

Research article

[urn:lsid:zoobank.org/pub:E5039C89-D341-4F71-9738-F4878F9E5E50](https://zoobank.org/pub:E5039C89-D341-4F71-9738-F4878F9E5E50)**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**Hossein ASHRAFI ^{1,*}, J. Antonio BAEZA ² & Zdeněk ĎURIŠ ³^{1,3}Department of Biology and Ecology, Faculty of Science, University of Ostrava, Ostrava, Czech Republic.²Department of Biological Sciences, 132 Long Hall, Clemson University, Clemson, SC 29634, USA and Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, FL 34949, USA and Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile.*Corresponding author: ashrafi.hossein.s@gmail.com²Email: jbaezam@clemson.edu³Email: zdenek.duris@osu.cz¹[urn:lsid:zoobank.org/author:9434EF55-A729-481B-A0BB-B2F82EC2BFC3](https://zoobank.org/author:9434EF55-A729-481B-A0BB-B2F82EC2BFC3)²[urn:lsid:zoobank.org/author:4A72F2F5-6C56-4800-91BE-E9E671AACDFE](https://zoobank.org/author:4A72F2F5-6C56-4800-91BE-E9E671AACDFE)³[urn:lsid:zoobank.org/author:0CF5D3F9-9663-4B76-BF91-713D9BE50BC3](https://zoobank.org/author:0CF5D3F9-9663-4B76-BF91-713D9BE50BC3)

Abstract. The present study focuses on shrimps belonging to the genus *Lysmata* Risso, 1816, collected from Madagascar during the Atimo Vatae expedition carried out in 2010. *Lysmata malagasy* sp. nov. is a new species belonging to the clade named “long accessory ramous” or “cosmopolitan” in previous phylogenetic studies. The new species can be distinguished from the only two other representatives of this group in the Indo-west Pacific, *L. ternatensis* De Man, 1902, and *L. trisetacea* (Heller, 1861), by the accessory ramus of the lateral antennular flagellum consisting of four elongated articles. *Lysmata lipkei* Okuno & Fiedler, 2010 is reported here from Madagascar with a remarkable extension of its known range after its original description from Japan. This species has also been reported from Singapore and, as alien species, from Brazil. Lastly, *L. kuekenthali* De Man, 1902 known from numerous localities in the Indo-West Pacific biogeographic area, is reported for the first time from Madagascar. Results of the present morphological and molecular analyses suggest that *L. hochi* Baeza & Anker, 2008 from the Caribbean Sea is a synonym of the Indo-West Pacific *L. kuekenthali*, and thus the latter species is alien in the western Atlantic.

Key words. *Lysmata malagasy* sp. nov., *L. lipkei*, *L. kuekenthali*, alien species, *L. hochi*.

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Introduction

The caridean shrimp genus *Lysmata* Risso, 1816 is the largest genus with 47 species in the relatively small family Lysmatidae Dana, 1852 (Chace 1997; Wicksten 2000; De Grave & Fransen 2011; De Grave *et al.* 2014). The species belonging to this genus live in the intertidal zone and down to 360 m depth in tropical, subtropical, and temperate regions worldwide (Crosnier & Forest 1973; Fransen 1991; Chace 1997; Anker & Cox 2011; Rhyne *et al.* 2012; Wang & Sha 2018). The genus was subdivided into several groups based on morphological features, ecological, and molecular data (Bauer 2000; Rhyne & Lin 2006; Baeza *et al.* 2009; Fiedler *et al.* 2010). The first division of the genus was conducted by Bauer (2000), suggesting the presence of two groups, the “cleaner” group mostly comprised of pair-living species that are active fish cleaners and feature conspicuous yellow and red colorations, and the “peppermint” group mostly comprised of species living in large aggregations that are not active fish cleaners, and with transverse or longitudinal red bands in the body. Rhyne & Lin (2006) added another group to Bauer’s division, characterized by having a long free (accessory) ramus of the lateral antennular flagellum.

In the first published comprehensive molecular phylogeny of the genus *Lysmata*, Baeza *et al.* (2009) named three different clades: 1) the ‘Tropical-American clade’ (occurring in the tropical western Atlantic and eastern Pacific), 2) the cleaner clade, and 3) the cosmopolitan clade, with the latter being the same as “long accessory ramous clade”, *sensu lato*. Lastly, a more comprehensive phylogenetic analysis conducted by Baeza (2010), revealed a fourth clade named the “morpho-variable clade” that includes *L. hochi* and *L. vittata*, together with two species belonging to genus *Exhippolyasmata* Stebbing, 1915, i.e., *E. ensirostris* (Kemp, 1914), and *E. oplophoroides* (Holthuis, 1948). In the same year, Fiedler *et al.* (2010) discriminated three groups based on the accessory ramus of the lateral antennular flagellum, establishing: 1) the “short accessory ramous” group (with the cleaner clade belonging to this group); 2) the “long accessory ramous” group, and 3) the “unguiform ramous” group. The latter group is similar to the “morpho-variable” clade defined by Baeza (2010) but excluding the genus *Exhippolyasmata*.

Importantly, free-living species in the genus appear to show a high potential for invading other regions, considering that four species so far have been recorded as alien: *L. hochi* Baeza & Anker, 2008 in India (Jose *et al.* 2020), *L. kempfi* Chace, 1997 in Turkey (Frogliola & Deval 2014), *L. lipkei* Okuno & Fiedler 2010 in Brazil (Alves *et al.* 2018), and *L. vittata* (Stimpson, 1860) in Brazil too (Soledade *et al.* 2013; Alves *et al.* 2018).

During the recent Atimo Vatae expedition to south Madagascar, conducted by the Museum national d’histoire naturelle (MNHN) under the “Our Planet Reviewed” program in 2010, three different species of the genus *Lysmata* were collected. After a detailed comparison of the captured specimens, one of them was identified as new to science. The remaining two species belong to currently known Indo-West Pacific representatives of the genus, *L. kuekenthali* (De Man, 1902), and *L. lipkei* Okuno & Fiedler, 2010. The new species is described, and the new records of the two other species are reported here.

Based on phylogenetic trees (Maximum Likelihood and Bayesian Inference) constructed using the 16S mitochondrial gene marker, the relationship of the new species with the other species of the “long accessory ramous” clade was examined. Also, new sequences belonging to *L. kuekenthali* and *L. lipkei* were compared with previously reported sequences retrieved from congeneric specimens to confirm their species affiliations, and to highlight their relationship to other currently recognized taxa.

Material and methods

Taxon sampling

The material from Madagascar was collected during the Atimo Vatae expedition in 2010 from intertidal and shallow subtidal zones in Fort-Dauphin (Tolagnaro), between April 27th and May 17th, and from

Lavanono, between May 23rd and June 13th, by means of SCUBA diving and light dredging. Moreover, a shrimp trawler was used to sample by dredging and trawling, conducting 119 hauls at depths between 50 and 700 m. The material of this expedition was deposited in MNHN, and during the visit of the collection by HA and ZĐ early in 2020, the examined specimens were loaned from the museum for this study.

In addition to material from Madagascar, two other specimens belonging to *L. kuekenthali* from the Gulf of Oman (Ashrafi *et al.* 2020) were included in this study. Moreover, sequence data from prior studies were used to construct phylogenetic trees (Table 1). The material from the Iranian coast in the Gulf of Oman was collected during a spring tide at night from the low intertidal zone. Shrimps belonging to the genus *Lysmata* are active at night, and thus, they can be captured during dark hours using a flashlight.

