal anterior spines on the first antennular segment and 2 on the second antennular segment; (5) the small forward directed tooth at about 3/5-th of the ventral median margin of the first antennular segment; in the holotype of *L. guamensis* a blunt tubercle is present in that position; (6) the threadlike tips of the spines on the ventral margin of the ischium of the first pereiopods; these are also present in the holotype of *L.*

guamensis. Differences with *L. guamensis* are: (i) the length of the exopod of the third maxilliped which reached to 2/3rd of the antepenultimate segment whereas it reaches half way this segment in *L. guamensis* (see Anker & Cox, 2011, fig. 1h); re-examination of the holotype of *L. guamensis* showed the exopod to be slightly more than half the length of the first segment; (ii) the presence of 3-5 barely visible subdivisions in the distal part of the ischium of the second pereiopods whereas there are 2 of these subdivisions visible in *L. guamensis* (see Anker & Cox, 2011, fig 2e, f); the subdivisions in *L. guamensis* are indeed hardly visible whereas they are slightly more pronounced in *L. wirtzi*; (iii) the merus of the third pereiopod is about 13 times as long as wide in *L. wirtzi*, whereas it is 22 times as long as wide in the holotype of *L. guamensis* (see Anker & Cox, 2011, fig. 3a); (iv) the merus of the third pereiopod of *L. wirtzi* has 6-8 articulating spines of which 2 proximoventral, the rest lateral, whereas in the holotype of *L. guamensis*, both left and right meri have 11 articulating spines of which 3 ventral and the other lateral (fig. 15A); in the type-description of *L. guamensis* only 6 ventrolateral spines are mentioned (Anker & Cox, 2011, fig. 3a); (v) the carpus of the third pereiopod is slightly shorter than the propodus in *L. wirtzi* and 8.5 times as long as wide, whereas it is as long as the propodus and 17 times as long as wide in the holotype of *L. guamensis* (Anker & Cox, 2011, fig. 3a); (vi) the propodus of the third pereiopod is 13 times as long as wide in *L. wirtzi*, whereas it is 20 times as long as with in the holotype of *L. guamensis* (Anker & Cox, 2011: fig. 3a); (vii) the merus of the fourth pereiopod is about 12 times as long as wide in the present specimens, whereas it is 21 times as long as wide in the holotype of *L. guamensis* (see Anker & Cox, 2011, fig. 3a); (viii) the merus of the fourth pereiopod of *L. wirtzi* has 5-7 articulating spines of which 2 proximoventral, the rest lateral, whereas the holotype of *L. guamensis* has 8-9 articulating spines of which 3 ventral and the other lateral (fig. 15B); in the type-description of *L. guamensis* only 6 ventrolateral spines are mentioned (Anker & Cox, 2011, fig. 3c); (ix) the carpus of the fourth pereiopod is 8.2 times as long as wide in *L. wirtzi*, whereas it is 16 times as long as wide in the holotype of *L. guamensis* (Anker & Cox, 2011, fig. 3a); (x) the propodus of the fourth pereiopod is 15 times as long as wide in *L. wirtzi*, whereas it is 25 times as long as wide in the holotype of *L. guamensis* (Anker & Cox, 2011, fig. 3c); (xi) the merus of the fifth pereiopod is 11 times as long as wide in *L. wirtzi*, whereas it is 14 times as long as wide in the holotype of *L. guamensis* (see Anker & Cox, 2011, fig. 3d); (xii) the merus of the fifth pereiopod of *L. wirtzi* has 1-2 articulating distolateral spines, whereas in the holotype of *L. guamensis* 4 articulating spines are present of which 2 proximoventral and 2 distolateral (Fig. 15C); in the type-description of *L. guamensis* only 2 distolateral spines are mentioned (Anker & Cox, 2011, fig. 3d); (xiii) the carpus of the fifth pereiopod is 10 times as long as wide in *L. wirtzi*, whereas it is 18.4 times as long as wide in the holotype of *L. guamensis* (Anker &

