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Molecular phylogeny of *Thoe* Bell, 1836 (Crustacea, Brachyura, Majoidea)

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ABSTRACT

Thoe Bell, 1836 is amphi-American in distribution and includes small spider crabs with cryptic habits and rare records in the literature and carcinological collections. The taxonomy of the three recent and two fossil species currently known in the genus has been revised. A phylogenetic reconstruction conducted here based on the mitochondrial markers COI and 16S rRNA supports the monophyletic status of *Thoe*. The resulting phylogeny suggests a western Atlantic to eastern Pacific radiation of the genus.

KEYWORDS

Decapoda, Eastern Pacific, Mithracidae, spider crab, taxonomy, Western Atlantic

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INTRODUCTION

The spider crabs form one of the largest brachyuran families, with almost 1000 described species (Davie et al., 2015). This group presents great morphological diversity, varying from the largest known arthropod, the giant Japanese spider crab *Macrocheira kaempferi* (Temminck, 1836), to very tiny crabs, such as species of *Thoe* Bell, 1836, ranging from 10 to 12 mm in carapace length. Recent species of *Thoe* are endemic to the Americas, with two species occurring in the western Atlantic, *Thoe aspera* Rathbun, 1901, and *Thoe puella* Stimpson, 1860 and one in the eastern Pacific, *Thoe erosa* Bell, 1836. Additionally, two fossil species, *Thoe asperoides*† Collins and Todd in Todd and Collins, 2005, from the Early Pleistocene of Panama, and the doubtful *Thoe vanuaensis*† Rathbun, 1945, likely from the Pliocene of Vanua Mbalavu, Fiji, are included in the genus.

Due to their small size and cryptic habits, as well as disruptive color and background matching, species of *Thoe* are rare in collections and difficult to find in their natural habitats. Thus, material of this genus deserves special attention to understand its distribution, taxonomy, and relationships, especially with the closely related *Hemus* A. Milne-Edwards, 1875, which occupy similar niches in tropical epifaunal fouling assemblages and similar morphology (Garth, 1958; Windsor and Felder, 2011; 2017). Indeed, previous molecular studies have shown that *Thoe*, *Hemus*, *Petramithrax* Windsor and Felder, 2014, and *Mithraculus* White, 1847 form a monophyletic clade (Windsor and Felder, 2014). However, considering the re-identification of a *T. aspera* specimen included in Windsor and Felder (2014) as *T. puella*, the phylogeny of *Thoe* and phylogenetic related species should be reviewed to include new information and new specimens positively identified as *T. aspera*. Also, the taxonomy and distributional range are updated based on new specimens collected and museum material examined.

Here we propose a molecular phylogenetic hypothesis for all extant species of *Thoe* including new sequences for *T. aspera*, to investigate the inter- and intraspecific relationships, based on partial sequences of the mitochondrial markers cytochrome oxidase subunit I (COI) and 16S rRNA. We take the opportunity to review in detail the taxonomy of the genus, including its fossil species, a more complete synonymic list, and updated remarks for all species. Also, we provide the first record of *T. aspera* for the coast of São Paulo, Brazil, and the first records for Martinique, and Trinidad and Tobago.

MATERIAL AND METHODS

Specimens examined are deposited in the collections of the Laboratório de Sistemática Zoológica, Universidade Estadual Paulista, Campus de Botucatu, Brazil (LSZ), Coleção de Crustáceos do Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, Brazil (CCDB), Muséum national d'Histoire naturelle, Paris, France (MNHN), Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP), Naturhistorisches Museum Basel, Switzerland (NMB F), Zoology Collection, Oxford University Museum of Natural History, England (OUMNH.ZC), Florida Museum of Natural History, University of Florida, United States (UF), National Museum of Natural History, Smithsonian Institution, United States (USNM), and Zoological Collection, University of Louisiana at Lafayette, United States (ULLZ) (now housed at USNM). The geographical names used follow the National Geographic Atlas of the World, 8th edition, Washington, DC.

We used the following abbreviations: CL, carapace length (along the dorsal midline, from the base of the rostral sinus to the posterior margin of the carapace); CW, carapace width (taken at the widest point, including lateral spines); P2–P5, pereopods 2 to 5 (P1 is the cheliped); G1, first gonopod; G2, second gonopod; ovig., ovigerous; juv., juvenile; RV, research vessel; stn, station; col., collector or collected by; det., determined by; m, meter of depth; EP, eastern Pacific; WA, western Atlantic; † indicates taxa exclusively known from fossils.

Comparative material

Hemus cristulipes A. Milne-Edwards, 1875. BRAZIL: 1 female (MZUSP 7212), Maranhão, R/V "Almirante Saldanha", stn. 1732A, 02°13'S 41°51'W, 30.x.1967, 69 m; 2 females (MZUSP 9146), Espírito Santo, Prof. R/V "W. Besnard", stn. 54, 18°54'08"S 39°15'04"W, i.1973, Rio Doce Project col.; 2 males, 2 females (MZUSP 11890), Rio de Janeiro, Bacia de Campos, stn. 03, Petrobrás Project col., Melo, G.A.S. det.; 1 female (MZUSP 11921), *ibidem*.

DNA extraction, PCR, and sequencing

Total genomic DNA was extracted from muscle tissue using the Omega Bio-tek EZNA Tissue DNA Kit. DNA extraction was conducted at the Laboratory of Molecular Biology at MZUSP. Partial sequences of the 16S and barcode regions of COI mitochondrial genes were amplified with the following primers, respectively: 16SF/16SR (Hultgren and Stachowicz, 2008) and LCO1490/HCO2198 (Folmer et al., 1994). PCR was performed in 20 µL reactions with reagent volumes and concentrations as follows: 0.4 µL of each primer (10 µM), 2 µL of Taq buffer (10X), 0.6 µL of MgCl2 (50 mM), 0.4 µL dNTPs (10 mM) and 0.2 µL Taq (PlatinumR Taq DNA Polymerase) (5 U/µL), 1 µL of genomic DNA and 15 µL of ultrapure water. PCR cycles, 16S: 94 °C for 30 s (denaturation), 48 °C for 30 s (annealing), and 72 °C for 60 s (extension) and, COI: 95 °C for 30 s (denaturation), 52 °C for 30 s (annealing), and 72 °C for 45-60 s (extension).

