

Shrimps of the genus *Thor* Kingsley, 1878 (Caridea, Thoridae): description of a new species using integrative data, remarks on *Thor manningi* Chace, 1972, and a world identification key

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ABSTRACT

Marine shrimps of the genus *Thor* Kingsley, 1878 are distributed in the eastern and western Atlantic, eastern Pacific, and Indo-West Pacific. *Thor manningi* Chace, 1972 was originally described from Antigua and since then has been recorded from other Atlantic localities, including the Caribbean Sea, Bermuda, USA, Brazil, and Ascension Island. Specimens previously identified as *T. manningi* from Panama and Brazil were analyzed using a combination of morphological and molecular approaches. The analyses yielded a new species from the Atlantic coast of Panama, herein described as *Thor paulae* sp. nov. Moreover, we provide additional morphological observations on *T. manningi*, mainly regarding mouthparts and pereopods. The new species is morphologically similar to the Pacific *Thor cocoensis* Wicksten and Vargas, 2001 and *Thor marguitae* Bruce, 1978. However, it can be separated from them by the carpus of the second pereopod, rostral dorsal dentition, and chela of the first pereopod, respectively. The two species studied here can be easily distinguished by the supraorbital prominence in *T. manningi*

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(*versus* absent in the new species), and the pterygostomial margin rounded and unarmed in *T. manningi* (*versus* angular, with tooth in the new species). *Thor manningi* is morphologically closer to the western Atlantic *Thor dobkini* Chace, 1972 and *Thor floridanus* Kingsley, 1878, but can be separated from both by the merus of the first pereopod (*T. dobkini*) and dactylus of fourth and fifth pereopods (*T. floridanus*, but with the possibility of overlap). We provide a comparative table with morphological characters of all 17 valid species of *Thor*, as well as a worldwide identification key to the genus.

KEYWORDS

Atlantic Ocean, Cytochrome Oxidase subunit I, Decapoda, Panama, 16S mtDNA.

INTRODUCTION

The small-sized (< 1 cm in total length) shrimps of the genus *Thor* Kingsley, 1878 have a wide diversity of lifestyles and sexual systems, including some species being symbiotic with anemones or corals and others living in association with seaweed or seagrass (Bauer, 1986; Chace, 1997; Khan *et al.*, 2004). *Thor* includes 16 valid species (De Grave and Fransen, 2011; Xu and Li, 2014; 2015; Anker and Baeza, 2021; WoRMS, 2022): four in the western Atlantic, three in the eastern Pacific, eight in the northwestern Pacific and Indo-West Pacific, and one with circumtropical distribution. Some species are known only from the type locality, such as *Thor spinipes* Bruce, 1983 (Australia, Northern Territory) and *Thor singularis* Xu and Li, 2015 (China, Hainan Island). In opposition, *Thor amboinensis* (de Man, 1888 [in de Man, 1887–1888]) and *Thor manningi* Chace, 1972, are widely distributed.

Titus *et al.* (2018) performed a molecular analysis of the circumtropical *T. amboinensis* and revealed the existence of at least five cryptic lineages: four in the Indo-West Pacific and one in the Western Atlantic. The latter lineage was recently described as *Thor dicaprio* Anker and Baeza, 2021; and the undescribed Indo-West Pacific species within that complex are treated herein as *T. amboinensis*.

Thor manningi was initially described from Antigua and new records have extended its distribution to other Caribbean localities, Bermuda, the eastern coast of the USA, Brazil (seamounts of the North Brazilian Chain, Fernando de Noronha, Ceará to São Paulo), and Ascension Island (Central Atlantic) (Chace, 1972; Manning and Chace, 1990; Christoffersen, 1998;

Coelho Filho, 2006). The occurrence of *T. manningi* in Brazil was probably based on the identification key proposed by Chace (1972), which was based on the analysis of specimens from the Caribbean Sea. In fact, a few morphological accounts (and figures) from Brazilian material of *T. manningi* have been provided by Almeida *et al.* (2008) based on material from Pernambuco, and the DNA sequences from São Paulo were made available by Terossi *et al.* (2017; 2018).