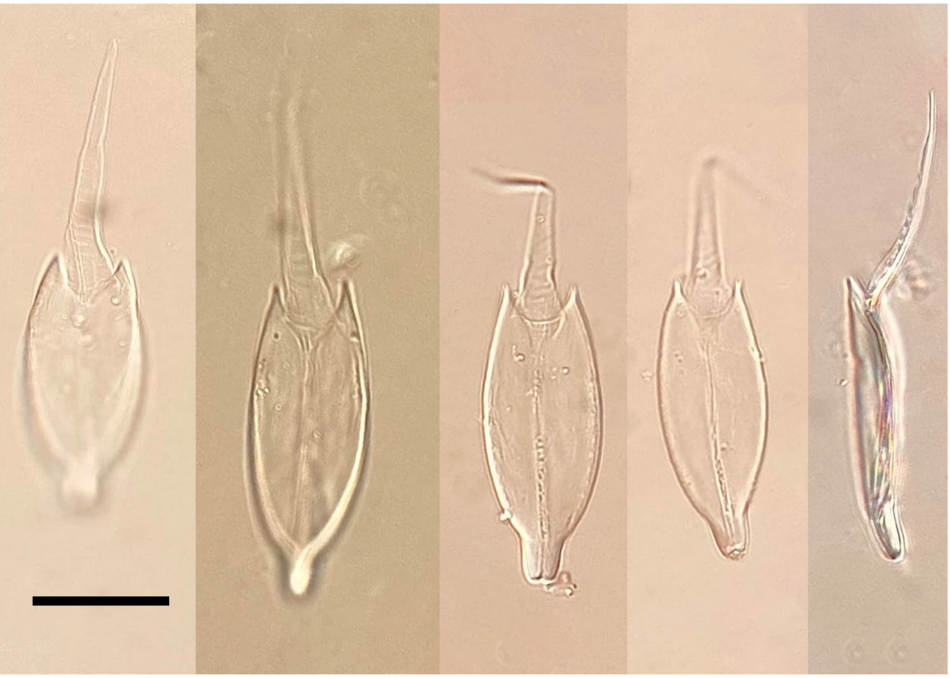

Fig. 13. *Lysmata wirtzi* spec. nov., ovigerous specimen, pocl. 3.9 mm, São Tomé, RMNH.CRUS.D.59490, tegumental scales, four scales on left side in dorsal view, scale on right side in lateral view. Scale = 0.05 mm.

Cox, 2011, fig. 3c); (xiv) the propodus of the fifth pereiopod is 16.5 times as long as wide in *L. wirtzi*, whereas it is 27.5 times as long as wide in the holotype of *L. guamensis* (Anker & Cox, 2011, fig. 3d). The most striking differences between the two species are the more slender ambulatory pereiopods and higher number of articulating spines in the meri of the ambulatory pereiopods in *L. guamensis* compared to these features in *L. wirtzi* spec. nov.

Colour patterns in *Lysmata* shrimps can be very helpful in distinguishing species. Unfortunately, the colour pattern in of *L. guamensis* is not known.

Remarks on tegumental scales. — The tegumental scales (figs. 2A, 13) are directed forward on first three abdominal pleons, carapace and anterior appendages and backward on the posterior three abdominal segments, telson and uropods. They have a narrow basal part which is falling in a pit in the surface of the carapace, abdomen or appendages, followed by an oval part with serrated margins and a tubercular midrib, the distal part is slender, seta-like, as described and figured by De Grave & Wood (2011: pp. 45-46, fig. 2) for other *Lysmata* species. When tegumental scales are abraded away, they leave a pitted surface.

Distribution remarks. — The species described here should currently be considered endemic to São Tomé and the Canary Islands. As it is a species native to

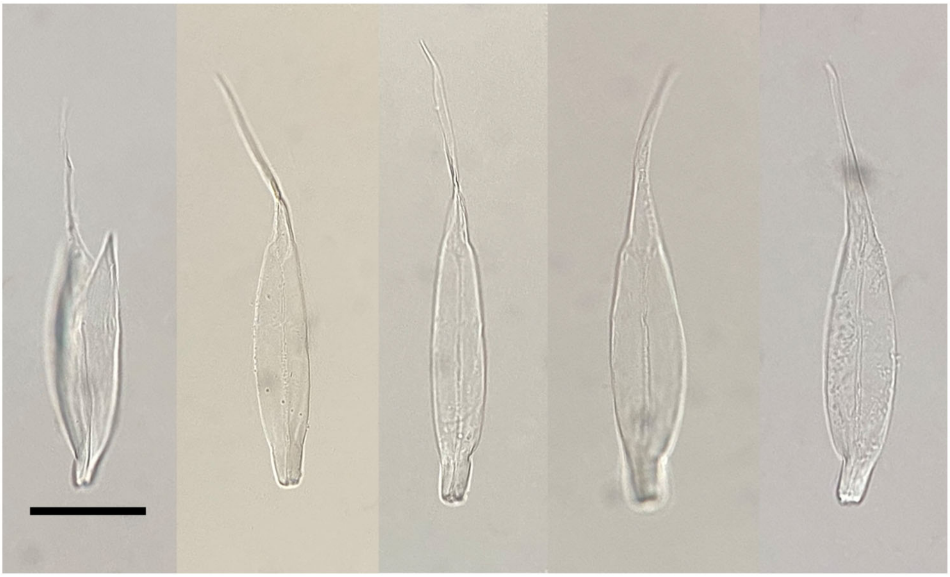

Fig. 14. *Lysmata guamensis* Anker & Cox, 2011, holotype, FLMNH UF Arthropoda 1229, ovigerous specimen, pocl. 4.15 mm, tegumental scales. Scale = 0.05 mm.