Sequencing reactions were purified using ExoSAP-IT™ (Thermo Fisher Scientific Inc.) and sent to be sequenced at the Instituto de Biotecnologia, Universidade Estadual Paulista (IBTEC-UNESP), Botucatu, state of São Paulo. Sequencing reactions were performed using 1 µL of purified PCR product in a 15 µL reaction containing 5 µL primer (0.5 pmol/µL), sequenced on an ABI 3500 automated DNA (Applied Biosystems) according to the manufacturer's instructions. Sequences were assembled, trimmed of primers, and checked for quality using Geneious 8.0.5 and 9.1.8 (Biomatters Ltd, Auckland, New Zealand). Sequences generated for this study have been deposited into GenBank (Tab. 1).

Table 1. Taxa included in the molecular phylogenetic and genetic distance analyses. Newly sequenced specimens are in bold. Abbreviation of institutional collections: CCDB, Coleção de Crustáceos do Departamento de Biologia - FFCLRP, Universidade de São Paulo; KAC, Keith A. Crandall lab collection; LSZ, Coleção do Laboratório de Sistemática Zoológica, Universidade Estadual Paulista; MZUSP, Museu de Zoologia, Universidade de São Paulo; ULLZ, University of Louisiana at Lafayette Zoological Collection; USNM, United States National Museum, Smithsonian Institution. GMx = Gulf of Mexico, water body names preceded by E, or W to indicate eastern or western, respectively, –, no sequence.

Taxon Name	Locality	Catalog No.	GenBank Accession Nos.	
			16S	COI
Mithracidae				
Thoe aspera	**W Atlantic Brazil**	**LSZ 185**	**MZ322947**	**MZ323413**
Thoe aspera	**W Atlantic Brazil**	**MZUSP 41773**	**MZ322965**	–
Thoe erosa	E Pacific Panamá	ULLZ 9073	KF453020	KF452939
Thoe puella	W Atlantic, Florida Keys	ULLZ 4533	KF452992	KF45290
Thoe puella	Caribbean, Colombia	ULLZ 9227	KF453027	KF45947
Thoe puella	Caribbean, Panama	ULLZ 13582	MK971356	MN183924
Thoe puella	Caribbean, Panama	ULLZ 13583	MK971561	MN183923
Petramithrax pygmaeus	E Pacific, Panama	ULLZ 10063	KF452972	KF452895
Hemus cristulipes	E GMx, Florida Keys	ULLZ 5783	KF452995	KF452915
Hemus magalae	Caribbean, Panama	USNM 1149374	KF453034	KF452958
Mithraculus forceps	Caribbean, Panama	ULLZ 13675	MK971651	MN184210
Mithraculus cinctimanus	Caribbean, Panama	ULLZ 13467	MK971628	MN184186
Mithraculus cinctimanus	Caribbean, Belize	ULLZ 12012	KF452986	KF452905
Omalacantha bicornuta	W Atlantic, Brazil	CCDB 5740	KX398194	KX398201
Omalacantha bicornuta	Caribbean, Panama	ULLZ 13563	MK971650	MN184209
Omalacantha bicornuta	Caribbean, Panama	ULLZ 13567	MK971631	MN184189
Outgroup				
Maja squinado	unknown	KAC 2168	DQ079723	–

Molecular data analysis

Sequences generated for this study were combined with those from Windsor and Felder (2014; 2017) and other sequences available from GenBank. Locality information and GenBank accession numbers for taxa included in the molecular analyses are provided in Tab. 1.

Multiple sequence alignment was performed using the MAFFT FFT-NS-I (Katoh et al., 2005) alignment algorithm for the individual molecular markers. The individual datasets were concatenated in Geneious. Phylogenetic trees were constructed using maximum likelihood in RAxML 7.0.4 (Stamatakis, 2006). In RAxML, we used the '-f ae' option with 1000 bootstrap replicates implemented on MEGA X (Tamura and Nei, 1993; Kumar et al., 2018). Also, a Bayesian Inference analysis of phylogeny was conducted using MrBayes (plugin v.2.2.2: Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) implemented in Geneious (9.1.8 v.) with four heated MCMC chains over 1,100,000 iterations, sampling every 200th tree. A burn-in of 10 % was discarded after visual inspection of the trace file for convergence. Likelihood and Bayesian parameters followed the General Time Reversible (GTR) model with a gamma distribution on the partitioned dataset. The resulting best tree was used to reflect phylogeny (Fig. 1).

Analyses to calculate the estimate of evolutionary divergence of 17 nucleotides of partial mitochondrial 16 S rRNA gene sequences over sequence pairs between species were conducted using the Tamura-Nei model implemented on MEGA X (Kumar et al., 2018) (Tab. 2). The rate variation among sites was modeled with a gamma distribution (shape parameter = 1). All ambiguous positions were removed for each sequence pair (pairwise deletion option).

