

## Research Article

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### Corresponding author:

Rodrigo Guéron; Email: [rggueron@gmail.com](mailto:rggueron@gmail.com)

# Refining southwestern Atlantic peppermint shrimp biodiversity: description of a new species of *Lysmata* (Decapoda: Lysmatidae) using an integrative systematic approach

Rodrigo Guéron<sup>1</sup> , J. Antonio Baeza<sup>2,3,4</sup> , Gabriel Lucas Bochini<sup>5</sup> , Mariana Terossi<sup>6</sup>  and Alexandre Oliveira Almeida<sup>1</sup> 

<sup>1</sup>Department of Zoology, Biosciences Center, Federal University of Pernambuco (UFPE), Avenida Professor Moraes Rêgo, 1235, 50670-901 Recife, PE, Brazil; <sup>2</sup>Department of Biological Sciences, 132 Long Hall, Clemson University, Clemson, SC 29634, USA; <sup>3</sup>Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, FL 34949, USA; <sup>4</sup>Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile; <sup>5</sup>Department of Biology, Faculty of Philosophy, Sciences and Letters at Ribeirão Preto (FFCLRP), University of São Paulo (USP), Avenida Bandeirantes, 3900, 14040-901 Ribeirão Preto, São Paulo, Brazil and <sup>6</sup>Department of Zoology, Institute of Biosciences, Federal University of Rio Grande do Sul (UFRGS), Avenida Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil

## Abstract

Currently, 14 of the 50 species of *Lysmata* are known to possess a long accessory branch with more than two articles. Historically, *Lysmata intermedia* and *Lysmata moorei* were the only two ‘long-branch’ species inhabiting the southwestern Atlantic. Here we describe, based on morphological, molecular and colour pattern data, a new species of *Lysmata* possessing a long accessory branch from Pernambuco, northeastern Brazil. Our maximum-likelihood analysis recovered *Lysmata elisa* sp. n. as a sister species to *Lysmata jundalini*. Both species are closely related to *Lysmata holthuisi* and *L. intermedia*. The four aforementioned species comprise the *L. intermedia* species complex. The new species may be morphologically distinguished from the other closely related species by different sets of characters, which include details of the dorsolateral antennular flagellum, armature of ischium of the second pair of pereopods, intraorbital process shape and relative proportions of pereopods. Our results reinforce the importance of refining biodiversity data through the application of integrative taxonomic approaches to expand the knowledge of local and global biodiversity. The biodiversity of *Lysmata* deserves special attention, as they are intensively exploited in the aquarium trade.

## Introduction

Lysmatidae Dana, 1852 is currently comprised of five genera (*Exhippolysmata* Stebbing, 1915, *Ligur* Sarato, 1885, *Lysmata* Risso, 1816, *Lysmatella* Borradaile, 1915 and *Mimocaris* Nobili, 1903), of which *Lysmata* is the most speciose with 50 valid species (Prakash and Baeza, 2017; De Grave and Anker, 2018; Wang and Sha, 2018; Ashrafi *et al.*, 2021; Guéron *et al.*, 2022). These shrimps are widely distributed from tropical to temperate regions and exhibit a wide diversity of social systems (e.g. pair-living, small groups or aggregations), mating systems (monogamous *vs* non-monogamous) and lifestyles (facultative or obligatory symbiosis, or free-living) (Bauer, 2000; Baeza, 2010a, 2013; Baeza *et al.*, 2016). Due to their beauty, bright coloration, ability to clean fish from parasites and controlling aquarium pests, shrimps belonging to the genus *Lysmata* are among the most desired marine invertebrates by aquarists worldwide and, thus, have been traded extensively over the last few decades (Calado *et al.*, 2003; Baeza and Behringer, 2017; Rhyne *et al.*, 2017; Vaughan *et al.*, 2017, 2018; Barton *et al.*, 2020).

Earlier molecular analyses suggested three subclades within *Lysmata*, which are represented by species with different sizes and shapes of the accessory branch in the dorsolateral antennular flagellum: (1) short, (2) long and (3) short/unguiform/absent (i.e. variable shape) (Baeza, 2010b; Fiedler *et al.*, 2010). Although paraphyly is observed among clades within *Lysmata* and it is evidenced by the homoplasy of the short accessory branch, the lineage containing only species bearing a long accessory branch is monophyletic (Baeza, 2010b; Fiedler *et al.*, 2010). Currently, 14 species of *Lysmata* are known to possess a long accessory branch with more than two articles (hereafter long-branch species), namely *L. argentopunctata* Wicksten, 2000, *L. chica* Wicksten, 2000, *L. galapagensis* Schmitt, 1904, *L. holthuisi* Anker, Baeza and De Grave, 2009, *L. intermedia* (Kingsley, 1878), *L. jundalini* Rhyne, Calado and dos Santos, 2012, *L. malagasy* Ashrafi, Baeza and Duriz, 2021, *L. moorei* Rathbun, 1901, *L. napoleoni* De Grave and Anker, 2018, *L. nilita* Dohrn and Holthuis, 1950, *L. seticaudata* Risso, 1816, *L. ternatensis* De Man, 1902, *L. trisetacea* (Heller, 1861) and *L. zacae* Armstrong, 1941.

Historically, *L. intermedia* and *L. moorei* were the only two long-branch species inhabiting the southwestern Atlantic (Christoffersen, 1980, 1998; Ramos-Porto *et al.*, 1995; Coelho Filho, 2006; Almeida *et al.*, 2007; Santos *et al.*, 2012; Barros-Alves *et al.*, 2015, 2016; Pachelle *et al.*,



2016, 2020). Recently, an individual collected along the coast of Espírito Santo, southeastern Brazil, was tentatively identified as *L. jundalini* after detailed morphological analysis, which increases the number of long-branch species in the region (Pachelle *et al.*, 2020). Between 2017 and 2019, we collected several shrimps belonging to the genus *Lysmata* among rocks close to sandstone reefs in Suape Bay and Praia dos Carneiros, Pernambuco, Brazil, that resemble *L. jundalini* in most taxonomic characters, but diverged in colour pattern. Additionally, molecular analysis confirmed that our specimens were genetically dissimilar to *L. jundalini sensu stricto* (see 'Discussion'). Thus, we described herein a new species of *Lysmata* from the southwestern Atlantic, which is closely related to *L. jundalini*, based on molecular, morphological and colour pattern data.

## Materials and methods

Specimens were collected along the sandstone reefs of Praia dos Carneiros (8°41'39.06"S 35°4'27.93"W) and Suape Bay (8°21'54.89"S 34°56'51.38"W), Pernambuco, northeastern Brazil, using artificial refuge structures (ARSs) following the methodology of Bochini *et al.* (2020). ARSs consisted of cube-shaped structures (25 × 25 × 25 cm<sup>3</sup>) made of plastic mesh filled with sets of polyvinyl chloride tubes of different diameters and sets of three shade nets tied together. These artificial structures work as 'attractors' for some benthic species and were placed in crevices at depths varying between 3 and 5 m using scuba diving.

The reef of Praia dos Carneiros is located within the largest federal marine conservation area in Brazil (Costa dos Corais Environmental Protection Area – ICMBio; <http://www.icmbio.gov.br/apacostadoscorais>). The Suape Bay reef is in a highly impacted area close to the Suape Industrial Port Complex – the most important port complex in northeastern Brazil.

After collection, shrimps were brought to the laboratory, where they were anaesthetized on ice, photographed and fixed in 70% ethanol. Drawings and measurements of the specimens were made with a camera lucida mounted on a Leica M50 stereomicroscope and Leica DME microscope. All shrimp carapace lengths were measured in millimetres from the post-orbital angle to the posterior margin of the carapace (pocl, mm). Due to protandric hermaphroditism reported in many species of *Lysmata* (see Baeza, 2018), individuals were classified solely as ovigerous (ov.) or non-ovigerous (non-ov.). Type material is deposited at Museu de Oceanografia Professor Petrônio Alves Coelho of Universidade Federal de Pernambuco (MOUFPE), Recife, Brazil and Coleção de Crustáceos do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul (DZ/UFRGS), Porto Alegre, Brazil.

## DNA sample preparation, extraction and sequencing

We dissected a small piece of pleonal muscle tissue and extracted total genomic DNA using the Qiagen DNeasy® Blood and Tissue Kit (Cat. No. 69504) following the manufacturer's protocol. Polymerase chain reaction (PCR) was used to amplify target regions of the mtDNA 16S rRNA gene (~557 bp; Schubart *et al.*, 2000) with specific primers, 16L2 (5'-TGCCTGTTTAT CAAAACAT-3') and 1472 (5'-AGATAGAAACCAACCTGG3'; Schubart *et al.*, 2000; Baeza *et al.*, 2009). PCR products were purified using an ExoSAP-IT kit and sequenced with ABI Big Dye Terminator Mix (Applied Biosystems, Waltham, USA) on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems automatic sequencer). All sequences were confirmed by sequencing both strands and a consensus sequence for the two strands was obtained using the computer program Bioedit v.7.2.5 (Hall, 2005) with ClustalW alignment (Thompson *et al.*, 1994). All new sequences were submitted to GenBank.

## Phylogenetic analysis

To examine the genetic dissimilarity between our newly collected specimens and other closely and distantly related species of *Lysmata*, we constructed a molecular phylogeny using fragments of the mtDNA 16S rRNA gene. In total, 31 sequences of species belonging to all previously recognized groups within *Lysmata* (e.g. short branch, long branch and variable branch shape [Baeza, 2010b; Fiedler *et al.*, 2010]) were used, two of which were generated by us and 29 were obtained from GenBank (Table 1). We included sequences from all long-branch species already sequenced (11 out of 14 described species). In addition, sequences of *Merguia rhizophorae* Rathbun, 1900 and *Merguia oligodon* De Man, 1888, also obtained from GenBank, were included in the analyses as outgroups (Table 1).