The taxonomy of this genus has not been completely clarified due to the morphological similarity among species, which hinders species identification, especially when they occur in the same region (Chace, 1972). This author reported difficulty in finding distinctive morphological characters among some species due to the occurrence of protandry. The sexual system of the four species reported from the western Atlantic has already been studied. Two species have been confirmed as gonochoric by Bauer and VanHoy (1996), *i.e.*, *Thor dobkini* Chace, 1972 and *Thor floridanus* Kingsley, 1878. Simple protandry has been reported in *T. dicaprio* (see Baeza and Piantoni, 2010 as *T. amboinensis*) and protandry with primary males (half the population does not change to female) in *T. manningi* (see Bauer, 1986).

This taxonomic context led us to analyze specimens previously identified as *T. manningi* from Panama and Brazil, using a combination of morphological and molecular data, as well as the morphology of the holotype from Antigua. Our findings result in the discovery of a new species of *Thor* from the Atlantic coast of Panama. In this study, we provide the description of the new species as well as additional morphological observations on *T. manningi*, including

illustration of their mouthparts. Both species were morphologically compared with congeners, and a world identification key for the genus is also provided.

MATERIALS AND METHODS

The specimens analyzed are deposited in the following collections: Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, Brazil (CCDB); Coleção de Crustáceos do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul, Brazil (DZ/UFRGS); Florida Museum of Natural History, USA (UF); Instituto de Ciências do Mar, Universidade Federal do Ceará, Brazil (LABOMAR); Laboratório de Invertebrados Marinhos do Ceará, Universidade Federal do Ceará, Brazil (LIMCE-UFC); National Museum of Natural History, Smithsonian Institution, USA (USNM).

Morphological data

Males were identified by the presence of the *appendix masculina* on the endopod of the second pair of pleopods and/or presence of the prehensile third pereopod, whereas females were identified by the presence of embryos or associated breeding material on their pleon, or by the absence of male diagnostic characters (Bauer, 1986). Mouthparts were dissected from specimens from samples CCDB 2593 (*T. manningi*), UF 44393, and UF 44518 (new species). Measurements and observations were performed with a Nikon SMZ800 stereomicroscope. The following measurements were taken: carapace length, length of the fifth and sixth pleonal segment, length, and proximal width of the telson, length of the endopod and exopod of the telson, length and greatest width of the scaphocerite, total length of the three articles of the third maxilliped, length from the articles of the first to the fifth pereopod (basis, ischium, merus, carpus, propodus, and dactylus, including the carpus articles of the second pereopod). Spiniform setae on the distal region of the flexor margin of the fifth pereopod were not counted since some specimens presented tufts of simple setae, making it impossible to see the structures. The illustrations of the morphology and the mouthparts were made, respectively, with

the aid of a Nikon SMZ800 stereomicroscope and Olympus CX31 microscope equipped with a camera lucida, later vectorized into the Adobe Illustrator® CS6. Abbreviations are: CL, carapace length; coll. (s), collector (s).

The identification key was based on, and modified from, a previous proposal: Chace (1997), a worldwide key with 10 species; Komai *et al.* (2015), an Indo-West Pacific key with nine species; and on all original descriptions from the 17 valid *Thor* species (present study).

Genetic data

Total genomic DNA was extracted from the muscle tissue of the pleon of the specimens, using the Qiagen Extraction Kit, following the manufacturer's recommendation. A region of ~600 base pairs (bp) of the 16S mtDNA (16S) and ~700 bp of the Cytochrome Oxidase subunit I (COI) genes were amplified from the extracted DNA through a polymerase chain reaction (PCR), using specific primers: 1472 (5'-AGATAGAAACCAACCTGG-3') / 16SL2 (5'-GCCTGTTTATCAAAAACAT-3') (Schubart *et al.*, 2000; 2002) for the 16S; and COL6b (5'-ACAAATCATAAAGATATYGG-3') / COH6 (5'-TADACTTCDGGRTGDCCAAARAAYCA-3') (Schubart and Huber, 2006) for the COI. PCR products were purified with ExoSAP-IT Kit, following the manufacturer's recommendation, and sequenced by ACTGENE (Análises Moleculares LTDA). All the sequences were confirmed by sequencing both strands, and the consensus sequence was obtained in the software Bioedit 7.0.5 (Hall, 2005). The non-specific readings were corrected manually, when necessary.

Sequences of five specimens of *T. manningi* were obtained from three locations: one from Panama, two from Brazil (São Paulo and Pernambuco), and three specimens of the new species from Panama. We also included *T. manningi* sequences obtained from GenBank from São Paulo and Puerto Rico.