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from the tissues of one of the fifth pereopods or fourth or fifth pleopods using the DNeasy Blood & Tissue Isolation Kit (QIAGEN) according to the manufacturer's protocol. The polymerase chain reaction was used to amplify a partial segment of the 16S rRNA gene (approximately 550 bp), using the primers AR pal (Palumbi & Benzie 1991) for forward and 1472 (Crandall & Fitzpatrick 1996) for reverse. A total volume of 20 μ l including 4 μ l 5x MyTaqTM Red Reaction buffer (comprising 15 mM MgCl₂ and 5 mM dNTPs), 1 μ l DNA template, 13.2 μ l dH₂O, 0.8 μ l of each primer, and 0.2 μ l MyTaqTM Red DNA polymerase were used for PCR. The thermocycler sequencing conditions were set according to Horká *et al.* (2016): 2.5 min at 90 °C, followed by 10 cycles of 50 s at 92 °C, 30 s at 42–48 °C, and 1 min at 72 °C, 36 cycles of 30 s at 92 °C, 40 s at 42–48 °C, and 1 min at 72 °C and a final extension step at 72 °C for 3 min. The final products were purified by the GenElute PCR Clean-up kit (Sigma-Aldrich), and sent to Macrogen, Amsterdam for forward and reverse sequencing (performed by an ABI3730XL DNA Sequencer), and therefore, complement sequences were used for the following steps.

Sequence alignment and tree construction

Obtained forward and reverse sequences were checked by eye and corrected if necessary in the case forward and reverse sequences were not a complete match, using Chromas ver. 2.4.1. Aligning 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. As a result, 358 out of 513 nucleotides were determined to be suitable for phylogenetic analysis.

The best-fit model for the nucleotide substitution (i.e., TIM3+F+I+G4) was selected based on AIC (Akaike Information Criterion) using the software IQ-TREE ver. 2.0.5 (Kalyaanamoorthy *et al.* 2017). The Maximum Likelihood analysis was conducted with the web server IQ-TREE with default options except for the number of bootstrap alignments set to 10000 with the 'ultrafast' option selected for 'bootstrap analysis'.

A Bayesian tree was constructed using MrBayes ver. 3.2.7 (Ronquist & Huelsenbeck 2003). The MCMC analysis was set for 8×10^6 generations with four chains and two independent runs. Each run was sampled every 500 generations, and the first 25% of trees in each run were discarded as "burn-in". The remaining trees were used for constructing the 50% majority rule consensus tree and also for calculating Bayesian posterior probabilities (bpp). The final tree was displayed using the online application ITOL (Letunic & Bork 2011).

Abbreviations used in the text

BI	=	Bayesian Inference
CL	=	carapace length (measured from the tip of the rostrum to the posterior margin of the carapace dorsally in the midline)
IWP	=	Indo-West Pacific
ML	=	Maximum Likelihood
MNHN	=	Muséum national d'Histoire naturelle, Paris
ZUTC	=	Zoological Museum of the University of Tehran

Results

Molecular analysis

In the present study, the two constructed phylogenetic trees (ML and BI; Figs. 1–2, respectively) somewhat differ from each other. The previously recognized “long accessory ramous” and “unguiform accessory ramous” clades are well (BI) or strongly (ML) supported by our analyses. The former clade forms a subclade consisting of *L. cf. trisetacea* (Heller, 1861), *L. intermedia* (Kingsley, 1878), *L. nilita* Dohrn & Holthuis, 1950, *L. moorei* (Rathbun, 1901), and *L. galapagensis* Schmitt, 1924 in both trees, with high support in the BI analysis. The other species that belong to this clade form a polytomy in the BI analysis, but they form a clade in the ML analysis that was not well-supported by bootstrap values.

The ‘Tropical American clade’ is sister to all other clades and species of *Lysmata* in the two (ML and BI) phylogenetic trees. Importantly, this ‘Tropical American clade’ does not cluster and forms a monophyletic clade with representatives from the “short accessory ramous” group. Thus, the “short accessory ramous” group does not appear to be monophyletic in the present analyses. Furthermore, *L. olavo* Fransen, 1991, is the single species that does not cluster together with any of the previously defined clades in the genus *Lysmata* (see Baeza *et al.* 2009 and Baeza 2010). In our analysis, the “unguiform ramous” group defined by Fiedler *et al.* (2010) is retrieved as a well-supported monophyletic clade.

The position of three problematic species mentioned by Fiedler *et al.* (2010) remains unresolved also in the present analyses. In addition to *Lysmata olavo* that does not cluster with any other groups (see above), two “peppermint shrimps”, *L. nayaritensis* Wicksten, 2000 and *L. californica* (Stimpson, 1866), form a monophyletic clade and cluster with members of the “cleaner clade”. The latter group is still monophyletic, although with relatively low support in the BI tree. However, the “cleaner clade” is paraphyletic in the ML tree as *L. nayaritensis* is nested inside.

Lysmata malagasy sp. nov. belongs to the “long accessory ramous” clade. However, the position of this species within the clade in the ML and BI phylogenetic trees is different. In the ML analysis, the new species is closest to *L. ternatensis*, and both form a poorly-supported subclade with *L. argentopunctata* Wicksten, 2000 and *L. seticaudata* (Risso, 1816). In the BI analysis, the new species does not cluster together with any other representative of the “long accessory ramous” clade.

The analysed specimens of *Lysmata kuekenthali* (De Man, 1902), *L. hochi* Baeza & Anker, 2008, *L. lipkei* Okuno & Fiedler, 2010, and *L. cf. anchisteus* Chace, 1972 form a well-supported clade that represents the “unguiform ramous” clade previously defined by Fiedler *et al.* (2010). The specimen of *L. hochi* is nested inside the group of *L. kuekenthali* specimens pointing to the possibility that *L. hochi* and *L. kuekenthali* might be the same species (see below).

Table 1. Specimen information about the material used to construct the phylogenetic tree.

Taxon	Source	Voucher number	GenBank accession number
<i>L. amboinensis</i>	Fiedler <i>et al.</i> 2010 Baeza <i>et al.</i> 2009		HQ315589 EU861488
<i>L. cf. anchisteus</i>	Fiedler <i>et al.</i> 2010		HQ315606
<i>L. ankeri</i>	Fiedler <i>et al.</i> 2010 Baeza <i>et al.</i> 2009		HQ315599 EU861501
<i>L. argentopunctata</i>	Baeza 2010		GQ227814
<i>L. boggei</i>	Baeza & Behringer 2017 Fiedler <i>et al.</i> 2010		MF632247 HQ315603
<i>L. californica</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		EU861499 HQ315596
<i>L. debelius</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		EU861492 HQ315595
<i>L. galapagensis</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		HQ315577 EU861480
<i>L. grabhami</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		HQ315593 EU861489
<i>L. gracilirostris</i>	Fiedler <i>et al.</i> 2010		EU861502
<i>L. hochi</i>	Fiedler <i>et al.</i> 2010		EU861507
<i>L. intermedia</i>	Baeza <i>et al.</i> 2009 De Grave <i>et al.</i> 2014		HQ315580 KF023094
<i>L. kuekenthali</i>	Baeza & Fuentes 2013 Present study-Madagascar Present study-Iran_1 Present study-Iran_2	MNHN-IU-2010-2377 MNHN-IU-2014-1246 MNHN-IU-2014-1247	KC962216 MW798242 MW798240 MW798241
<i>L. lipkei</i>	Baeza <i>et al.</i> 2009 Present study	MNHN-IU-2010-4898	HQ315574 MW798243
<i>L. malagasy</i>	Present study	MNHN-IU-2010-4890	MW798244
<i>L. moorei</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		HQ315578 EU861481
<i>L. nayaritensis</i>	Fiedler <i>et al.</i> 2010		EU861506
<i>L. nilita</i>	Fiedler <i>et al.</i> 2010		EU861482
<i>L. olavoi</i>	Fiedler <i>et al.</i> 2010		EU861494
<i>L. pedersenii</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		HQ315601 EU861504
<i>L. rafa</i>	Baeza <i>et al.</i> 2009 Fiedler <i>et al.</i> 2010		HQ315604 EU861495
<i>L. seticaudata</i>	De Grave <i>et al.</i> 2014 Baeza 2010		KF023083 GQ227827
<i>L. ternatensis</i>	Baeza <i>et al.</i> 2009 Aznar-Cormano <i>et al.</i> 2015		HQ315584 KP725548
<i>L. cf. trisetacea</i>	Fiedler <i>et al.</i> 2010		EU861483
<i>L. wurdemanni</i>	Baeza & Prakash 2019		MG957483
<i>Gelastocaris paronae</i>	Present study	MNHN-IU-2018-1318	MW798245