We performed the initial sequence alignment using MUSCLE as implemented in MEGA X (Kumar *et al.*, 2018). The aligned sequences contained multiple indels or 'islands' and were considered ambiguous. Therefore, we used the program GBlocks v0.91b (Castresana, 2000) with the less stringent setup to identify and omit highly divergent and misaligned positions of the mtDNA 16S rRNA gene. The resulting alignment consisted of 425 bp. Aligned sequences were analysed with the program jModelTest 2 (Darriba *et al.*, 2012), which compares different models of nucleotide substitution in a hierarchical hypothesis testing framework to select a model that best fits the data. The optimal model found by jModelTest 2 (selected by the Akaike information criterion) was TrN + G. The parameters calculated were as follows: assumed nucleotide frequencies: A = 0.3384, C = 0.0926, G = 0.2039, T = 0.3652; replacement rate matrix with replacement: A – C = 1.0000, A – G = 7.2896, A – T = 1.0000, C – G = 1.0000, C – T = 10.4018, G – T = 1.0000; rates for variable locations assumed to follow a gamma distribution (G) with shape parameter = 0.4260. This model was used in the web server IQ-TREE (Trifinopoulos *et al.*, 2016, <http://iqtree.cibiv.univie.ac.at>) for maximum-likelihood (ML) analysis. The robustness of the ML tree topologies was evaluated by bootstrapping the observed data 2000 times. Additionally, we calculated pairwise genetic distances (intra- and interspecific) between sequences using the TrN model using MEGA X (Kumar *et al.*, 2018).

## Results

### Taxonomy

Order DECAPODA Latreille, 1802  
 Infraorder CARIDEA Dana, 1852a  
 Family LYSMATIDAE Dana, 1852b

*Lysmata* Risso, 1816

*Lysmata elisa* sp. n.

urn:lsid:zoobank.org:act:FCD33BD2-83D5-4DEA-BD16-4F921EB9D230

(Figures 1–4)

(?) *Lysmata* cf. *jundalini* – Pachelle *et al.*, 2020: 68, Figure 8.

### Type material

**Brazil, Pernambuco, Cabo de Santo Agostinho, Suape Bay.**

Holotype: ov. specimen (pocl 4.18 mm), MOUFPE 21022, GenBank 16S gene (OQ382885), depth 3–5 m, collectors G. L. Bochini, G. O. Soledade, P. Santos, R. Guéron and A. O. Almeida, 26/X/2018. Paratypes: one non-ov. specimen (pocl 4.75 mm), DZ/UFRGS 6936, GenBank 16S gene (OQ382884), same collection data as for holotype, 26/VI/2018; four non-ov. specimens (pocl 3.07, 3.91, 3.98, 4.16 mm), MOUFPE 21023, same collection data as for holotype, 26/VI/2018; seven non-ov. specimens (pocl 3.49, 3.93, 4.33, 4.36, 4.40, 4.94, 5.21 mm), MOUFPE 21024, same collection data as for holotype, 16/VIII/2019; one non-ov. specimen (pocl 5.20 mm), DZ/UFRGS 6940, same depth data as for

**Table 1.** *Lysmata* species and other caridean shrimps used for phylogenetic reconstruction using mitochondrial 16S RNA marker

| Species   | Collection site            | Catalogue number     | GenBank  |
|---|----------------------------|----------------------|----------|
| <i>Lysmata amboinensis</i> (De Man, 1888)                   | Aqua. Store, FL, USA       | UMML 32.9451         | EU861488 |
| <i>Lysmata ankeri</i> Rhyne and Lin, 2006                   | Fort Pierce, FL, USA       | UMML 32.9452         | EU861501 |
| <i>Lysmata argentopunctata</i> Wicksten, 2000               | Cabo San Lucas, Mexico     | CNCR 20998           | GQ227814 |
| <i>Lysmata boggessi</i> Rhyne and Lin, 2006                 | St. Petersburg, FL, USA    | UMML 32.9454         | EU861505 |
| <i>Lysmata</i> cf. <i>trisetacea</i> (Heller, 1861)         | Kapapa Island, HI, USA     | Not vouchered        | HQ315586 |
| <i>Lysmata</i> cf. <i>trisetacea</i> (Heller, 1861)         | Kapapa Island, HI, USA     | Not vouchered        | HQ315576 |
| <i>Lysmata debelius</i> Bruce, 1983                         | Aqua. Store, FL, USA       | UMML 32.9456         | EU861492 |
| <i>Lysmata galapagensis</i> Schmitt, 1924                   | Islas Secas, Panama        | UMML 32.9457         | EU861480 |
| <i>Lysmata grabhami</i> (Gordon, 1935)                      | Aqua. Store, FL, USA       | UMML 32.9459         | EU861489 |
| <i>Lysmata hochi</i> Baeza and Anker, 2008                  | Long Key, FL, USA          | UMML 32.9460         | EU861507 |
| <i>Lysmata holthuisi</i> Anker, Baeza and De Grave, 2009    | Chumical, Panama           | UMML 32.9466         | EU861483 |
| <i>Lysmata intermedia</i> (Kingsley, 1879)                  | Sebastian Inlet, FL, USA   | Not vouchered        | HQ315579 |
| <i>Lysmata intermedia</i> (Kingsley, 1879)                  | Bahia, Brazil              | Not vouchered        | HQ315581 |
| <i>Lysmata intermedia</i> (Kingsley, 1879)                  | Sergipe, Brazil            | MZUSP 37512          | MH102008 |
| <i>Lysmata intermedia</i> (Kingsley, 1879)                  | Bocas del Toro, Panama     | UMML 32.9461         | EU861484 |
| <i>Lysmata</i> cf. <i>intermedia</i> (Kingsley, 1879)       | Carrie Bow, Belize         | UMML 32.9606         | GQ227817 |
| <i>Lysmata jundalini</i> Rhyne, Calado and dos Santos, 2012 | NA                         | Not vouchered        | KF023094 |
| <i>Lysmata jundalini</i> Rhyne, Calado and dos Santos, 2012 | Puerto Rico                | Not vouchered        | HQ315582 |
| <i>Lysmata kuekenthali</i> (De Man, 1902)                   | NA                         | UMML 32.9467         | KC962216 |
| <i>Lysmata lipkei</i> Okuno and Fiedler, 2010               | Sesoko Is., Okinawa, Japan | Not vouchered        | HQ315574 |
| <i>Lysmata malagasy</i> Ashrafi, Baeza and Đuriš, 2021      | Madagascar                 | MNHN-IU-2010-4890    | MW798244 |
| <i>Lysmata moorei</i> (Rathbun, 1901)                       | Galeta, Panama             | UMML 32.9462         | EU861481 |
| <i>Lysmata elisa</i> sp. n.                                 | Pernambuco, Brazil         | MOUFPE 21022         | OQ382885 |
| <i>Lysmata elisa</i> sp. n.                                 | Pernambuco, Brazil         | DZ/UFRGS 6936        | OQ382884 |
| <i>Lysmata nilita</i> Dohrn and Holthuis, 1950              | Giglio, Italy              | SMF 32005            | EU861482 |
| <i>Lysmata pedersenii</i> Rhyne and Lin, 2006               | Carrie Bow, Belize         | UMML 32.9464         | EU861504 |
| <i>Lysmata rauli</i> Laubenheimer and Rhyne, 2010           | Sergipe, Brazil            | MZUSP 37509          | MH102012 |
| <i>Lysmata seticaudata</i> (Risso, 1816)                    | Portugal                   | UMML 32.9614         | GQ227827 |
| <i>Lysmata seticaudata</i> (Risso, 1816)                    | Corsica, France            | OUMNH.ZC.2007-24-003 | KF023083 |
| <i>Lysmata ternatensis</i> De Man, 1902                     | Akajima, Keramas, Japan    | Not vouchered        | HQ315584 |
| <i>Lysmata wurdemanni</i> (Gibbes, 1850)                    | Port Aransas, TX, USA      | Not vouchered        | EU135797 |
| <i>Merguia oligodon</i> (De Man, 1888)                      | Africa                     | OUMNH.ZC.2002-04-01  | GQ227826 |
| <i>Merguia rhizophorae</i> (Rathbun, 1900)                  | Bocas del Toro, Panama     | UMML 32.9471         | EU861508 |

Catalogue numbers, Museum or collection: CNCR, Colección de Crustáceos, Instituto de Biología, Departamento de Zoología, Universidad Nacional Autónoma de México, México; DZ/UFRGS, Coleção de Crustáceos do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; MOUFPE, Museu de Oceanografia Professor Petrônio Alves Coelho of Universidade Federal de Pernambuco, Recife, Brazil; MNHN, Museum National d'Histoire Naturelle, Paris, France; MZUSP, Museum of Zoology of the University of São Paulo, São Paulo, Brazil; OUMNH.ZC, Oxford University Museum of Natural History, Zoological Collection, Oxford, England; SMF, Senckenberg Museum, Frankfurt, Germany; UMML, University of Miami Marine Laboratories, Rosenstiel School of Marine Science, University of Miami, Miami, Florida, USA. Abbreviation: NA, not available.

holotype, collectors R. Guéron, W. M. Nascimento, K. Pasinato and P. H. Paixão, 09/IX/2022.

**Brazil, Pernambuco, Tamandaré, Praia dos Carneiros.** Paratype: one non-ov. specimen (podl 3.84 mm), MOUFPE 21025 depth 3–5 m, collectors G. L. Bochini, G. O. Soledade, P. Santos, R. Guéron and A. O. Almeida, 04/IV/2018.

#### Zoobank access

<https://zoobank.org/urn:lsid:zoobank.org:pub:FEBFC12D-B277-45A9-989A-36F49D2C67E0>

#### Etymology

The species is named in honour of Maria Elisa Guéron, Rodrigo Guéron's grandmother.