Available sequences from other species of *Thor* (*T. amboinensis* complex and *Thor hainanensis* Xu and Li, 2014) and the outgroup composed of *Thinora maldivensis* Borradaile, 1915 were retrieved from Genbank. This latter species was chosen for its morphological and phylogenetic proximity to *Thor*

(see De Grave *et al.*, 2014 and Komai *et al.*, 2015), although there was only one sequence available for the 16S; and *Eualus cranchii* (Leach, 1817 [in Leach, 1815–1875]) that was selected because it belongs to the same family (De Grave *et al.*, 2014, as *Thoralus cranchii*).

The final sequences were aligned by the MUSCLE method (Edgar, 2004), implemented in the Cyberinfrastructure for Phylogenetic Research (CIPRES) platform (Miller *et al.*, 2010). For each gene, genetic distance matrices and phylogenetic trees were generated separately by the methods of Maximum Likelihood (ML) and Bayesian Inference (BI). The best substitution model was defined by the software JModelTest 2 (Darriba *et al.*, 2012) implemented on the CIPRES platform, using the Bayesian Information Criterion.

ML was performed with RAxML (Stamatakis, 2014), implemented on the CIPRES platform with the standard GTR model. The topology consistency was measured by the bootstrap method and the ML trees were viewed and edited in Mega 7 (Kumar *et al.*, 2016). Only support values above 90 % are shown.

BI was carried out in the MrBayes 3.2.6 (Ronquist *et al.*, 2012) implemented on the CIPRES platform. The data from the obtained substitution model were analyzed in Tracer v1.6. (Rambaut *et al.*, 2018). The first 15 % of the parameters and trees was discarded as burn-in. The final tree was generated, using the software Tree Annotator 1.8.4 (Drummond *et al.*, 2012). The tree was viewed and edited in the software Fig Tree 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>). Only support values of posterior probabilities above 0.90 are shown.

The genetic distance matrices were calculated for each gene by pairwise comparisons between sequences, using the p-distance with the software MEGA (Kumar *et al.*, 2016).

RESULTS

Systematics

Family Thoridae Kingsley, 1879

Genus *Thor* Kingsley, 1878

Thor paulae sp. nov.

(Figs. 1, 2)

Zoobank: [urn:lsid:zoobank.org:pub:E6AC08C7-EE6E-4EBB-B6BD-F1B2250C8255](https://zoobank.org/pub/E6AC08C7-EE6E-4EBB-B6BD-F1B2250C8255)

Type material. Panama: Holotype, ovigerous female (CL 2.7 mm), UF 60011, Panama, Bocas del Toro, Seagal (09°17'20.4"N 82°17'45.6"W), colls. M. Leray, F. Michonneau and R. Lasley, 27 May 2016. Paratypes: 1 male with *appendix masculina* and 8 females (6 ovigerous and 2 non-ovigerous adults, CL 2.2–2.7 mm), UF 44518 (photo available, one dissected specimen), same data as holotype; 1 male with *appendix masculina* (CL 1.9 mm), UF 44289, Panama, Bocas del Toro, Ponsak (09°17'38.4"N 82°19'55.2"W), colls. M. Leray, F. Michonneau and R. Lasley, 13 May 2016; 7 females (5 ovigerous and 2 non-ovigerous adults, CL 2.0–2.5 mm), UF 44393 (photo available, one dissected specimen), Panama, Bocas del Toro, Punta STRI (Smithsonian Tropical Research Institute) (09°20'56.4"N 82°15'46.8"W), colls. M. Leray, F. Michonneau and R. Lasley, 09 May 2016.

Etymology. The new species is named in honor of our great friend, Dra. Paula Beatriz de Araujo (Federal University of Rio Grande do Sul, Brazil), who has devoted her career to the study of biology, ecology, and systematics of crustaceans.

Diagnosis. Supraorbital tooth vestigial or absent. Pterygostomial margin angular, with one tooth. Telson with 3 pairs of dorsolateral spiniform setae; posterior margin with 3 pairs of simple setae. Merus of first pereopod with 1 or 2, rarely 3 or 4, spiniform setae on flexor proximal region. Dactylus of fourth and fifth pereopods with 2 or 3, rarely 1 or 4, spiniform setae on flexor margin.