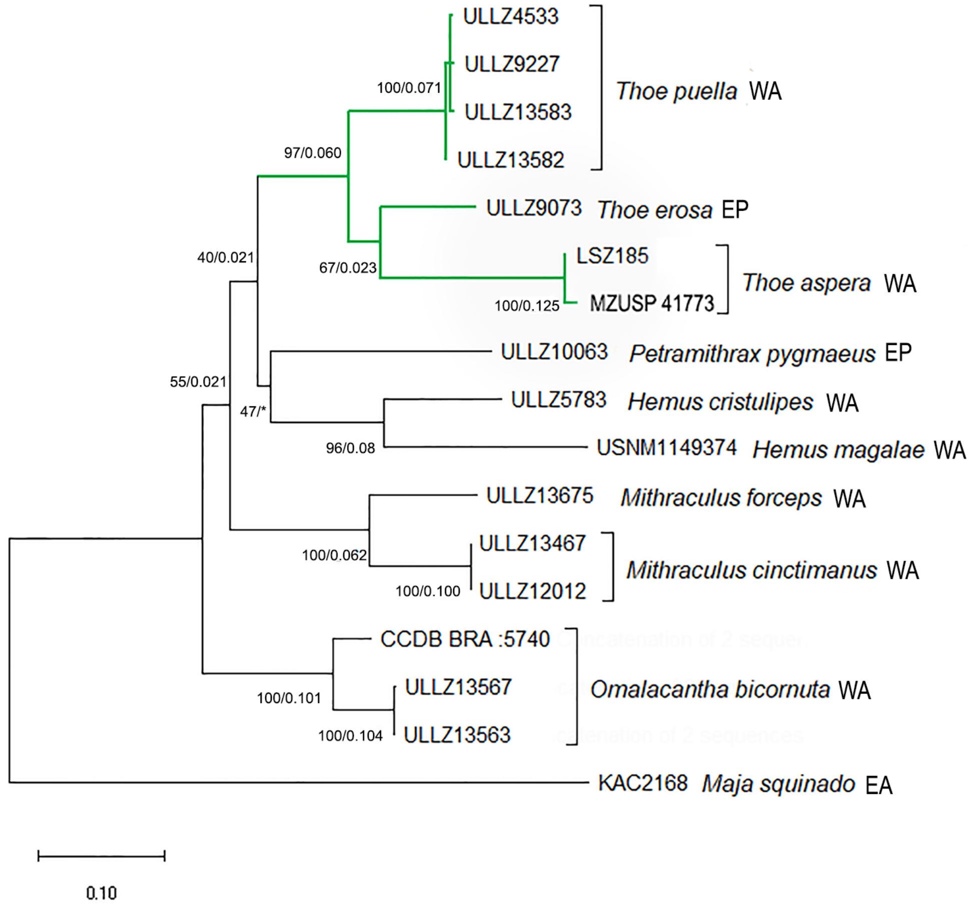

Figure 1. Molecular phylogenetic tree represented as maximum likelihood and Bayesian topology of two partial mitochondrial (COI and 16S) sequences showing *Thoe* inter- and intra-generic relationship, based on 5 close genera and 17 sequences including *Maja squinado* as outgroup with maximum likelihood bootstrap values and Bayesian posterior probabilities (* different topology). Note: ULLZ 9227 of Windsor and Felder (2014) reidentified as *Thoe puella* Stimpson, 1860.

Table 2. Pairwise evolutionary divergence of partial 16 S rDNA sequences using Tamura-Nei model among *Thoe* and other Mithracidae species using *Maja squinado* as outgroup.

	T. aspera	***T. erosa***	***T. puella***	***M. cinctimanus***	***P. pygmaeus***	***O. bicornuta***	***H. cristulipes***	***M. forceps***	***H. magalae***	***M. squinado***
Thoe aspera										
Thoe erosa	0.13									
Thoe puella	0.15	0.09								
Mithraculus cinctimanus	0.21	0.17	0.18							
Petramithrax pygmaeus	0.22	0.17	0.17	0.25						
Omalacantha bicornuta	0.22	0.20	0.19	0.22	0.23					
Hemus cristulipes	0.22	0.15	0.16	0.22	0.21	0.22				
Mithraculus forceps	0.22	0.16	0.18	0.08	0.25	0.24	0.24			
Hemus magalae	0.25	0.21	0.24	0.22	0.26	0.25	0.14	0.26		
Maja squinado	0.35	0.32	0.31	0.34	0.38	0.30	0.37	0.36	0.35	

RESULTS

Two specimens of *T. aspera* from the Brazilian coast were sequenced, and the mitochondrial loci COI and 16S were successfully amplified. Nodes of maximum likelihood bootstrap support are shown on the maximum likelihood phylogenetic tree (Fig. 1).

Thoe forms a highly supported (97 %) monophyletic group. The western Atlantic species *T. puella* forms the basal branch of the genus, while the eastern Pacific species *T. erosa* Bell, 1836 is supported (67 %) as a sister group to the Atlantic species *T. aspera*. This divergence is probably due to the misidentification of the specimen ULLZ 9227 used in their analysis which has since been redetermined as *T. puella* (Darryl Felder, pers. comm. to AMW).

The clade composed of *Petramithrax pygmaeus* (Bell, 1836a) and *Hemus* has low support (40 %) as a sister group to *Thoe* (Fig. 1). This could be a result of the different sequences used by Windsor and Felder (2014) and the present study. All three genera include very small crabs that inhabit subtidal reefs and are commonly associated with *Pocillopora* Lamarck, 1816 and other corals, sponges, shell hash, and reef rubble (Rathbun, 1925; Garth, 1958). *Mithraculus* is basal to the clade formed by *Petramithrax*, *Hemus*, and *Thoe*.

In the evolutionary divergence analysis, a total of 484 positions were obtained in the final dataset. The genetic distance between the Pacific species *T. erosa* and the Atlantic congener *T. puella* is lower (0.09) than between two Atlantic species, *T. aspera* and *T. puella*, which shows the rate of 0.15 base substitutions per site (Tab. 2), corroborating the phylogenetic results.

Systematics

Superfamily Majoidea Samouelle, 1819

Family Mithracidae MacLeay, 1838

Thoe Bell, 1836

Thoe Bell, 1836a: 170 [Type species: *Thoe erosa* Bell, 1836, by monotypy, gender feminine].

Platypes Lockington, 1877a: 41 [Type species: *Platypes edentata* Lockington, 1877a, accepted as *Thoe erosa*, by monotypy, gender feminine].

Diagnosis. See Windsor and Felder (2014: 167).

Included species. *Thoe aspera* Rathbun, 1901 (WA), *Thoe erosa* Bell, 1836 (EP), *Thoe puella* Stimpson, 1860 (WA), *Thoe asperoides*† Collins and Todd, 2005, *Thoe vanuaensis*† Rathbun, 1945.