#### Ecology

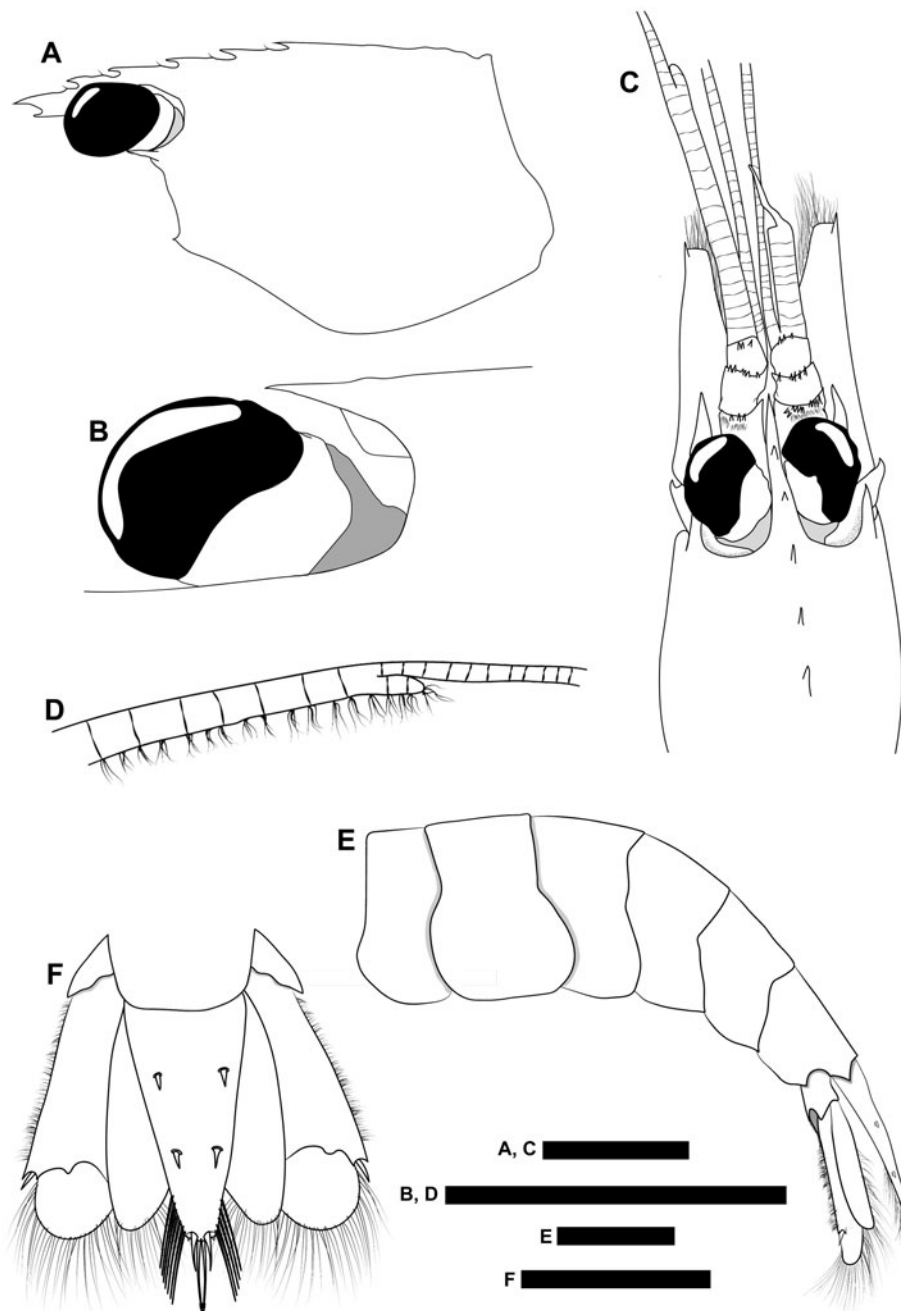
All specimens of *Lysmata elisa* sp. n. were collected using ARSs installed on sandstone reefs (beachrock) between 3 and 5 m. They are probably free-living, not associating with other organisms.

#### Type locality

Brazil, Pernambuco, Cabo de Santo Agostinho, Suape Bay.

#### Distribution

Currently known only from the type locality, Suape Bay and Praia dos Carneiros, both localities situated on the state of Pernambuco coast, northeastern Brazil.



**Figure 1.** *Lysmata elisa* sp. n., holotype (MOUFPE 21022): (A) carapace, lateral view; (B) intraorbital region, dorsolateral view; (C) frontal region, dorsal view; (D) dorsolateral antennular flagellum and accessory branch, lateral view; (E) pleon and telson, lateral view; (F) telson, dorsal view. Scale bars: A–F, 2 mm.

### Description

Rostrum (Figure 1A, C) straight, about 0.56 times as long as carapace, reaching half of the second article of the antennular peduncle; dorsal margin bearing five teeth evenly distributed with single seta between each tooth, third tooth close to post-orbital margin, fourth and fifth teeth situated on carapace posterior to post-orbital margin; ventral margin bearing two teeth, second tooth covered by the cornea. Carapace (Figure 1A, C) smooth, with rounded posteroventral margin; pterygostomial angle with minute and acute tooth; antennal tooth strong, slightly separated from ventral orbital angle, not reaching middle of cornea; intraorbital process (Figure 1B) triangular shaped in dorsolateral view, 1.53 times as wide as it is high, with rounded tip, no setation observed.

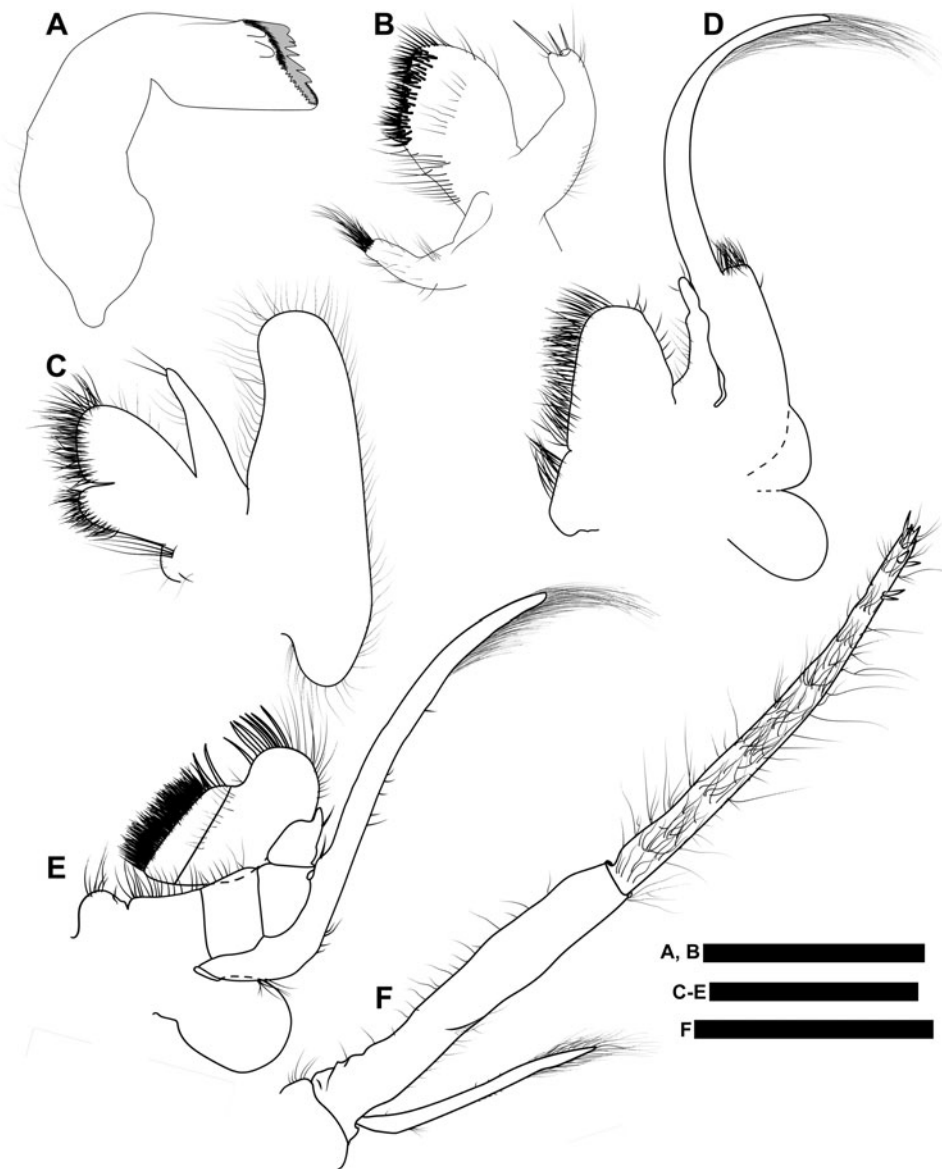
Antennular peduncle (Figure 1C) 0.63 times as long as scaphocerite, first article 2.96 times as long as second article, second

article 1.21 times as long as third article; all three articles bearing groups of spinules on distodorsal margin. Stylocerite (Figure 1C) overreaching first article of antennular peduncle. Dorsolateral antennular flagellum long; accessory branch (Figure 1C, D) with two free articles, fused portion with 18 articles, free portion 0.08 times as long as fused portion. Scaphocerite 3.38 times as long as it is wide; scaphocerite distolateral tooth overreaching distal margin of blade.

Pleon smooth (Figure 1E); first three pleonites with margins ventrally rounded; fourth pleonite angulated postero-ventrally with subtle posterolateral tooth; fifth pleonite with well-developed, distally projecting posterolateral tooth; sixth with acute posteroventral tooth and pair of posterior teeth on each side of telson.