Description. Rostrum (Fig. 1A, B) slightly descending, falling short of distal margin of first article of antennular peduncle to reaching distal margin of second article; dorsal margin armed with 4–5 teeth, posteriormost tooth located at about rostral base; ventral margin with minute subapical tooth, rarely 2 teeth or toothless. Supraorbital tooth vestigial or absent. Antennal tooth present, acute. Pterygostomial margin angular, with 1 tooth.

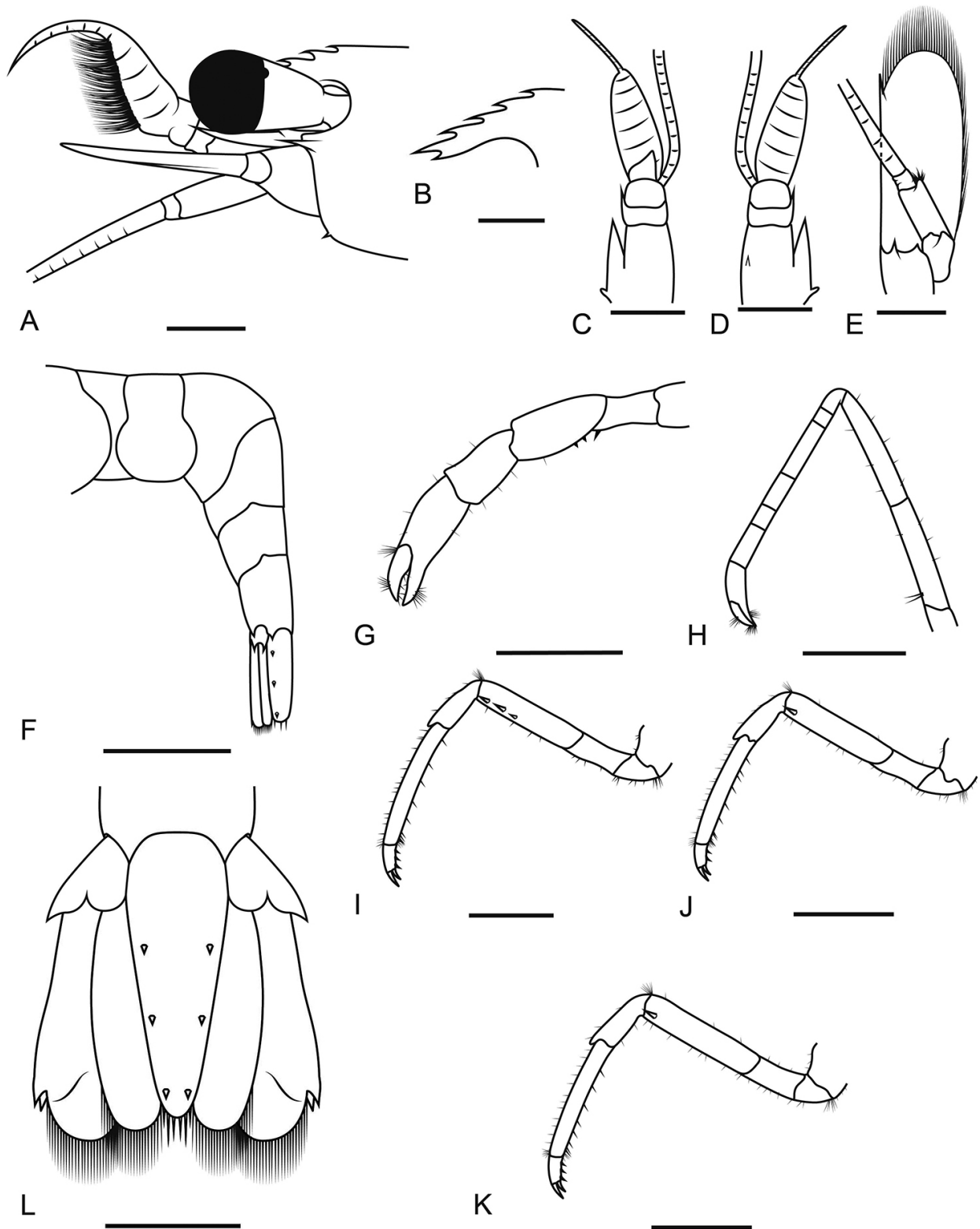


Figure 1. *Thor paulae* sp. nov. Panama, Bocas del Toro. Holotype, female (UF 60011). **A**, Carapace and cephalic appendages, left lateral view; **B**, rostrum, left lateral view; **C**, left antennule, dorsal view; **D**, left antennule, ventral view; **E**, left antenna, ventral view; **F**, pleon, left lateral view; **G**, left first pereopod, lateral view; **H**, left second pereopod, lateral view; **I**, left third pereopod, lateral view; **J**, left fourth pereopod, lateral view; **K**, left fifth pereopod, lateral view; **L**, telson and uropods, dorsal view. Scale bars: A, F–K: 0.83 mm; B: 1.0 mm; C–E: 0.625 mm; L: 0.25 mm.