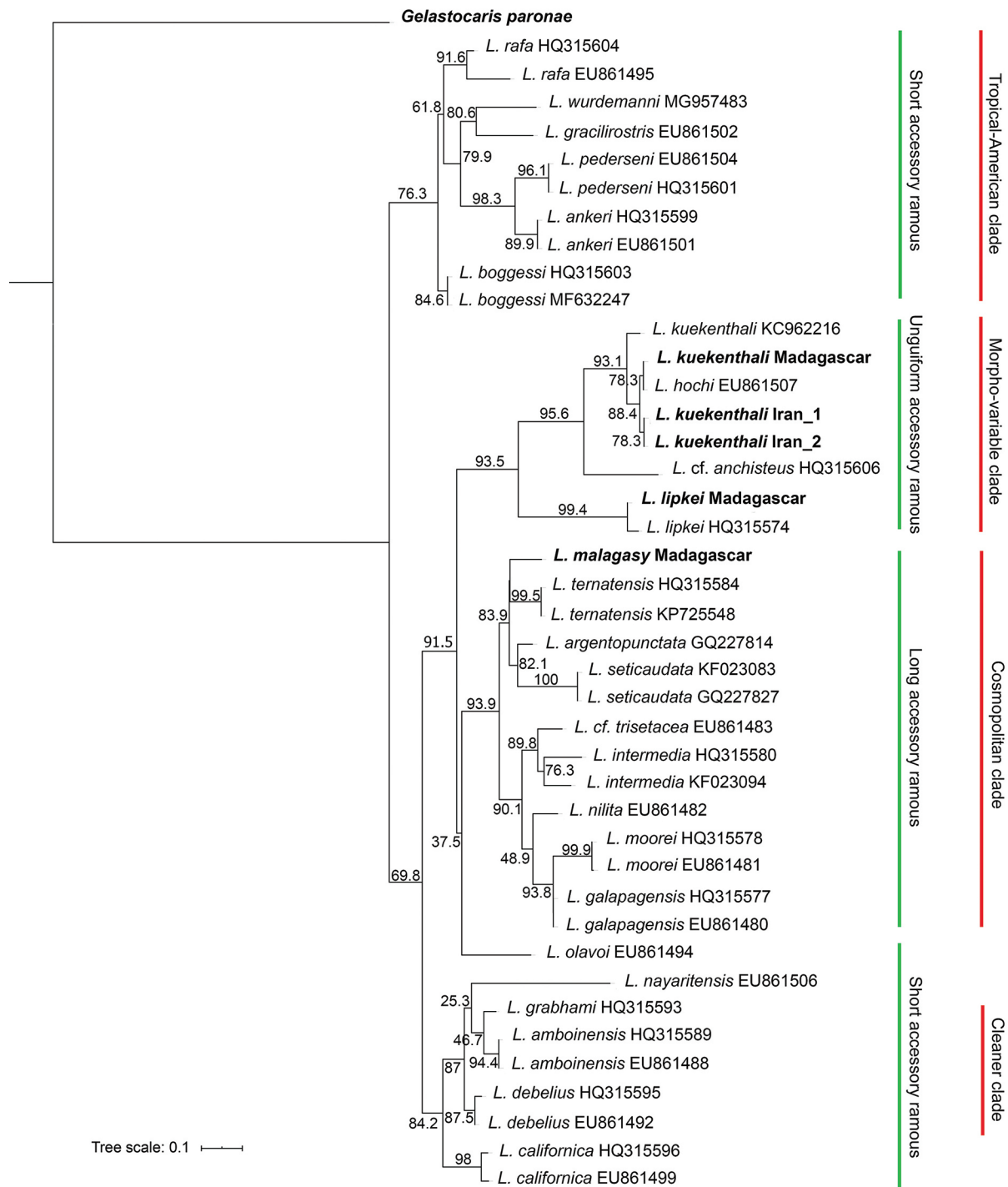
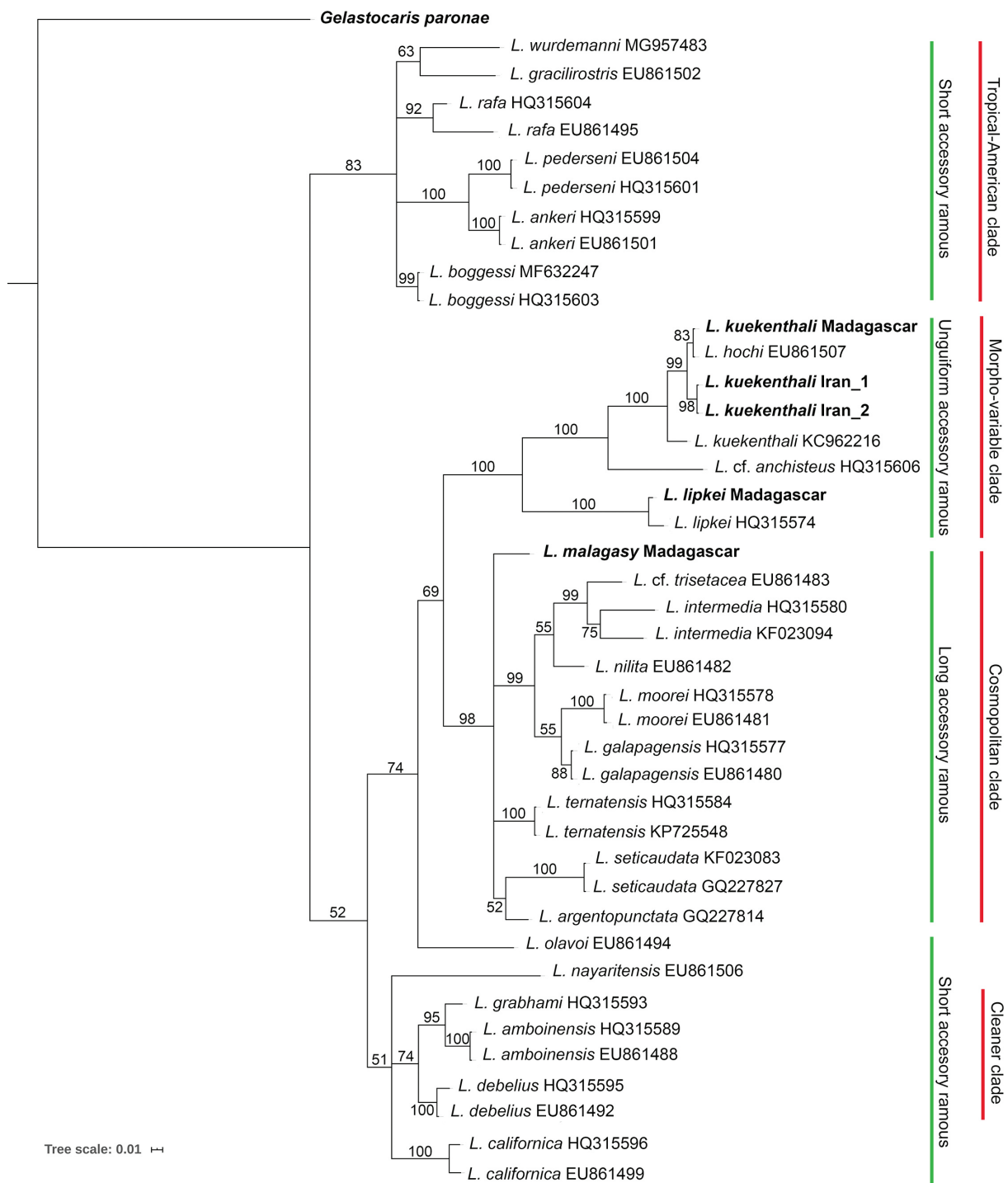


Fig. 1. Phylogenetic tree obtained by Maximum Likelihood analysis based on partial sequences of 16S. Bootstrap support is indicated above or below the branches before the nodes. The material of the present study is shown in bold format. The green vertical lines show the clades defined by Fiedler *et al.* (2010), and the red ones by Baeza *et al.* (2009) and Baeza (2010).