Telson (Figure 1F) 1.52 times as long as sixth pleonite, 2.32 times as long as it is wide, tapering posteriorly; lateral margins





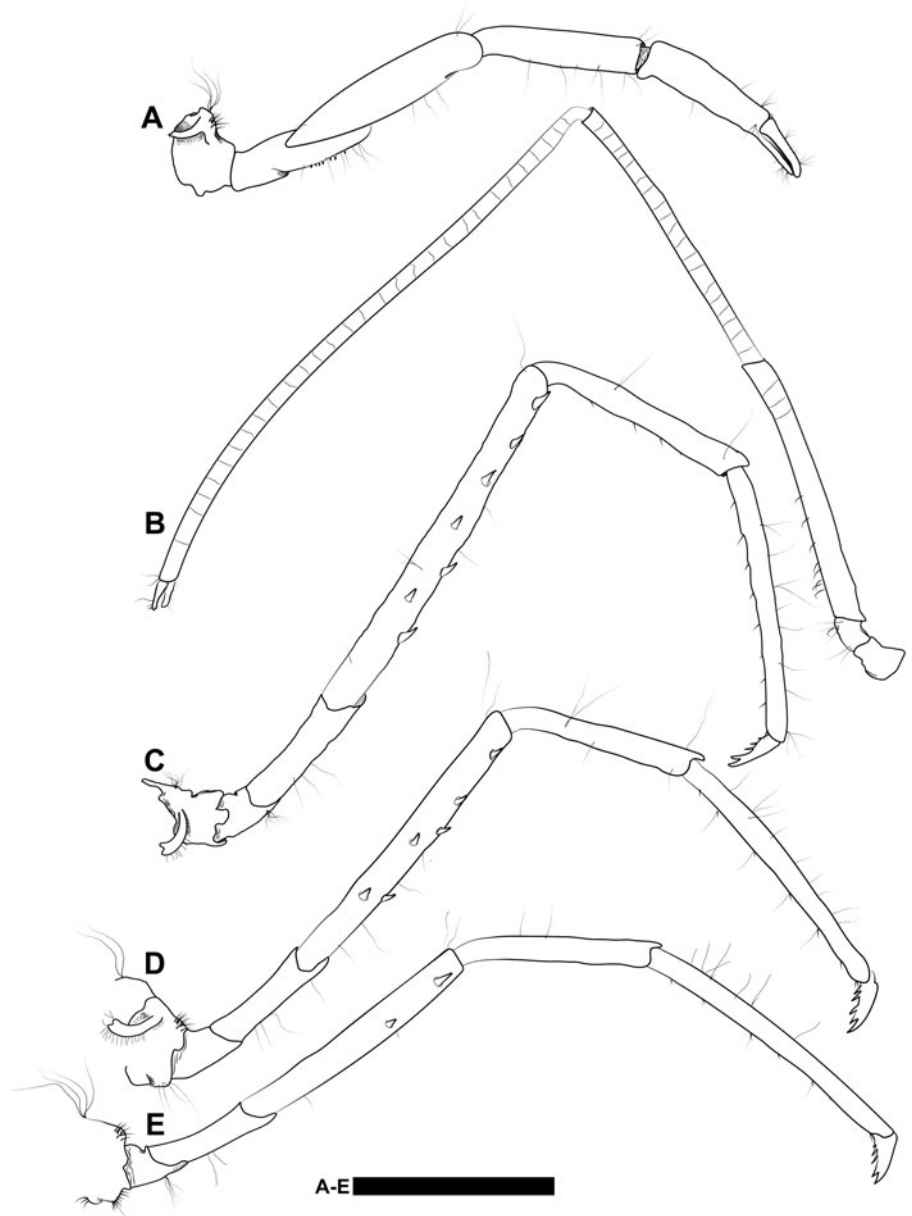
**Figure 2.** *Lysmata elisa* sp. n., paratype (MOUFPE 21023; carapace length: 3.91 mm): (A) right mandible, ventral view; (B) right maxillula; (C) right maxilla; (D) left first maxilliped; (E) right second maxilliped; (F) right third maxilliped. Scale bars: A–E, 1 mm; F, 2 mm.

of telson with numerous long plumose setae on distal half; dorsal surface with two pairs of spines, first pair at 0.33 and second at 0.63 of telson length; posterior margin with three pairs of spiniform setae: one pair of short and stout setae in the outermost position, one pair of long, stout and posteriorly acute setae, and one pair of long plumose setae in the innermost position. Uropod (Figure 1E, F) with protopodite 0.38 times as long as exopod in lateral view, posterolateral lobe with strong tooth bearing four long setae on margin; exopod with diaeresis bearing two strong teeth laterally, separated by slender and longer setae in between; endopod subequal to exopod length.

Mandible (Figure 2A) without palp and incisor process, molar process well-developed bearing five marginal teeth. Maxillula (Figure 2B) with curved palp shallowly bilobed distally, left lobe bearing one terminal strong and long plumose seta and eight marginal plumose setae that extend to distolateral margin of the right lobe, outer basolateral margin of palp bearing row of plumose setae; upper endite bearing several long plumose setae in both lateral margins, strong serrate setae densely gathered on distomesial margin, row of scattered long plumose setae on mesial region;

lower endite sub similar when compared to palp bearing scattered long plumose setae in both lateral margins, strong and long serrate setae densely gathered terminally. Maxilla (Figure 2C) with slender palp, bearing two terminal strong and long plumose setae and row of four plumose setae on lateral margin; upper endite deeply bilobed, distomesial margin bearing strong and long serrate setae densely gathered; lower endite rounded, feebly developed, bearing very long plumose setae distally; scaphognathite well developed, distal margin entirely covered with plumose setae.

First maxilliped (Figure 2D) with basal endite shallowly bilobed, distal margin entirely covered with plumose setae densely gathered, inner distolateral margin with scattered plumose setae, dorsomesial region with rows of plumose setae; endopod overreaching distal margin of caridean lobe bearing row of scattered long plumose setae on basolateral margin and three long plumose setae on distal margin; epipod deeply bilobed; exopod well-developed, distinctly curved, bearing several long plumose setae on distal half; caridean lobe small, not distinctly separated from flagellum, with dense plumose setae terminally. Second maxilliped (Figure 2E) with coxa short with long spiniform setae on



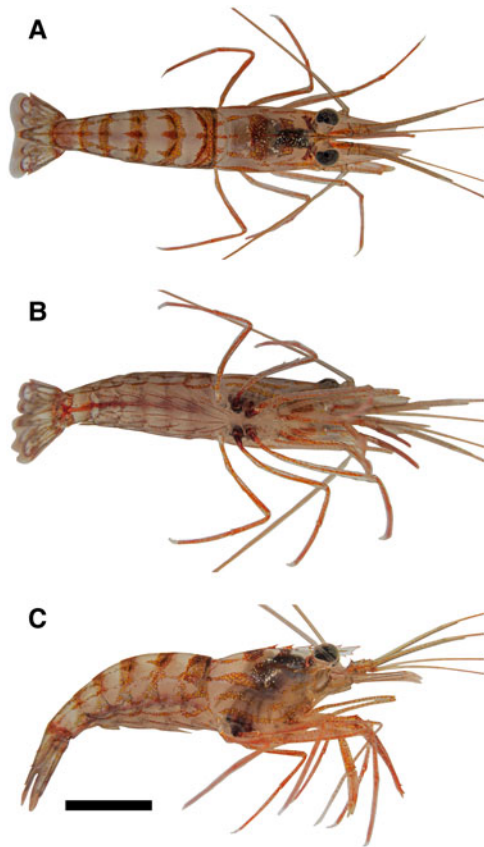
**Figure 3.** *Lysmata elisa* sp. n., paratype (MOUFPE 21024; carapace length: 4.33 mm): (A) first pereopod, lateral view; (B) second pereopod, lateral view; (C) third pereopod, lateral view; (D) fourth pereopod, lateral view; (E) fifth pereopod, lateral view. Scale bars: A–E, 2 mm.

inner lateral mesial margin; basis with plumose setae on mesial margin; endopod stout; ischium subquadrate with plumose setae on mesial margin; merus without apparent setaetion; carpus short, with one distodorsal robust plumose seta; propodus longer than wide, with anterior margin broadly rounded, distolateral margin with numerous long plumose setae; dactylar segment bearing rows of robust serrate setae on distal margin; exopod well-developed, slightly curved, bearing several long plumose setae on distal half; epipod medially rounded. Third maxilliped (Figure 2F) with long endopod, overreaching scaphocerite, ultimate segment with six distal and two subdistal spines; penultimate segment about 0.53 times as long as ultimate segment; exopod about 0.80 times as long as antepenultimate segment of endopod, bearing long plumose setae on distal half, eight short and simple setae on mediolateral margin, and tuff of plumose setae near base.

First pereopod (Figure 3A) with simple chela, overreaching scaphocerite by length of fingers when extended; ischium with row of seven (left) and eight (right) spinules and scattered setae on ventrolateral margin; merus with row of hook-like setae on dorsal margin, 1.10 times as long as carpus; carpus 4.84 times as long as it is high; chela 1.15 times as long as carpus, palm 1.87 times as long as dactylus, chela 4.74 times as long as it is

high; fingers conspicuously gaping when closed, tip tapering. Second pereopod (Figure 3B) with ischium with seven (left) and eight (right) scattered hook-like setae on ventral margin; merus with 17 (left) and 16 (right) articles, 1.13 times as long as ischium; carpus with 29 articles in both left and right sides, 2.05 times as long as merus; chela small, with palm 2.16 times as long as fingers.

Third to fifth pereopods (Figure 3C–E) are similar, decreasing in length from third to fifth. Third pereopod (Figure 3C) with ischium unarmed; merus with seven stout spines in both left and right sides, 2.46 times as long as ischium; carpus with two (left) and five (right) spiniform setae, 0.56 times as long as merus; propodus with nine (left) and eight (right) spiniform setae on ventromesial margin and pair of spines on ventrodistal margin, 1.31 as long as carpus; dactylus biunguiculate, terminal unguis longer than ventral, flexor margin bearing three spines on left and right sides. Fourth pereopod (Figure 3D) with ischium unarmed; merus with seven stout spines, 2.01 times as long as ischium; carpus with two spiniform setae, 0.65 times as long as merus; propodus with seven spiniform setae on ventromesial margin and pair of spines on ventrodistal margin, 1.33 as long as carpus; dactylus biunguiculate, terminal unguis longer than



**Figure 4.** Live colour pattern of *Lysmata elisa* sp. n., paratype (DZ/UFRGS 6940): (A) dorsal view; (B) ventral view; (C) lateral view. Scale bar: 5 mm.

ventral one, flexor margin bearing three spines on left and right sides. Fifth pereiopod (Figure 3E) with unarmed ischium; merus with two stout spines in both left and right sides, 2.21 times as long as ischium; carpus unarmed, 0.69 times as long as merus; propodus with eight spiniform setae on ventromesial margin and pair of spines on ventrodistal margin, 1.64 as long as carpus; dactylus biunguiculate, terminal unguis longer than ventral, flexor margin bearing three spines on left and right sides.