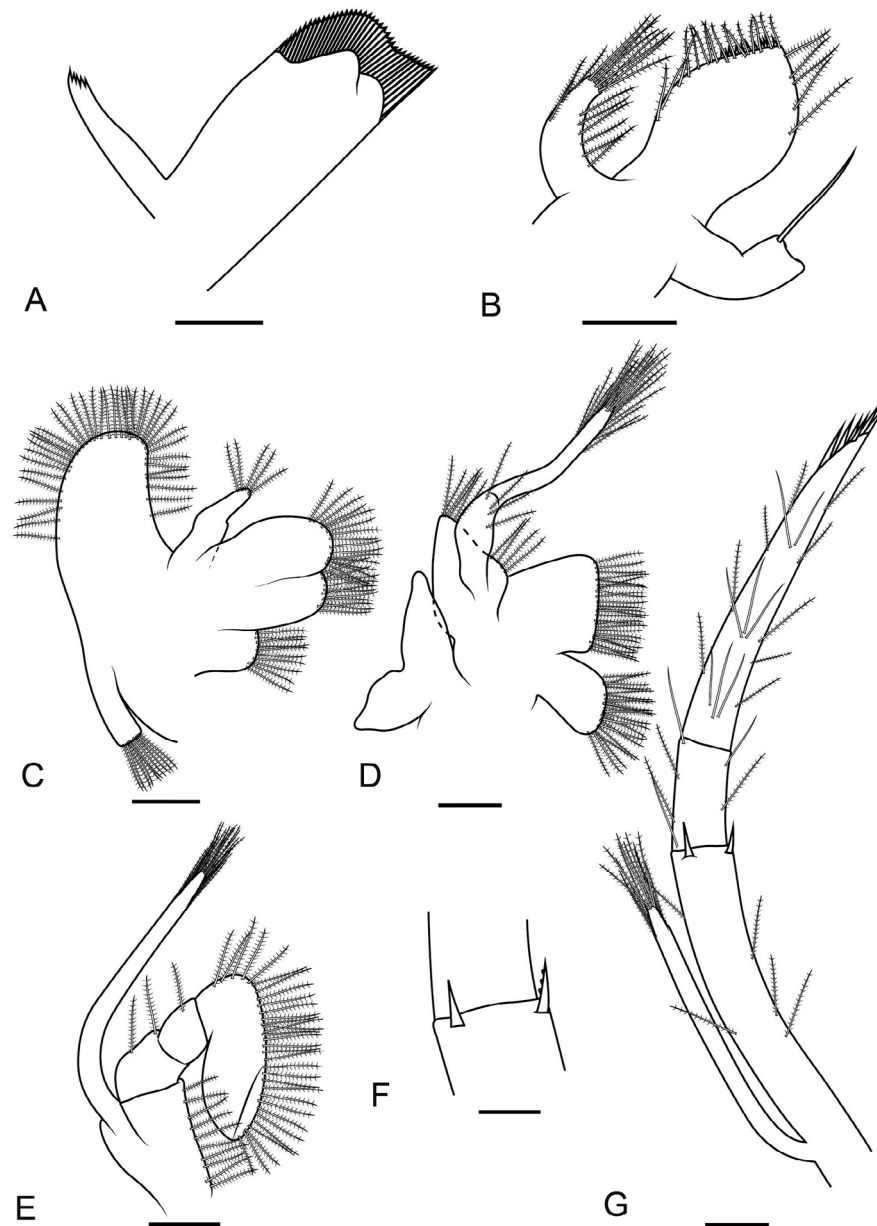


Figure 2. *Thor paulae* sp. nov. Panama, Bocas del Toro. Paratypes, females (A, B, D, E - UF 44393; C, F, G - UF 44518). **A**, Right mandible, ventral view; **B**, right maxillule, ventral view; **C**, left maxilla, ventral view; **D**, left first maxilliped, ventral view; **E**, left second maxilliped, ventral view; **F**, detail of the third maxilliped with papillose seta, ventral view; **G**, left third maxilliped, ventral view. Scale bars: A–E, G: 0.25 mm; F: 0.06 mm.