Remarks. Windsor and Felder (2014: 167) indicated the authority of the genus *Thoe* to Chun (1879), however the authors probably referred, by mistake, to the homonymous Ctenophora genus *Thoe* Chun, 1879. According to the ICZN (1999, art. 23), applying the principle of priority, *Thoe* Bell, 1836 should be maintained and a new name for the Ctenophora genus should be designated.

Thoe vanuaensis† from the Pliocene of Vanua Mbalavu, Fiji, was described from a fragment of the left cheliped, including the partially preserved fixed and movable fingers. The type material is deposited in the USNM Department of Paleobiology Collections (USNM MO 498434). Although clearly a majoid cheliped, the generic placement of this species seems to not be supported by its morphology. The clear gap between fingers, the few small tubercles on the fixed finger, and the absence of tubercles or teeth on the dactyl are characteristics of several groups among the majoid families. *Thoe vanuaensis* † has sparse tubercles on the upper face of the fixed finger, differing from the recent species of *Thoe* that have the propodi surface without any tubercles or spines. It is important to note that this species is from Fiji, considering that *Thoe* recent species are all endemic to the Americas, its assignment to this genus is doubtful and a detailed examination of this material is necessary to determine its placement in another genus.

The other fossil species, *Thoe asperoides*† from the Late Miocene of Panama, on the other hand, resembles the recent species *T. aspera*. The holotype (NMB F1681) is a fragment of the carapace that resembles *T. aspera* in overall carapace shape and the regions are well delimited with numerous tubercles. This species has another attributed record, a fixed finger fragment, from the Late Pliocene-Early Pleistocene of Panama (NMB F1682) (Collins and Todd, 2005).

***Thoe aspera* Rathbun, 1901**
(Fig. 2A–D)

Thoe aspera Rathbun, 1901: 63, text-fig. 10 [type locality: Ensenada Honda, Culebra, Puerto Rico, type material: male holotype (USNM 23773)]. — Rathbun, 1925: 352, text-fig. 114, pl. 124, figs. 4–5. — Rathbun, 1933: 22. — Vélez, 1978: 74, text-fig. 4. — Coelho, 1971: 141. — Coelho, 1972: 214. — Fausto-Filho, 1974: 82. — Fausto-Filho, 1975: 82. — Markham et al., 1990: 431. — Melo, 1996: 250, 1 text-fig. — Coelho et al., 2008: 24. — Alves et al., 2012: 57. — Windsor and Felder, 2014: 167.

Type material examined. Adult male, holotype (cl 10 mm, cw 7.84 mm), 1 female, paratype (USNM 23773), Puerto Rico, Ensenada Honda, Culebra Island, 18°18'18.0"N 65°18'05.0"W, R/V "Fish Hawk", 9–10.ii.1899 (Fig. 2C, D).

Additional material examined. 1 juvenile male (UF 44442), Panama, Bocas del Toro Province, Runway, 23.v.2016, Leray, M., Michonneau, F. and Lasley, R. col.; 1 female (UF 44492), Panama, Bocas del Toro Province, Seagal, 09°17'21.3"N 82°17'44.6"W, 25.v.2016, Leray, M., Michonneau, F. and Lasley, R. col.; 1 female (UF 44330), Mexico, Punta Puebla, 16.v.2016, Leray, M., Michonneau, F., Lasley, R. col.; 1 male (MNHN IU 2014-16077), Martinique, Grande anse du Diamant, Madibenthos Expedition, stn. AR129, 14°28'07.9968"N 61°01'08.0004"W, depth 6 m, 15.ix.2016; 1 ovigerous female (MNHN IU 2014-16221), Martinique, Le Robert, Madibenthos Expedition, stn. AB193, 14°41'18.9996"N 60°50'9.996"W, depth 18 m, 19.ix.2016; 1 ovigerous female (MNHN IU 2014-16238), Martinique, Grande anse du Diamant, Madibenthos Expedition, stn. AR129, 14°28'07.9968"N 61°01'08.0004"W, 6 m, 15.ix.2016; 1 ovigerous female (MNHN IU 2017-1638), Martinique, Le Vauclin, Madibenthos expedition, stn. AB130, 14°32'00.0024"N 60°48'56.9988"W, depth 1 m, 20.ix.2016; 2 females (USNM 1269593), Trinidad And Tobago, Man-O-War Bay, Charlottleville, 3.vii.1939, Hardy, J.D. col., i.2015, Windsor, A. det.; 1 male, 2 juvenile males (cl 7.5 mm, cw 6.78 mm) (MZUSP 41773), Brazil, Pernambuco, Suape, depth 4 m, 26.x.2018, Bochini, G. and Almeida A. col.; 1 female, (LSZ 185), Brazil, São Paulo, Ilhabela, Ilha da Vitória, depth 5 m, up to coral *Madracis decactis* fragments, 14.xii.2017, Moraes, I.R.R. and Cobo, V.J. col (Fig. 2A, B).

Emended diagnosis. Carapace armed with sharp spines and tubercles, 2 short spines at posterolateral angles. Rostral spines separated by a large V-shaped sinus. Basal article of antenna longer than broad, with 2