#### Colour in life

Colour pattern description is based on the paratype (voucher number DZ/UFRGS 6940; Figure 4A–C) approximately 72 h after being brought to the laboratory from the field. Body semi-translucent with thin longitudinal stripes formed by the combination of dense red and yellowish dots. Dorsal carapace with inverted trident, oriented posteriorly, lateral region with less evident oblique stripes. Pleon with nine (three dorsal and six lateral) thin longitudinal stripes that may be either continuous or discontinuous; dorsal stripes parallel that converge on the distal margin of the sixth pleonite; evident gapping of chromatophores between the stripes that are interrupted by transversal bands on the transition between each pleonite. Base of eyestalk with two broad longitudinal red bands running from base to proximal margin of cornea. Pereiopods semi-translucent with red spots that may vary from few or very dense; coxa of third and fourth pereiopod with conspicuous dark blue spot, barely reaching the coxa of fifth pereiopod. Protopodite of uropods with semi-translucent base, while the distal half region is bright red (Figure 4A–C).

#### Morphological variation

Rostral formula (dorsal + post-orbital/ventral teeth) varies little in *L. elisa* sp. n.: 2 + 3/2; 3 + 2/2; 3 + 2/3; 3 + 3/2; and 3 + 3/3;

rostrum length ranges from the proximal margin of the second article to beyond half of the third article of the antennular peduncle. Ratio of fused vs free portion of the dorsolateral antennular flagellum varies between 0.05 and 0.21, with a mean value of about 0.12; accessory branch articles vary between 2 and 5, whereas fused portion articulation varies between 11 and 25. The number of spines in the ultimate segment of the third maxilliped varies between 7 and 10; ratio of penultimate vs ultimate segment varies between 0.44 and 0.53.

Ratios of the first pereiopod also vary; length of merus vs carpus varies between 1.03 and 1.95; carpal length vs height varies between 4.38 and 6.23; length of palm vs dactylus varies between 1.82 and 2.52; length of chela vs carpus varies between 0.91 and 1.59; length of dactylus vs chela varies between 0.28 and 0.37; chela length vs height varies between 4.55 and 5.30. The number of hook-like setae on the ischium of the second pereiopod varies between 3 and 8; meral and carpal articles of the second pereiopod vary between 12–23 and 24–31, respectively. The number of meral and carpal articles also varies between left and right sides, with a considerable difference between meri (1–6), while the difference between carpi is smaller (1–2). The number of spines of the merus of the third, fourth and fifth pereiopod varies between 5–10, 4–8 and 1–3, respectively. The number of spines also varies between left and right sides: 1–3 on third, and 1 on fourth and fifth pereiopods. The number of spiniform setae of the propodus of third, fourth and fifth pereiopod varies between 6–10, 5–8 and 6–9, respectively, with an additional pair of distal spiniform setae always present. The number of spines also varies between left and right sides: 1–3 on third, 1 on fourth and 1–2 on fifth pereiopods. The number of spines on the flexor margin of dactylus varies between 3 and 4.

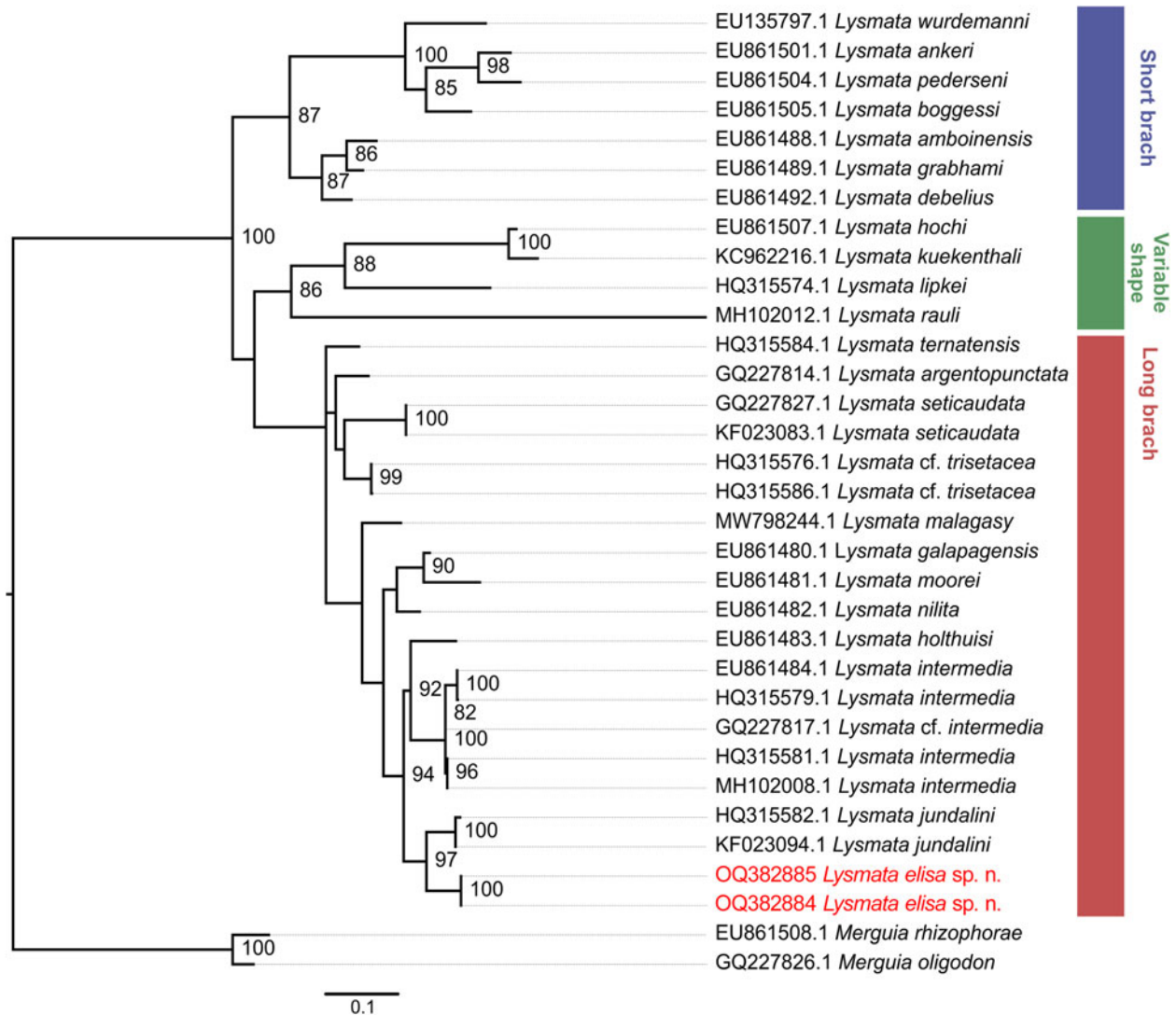
#### Phylogenetic analysis

The ML analysis placed the new species within the ‘long-branch’ clade of *Lysmata* (Figure 5), recognized by earlier studies (Baeza, 2010b; Fiedler *et al.*, 2010). The two sequences of *L. elisa* sp. n. from Suape Bay are identical (genetic distance = 0.000). *L. elisa* sp. n. is sister (ML = 97) to *L. jundalini*, represented in our study by two specimens, one collected in Puerto Rico (the species’ type locality) and a second specimen from an unknown locality. Genetic distance between *L. elisa* sp. n. and *L. jundalini* varied between 0.070 and 0.079. Additionally, our molecular analysis showed that the clade *L. elisa* sp. n. + *L. jundalini* is sister to a well-supported (ML = 94) clade composed of *L. intermedia* and *L. holthuisi* (Figure 5). Genetic distance between *L. elisa* sp. n. and *L. intermedia* varied between 0.095 and 0.101 and was 0.124 between *L. elisa* sp. n. and *L. holthuisi*. These values are higher than or similar to interspecific distances observed in the present study for other pairs of morphologically similar sister species based on the 16S gene, including *L. ankeri* Rhyne and Lin, 2006 vs *L. pedersenii* Rhyne and Lin, 2006 (0.078), *L. grabhami* (Gordon, 1935) vs *L. amboinensis* (De Man, 1888) (0.052) and *L. hochi* Baeza and Anker, 2008 vs *L. kuekenthami* (De Man, 1902) (0.047).

#### Discussion

In this study, we describe a new species of *Lysmata* from Brazil (Pernambuco) based on integrative systematic data. This new species is close (based on morphology, genetics, and colour pattern) to the eastern Pacific *L. holthuisi*, and both western Atlantic *L. intermedia* and *L. jundalini*. *Lysmata intermedia* was described from USA (Florida) and has been extensively recorded along the Brazilian coast (Ceará to São Paulo; Christoffersen, 1980; Ramos-Porto *et al.*, 1995; Almeida *et al.*, 2007; Santos *et al.*, 2012; Barros-Alves *et al.*, 2015, 2016; Pachelle *et al.*, 2016,





**Figure 5.** Phylogenetic tree obtained from ML analysis of the partial mtDNA 16S rRNA gene for *Lysmata* and *Merguia* shrimps. Numbers near the branches represent approximate likelihood-ratio test and bootstrap values obtained from ML in the webserver W-IQ-TREE (Trifinopoulos et al., 2016; <http://iqtree.cibiv.univie.ac.at/>). Low node values ( $\leq 60$ ) were removed from the final topology. Names in red indicate the sequences of the species described in the present study.