Pleurae (Fig. 1F) of pleonal segments 1–3 rounded posteroventrally; pleurae of pleonal segments 4–6 acute posteroventrally. Sixth segment 1.6 times as long as fifth; telson 1.1 times as long as sixth segment. Telson (Fig. 1L) 2.5 times longer than proximal width, with 3 pairs of dorsolateral spiniform setae and posterior margin with 3 pairs of simple setae, intermediate pair longest and outer shortest.

Cornea generally wider and slightly shorter than eyestalk. First article of antennular peduncle with tooth on median region of ventral margin (Fig. 1D); acute stylocerite of variable length from reaching distal margin of first article of antennular peduncle to distal margin of second article of antennular peduncle (Fig. 1C); stylocerite with tooth on proximal dorsolateral margin; second article of antennular

peduncle with tooth on lateral margin with variable length from reaching half to slightly exceeding distal margin of third article of antennular peduncle; third article of antennular peduncle with triangular plate articulated on dorsodistal margin; inner flagellum overreaching outer flagellum; inner flagellum slender and elongate; outer flagellum stout, with dense row of aesthetascs (Fig. 1A). Antennal basicerite with 2 ventral teeth; carpocerite variable in length, not reaching or slightly exceeding half-length of scaphocerite; scaphocerite 2.5 times longer than median width, overreaching distal margin of third article of antennular peduncle, with tooth on lateral distal margin (Fig. 1E); antennal flagellum long, filiform, articulated slightly broader at base than tip.

Mandible asymmetrical (Fig. 2A), molar process with serrated surface, incisor process with 5 teeth, palp absent. Maxillule (Fig. 2B) with distally truncated and undivided endopod, with distal simple seta; endite with upper lacinia broad, with somewhat acute distomedial angle, with numerous plumose setae and 11 spiniform setae; lower lacinia slender, with numerous plumose setae distally. Maxilla (Fig. 2C) with coxal endite distally truncated and bilobed basal endite slightly rounded, numerous plumose setae on both endites; short endopod, distally slender, with plumose setae; exopod (scaphognathite) well-developed, rounded, truncated terminal margin, with numerous plumose setae.

First maxilliped (Fig. 2D) with coxal and basal endites similar in length, covered by numerous plumose setae; both endites with distal margin slightly rounded; undivided endopod, with plumose setae; exopod well developed and undivided, with some plumose setae on proximal region and numerous plumose setae on distal region; proximal and distal lobes of large epipod similar in width. Second maxilliped (Fig. 2E) with protopodite with plumose setae; endopod with 4 articles, merus 3.1 times as long as dactylus, carpus 3 times as long as dactylus, propodus 10 times as long as dactylus, propodus and dactylus with numerous plumose setae; long, slender, undivided exopod, some plumose setae on proximal region and numerous plumose setae on distal region. Third maxilliped (Fig. 2G) overreaching antennular peduncle; antepenultimate article 0.9 times as long as ultimate article, with some plumose setae, distal region unarmed or with 1 papillose seta

(Fig. 2F) and 0 or 1 spiniform seta, with variable positions; penultimate article 0.3 times as long as ultimate article, with some simple and plumose setae; ultimate article with many simple and plumose setae, tip with 7 or 8 spiniform setae; exopod not reaching distal margin of antepenultimate article, with tuft of plumose setae on tip.