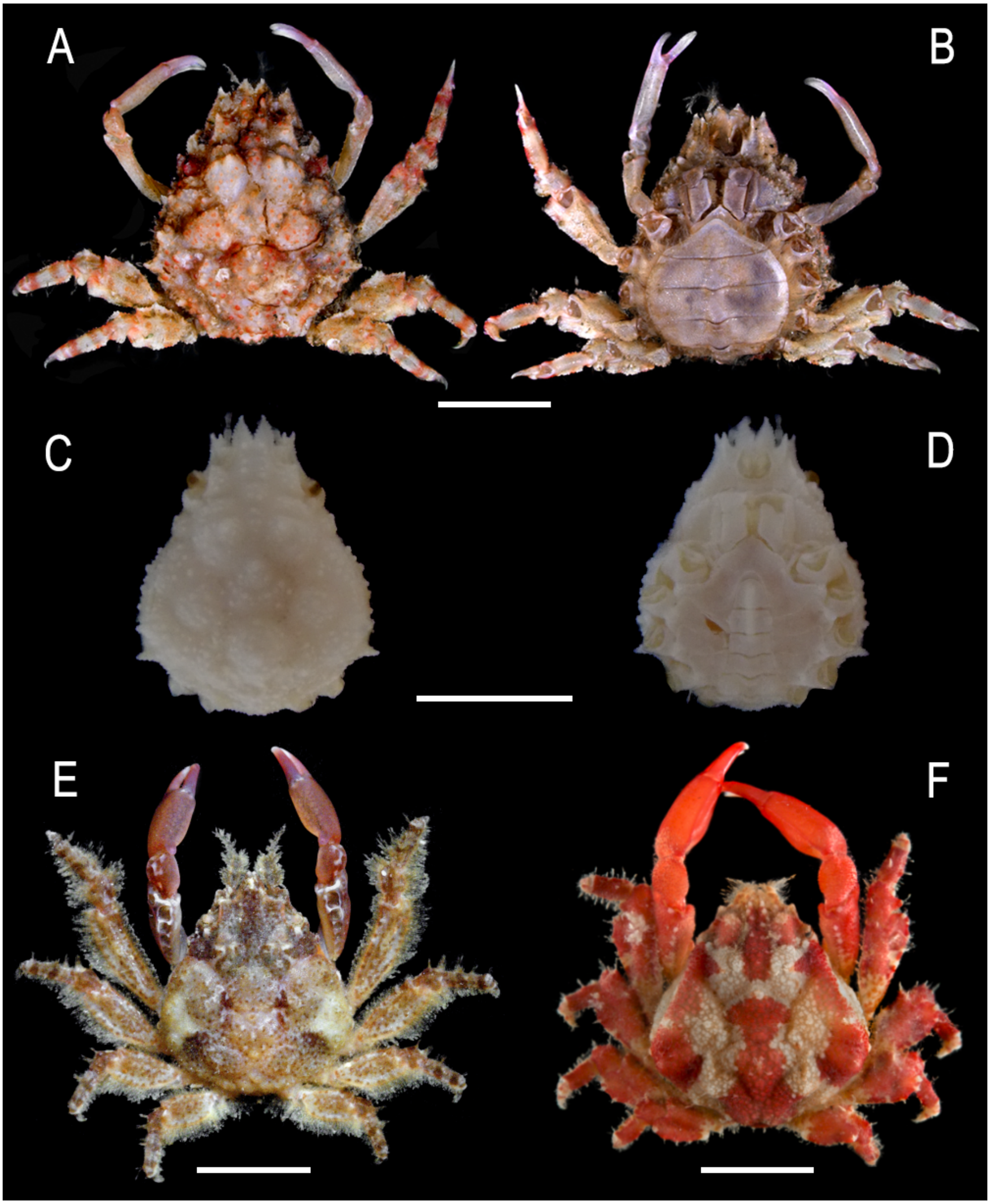

Figure 2. **A**–**D** *Thoe aspera* Rathbun, 1901. **A**, **B**, Female, CL 7.5 mm, CW 6.78 mm, Brazil (LSZ 185). **C**, **D**, Male lectotype, CL 9.9 mm, CW 7.84 mm, Puerto Rico (USNM 23773). **A**, **C**, Habitus. **B**, **D**, Ventral view. **E**, *Thoe erosa* Bell, 1836, habitus, male, CL 8.6 mm, Panama (eastern Pacific) (ULLZ 9738). **F**, *Thoe puella* Stimpson, 1860, habitus, male, CL 10 mm, CW 11 mm, Guadeloupe (MNHN IU 2013 4256). Credit of photos: E, D. Felder; F, J. Poupin. Scale bars: 0.5mm.

distal spines. Palm of cheliped 3 times longer than wide. Merus of legs (P2–P5) with moderately dilated crests (meral extensions) in lateral margin.

Habitat. Reef zone, between coral fragments and among algae covering coral rubble (Markham et al., 1990).

Type locality. Ensenada Honda, Culebra, Puerto Rico.

Distribution. Western Atlantic: México, Puerto Rico, Panama, Martinique, Trinidad and Tobago, Colombia and Brazil (in the states of Pernambuco, Alagoas, and São Paulo) (Rathbun, 1901; Coelho, 1971;

Melo, 1996; Santos and Coelho, 1997; Castaño and Campos, 2003; Alves et al., 2012; Giraldes et al., 2015).

Remarks. Coelho (1971) was the first to report *T. aspera* from the Brazilian coast based on a male collected in the intertidal zone of Candeias reef, in Pernambuco State. Fausto-Filho (1975) collected the second record of this species in Brazil from Maceió, Alagoas State. After that, this species was reported only a couple of times from the coast of Pernambuco, in Praia do Paiva (Austregésilo-Filho and Ramos-Porto, 1995), Jaboatão dos Guararapes (Santos and Coelho, 1997) and Porto de Galinhas (Giraldes et al., 2015). This study presents the first and the southern-most record of *T. aspera* in São Paulo, Brazil.

The female specimen (LSZ 185) from Ilha da Vitória was found in fragments of the coral *Madracis decactis* (Lyman, 1859) at 5 m depth. The female shows two spines at the posterolateral margin of the carapace and the carapace regions are well delimited as observed in the male holotype (Fig. 2A–D). Color in life of *T. aspera* is beige with red spots and the chelipeds are pinkish (Fig. 2A, B).

The specimens from MNHN-Paris collected during Madibenthos Expedition (2016) extends the distribution range of *T. aspera* to Martinique (MNHN IU 2014-16077, MNHN IU 2014-16221, MNHN IU 2014-16238), and the specimen USNM 1269593 represents the first record for Trinidad and Tobago.

Thoe aspera was not listed as a valid species in Ng et al. (2008) and, according to Coelho et al. (2008), the former authors forgot to include this species in their catalogue.