2020). *Lysmata jundalini* was described from Puerto Rico and first recorded off the Brazilian coast (Couves Island, São Paulo) in 2018 after reanalysis of material previously identified as *L. cf. intermedia* (Terossi et al., 2018). This same material was analysed again by Pachellet et al. (2020) and identified as *L. intermedia*. However, it is noteworthy to mention that the latter authors tentatively identified a separate individual as *L. jundalini*, which was collected at 15 m depth in Guarapari, Espírito Santo State, south-eastern Brazil. The authors commented that there is no record of the specimen's colour pattern, although Pachellet et al. (2020: 71) stated that the individual 'corresponds to *L. jundalini* in most taxonomically important morphological characters, including the number of subdivisions in the fused portion of the lateral antennular flagellum and the relatively longer first pereopod carpus'. We did not have access to this material; thus, we cannot determine whether this material represents *L. elisa* sp. n., *L. jundalini*, or a different species. Continued sampling is warranted to resolve the occurrence of *L. jundalini* in the southwestern Atlantic.

*Lysmata elisa* sp. n. resembles *L. holthuisi*, *L. intermedia* and *L. jundalini* by the number of rostral teeth (5–6 dorsal and 2–3 ventral) and length (reaching from proximal margin of the second to beyond half of the third antennular article), number of meral (12–

23) and carpal (24–31) articles of the second pair of pereopods and meral (5–10) and propodal (6–10) armature of the third pair of pereopods. Nevertheless, the new species can be distinguished from the other three by the pterygostomial tooth being minute in the new species vs well-developed in the others (D'Udekem D'Acoz, 2000; Anker et al., 2009; Rhyne et al., 2012). This character is also useful for distinguishing *L. holthuisi* from *L. argentopunctata* and *L. chica*, both of which present a minute pterygostomial tooth (Anker et al., 2009). Other specific characters are discussed below for each species.

The main characters that distinguish the new species from *L. holthuisi* are the number of free articles of the dorsolateral antennular flagellum (2–5 vs 6–7 in *L. holthuisi*), number of ventral teeth on the flexor margin of dactyli of pereopods 3–5 (3–4 vs 2 in *L. holthuisi*), ratio of penultimate vs ultimate segment of the third maxilliped (0.44–0.53 vs 0.73 in *L. holthuisi*) and armature of the fourth pleonite (posterolateral tooth present vs absent) (Anker et al., 2009; present study; see Table 2). Morphologically, *L. elisa* sp. n. can be separated from its sister species *L. jundalini* by the palm vs dactylus ratio of the first pereopod (1.82–2.52 vs 3 in *L. jundalini*), and the armature of ischium of the second pair of pereopods (3–8 hook-like setae vs 12 in *L. jundalini*) (Rhyne et al., 2012; present study; see Table 2). New morphological



**Table 2.** Important characters to delimit the four species belonging to the *L. intermedia* species complex

| Character   | <i>Lysmata elisa</i> sp. n.   | <i>Lysmata holthuisi</i> | <i>Lysmata intermedia</i>                                   | <i>Lysmata jundalini</i> |
|---|---|--------------------------|---|--------------------------|
| Intraorbital process shape  | Triangle-shaped, 1.53 times as wide as it is high, with a rounded tip | NA                       | More than 4 times as wide as it is high, with an acute tip* | NA                       |
| Pterygostomial tooth  | Minute  | Well-developed           | Well-developed  | Well-developed           |
| No. of free articles in the dorsolateral antennular flagellum         | 2–5   | 6–7                      | 3–4   | 3                        |
| No. of fused articles in the dorsolateral antennular flagellum        | 11–25   | NA                       | 9–17  | 24                       |
| Ratio of fused vs free portion of the antennular flagellum            | 0.05–0.21   | 0.19–0.29                | 0.13–0.15   | 0.15                     |
| Ratio of penultimate vs ultimate segment of the third maxilliped      | 0.44–0.53   | 0.73                     | 0.5   | NA                       |
| Relative size of the first pereopod carpus (length vs height)         | 4.38–6.23   | NA                       | 3.00–3.50*  | 4.50–5.00*               |
| Ratio of palm vs dactylus of the first pereopod                       | 1.82–2.52   | 1.8–1.85                 | NA  | 3                        |
| Armature of ischium of the second pair of pereopods                   | 3–8   | NA                       | NA  | 12                       |
| No. of ventral teeth on the flexor margin of dactyli of pereopods 3–5 | 3–4   | 2                        | 4–6   | 3                        |

The morphological data of *L. jundalini* and *L. holthuisi* were retrieved from their respective original descriptions (Rhyne *et al.*, 2012 and Anker *et al.*, 2009, respectively), while data of *L. intermedia* were retrieved from its redescription published by D'Udekem D'Acoz (2000). The data followed by an asterisk were retrieved from Pachelles *et al.* (2020). Abbreviation: NA, not available.

characters, such as the relative size of the first pereopod carpus and the number of fused articles in the antennular flagellum were proposed by Pachelles *et al.* (2020) to differentiate *L. intermedia* from *L. jundalini*. Only the former is useful to distinguish *L. elisa* sp. n. from *L. intermedia* due to an overlap in the number of articles in the fused portion of the antennular flagellum (Table 2). In *L. elisa* sp. n., the carpus is 4.38–6.23 times as long as it is high, while in *L. intermedia* it is 3.00–3.50 times as long as it is high (Pachelles *et al.*, 2020; present study; see Table 2). Pachelles *et al.* (2020) also showed that the intraorbital process shape is taxonomically informative in *Lysmata*. In the new species, the intraorbital process is triangle-shaped, 1.53 times as wide as it is high, with a rounded tip, while in *L. intermedia* it is more than four times as wide as it is high, with an acute tip (see Figure 7C in Pachelles *et al.*, 2020).

Species of the *L. intermedia* complex can also be separated by their colour in life, as can species of the *L. wurdemanni* (Gibbes, 1850) and *L. vittata* (Stimpson, 1860) complex, and the sister species *L. amboinensis* and *L. grabhami* (Rhyne and Lin, 2006; Baeza, 2010b; Baeza and Behringer, 2017; Aguilar *et al.*, 2022; Guéron *et al.*, 2022). *Lysmata elisa* sp. n. can be distinguished from *L. holthuisi* by the absence of a dense cover of chromatophores between the longitudinal stripes along the entire pleon, absence of a mediodorsal V-shaped band crossing the most-posterior post-rostral tooth and absence of a conspicuous coloured accessory branch of lateral flagellum, which is bright yellow in the latter species (all characteristics present in *L. holthuisi*; see Figure 4 in Anker *et al.*, 2009). In *L. jundalini*, the left and right dorsal stripes, adjacent to the central stripe, do not reach the distal margin of the sixth pleonite, while in *L. elisa* sp. n. the three dorsal stripes (central + adjacent) converge at the distal margin of the sixth pleonite forming a transverse band that extends to the proximal margin of the tail fan (see Figure 4 in Rhyne *et al.*, 2012 and Figure 10 in Pachelles *et al.*, 2020). Another diagnostic feature in *L. jundalini* is the brilliant orange coloration on the dorsal region of its pereopods 3–5, which is reddish in the new species. *Lysmata elisa* sp. n. can be distinguished from *L. intermedia* by the presence of a conspicuous dark blue spot on the coxa of fourth pereopod, which spreads to the coxa of the third pereopod (absent in *L. intermedia*). This same character is used to distinguish *L. jundalini* from *L. intermedia* (Rhyne *et al.*, 2012). Also, *L. intermedia* presents thin longitudinal stripes with a dense cover of chromatophores between them which goes parallelly from the proximal margin of the pleon to the distal margin of the telson, without converging (see Figure 5 in Rhyne *et al.*, 2012 and Figure 9 in Pachelles *et al.*, 2016).

Five species of the long-branch group can be readily distinguished from *L. elisa* sp. n. by the number of fused (11–25), free articles (2–5) and/or the ratio between length of free and fused portion of the dorsolateral antennular flagellum (0.05–0.21): *L. argentopunctata* (13–15 fused and 13–17 free, ratio 0.5; Wicksten, 2000; Anker *et al.*, 2009), *L. moorei* (8–13 fused and 7–16 free, no data on ratio; Rathbun, 1901; Pachelles *et al.*, 2020), *L. napoleoni* (6–9 fused and 10–13 free, ratio 1.1–2.2; De Grave and Anker, 2018), *L. seticaudata* (20–38 fused and 8–15 free, ratio 0.5–0.6; Dohrn and Holthuis, 1950), *L. ternatensis* (no data on fused and 10–18 free, no data on ratio; Chace, 1997; Madhavan *et al.*, 2019) and *L. trisetacea* (no data on fused and 7–10 free, no data on ratio; Chace, 1997; Wicksten, 2000).

An additional set of characters is also useful for differentiating the new species from the five listed above; specifically, the absence of a pterygostomial tooth (present in the new species), and carpal articles in the second pereopod that distinguish *L. moorei* (17) and *L. trisetacea* (19–24) from *L. elisa* sp. n. (24–31) (Rathbun, 1901; Chace, 1997). *Lysmata elisa* sp. n. also differs from *L.*

*moorei* by the shape of the intraorbital process, which is more than 6 times as wide as it is high in the latter *vs* 1.53 times in the former (see Figure 13C in Pachelle *et al.*, 2020). The fourth pleonite with the posterolateral angle rounded of *L. napoleoni*, *L. seticaudata* and *L. ternatensis* (Chace, 1997; D'Udekem D'Acoz, 2000; De Grave and Anker, 2018) also distinguishes from *L. elisa* sp. n., which possesses a pointed posterolateral angle.

Other species of the long-branch group may possess a similar number of articles in the free portion of the accessory branch (3–6) to that reported herein for *L. elisa* sp. n. However, other sets of characters are important to distinguish them. For instance, the new species may be distinguished from *L. malagasy* by possessing 11–25 articles in the fused portion of the antennular flagella (*vs* 8–9), a subtle posterolateral tooth on fourth pleonite (*vs* absent), merus and carpus of the second pereopod with 12–23 and 24–31 articles, respectively (*vs* 8 and 23) and propodus of the third pereopod bearing 6–9 spiniform setae (*vs* 16) (Ashrafi *et al.*, 2021). *Lysmata chica* and *L. galapagensis* present a smaller number of articles in the fused portion of the antennular flagella (10–11 and 6–13, respectively) and in the merus of the second pereopod (10–13 and 7–9, respectively) compared to the new species (Wicksten, 2000). Additionally, *L. galapagensis* presents no pterygostomial tooth on the anteroventral margin of the carapace (Wicksten, 2000). *Lysmata nilita* from the Mediterranean Sea resembles *L. elisa* sp. n. by the number of fused and free portion of the antennular flagellum; nevertheless they may be separated by the ratio of free *vs* fused portion of the antennular flagellum (0.20–0.33 in *L. nilita* *vs* 0.05–0.21 in *L. elisa* sp. n.) and the number of carpal articles in the second pereopod (30–35 in *L. nilita* *vs* 24–31 in *L. elisa* sp. n.) (Dohrn and Holthuis, 1950).