Tree scale: 0.01

Fig. 2. Phylogenetic tree obtained by Bayesian inference analysis based on partial sequences of 16S. Support for each node is indicated as posterior probabilities above or below the branches before the nodes. The material of the present study is shown in bold format. The green vertical lines show the clades defined by Fiedler *et al.* (2010), and the red ones by Baeza *et al.* (2009) and Baeza (2010).

Systematics

Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Infraorder Caridea Dana, 1852
Family Lysmatidae Dana, 1852
Genus *Lysmata* Risso, 1816

Lysmata malagasy sp. nov.

[urn:lsid:zoobank.org:act:62A66440-6F8E-4BD3-94E3-5CAD9D2D336E](https://doi.org/10.21203/rs.3.rs-6246644/v1)

Figs 3–7

Etymology

The new species is named after ‘Malagasy’, the native inhabitants of Madagascar where the specimen was collected; the term ‘Malagasy’ is English version of the word ‘Malgache’ in French used for both people and their language in Madagascar; used as a noun in apposition.

Type material

Holotype

MADAGASCAR • 1 ovigerous hermaphrodite (CL 8.8 mm); southern Madagascar; 24°58'4.8" S, 47°06'8.4" E; depth 3–8 m; 6 May 2010; MNHN exped.; Atimo-Vatae; Stn TR05 1; GenBank MW798244; MNHN-IU-2010-4890.

Description

Medium-sized lysmatid shrimp

CARAPACE (Figs 3, 4A–C). Smooth with scattered setae on dorsal margin, antennal tooth strong, pterygostomial margin slightly produced, pointed; with two postrostral dorsal teeth located anteriorly at about 0.2 and 0.4 of carapace length. Rostrum elongated, approximately half of CL, reaching to about

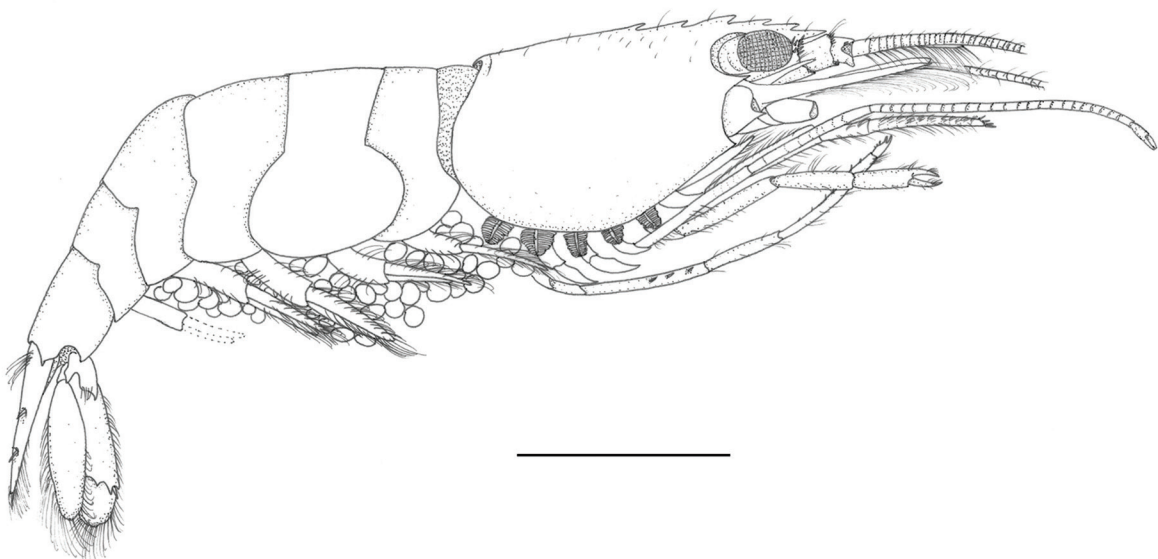


Fig. 3. *Lysmata malagasy* sp. nov., holotype (MNHN-IU-2010-4890), habitus, lateral view. Scale bar: 5 mm.

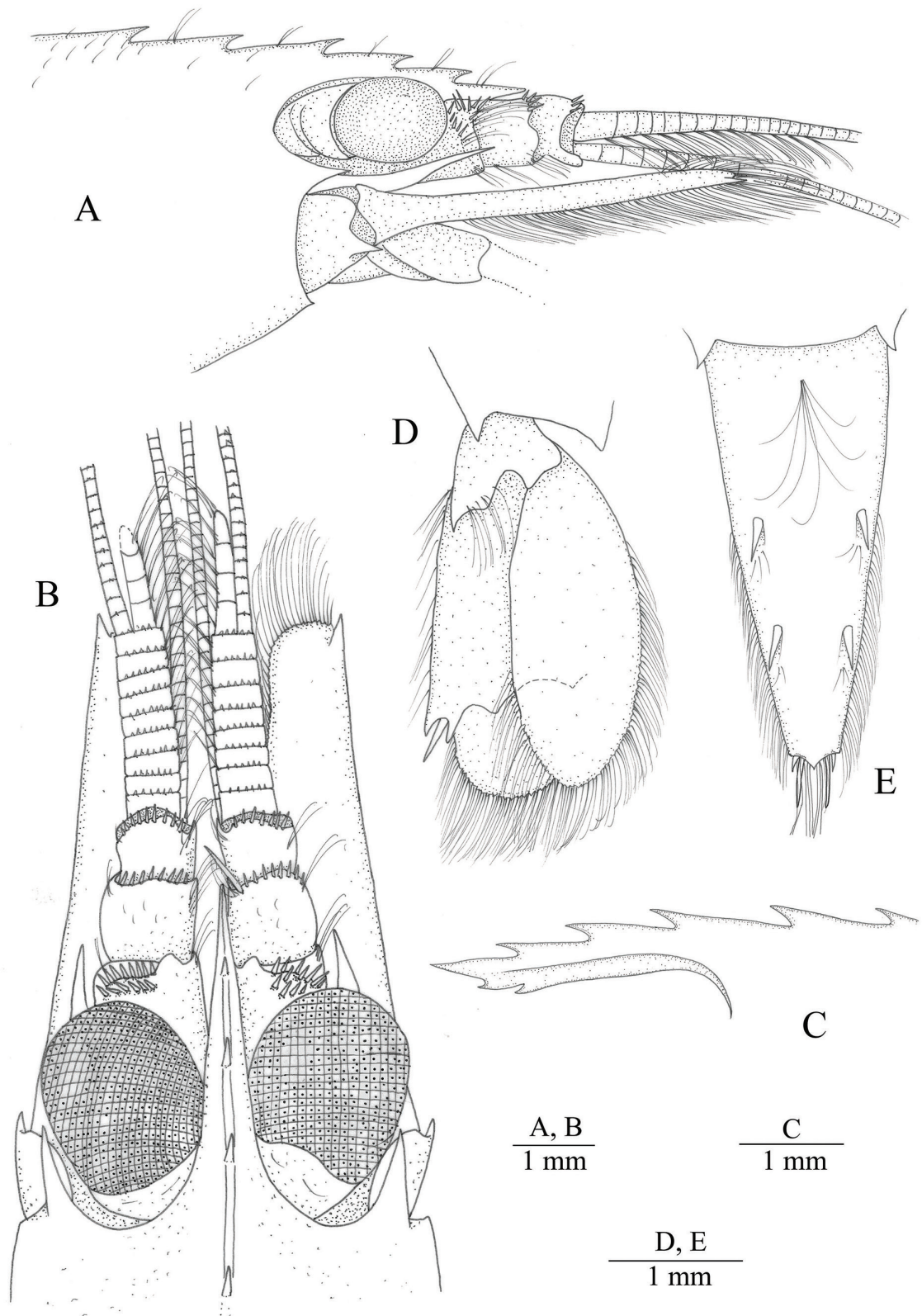


Fig. 4. *Lysmata malagasy* sp. nov., holotype (MNHN-IU-2010-4890). **A.** Anterior region, lateral view. **B.** Same, dorsal view. **C.** Rostrum, lateral view. **D.** Uropods, dorsal view. **E.** Telson, dorsal view.

end of second antennular article, straight in lateral view, bearing evenly distributed three teeth dorsally; ventral margin with two teeth at distal-third.