***Thoe erosa* Bell, 1836**

(Figs. 2E, 3)

Thoe erosa Bell, 1836a: 170 [type locality: Galápagos Island, type material: 1 female syntype (OUMNH. ZC.13734), 1 female syntype (OUMNH. ZC.13735)]. — Bell, 1836b: 48, pl.19, fig. 4k-o. — H. Milne-Edwards, 1838: 140. — A. Milne-Edwards, 1875: 121, pl. 19, 4a-d. — Nobili, 1901: 30. — Rathbun, 1910: 575. — Rathbun, 1925: 351, pl. 249, figs. 1–6. — Boone, 1927: 149, text-fig. 145. — Garth, 1946: 386. — Garth, 1958: 426. — DiMauro, 1982: 163. — Hendrickx, 1995: 132. — Ng et al., 2008: 120. — Windsor and Felder, 2014: 167, fig. 3o, fig. 4p.

Thoe sulcata Stimpson, 1860: 177 [type locality: Lower California, Cape St. Lucas, type material: non-extant]. — A. Milne-Edwards, 1875: 121, pl. 19, figs. 5-5e. — A. Milne-Edwards, 1878: 121. — Streets and Kingsley, 1877: 104. — Rathbun, 1910: 575. — Rathbun, 1923: 635. — Rathbun, 1924: 379. — Rathbun, 1925: 349, pl. 125, figs. 3, 4. — Crane, 1937: 59. — Steinbeck and Ricketts, 1941: 466, pl. 24, fig. 2.

Platypes edentata Lockington, 1877a: 41[type locality: Mexico, Mazatlán: type material: deposited on Peabody Academy of Science, probably non-extant]. — Lockington, 1877b: 65.

Thoe edentata — Cano, 1889: 101, 183.

Thoe panamensis Nobili, 1901: 30 [type locality: Ecuador, Flamenco Island, type material: non-extant]. — Rathbun, 1910: 575. — Rathbun, 1925: 351, pl. 125, figs. 5, 6, text-fig. 113. — Finnegan, 1931: 624.

Thoe sulcata panamensis — Crane, 1947: 71, text-fig. 2A. — Garth, 1948: 28. — Hendrickx, 1995: 132.

Thoe sulcata sulcata — Crane, 1947: 71, text-fig. 2B. — Garth 1948: 28. — Hendrickx, 1995: 132.

Material examined. 1 male, Panama, Eastern Pacific (ULLZ 9738).

Diagnosis (as in Garth, 1958). Only 1 anterior tooth or lobe on basal antennal article. Double row of deep excavations on merus of pereiopods. Fingers of males strongly arched; gap entire except for 1 tooth on dactyl.

Habitat. Sandy mud.

Type locality. Eastern Pacific, Ecuador, Galápagos Island, depth 12.8 m; Hugh Cuming coll.

Distribution. Panama, México (from Tepoca Bay, Gulf of California, to the state of Oaxaca as *Thoe sulcata*), Costa Rica, Ecuador (Santa Helena Bay to