In the present study, we considered *L. zacae* as a long-branch species morphologically different than *L. elisa* sp. n. Despite neither *L. zacae*'s original description, nor its redescription explicitly state the number of accessory branch articles (Armstrong, 1941; Okuno, 1996), the latter author stated that this species possesses a 'dorsal antennular flagellum distinctly biramous', while Chace (1997) placed it in the group of species with 'distinct accessory branch of 3–16 articles'. The new species may be readily distinguished from *L. zacae* by the number of rostral ventral teeth (2–3 in *L. elisa* sp. n. *vs* 4 in *L. zacae*), presence of pterygostomial tooth (*vs* absent), antennular peduncle 0.63 times as long as scaphocerite (*vs* almost as long as scaphocerite), stylocerite overreaching first article of antennular peduncle (*vs* stylocerite short, reaching the proximal third of first article of antennular peduncle) and the number of carpal articles in the second pereopod (24–31 in *L. elisa* sp. n. *vs* 34–38 in *L. zacae*) (Armstrong, 1941; Okuno, 1996).

*Lysmata elisa* sp. n. is easily distinguished from two other exotic/invasive congeneric in the southwestern Atlantic, *L. lipkei* Okuno and Fiedler, 2010 and *L. rauli* Laubenheimer and Rhyne, 2010 and from the putatively ampho-Atlantic *L. uncicornis* Holthuis and Maurin, 1952. While the new species exhibits a long accessory branch in the dorsolateral flagellum, the other three species above possess one article in the accessory branch in the dorsolateral flagellum (Holthuis and Maurin, 1952; Laubenheimer and Rhyne, 2010; Okuno and Fiedler, 2010). Additionally, the new species may be differentiated from *L. lipkei* and *L. rauli* by the number of meral articles in the second pereopod (12–23 *vs* 23–27 in *L. lipkei* and 5–11 in *L. rauli*; Laubenheimer and Rhyne, 2010; Okuno and Fiedler, 2010; Guéron *et al.*, 2022), and from *L. uncicornis* by the shape of the fourth pleonite (posterolateral margin angle pointed *vs* posterolateral angle rounded in *L. uncicornis*; Holthuis and Maurin, 1952; Giraldes *et al.*, 2018 as *L. arvoredensis* Giraldes, Macedo, Brandão, Baeza and Freire, 2018).

Molecular analysis supports our morphological and colour pattern findings, which separate *L. elisa* sp. n. as a distinctive and well-supported lineage different than (sister to) *L. jundalini*. It is worth mentioning that one of the sequences of *L. jundalini* is from the type locality, Puerto Rico (Fiedler *et al.*, 2010). The *L. elisa* sp. n. + *L. jundalini* clade is sister to a second well-supported clade containing *L. intermedia* and *L. holthuisi* (Figure 5). All the four species above belong to the *L. intermedia* species complex (Rhyne *et al.*, 2012). The genetic distances between *L. elisa* sp. n. and *L. jundalini* varied between 0.070 and 0.079. The minimum genetic distances between *L. elisa* sp. n. and the other two species of the *L. intermedia* complex are 0.095 (*L. intermedia*) and 0.124 (*L. holthuisi*). These values are higher than or similar to interspecific distances observed in the present study for other pairs of morphologically similar sister species (see 'Results').

## Conclusion

*Lysmata elisa* sp. n. represents the 51st species belonging to *Lysmata* described worldwide and the number of species currently recorded in the southwestern Atlantic increases to 12. The new species belongs to the so-called 'long-branch' clade *sensu* Fiedler *et al.* (2010), which contains now 15 species described worldwide possessing a dorsolateral antennular flagellum with a long and multi-articulated accessory branch.

Our results reinforce the importance of refining biodiversity data through the application of integrative taxonomic approaches (i.e. combining morphological data with other data sources) to expand knowledge of local and global biodiversity. In earlier studies, integrative taxonomy proved to be an effective tool in resolving taxonomic confusions previously caused by morphological similarity between different taxa and the discovery of species not yet known, especially in peppermint shrimp (Rhyne and Lin, 2006; Baeza and Prakash, 2019; Aguilar *et al.*, 2022; Guéron *et al.*, 2022). The biodiversity of this group of shrimps deserves special attention, as they are intensively exploited in the aquarium trade (Baeza and Behringer, 2017). Despite its popularity, the difficulty of accurately identifying shrimps belonging to *Lysmata* is often documented in the literature, even for specialists (Rhyne and Lin, 2006; Soledade *et al.*, 2013; Baeza and Behringer, 2017). This problem, which is also observed in other groups of animals, may cause impacts on conservation and protection of *Lysmata* shrimps, which have the risk of being overexploited.

Finally, the discovery of the new species together with data from *L. intermedia* and *L. holthuisi* may shed light on biogeographic events (e.g. closure of Panama isthmus and Amazon River plume) responsible for diversification of marine organisms distributed along the tropical eastern Pacific and western Atlantic. Therefore, the *L. intermedia* complex represents a study model that may be used for future phylogeographic studies of marine taxa.

**Data.** Data are available on request from the authors.

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R. G., G. L. B., M. T. and A. O. A.; analysis and interpretation of data: R. G., J. A. B., G. L. B., M. T. and A. O. A.; preparation of figures/illustrations: R. G.; writing – original draft: R. G.; writing – critical review and editing: R. G., J. A. B., G. L. B., M. T. and A. O. A.