PLEON (Fig. 3). Smooth; first pleuron obtusely angulate anteriorly, rounded postero-ventrally; second and third pleura rounded antero- and postero-ventrally; fourth pleuron angulated postero-ventrally, not pointed; fifth pleuron produced postero-ventrally, subacute; sixth pleuron with triangular projections postero-laterally.

TELSON (Fig. 4E). Elongated, slightly more than twice as long as broadest part, tapering posteriorly; dorsal surface with antero-median tuft of long setae and two pairs of spines about 0.1 of telson length and situated at 0.5 and 0.75 of telson length; distal half of lateral margins furnished with setae; posterior margin broadly triangular, projecting medially into acute apex, with two pairs of slender submedian setae and two pairs of laterally placed spines, mesial spines long, about 1.2 times as long as dorsal spines and more than three times as long as lateral ones, latter small, about 2.5 times as short as dorsal spines.

ANTENNULE (Fig. 4A–B). With peduncle stout; basal peduncular segment longer and stouter than others, reaching about to base of most anterior dorsal rostral tooth, with group of spinules antero-dorsally; stylocerite slender, acute, falling short of reaching to middle of second antennular segment; second peduncular segment stouter and longer than third one, with few spinules along antero-dorsal margin; third segment about 0.7 as long as second one, with row of spinules furnishing distal margin. Lateral (= upper) flagellum biramous, fused part consisting of eight or nine articles (right and left antennule in holotype, respectively), each article of fused part with row of small spinules situated on anterior margin, short free ramus (= accessory ramus) comprising of four elongated articles; aesthetascs present from distal end of first article of fused part to end of short free ramus. Longer free ramus of upper flagellum filiform, each article with one or two small spinules on anterior margin. Lower antennular flagellum filiform, long.

ANTENNA (Fig. 4A–B). With scaphocerite about 0.8 as long as CL, elongated, five times as long as broad, lateral margin straight, distolateral tooth acute, slightly overreaching blade, slightly overreaching fused part of lateral antennular flagellum, basicerite with acute inferior tooth, falling short of middle of cornea, superior margin rounded; carpocerite small, reaching to about end of first antennular segment.

EYES. With cornea about 0.2 of CL, stalk about a third of cornea.

MOUTH PARTS. Not dissected except for third maxilliped. Second maxilliped with podobranch. Third maxilliped (Fig. 5A) pediform, bearing broadly hooked lateral plate, group of short distolateral setae, strap-like epipod, and arthrobranch. Endopodite stout, with numerous slender serrulate setae dorsally as well as ventrally; antepenultimate segment long, slender, more than nine times as long as deep; penultimate segment about 0.4 as long as antepenultimate one, four times as long as deep; ultimate segment long, slender, slightly tapering distally, approximately 0.75 as long as antepenultimate segment, bearing three terminal spinules and single similar subterminal one. Exopodite feebly developed, reaching to distal two thirds of antepenultimate segment, distal half with numerous slender marginal setae.

FIRST PEREIOPOD (Fig. 5B–C). As in other lysmatid shrimps, similar, equal, smaller than other pereio-pods, slightly overreaching scaphocerite when extended; coxa with strap-like epipod and tuft of numerous long setobranchs; basis small, with no special structures; ischium about three times as long as basis, with several small spinules and several thick setae on ventral margin; merus nearly twice as long as ischium, about 5.5 times as long as broadest part in midlength, with few thick setae on mid-ventral margin; carpus about 0.8 times as long as merus, more than three times as long as broad, furnishing with setal brush disto-ventro-mesially; chela with palm elongated, more than 1.5 times as long as fingers, lacking thick setae; fingers simple, without gap when closed.

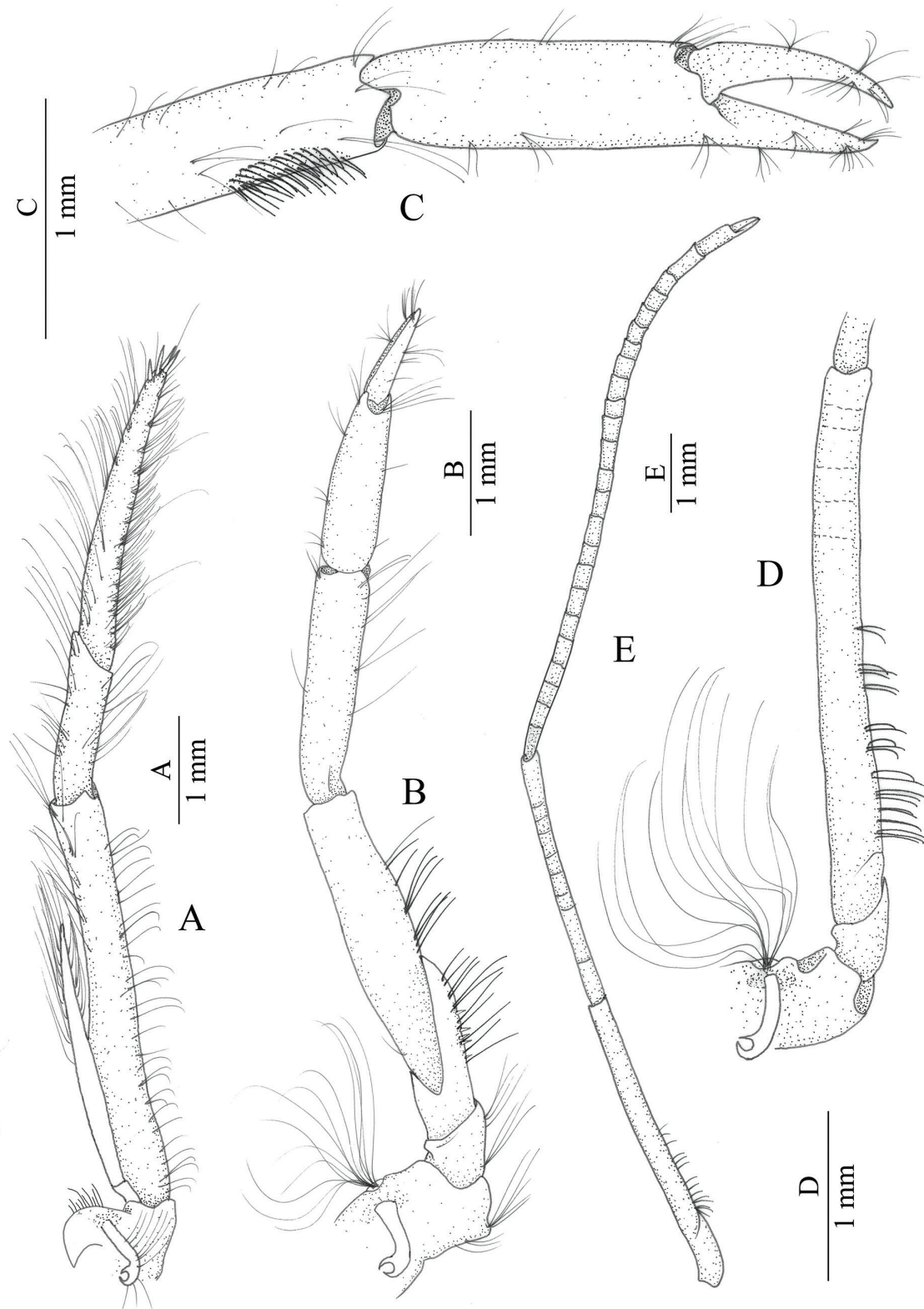


Fig. 5. *Lysmata malagasy* sp. nov., holotype (MNHN-IU-2010-4890). **A.** Third maxilliped, lateral view. **B.** First pereopod, lateral view. **C.** Same, mesial view. **D.** Proximal parts of second pereopod, lateral view. **E.** Distal parts of second pereopod, lateral view.