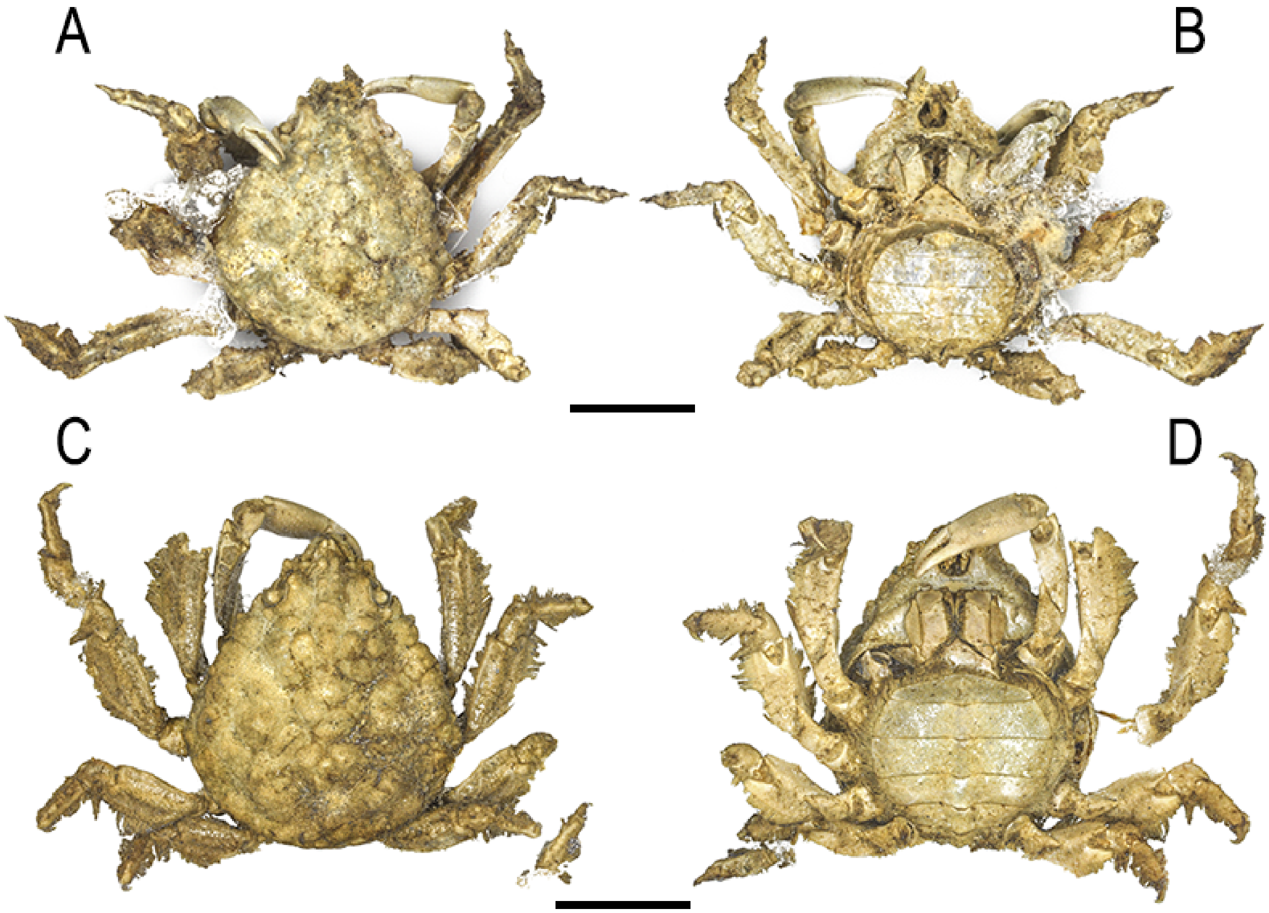

Figure 3. A–D, *Thoe erosa* Bell, 1836. **A**, **B**, Female syntype, CL 9.9 mm, CW 9.5 mm (OUMNH.ZC.13734). **C**, **D**, Female syntype, CL 11.6 mm, CW 10.5 mm (OUMNH.ZC.13735). Credit of photos: K. Child. Scale bars: 0.5mm.

Galápagos Islands as *T. erosa*). From Gorgona Island, Colombia, to South of Salinas, Ecuador, Flamenco Island as *T. panamensis* (Nobili, 1901; Rathbun, 1910; Hendrickx, 1995; Garth, 1939).

Remarks. Much confusion remains around the type material of *T. erosa*. Bell (1836a) described *T. erosa*, given the measurement "5 lin., lat. 4," (CL 10.5 mm, CW 8.4 mm) and later, in 1836b, included a different measurement: "length 6 lines, breadth 5 lines" (CL 12.7 mm, CW 10.5 mm). It is clear he based his descriptions on more than one specimen because he included male and female characteristics (Bell, 1836a; 1836b) suggesting a syntype series (see Garth, 1958: 426); however, no differences were mentioned about size, number of individuals, and the measurements differed in both publications. The type material of this species was considered lost by several authors (e.g., Rathbun, 1925; Garth, 1958). Di Mauro (1982) mention two syntype females deposited at the Oxford Museum collection for *T. erosa*. Di Mauro clearly only considered the Bell's (1836b) publication in his study, and indicated the larger female specimen, OUMNH.ZC.13735 (CL 12.7 mm, CW 10.5 mm), as the specimen measured by Bell (1836b). Di Mauro (1982) also provided the measurements for the other female (OUMNH.ZC.13734) being 11 mm CL and 9 mm CW (Fig. 3), very similar to what was provided by Bell (1836a). Consulting the Oxford Museum collections, we found further minor discrepancies in the size of the specimens: OUMNH.ZC.13735 11.6 mm CL, 10.5 mm CW, and OUMNH.ZC.13734 with 9.9 mm CL, 9.5 mm CW. It is important to note that the specimens were dry preserved, and the specimen OUMNH.ZC.13734 had the legs fixed with superglue (Fig 3). Bell (1836b) illustrated a male, whose chelipeds are distinctly more robust than in females and juveniles; however, the deep excavations on the merus of the cheliped are visible in both, including in the preserved material in the Oxford collection (Fig. 3A, C). The male illustrated by Bell (1836b) was not found in the OUMNH.ZC collections and it is probably lost. We agree with Di Mauro (1982) that both females are part of the syntype series, and they are here illustrated for the first time (Fig. 3A–D).

Lockington (1877a) sent the type-material of *Platypes edentata* to the Peabody Academy of Science in Salem, Massachusetts. Streets and Kingsley (1877: 104) examined the specimens and attested them as "plainly" *T. sulcata*. While reviewing this species, Windsor and Felder (2014) observed morphological variability among specimens forming a morphological continuum between species and subspecies. The review and the comparison of the distinguishing morphological characters of *T. erosa, T. panamensis,* and *T. sulcata* proposed by Garth (1958: 431–432), along with his notes, led Windsor and Felder (2014) to synonymize all Pacific species.

Thoe erosa is the most easily distinguishable species of the genus by having the carpus and merus of the chelipeds deeply excavated without crested margins, while in *T. puella* and *T. aspera* the cheliped surface is not excavated and have crested margins (Fig. 2A, B, E, F).

Color in life is light yellowish, with darker regions from brownish to dark red. Chelipeds are light brown to pinkish on fingers (Fig. 2E).

Thoe puella **Stimpson, 1860**

(Figure 2F)

Thoe puella Stimpson, 1860: 179 [type locality: Florida, Tortugas, type material: non-extant]. — A. Milne-Edwards, 1873: 122, pl. 19, 3-3e. — Rathbun, 1897: 11. — Rathbun, 1925: 348, pl. 125, fig. 1, 2. — Rodríguez, 1980: 277. — Ramos, 1986: 69, fig. 1. — Marcano and Bolaños, 2001: 76. — Ng et al., 2008: 120. — Windsor and Felder, 2014: 167. — García and Capote, 2015: 11, fig. 5i and 5j. — Carmona-Suarez and Poupin, 2016: 378, fig. 8k.

Pisa latipes Desbonne, in Desbonne and Schramm, 1867: 19 [type locality: Guadeloupe, type material: non-extant].

Material Examined. 1 male (MNHN IU 2013 4256), Guadeloupe, Karubenthos 2012 [lot JL489-5], stn. GM09, depth 1 m, Poupin, J. det.; 1 male, 1 ovigerous female (MZUSP 33887), Panama, North of Boca del Drago, stn. 12, depth 0.5–2 m, in and under coral rubble, 01.v.2015, A. Anker col., 21.xii.2021, Colavite, J. det.

Diagnosis (as in Rathbun, 1925). Carapace margins perpendicular and nearly straight. Basal antennal articles not grooved. Margins of merus joints of ambulatory legs thin.

Habitat. Solid substrates and rubble. Found in rocky and coralline bottoms, reef corals, in shallow waters (Garth, 1978; Carmona-Suarez and Poupin, 2016).

Type locality. Dry Tortugas, Florida, United States of America.