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## References

- Aguilar R, Prakash S, Ogburn MB, Lohan KMP, MacDonald KS III, Driskell AC, Ahnyong ST, Leray M, McIlroy SE, Tuckey TD and Baeza JA** (2022) Unresolved taxonomy can confound invasive species identification: the *Lysmata vittata* (Stimpson 1860) (Decapoda: Caridea: Lysmatidae) species complex and recent introduction of *Lysmata vittata sensu stricto* in the Western Atlantic. *Journal of Crustacean Biology* **42**(1), 1–18.
- Almeida AO, Guerrazzi MC and Coelho PA** (2007) Stomatopod and decapod crustaceans from Camamu Bay, state of Bahia, Brazil. *Zootaxa* **1553**(1), 1–45.
- Anker A, Baeza JA and De Grave S** (2009) A new species of *Lysmata* (Crustacea, Decapoda, Hippolytidae) from the Pacific Coast of Panama, with observations of its reproductive biology. *Zoological Studies* **48**(5), 682–692.
- Armstrong JC** (1941) The Caridea and Stomatopoda of the second Templeton Crocker-American Museum Expedition to the Pacific Ocean. *American Museum Novitates* **1137**, 1–14.
- Ashrafi H, Baeza JA and Đuriš Z** (2021) The caridean shrimps of the genus *Lysmata* Risso, 1816 (Decapoda: Lysmatidae) from Madagascar collected during the Atimo-Vatae Expedition: a new species and two new records. *European Journal of Taxonomy* **774**, 155–177.
- Baeza JA** (2010a) The symbiotic lifestyle and its evolutionary consequences: social monogamy and sex allocation in the hermaphroditic shrimp *Lysmata pederseni*. *Naturwissenschaften* **97**(8), 729–741.
- Baeza JA** (2010b) Molecular systematics of peppermint and cleaner shrimps: phylogeny and taxonomy of the genera *Lysmata* and *Exhippolysmata* (Crustacea: Caridea: Hippolytidae). *Zoological Journal of the Linnean Society* **160**(2), 254–265.
- Baeza JA** (2013) Molecular phylogeny of broken-back shrimps (genus *Lysmata* and allies): a test of the ‘Tomlinson-Ghiselin’ hypothesis explaining the evolution of hermaphroditism. *Molecular Phylogenetics and Evolution* **69**(1), 46–62.
- Baeza JA** (2018) Sexual systems in shrimps (Infraorder Caridea Dana, 1852), with special reference to the historical origin and adaptive value of protandric simultaneous hermaphroditism. In Leonard J (ed.), *Transitions between Sexual Systems*. Cham, Switzerland: Springer, 269–310.
- Baeza JA and Behringer DC** (2017) Integrative taxonomy of the ornamental ‘peppermint’ shrimp public market and population genetics of *Lysmata boggsi*, the most heavily traded species worldwide. *PeerJ* **5**, e3786.
- Baeza JA, Guéron R, Simpson L and Ambrosio LJ** (2016) Population distribution, host-switching, and chemical sensing in the symbiotic shrimp *Lysmata pederseni*: implications for its mating system in a changing reef seascape. *Coral Reefs* **35**, 1213–1224.
- Baeza JA and Prakash S** (2019) An integrative taxonomic and phylogenetic approach reveals a complex of cryptic species in the ‘peppermint’ shrimp *Lysmata wurdemanni sensu stricto*. *Zoological Journal of the Linnean Society* **185**(4), 1018–1038.
- Baeza JA, Schubart CD, Zillner P, Fuentes S and Bauer RT** (2009) Molecular phylogeny of shrimps from the genus *Lysmata* (Caridea: Hippolytidae): the evolutionary origins of protandric simultaneous hermaphroditism and social monogamy. *Biological Journal of the Linnean Society* **96**(2), 415–424.
- Barros-Alves SP, Alves DFR, Hirose GL and Cobo VJ** (2016) New records of caridean shrimps, *Lysmata ankeri* and *L. cf. intermedia*, from southeast coast of Brazil. *Marine Biodiversity Records* **9**, 34..
- Barros-Alves SP, Alves DFR, Silva SLR, Guimarães CRP and Hirose GL** (2015) New records of decapod crustaceans from the coast of Sergipe state, Brazil. *Check List* **11**(5), 1768.
- Barton JA, Humphrey C, Bourne DG and Hutson KS** (2020) Biological controls to manage *Acropora*-eating flatworms in coral aquaculture. *Aquaculture Environment Interactions* **12**, 61–66.
- Bauer RT** (2000) Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. *Journal of Crustacean Biology* **20**(5), 116–128.
- Bochini GL, Cunha AM, Terossi M and Almeida AO** (2020) A new genus and species from Brazil of the resurrected family Macromaxillocarididae Alvarez, Illife & Villalobos, 2006 and a worldwide list of Stenopodidae (Decapoda). *Journal of Crustacean Biology* **40**(6), 704–714.
- Calado R, Araújo R, Narciso L, Lin J and Rhyne AL** (2003) Marine ornamental decapods popular, pricey, and poorly studied. *Journal of Crustacean Biology* **23**(4), 963–973.
- Castresana J** (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**(4), 540–552.
- Chace FA Jr.** (1997) The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 7: families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae. *Smithsonian Contributions to Zoology* **587**, 1–106.
- Christoffersen ML** (1980) *Taxonomia e distribuição geográfica dos Alpheoidea (Crustacea, Decapoda, Natantia) do Brasil, Uruguai e norte da Argentina, incluindo considerações sobre a divisão do sul do continente em províncias biogeográficas marinhas* (PhD thesis). University of São Paulo, São Paulo, Brazil.
- Christoffersen ML** (1998) Malacostraca – Eucarida. Caridea. Crangonoidea and Alpheoidea (except Glyphocrangonidae and Crangonidae). In Young PS (ed.), *Catalogue of Crustacea of Brazil*. Rio de Janeiro, Brazil: Museu Nacional, 351–372.
- Coelho Filho PA** (2006) Checklist of the decapods (Crustacea) from the outer continental shelf and seamounts from northeast of Brazil – REVIZEE Program (NE III). *Zootaxa* **1184**(1), 1–27.
- Darriba D, Taboada GL, Doallo R and Posada D** (2012) JModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**, 772.
- De Grave S and Anker A** (2018) A new, distinctly coloured species of *Lysmata* Risso, 1816 (Malacostraca: Decapoda: Lysmatidae) from the south-central Atlantic. *Zootaxa* **4429**(2), 390–400.
- Dohrn PFR and Holthuis LB** (1950) *Lysmata nilita*, a new species of prawn (Crustacea: Decapoda) from the Western Mediterranean. *Pubblazioni della Stazione Zoologica di Napoli* **22**, 339–347.
- D’Udekem D’Acoz C** (2000) Redescription of *Lysmata intermedia* (Kingsley, 1879) based on topotypical specimens, with remarks on *Lysmata seticaudata* (Risso, 1816) (Decapoda, Caridea, Hippolytidae). *Crustaceana* **73**, 719–735.
- Fiedler GC, Rhyne AL, Segawa R, Aotsuka T and Schizas NV** (2010) The evolution of euhermaphroditism in caridean shrimps: a molecular perspective of sexual systems and systematics. *BMC Evolutionary Biology* **10**, 1–14.
- Gan Z and Li X** (2016) *Lysmata leptodactylus*, a new species of lysmatid shrimp (Crustacea: Decapoda: Caridea) from China. *Zootaxa* **4138**(1), 181–188.
- Giraldes BW, Macedo TP, Brandão MC, Baeza JA and Freire AS** (2018) *Lysmata arvoredensis* nov. sp. a new species of shrimp from the south coast of Brazil with a key to species of *Lysmata* (Caridea: Lysmatidae) recorded in the southwestern Atlantic. *PeerJ* **6**, e5561.
- Guéron R, Almeida AO, Aguilar R, Ogburn MB, Prakash S and Baeza JA** (2022) Delimiting species within the *Lysmata vittata* (Stimpson, 1860) (Decapoda: Lysmatidae) species complex in a world full of invaders. *Zootaxa* **5150**(2), 189–216.
- Hall TA** (2005) BioEdit v.7.0.5. Biological sequences alignment editor for Windows. Ibis Therapeutics a division of Isis Pharmaceutical. Available at <http://www.mbio.ncsu.edu/BioEdit/bioedit.html>, accessed online 29 March 2021.
- Holthuis LB and Maurin C** (1952) Note sur *Lysmata uncinicornis* nov. spec. et sur deux autres espèces intéressantes de crustacés décapodes macroures de la côte Atlantique du Maroc. *Proceedings of the Koninklijke Nederlandse Akademie Wetenschappen, Amsterdam* **55**(2), 197–202.
- Kumar S, Stecher G, Li M, Knyaz C and Tamura K** (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35**(6), 1547–1549.



- Laubenheimer H and Rhyne AL** (2010) *Lysmata rauli*, a new species of peppermint shrimp (Decapoda: Hippolytidae) from the southwestern Atlantic. *Zootaxa* 2372(1), 298–304.
- Madhavan M, Purushothaman P, Akash S, Bharathi S, Jose S, Dhinakaran A, Ravi C, Kumar TTA and Lal KK** (2019) New record of *Thor hainanensis* Xu & Li, 2014 and taxonomical remarks on *Lysmata ternatensis* de Man, 1902 (Decapoda: Thoridae & Lysmatidae) from the Lakshadweep Islands, India. *Zootaxa* 4624(3), 351–364.
- Okuno J** (1996) *Lysmata zaca* Armstrong, 1941, rediscovery from southern Japan and New Caledonia (Crustacea, Decapoda, Hippolytidae). *Species Diversity* 1(1), 49–54.
- Okuno J and Fiedler GC** (2010) *Lysmata lipkei*, a new species of peppermint shrimp (Decapoda, Hippolytidae) from warm temperate and subtropical waters of Japan. In Fransen CHJM, De Grave S and Ng PKL (eds), *Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume*. Crustaceana Monographs 14. Leiden, The Netherlands: Brill, 597–610.
- Pachelle PPG, Anker A, Mendes CB and Bezerra LEA** (2016) Decapod crustaceans from the state of Ceará, northeastern Brazil: an updated checklist of marine and estuarine species, with 23 new records. *Zootaxa* 4131(1), 1–63.
- Pachelle PPG, Carvalho L, Alves DFR and Anker A** (2020) A revision of the Brazilian species of *Lysmata* Risso, 1816 (Decapoda: Caridea: Lysmatidae), with discussion of the morphological characters used in their identification. *Zootaxa* 4789(1), 55–90.
- Prakash S and Baeza JA** (2017) A new species of *Lysmata* Risso, 1816 (Crustacea, Decapoda, Lysmatidae) from the Gulf of Mexico. *Zootaxa* 4363(4), 576–582.
- Ramos-Porto M, Carvalho PVVDBC and Botter-Carvalho ML** (1995) Registro de *Lysmata intermedia* (Kingsley, 1878) (Decapoda, Hippolytidae) no litoral pernambucano. *Trabalhos do Instituto Oceanográfico da Universidade Federal de Pernambuco* 23, 107–111.
- Rathbun MJ** (1901) Investigations of the aquatic resources and fisheries of Porto Rico by the United States Fish Commission Steamer Fish Hawk in 1899. The Brachyura and Macrura of Porto Rico. *Bulletin of the United States Fish Commission* 20, 1–127.
- Rhyne AL, Calado R and dos Santos A** (2012) *Lysmata jundalini*, a new peppermint shrimp (Decapoda, Caridea, Hippolytidae) from the Western Atlantic. *Zootaxa* 3579(1), 71–79.
- Rhyne AL and Lin J** (2006) A western Atlantic peppermint shrimp complex: redescription of *Lysmata wurdemanni*, description of four new species, and remarks on *Lysmata rathbunae* (Crustacea: Decapoda: Hippolytidae). *Bulletin of Marine Science* 79(1), 165–204.
- Rhyne AL, Tlusty MF, Szczebak JT and Holmberg RJ** (2017) Expanding our understanding of the trade in marine aquarium animal. *PeerJ* 5, e2949.
- Santos PS, Soledade GO and Almeida AO** (2012) Decapod crustaceans on dead coral from reef areas on the coast of Bahia, Brazil. *Nauplius* 20(2), 145–169.
- Schubart CD, Neigel JE and Felder DL** (2000) Use of the mitochondrial 16S rRNA gene for phylogenetic and population studies of Crustacea. *Crustacean Issues* 12, 817–830.
- Soledade GO, Baeza JA, Boehs G, Simões SM, Santos PS, Costa RC and Almeida AO** (2013) A precautionary tale when describing species in a world of invaders: morphology, coloration and genetics demonstrate that *Lysmata rauli* is not a new species endemic to Brazil but a junior synonym of the Indo-Pacific *L. vittata*. *Journal of Crustacean Biology* 33(1), 66–77.
- Terossi M, Almeida AO, Buranelli RC, Castilho AL, Costa RC, Zara FJ and Mantelatto FL** (2018) Checklist of decapods (Crustacea) from the coast of the São Paulo state (Brazil) supported by integrative molecular and morphological data: I. Infraorder Caridea: families Hippolytidae, Lysmatidae, Ogyrididae, Processidae and Thoridae. *Zootaxa* 4370(1), 76–94.
- Thompson JD, Higgins DG and Gibson TJ** (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22(22), 4673–4680.
- Trifinopoulos J, Nguyen LT, von Haeseler A and Minh BQ** (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44(W1), W232–W235.
- Vaughan DB, Grutter AS, Costello MJ and Hutson KS** (2017) Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses. *Fish and Fisheries* 18(4), 698–716.
- Vaughan DB, Grutter AS, Ferguson HW, Jones R and Hutson KS** (2018) Cleaner shrimp are true cleaners of injured fish. *Marine Biology* 165(7), 118.
- Wang YR and Sha ZL** (2018) Description of two new species of *Lysmata* Risso, 1816 (Decapoda, Lysmatidae) from the China seas, with remarks on *Lysmata vittata* (Stimpson 1860). *Zootaxa* 4392(1), 28–40.
- Wicksten MK** (2000) The species of *Lysmata* (Caridea: Hippolytidae) from the Eastern Pacific Ocean. *Amphipacifica* 2(4), 3–22.