SECOND PEREIOPODS (Fig. 5D–E). Subequal, similar, about 2.5 times as long as CL, more slender than other pereio pods, coxa with strap-like epipod and tuft of numerous setob rachs; basis short; ischium long, about 7 times as long as basis, with relatively thick setae on ventral margin at proximal-half, distal half with several weak subdivisions; merus long, about 0.8 as long as ischium, with eight articles; carpus long, more than twice as long as merus, subdivided into 23 articles; chela small, with palm about 1.5 times as long as fingers, fingers simple.

THIRD PEREIOPOD (Fig. 6A–B). Longer than other walking pereio pods; coxa with strap-like epipod and tuft of numerous setob rachs; merus more than three times as long as ischium, with two rows of spines on latero-ventral margin, one row with five and other row with three spines; carpus about 0.5 times as long as merus, with two rows of spines, each row with three spines; propodus about 1.3 times as long as carpus, bearing two rows of spines on ventral margin and one pair distally, each row with eight spines; dactylus biunguiculate, superior unguis slightly longer than inferior, inferior unguis slightly broader at base than superior, flexor margin with three accessory spines.

FOURTH PEREIOPOD (Fig. 6C–D). Generally similar to third one, carpus with only one spines on ventral margin, propodus with single row of seven spines ventrally and one pair distally.

FIFTH PEREIOPOD (Fig. 6E). Generally similar to fourth pereio pod; with coxa bearing setob rachs, without strap-like epipod; merus with only one row of three spines implemented ventrally; carpus unarmed, propodus with two small transverse row of cleaning setae distally on ventro-mesial margin.

UROPOD (Fig. 4D). With dorso-distal end of protopod acute; rami subequal, broadly subovate; exopod approximately twice as long as broad, with lateral margin straight ending distolaterally into ‘trispinose’ arrangement of two strong teeth – acute lateral and subacute mesial one, with slender and longer movable spine between teeth; mesial distolateral tooth situated laterally on diaeresis, latter sinuous, with obtuse median projection and subacute projection mesially.

Color pattern

BODY (Fig. 7). Transparent to semi-transparent with one broad reddish brown coloured stripe mid-dorsally on carapace and four similar irregular longitudinal stripes on the sides, all continuing posteriorly to end of sixth pleonite; lateral pleonal stripes regular in shape. Reddish-brown broad stripes interspaced with narrow whitish longitudinal paths with series of white dots in midline. Outer antennular flagella bright red, inner flagellum pinkish; third maxillipeds and pereio pods pinkish proximally with gentle gradient toward distal parts, darker in articulations, distal margin of palm and fingers of first pereio pods pinkish red; uropods and telson reddish brown without any stripes; eggs kiwi-fruit-flesh green.

Remarks

The phylogenetic analysis places the present new species into the “long accessory ramous” clade of the genus *Lysmata* in both ML (Fig. 1) and BI (Fig. 2) analyses. In the ML analysis, *L. malagasy* sp. nov. forms a subclade; however, not well-supported, together with *L. ternatensis*, *L. argentopunctata* and *L. seticaudata*, with *L. ternatensis* being the closest species to the new species. In the BI analysis, the relationships of the new species to other species belonging to the “long accessory ramous” clade is not clear as *L. malagasy* sp. nov. forms no subclade with any other species of the clade.

Considering the division of the genus into three clades morphologically distinguishable by the state of the shorter free (= accessory) ramus of the lateral antennular flagellum i.e., short with one article, unguiform with one finger-like article, or long with multiple articles (Fiedler *et al.* 2010), the new species *L. malagasy* sp. nov. belongs to the third group, i.e., the “long accessory ramous” which represents a well-supported monophyletic clade in previous phylogenetic studies (Baeza *et al.* 2009; Baeza 2010;

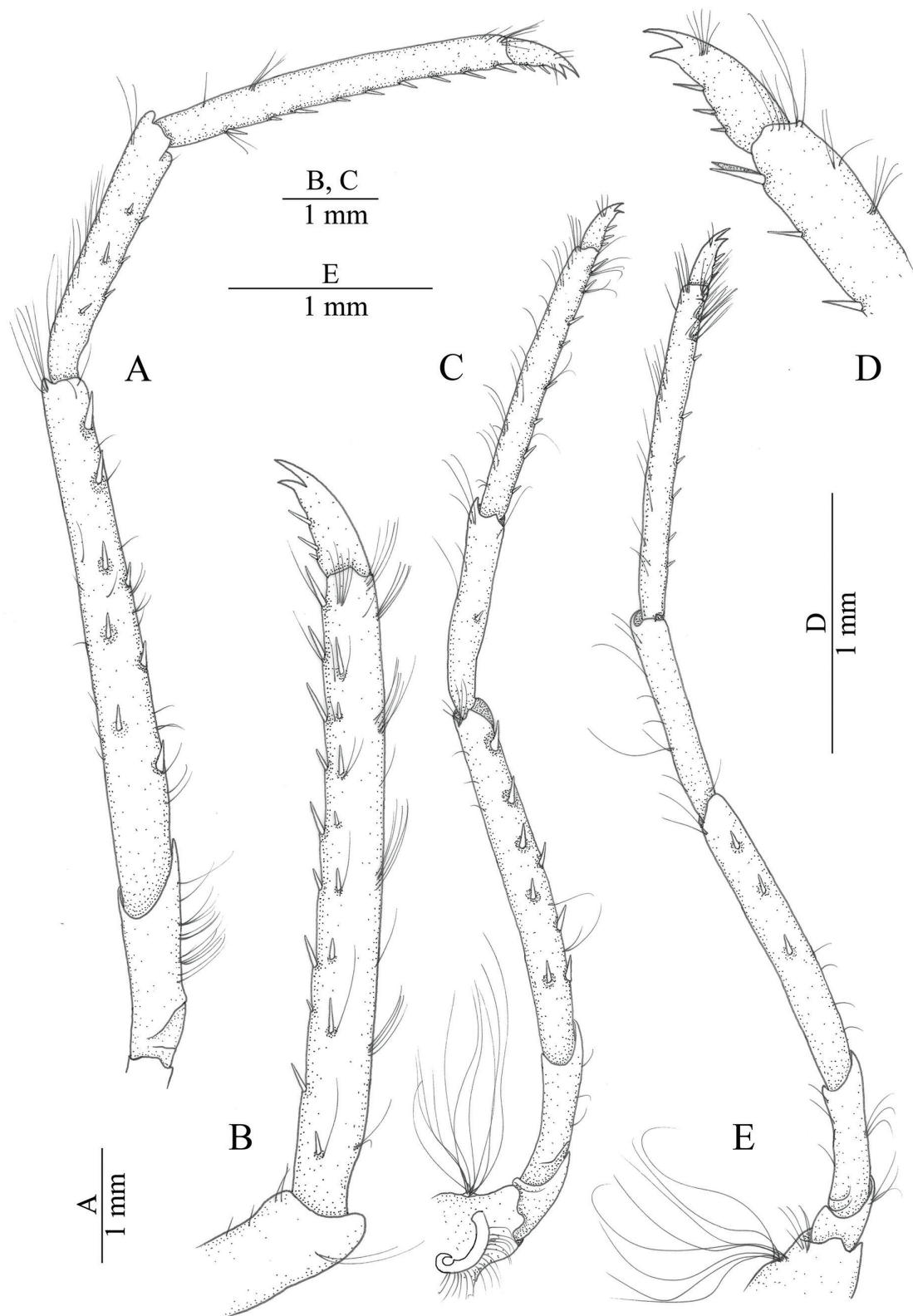


Fig. 6. *Lysmata malagasy* sp. nov., holotype (MNHN-IU-2010-4890). **A.** Third pereiopod, lateral view. **B.** Same, mesial view. **C.** Fourth pereiopod, lateral view. **D.** Dactylus of fourth pereiopod, mesial view. **E.** Fifth pereiopod, lateral view.