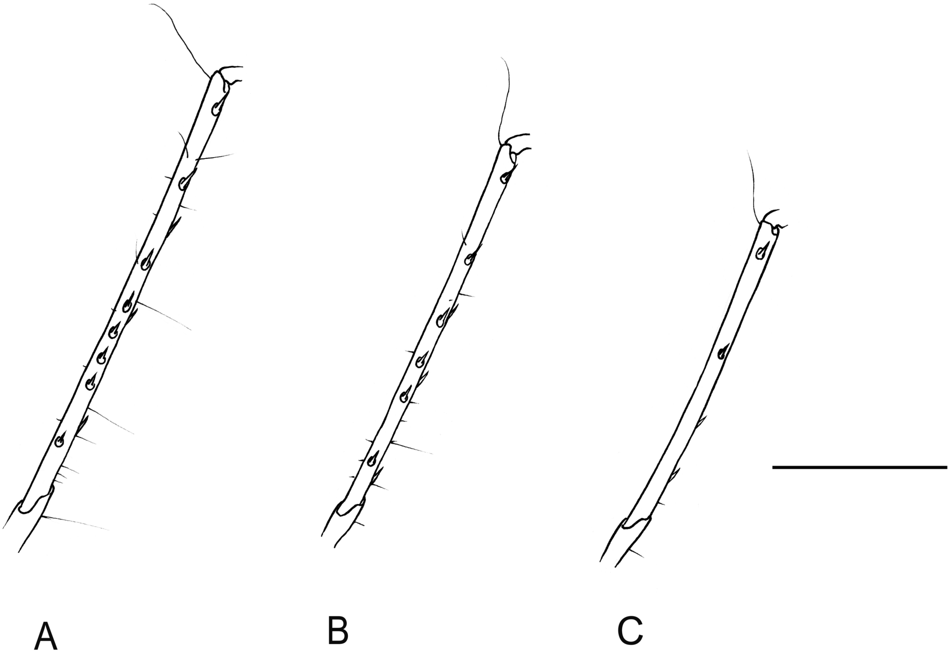

Fig. 15. *Lysmata guamensis* Anker & Cox, 2011, holotype, FLMNH UF Arthropoda 1229, ovigerous specimen, pocl. 4.15 mm. A, Right third pereiopod merus, lateral view; B, right fourth pereiopod merus, lateral view; C, right fifth pereiopod merus, lateral view. Scale = 2 mm.

shaded environments (scyophilous), we do not rule out the possibility of finding further specimens of this species in other islands of the eastern Atlantic, or even along the African coast.

DNA analyses

In the present study, the clade characterized by a long (multiarticulate) accessory ramous of the antennulae, as recognized by Baeza et al. (2009), Baeza (2010) and Fiedler et al. (2010), is recovered with high support (bootstrap value 98) in the phylogenetic reconstruction (fig. 16). The short accessory ramous clade (bootstrap value 76) and the variably shaped accessory ramous clade (bootstrap value <50) are recovered but not well supported.

The present specimen clusters together with *L. olavoi*, though with low support (bootstrap value <50). Both species are positioned basally within *Lysmata*, occupying an isolated position and not clustering with any of the previously recognized clades (fig. 16).

DISCUSSION

Lysmata wirtzi spec. nov. and *Lysmata guamensis* share many morphological features. The most striking differences between the species are the more robust and slightly shorter ambulatory pereiopods in the new species and the lower number of articulating spines on the meri of the ambulatory pereiopods in *L. wirtzi* compared to these features in *L. guamensis*.

Morphologically similar but genetically different pairs of species of which one sister species is occurring in the Atlantic and the other in the Indo-West Pacific have been recognized previously. Morphological differences between the Indo-West Pacific *Lysmata amboinensis* (De Man, 1888) and the Atlantic *L. grabhami* (Gordon, 1935) for instance, have not been observed. This was noted by Hayashi (1975) who synonymized the species. Observations on differences between the colour patterns of both species lead Manning & Chace (1990) to recognized them as separate species again. Genetic differences between the species confirmed their separate taxonomic status (Baeza et al., 2009; Baeza, 2010). Another shrimp species that was initially thought to have a circumtropical distribution, *Thor amboinensis* (De Man, 1888), was recently recognized to comprise a complex of species and was subsequently split based on differences in colour pattern and molecular analyses (Anker & Baeza, 2021). It is expected that *L. guamensis* and *L. wirtzi* spec. nov. might belong to such a species complex and when further material becomes available this will be confirmed by molecular data and information on their colour patterns.