Distribution. South Florida, Bahamas, Belize, Cuba, Jamaica, Guadeloupe, Curaçao, Bonaire and Saint Maarten, Dry Tortugas, Greater Antilles, Guadeloupe, Colombia, Venezuela (Rathbun, 1897; 1901; Garth, 1958; Powers, 1977; Keith, 1985; Castaño and Campos, 2003; García and Capote, 2015; Carmona-Suarez and Poupin, 2016; Diez and Espinosa, 2018).

Remarks. The type material of *T. puella* is probably lost, as are several other species described by Stimpson due to the Great Chicago Fire of 1871 (Mayer, 1918).

Thoe puella and *T. aspera*, both western Atlantic species, can be easily distinguished by: (i) the basal article of antenna without spines in *T. puella* (vs. basal article of antenna with two distal spines in *T. aspera*, one visible in dorsal view); (ii) the carapace with sparse tubercles, branchial region well defined and laterally projected (vs. carapace with sparse spines and tubercles, branchial region less defined, with two distinct posterolateral spines); and (iii) rostral spines blunt in *T. puella* (vs. rostral spines acute, with a distinct V sinus in *T. aspera*) (Fig. 2A, B, F). The color of each *Thoe* species and carapace characteristics usually match the background of their habitats, making them difficult to observe *in situ*. Each one has a unique color pattern that can be used as an informative character to distinguish each species in the field (Fig. 2A, E, F).

Color in life is beige with some darker spots that vary from pinkish to dark red. Chelipeds are vivid red.

DISCUSSION

Small crabs are frequently overlooked in systematic studies and molecular phylogenies, possibly due to the difficulty of morphological identification and sample collection. *Thoe* species, specifically, are difficult to find in their natural habitats due to cryptic behavior, and consequently are rarely found in biological collections. Previous phylogenetic hypotheses involving this genus were based on a misidentified specimen (see Results). The reidentification of the specimen (ULLZ 9227) and provision of new sequences for *T. aspera* have modified the intraspecific relationships of this genus.

Monophyly of the genus is consistently well supported (Fig. 1). The western Atlantic species *T. puella* forms the basal branch of the genus, while the eastern Pacific species *T. erosa* is the sister group to the western Atlantic species *T. aspera*, differing from the hypothesis previously presented by Windsor and Felder (2014). The genetic distance also supports the phylogenetic results, with the Pacific species *T. erosa* and the Atlantic *T. puella* more genetically similar than the Atlantic species, *T. aspera* and *T. puella*, suggesting an older divergence between Atlantic species (Tab. 2). This hypothesis of western Atlantic to eastern Pacific radiation is also observed for other amphi-Atlantic majoids (e.g., Tamburus and Mantellato, 2021), probably due the closure of the Central American Seaway.

The relationship between other miniature mithracids, *Petramithrax pygmaeus* and *Hemus* spp., could not be elucidated here, with *Petramithrax* and *Hemus* forming a clade with low support, and this clade forming the sister group to *Thoe,* also with low support (both < 50%, Fig. 1). However, the intergeneric relationship of *Thoe* has been tested in a more inclusive context by Windsor and Felder (2014) in which *Petramithrax* is the sister taxon to *Thoe* and *Hemus* forming a basal clade in this group. *Mithraculus* is basal to *Petramithrax*, *Hemus*, and *Thoe* and the three genera form a well-supported monophyletic Mithracidae clade (Fig. 1) (Windsor and Felder, 2014).

Morphologically, *Petramithrax* is distinct from either *Thoe* or *Hemus*. This genus has slender pereopods without meral extensions, while the pereopods of *Thoe* and *Hemus* have wide meral extensions, in *Petramithrax* the carapace is as long as wide, while in *Thoe* and *Hemus* the carapace is distinctly longer than wide.

Despite the general similarities, *Thoe* and *Hemus* differ from each other mostly in the carapace, rostral, and antennal shape. *Thoe* species have a pyriform carapace, while *Hemus* exhibits a triangular or rectangular carapace, the rostral spines are small, markedly bifurcated, forming a distinct V-shaped sinus in *Thoe,* while the rostral spines are broad, trapezoidal, without the V sinus shape in *Hemus*, the first and second movable antennal articles are large and cylindrical in *Thoe*, while the first and second movable antennal articles are wide and flat in *Hemus*.

The relationship with Planoterginae, unfortunately, could not be tested here. *Thoe* was suggested as a putative link between Planoterginae and Mithracidae (Ng et al., 2008: 99). This monogeneric subfamily of miniature crabs has only two representatives, *Planotergum mirabile* Balss, 1935 known from Western Australia, Queensland, Java Sea, and Singapore (Johnson, 1965) and *P. kowalevski* Marin, Spiridonov and Ng, 2019 from the Red Sea. *Planotergum* resembles the American genus *Hemus* and it was suggested that *Hemus* should be included in Planoterginae due to the morphological affinities between them (Števčić, 1991; Garth, 1958; Hendrickx, 1999). Nevertheless, the phylogenetic results of Windsor and Felder (2014) definitively place *Hemus* within Mithracidae as a sister to a clade containing *Thoe* and *Petramithrax*. Windsor and Felder (2014) did not include Planoterginae species in their analyses, but suggested that the morphological similarities between *Planotergum*, *Hemus*, and *Thoe* could be a result of convergence (see also Windsor and Felder, 2011). Although our results show that the relation between *Petramithrax*, *Hemus*, and *Thoe* is beyond doubt, a phylogenetic analysis including *Planotergum* is needed to clarify if the morphological resemblance is due to convergence or not.

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Authors contribution

Conceptualization and Design: JC, WS. Performed research: JC, AMW, WS. Acquisition of data: IRRM, ALC. Analysis and interpretation of data: JC, AMW, WS. Preparation of figures/tables/maps: JC, MM, LL. Writing - original draft: JC, MM, LL, IRRM. Writing - critical review & editing: AMW, WS.

Conflicts of interest

The authors declare no conflicts of interest.

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Data availability

All study data are included in the article, including GenBank accession numbers.

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