Fiedler *et al.* 2010; Baeza & Fuentes 2013). In the study of Baeza *et al.* (2009), Baeza (2010), and Baeza & Fuentes (2013), this clade was named the “cosmopolitan clade”. The Atlantic representatives of this clade are *Lysmata intermedia*, *L. jundalini* Rhyne, Calado & dos Santos, 2012, *L. moorei*, *L. napoleoni* De Grave & Anker, 2018, *L. nilita*, and *L. seticaudata*. The eastern-Pacific representatives of this group are *L. argentopunctata*, *L. chica* Wicksten, 2000, *L. galapagensis*, and *L. holthuisi* Anker, Baeza & De Grave, 2009. However, only two species with long accessory ramus have been described from the Indo-West Pacific, *L. ternatensis* De Man, 1902, and *L. trisetacea*, in addition to *L. zaca* Armstrong, 1941 only being reported from the West Pacific.

Lysmata ternatensis shares with *L. malagasy* sp. nov. some traits like the rostral armament, i.e., 5–6 teeth on upper (including postrostral ones) and 2–3 on lower margins, the carapace with the pterygostomial tooth, the stylocerite not extending beyond midlength of the second antennular article, and the second pereopod with the carpus composed of about 24 articles. Although no information about the carpal and meral spinulation of the three last pereopods was provided by De Man (1902), it seems that these two species are similar in the latter character according to Xu & Li (2015). Importantly, as discussed by De Grave & Anker (2018), and according to personal observations by one of the authors (HA) on other congeners, i.e., *L. vittata* and *L. kuekenthali*, characters like the rostral armament, second pereopod carpal segmentation, and carpal and meral spinulation on three last pereopods, especially the third one, can be highly variable within a species and consequently untrustworthy for separating taxa. However, based on the original description (De Man 1902) and other published reports on *L. ternatensis* (e.g., Chace 1997; Xu & Li 2015; Madhavan *et al.* 2019), the accessory ramus of the lateral antennular flagellum in *L. ternatensis* consists of 10 segments (10 to 15 segments were reported



Fig. 7. Color pattern of the live holotype specimen of *Lysmata malagasy* sp. nov. (MNHN-IU-2010-4890). Photo by Tin-Yam Chan. Copyright MNHN.

for material from the China Sea by Xu & Li in 2015), thus their distinctly higher number clearly distinguishes *L. ternatensis* from *L. malagasy* sp. nov. In the latter, the accessory ramus consists of only four elongated articles. This can be the most reliable morphological character applicable to separate these two species. This difference can also be applied for distinguishing *L. malagasy* sp. nov. from the synonymized species under the name of *L. ternatensis*, *Hippolysmata acicula* Rathbun, 1906, *Lysmata affinis* Borradaile, 1915, and *Palaemon dentatus* De Haan, 1841. In the description of *Hippolysmata acicula*, Rathbun (1906) stated nothing about the state of the accessory ramus of the lateral antennular flagellum. However, the holotype material was re-examined by Chace (1997), who reported that the accessory ramus was comprised of 10 segments compared to four in the new species. In the description of *Lysmata affinis*, Borradaile (1915) only stated that *L. affinis* is related to *L. seticaudata* (Risso, 1816) and *L. chiltoni* Kemp, 1914; with no more information about the status of the antennular flagellum. However, Borradaile (1917) provided more information about *L. affinis*, and he described the accessory ramus of the antennular flagellum being as long as the fused part. This character can be used to distinguish between *L. affinis* and *L. malagasy* sp. nov. as in the latter one, the fused part of the antennular flagellum is much longer than the accessory ramus. Holthuis (1947) stated that in *L. dentata* (originally as *Palaemon dentatus*), the fused part and accessory ramus of the antennular flagellum are equal in size as in *L. affinis*. Thus, the same argument can be used to differentiate between *L. dentata* and *L. malagasy* sp. nov.

Two differences are notable between *L. trisetacea* and *L. malagasy* sp. nov.: 1) the pterygostomial angle is without a tooth in the former species while the latter bears a small acute tooth there; and 2) the accessory ramus of the outer antennular flagellum of *L. trisetacea* consists of at least eight segments (Kemp 1914; Chace 1997) and is subequal in length to the fused portion of the flagellum (Heller 1862; Kemp 1914; Holthuis 1947) whereas in the new species, the accessory ramus includes four elongated segments and is noticeably shorter in length than the fused part. However, it is worth to notice that *L. trisetacea* Heller, 1861, and its synonyms *L. pusilla* Heller, 1862, and *L. chiltoni* Kemp, 1914, should be treated more carefully as there is a considerable difference between the proportion of the length of the free accessory ramus to that of the fused part of the outer flagellum. In the description of *L. pusilla*, Heller (1862) noted that the accessory ramus is about twice as long as the fused part while Kemp (1914) described *L. chiltoni* with the fused part and accessory ramus being equal in length.

Armstrong (1941), in the description of *L. zacaе*, only mentioned that the lateral antennular flagellum is biramous. Okuno (1996) re-examined the type material of *L. zacaе*, and yet did not describe the exact status of the lateral antennular flagellum. There are three characters which can be used to differentiate the new species from *L. zacaе* as follows: first, the shape of the pterygostomial angle bearing a small tooth in *L. malagasy* sp. nov. vs rounded in *L. zacaе*; second, the very short stylocerite in *L. zacaе* reaching to the proximal third of the basal antennular segment compared to longer one in the new species overreaching the basal antennular segment; and third, the scaphocerite reaching to the end of the antennular peduncle in *L. zacaе* while it distinctly surpassing the antennular peduncle in *L. malagasy* sp. nov.

Other members of the “long accessory ramous” clade of the genus *Lysmata* from other geographical regions can be more or less distinguishable from the new species by the number of segments of the fused part and of the accessory ramus of the lateral flagellum; *L. intermedia* with 17–18 and 3–4 articles (d’Udekem d’Acoz 2000), *L. jundalini* 18–24 and 3–4 (Rhyne *et al.* 2012), *L. moorei* 7–13 and 7–16 (Rathbun 1901; Pachelles *et al.* 2020), *L. napoleoni* 6–9 and 10–13 (De Grave & Anker 2018), *L. nilita* 21–27 and 4–7 (Dohrn & Holthuis 1950), *L. seticaudata* 20–38 and 8–15 (Dohrn & Holthuis 1950), *L. argentopunctata* 13–15 and 13–17 (Wicksten 2000), *L. chica* 10–11 and 3–6 (Wicksten 2000), *L. galapagensis* 6–13 and 5–7 (Schmitt 1924), and *L. holthuisi* 17 and 6–7 articles (Anker *et al.* 2009), respectively.

Lysmata kuekenthali (De Man, 1902)

Hippolyte kükenthali De Man, 1902: 850.

Hippolysmata kükenthali – Kemp 1914: 115, p. 6 fig. 2.

Hippolysmata (Hippolysmata) kükenthali – Holthuis 1947: 69.

Diagnosis

Carapace with rostrum reaching to between end of first antennular article to middle of third one, slightly up-turned distally, with four to seven teeth (mostly six) on dorsal margin including the Postrostral teeth, with greater gap between most posterior tooth and preceding one, bearing one to three teeth on ventral margin; antennal tooth strong, surpassing anterior margin of carapace, not fused with lower orbital angle; pterygostomial margin varying from rounded to bearing small tooth. Antennule with stylocerite subacute, falling short of end of first antennular segment; lateral flagellum with accessory free ramus composed of small one-segmented finger-like projection. Antenna with inferior tooth of basicerite small, subacute; scaphocerite slightly overreaching antennular peduncle, disto-lateral tooth slightly surpassing blade, blade with anterior margin relatively straight, lateral margin slightly concave; carpuccerite not reaching to end of second antennular segment.