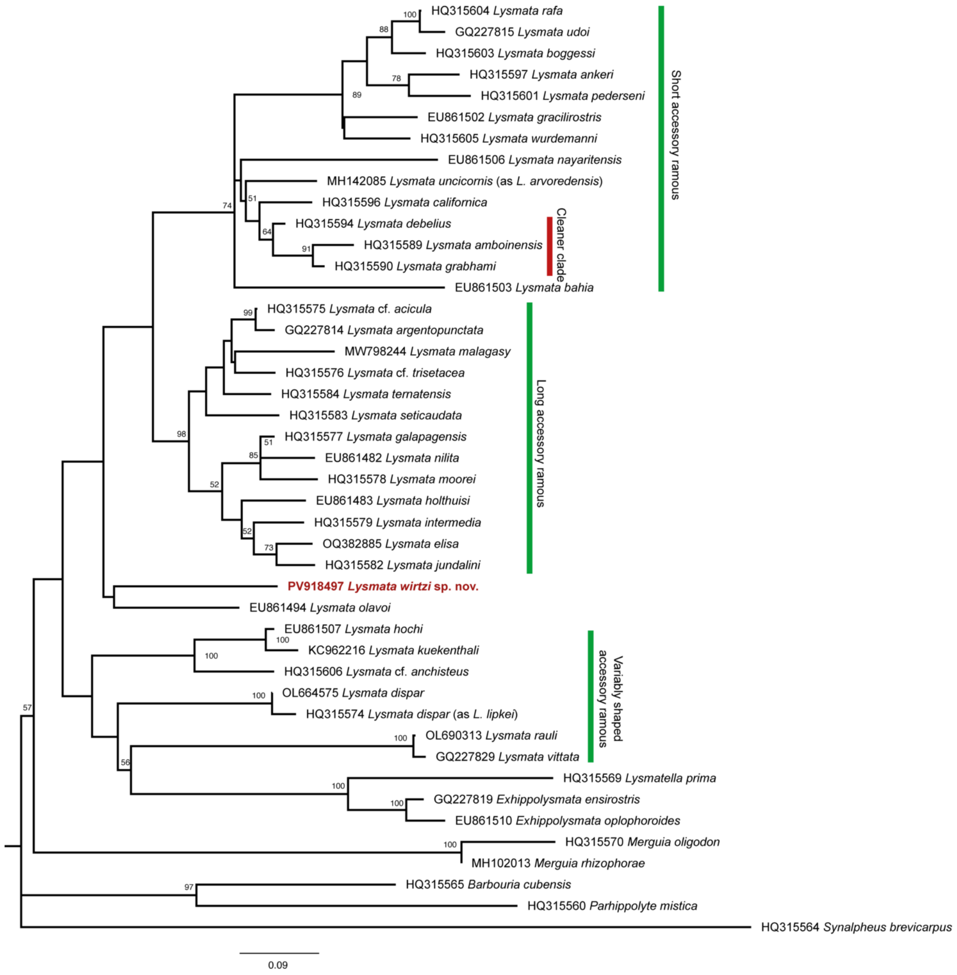

Fig. 16. Phylogenetic tree obtained from Maximum Likelihood (ML) analysis of the partial 16S rRNA gene for *Lysmata* Risso, 1816, and representatives of related genera. Numbers near the branches represent bootstrap values. Low node values ($\leqslant 50$) were removed from the final topology. Name in red indicates the new sequence obtained in this study.

The population of *L. wirtzi* spec. nov. on Tenerife seems under thread. Despite its relatively good state of conservation in 2014 (which has since deteriorated significantly), the ‘Cueva Marina de San Juan’ on Tenerife was (and still is) subjected to a series of main impacts, such as recreational and scientific diving (with medium to high attendance), land-to-sea discharges (urban wastewater), and the effects of a golf course near a banana plantation (likely contributing fertilisers and biocides) (Monterroso et al., 2015; Riera et al., 2016). Another pressure not mentioned in these studies has been the illegal collection of spiny lobsters for commercialisation and consumption, as well as the collection of other invertebrates for the aquarium trade.

ACKNOWLEDGEMENTS

The holotype specimen was collected while Peter Wirtz was diving at Atlantic Diving Base, Santana Bay and supported by a grant from CCMAR through projects UIDB/04326/2020, UIDP/04326/2020 and LA/P/0101/2020. We are very thankful for Amanda Bemis and Gustav Paulay from the Florida Museum of Natural History for making the holotype of *Lysmata guamensis* available to us for comparison. We thank Laura van Hoek for carrying out the DNA extractions and Polymerase Chain Reactions. Comments and suggestions by Sammy De Grave and an anonymous reviewer helped improving this manuscript.

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First received 25 April 2025.
Final version accepted 14 July 2025.