First pereopods small, robust; chela with very narrow gap between fingers at their proximal half when closed, fingers with small accessory tooth distally. Second pereopods subequal, carpus with 17–22 segments. Third to fifth pereopods generally similar, merus with two or three spinules on disto-lateral margin, dactylus biunguiculate, with two accessory spinules on flexor margin.

Pleon with three anterior pleura rounded antero- and postero-ventrally, fourth pleuron obtusely angulated postero-ventrally, fifth pleuron with small acute tooth postero-ventrally, sixth pleuron with triangular projection on postero-lateral angle flanking telson. Posterior margin of telson with subacute median projection and bearing two pairs of spines posteriorly, mesial spiniform setae longer than lateral ones.

Material examined

MADAGASCAR • 1 hermaphrodite; southern Madagascar; 25°4'23" S, 46°57'8" E; depth 14–18 m; 8 May 2010; MNHN exped.; Atimo-Vatae; Stn. TB06; GenBank MW798242; MNHN-IU-2017-2377.

IRAN • 5 hermaphrodites; Ramin; Gulf of Oman; 25°16'7.05" N, 60°45'2.71" E; 5 Nov. 2008; A. Sari leg.; sandy/rocky with cobbles; GenBank MW798240; MNHN-IU-2014-1246 • 4 hermaphrodites; Ramin; Gulf of Oman; 25°16'7.05" N, 60°45'2.71" E; 16 May 2018; H. Ashrafi leg.; sandy/rocky with cobbles; GenBank MW798241; MNHN-IU-2014-1247 • 13 hermaphrodites; same collection data as for preceding; ZUTC 6840 • 8 hermaphrodites; Djod; Gulf of Oman; 25°26'40" N, 59°30'45" E; 18 May 2018; H. Ashrafi leg.; sandy/rocky with cobbles; ZUTC 6841 • 8 hermaphrodites; same collection data as for preceding; 7 Feb. 2009; H. Salehi leg.; sandy/rocky with cobbles; ZUTC 6842.

Ecology

No information about the ecology of the specimen collected in Madagascar is available. However, the specimens collected in the Gulf of Oman (by HA) were found at night in the lower intertidal zone in a deep tidal pool surrounded by large rocks, together with *Palaemon pacificus* (Stimpson, 1860). More than 100 individuals of *L. kuekenthali*, and around 30 of *P. pacificus*, were in the same tidal pool.

Distribution

Although this species has been recorded from many localities in the Indo-West Pacific (see Kemp 1914; Holthuis 1947; Chace 1997; Anker & De Grave 2016; Ashrafi *et al.* 2020), this is the first record of this species from Madagascar.

Lysmata lipkei Okuno & Fiedler, 2010

Fig. 8

Lysmata lipkei Okuno & Fiedler 2010: 599, figs 1–4.

Diagnosis

Carapace with rostrum reaching to about middle of second antennular article, armed with 4–5 teeth on dorsal margin (including two postorbital ones) and 2–4 on ventral margin; antennal tooth well-developed; pterygostomial angle with small acute tooth. Antennule with stylocerite subacute, falling short of reaching to end of first antennular segment; lateral flagellum with accessory ramus consisting of short one-segmented finger-shaped article. Antenna with inferior tooth of basicerite strong; scaphocerite distinctly surpassing antennular peduncle, lateral margin slightly concave, distolateral tooth slightly overreaching blade; carpocerite small, not reaching to end of first antennular article.

First pereopod robust, chela with fingers bearing a narrow gap when closed, especially on proximal half. Second pereopods unequal in size, longer one with 27–32 and shorter one with 23–27 carpal segments. Third pereopod with merus armed with spinules on distal 0.6 of segment length; carpus unarmed; dactylus biunguiculate, ventral margin with two or three accessory spines, decreasing in size toward



Fig. 8. Color pattern of the live ovigerous hermaphrodite, *Lysmata lipkei* Okuno & Fiedler, 2010. Photo by Tin-Yam Chan & Chia-Wei Lin. Copyright MNHN.

proximal margin (in case of having three accessory teeth, proximal one very small). Fifth pereopod with merus armed with 1–3 spinules disto-ventrally.

Pleon with three anterior pleura rounded antero- and postero-ventrally, fourth pleuron angled postero-ventrally, fifth pleuron with small acute tooth postero-ventrally. Posterior margin of telson with small acute median projection and two pairs of spines, with mesial pair stronger and longer than lateral pair.

Material examined

MADAGASCAR • 1 hermaphrodite; southern Madagascar; 25°26.4' S, 44°56.1' E; depth 14–18 m; 29 May 2010; MNHN exped.; Atimo-Vatae; Stn. BS03; GenBank MW798243; MNHN-IU-2010-4898.

Remarks

Although the lateral flagella of the two antennules in the single studied specimen of *L. lipkei* from Madagascar are broken, all other morphological characters, as well as molecular data, are consistent with the description and variability provided by Okuno & Fiedler (2010), except for one character – the number of accessory spinules on the flexor margin of the biunguiculate dactyli of the last three pereopods. In the original description, there are three accessory spinules decreasing in size proximally, while only two accessory spinules are seen in the material of the present study. This single difference can be interpreted as inter-population variation, as specimens of Japan and Madagascar are very close genetically.

Distribution

This is the seventh record of *L. lipkei*. After being originally described from Japan by Okuno & Fiedler (2010), reported again from Japan by De Grave *et al.* (2012), and subsequently reported from Singapore by Anker & De Grave (2016); this species, based on morphological and genetic data, was recorded from the south-western Atlantic Ocean, Brazil, and classified as alien there by Alves *et al.* (2018) as well two other records from Brazil (Pachelle *et al.* 2016, 2020). The present report on *L. lipkei* from Madagascar significantly extends its known Indo-West Pacific range to the south-west Indian Ocean.

Discussion

Although the western Atlantic *L. hochi* has recently been reported from India as a non-indigenous species (Jose *et al.* 2020), the present results of the phylogenetic reconstruction allow to suggest contrarily that *L. hochi* is in fact the IWP species *L. kuekenthali* introduced to the Caribbean Sea. The only morphological difference between *L. hochi* and *L. kuekenthali* stated by Jose *et al.* (2020) is the bifid stylocerite of the former species. However, in the original description of *L. hochi*, Baeza & Anker (2008: 149) reported on the stylocerite as being “usually bifid”. It is thus evident that this character varies in the latter species.

The present material of *L. kuekenthali* from the Gulf of Oman shows variability in the pterygostomial angle which is rounded in larger specimens (see also remarks for *L. kuekenthali* by Kemp in 1914 and Chace in 1997) but with a small tooth in smaller specimens. All other characters are completely consistent between *L. hochi* and *L. kuekenthali*. Additionally, the color pattern shown for *L. hochi* by Baeza & Anker (2008: fig. 2) and Jose *et al.* (2020: fig. 2) is very similar to that of *L. kuekenthali* (Ashrafi *et al.* 2020: fig. 1d).

The western Atlantic *L. hochi* might be conspecific with the IWP *L. kuekenthali*. However, additional studies focusing on both color pattern as well as morphological and genetic characters from specimens collected from more localities are needed to support this last claim, considering that *L. kuekenthali* was suggested to represent a species complex by Anker & De Grave (2016).

In the past decade, four species of *Lysmata* have been reported as alien and/or invasive (Soledade *et al.* 2013; Frogliá & Deval 2014; Alves *et al.* 2018; Jose *et al.* 2020). Among all the possible mechanisms

involved in the introduction of invertebrates, including crustaceans (e.g., ship transport and intentional introductions – Rodríguez & Suárez 2001; Hänfling *et al.* 2011), the aquarium trade seems to play an important role in shrimps (Rhyne *et al.* 2009; Baeza & Behringer 2017). Peppermint shrimps are highly popular in the aquarium trade given their striking coloration, the ability for controlling pests, and for cleaning fish from parasites (Bauer 2000; Rhyne *et al.* 2004; Calado 2008; Rhyne *et al.* 2009).

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