Pereopods without epipods. First pereopod (Fig. 1G) of variable length, not reaching or exceeding half-length of scaphocerite; ischium, merus, carpus, and propodus 2.0, 3.2, 2.8, 3.9 times as long as basis, respectively; ischium with 1 spiniform seta on distal flexor region; merus with 1 or 2, rarely 3 or 4, spiniform setae on flexor proximal region; chela slender, fingers 0.6 times as long as palm, both with short setae on cutting edge and tufts of setae on lateral edge. Second pereopod (Fig. 1H) with ischium, merus, carpus, and propodus 4.3, 4.6, 7.2, 2.6 times as long as basis, respectively; ischium with 2 simple and long setae on proximal flexor region; carpus subdivided into 6 articles, length ratio of carpal articles from proximal to distal 2:1:4:3:2.5:3; chela slender, fingers 0.7 times as long as palm, both with tufts of setae on lateral margin. Third pereopod (Fig. 1I) with ischium, merus, carpus, and propodus 2.2, 4.3, 2.1, 5.1 times as long as basis, respectively; merus with 1 to 3 lateral spiniform seta on distal region; carpus with tip of dorsal region projected anteriorly; flexor region of propodus with 7 to 16 spiniform setae, distal setae paired; male specimen (UF 44289) with tuft of setae on distal region of flexor margin; dactylus 0.2 times as long as propodus, distally biunguiculate with 2 or 3, rarely 4, spiniform setae on flexor margin. Fourth pereopod (Fig. 1J) with ischium, merus, carpus, and propodus 2.3, 4.9, 2.5, 5.7 times as long as basis, respectively; merus with 1 spiniform seta on distal region, tuft of setae on distal dorsal region; carpus with tip of dorsal region projected anteriorly; flexor region of propodus with 8 to 12 spiniform setae, distal setae paired; dactylus 0.2 times as long as propodus, distally biunguiculate with 2 or 3 spiniform setae on flexor margin. Fifth pereopod (Fig. 1K) with ischium, merus, carpus, and propodus 2.2, 4.2, 2.2, 5.4 times as long as basis, respectively; merus unarmed (rarely) or with 1 spiniform seta on distal region, tuft of setae on distal dorsal region; carpus with tip of dorsal region projected anteriorly; flexor region of propodus with

8 to 15 spiniform setae, distal setae paired, some specimens with tuft of simple setae on distal region of flexor margin; dactylus 0.2 times as long as propodus, distally biunguiculate with 2 or 3, rarely 1, spiniform setae on flexor margin.

Exopod of uropod 1.1 times as long as endopod (Fig. 1L); exopod with distolateral tooth and spiniform setae between distolateral tooth and margin of blade.

Type locality. Panama, Bocas del Toro, Isla Cristóbal, NW side, "Seagal".

Distribution. Western Atlantic — Panama (this study).

Variations. One male paratype (UF 44289, 1.9 mm CL) presented a tuft of setae on the distal region of the flexor margin of the propodus of the third pereopod. This tuft was absent in the other male paratype examined (UF 44518, 2.2 mm CL).

Thor manningi Chace, 1972

(Fig. 3)

Thor manningi Chace, 1972: 130, 137, figs. 59–61; Birkeland *et al.*, 1976: 138; Heck and Wetstone, 1977: 138; Carvacho, 1979: 464; Gore, 1981: 138, 152; Markham and McDermott, 1980: 1270; Carvacho, 1982: 18; Cubit and Williams, 1983: 25; Williams, 1984: 134, 137, fig. 96; Bauer, 1985: 150, 152–158; Bauer, 1986: 11–13, 15, 19, 23, 25, 27–29, figs. 1, 8, 9, 12; Martínez Iglesias, 1986: 5, 18, 19, fig. 9B; Young, 1986: 112; Manning and Chace, 1990: 24; Markham *et al.*, 1990: 423; Bauer and VanHoy, 1996: 53–56, 61–71; Duarte and Nalesso, 1996: 143, 148; Hernández-Aguilera *et al.*, 1996: 41; Christoffersen, 1998: 353; Álvarez *et al.*, 1999: 7; Morgado and Tanaka, 2001: 177; Wicksten, 2005: 100, 107, fig. 7; Coelho Filho, 2006: 10; De Grave *et al.*, 2006: 5363.2; Almeida *et al.*, 2008: 23, 28, 38, figs. 2–3; Felder *et al.*, 2009: 1059; Amaral *et al.*, 2010: 249; De Grave and Franssen, 2011: 434; Almeida *et al.*, 2012: 2, 24, 26, 28, 35, app. II; De Grave and Anker, 2017: 33; Tavares *et al.*, 2017: 157, 162, 107–172, fig. 4C; Terossi *et al.*, 2017: fig. 2, tab. S1; Mariño *et al.*, 2018: 4–6; Terossi *et al.*, 2018: 79, 87, fig. 2; Romero-Rodríguez and Álvarez, 2020: 560, 561, 563, 565, 567, 568, fig. 1A.

Thor floridanus — (?) Fausto-Filho, 1970: 56; (?) Coelho and Ramos, 1972: 152; (?) Heck, 1977: 338; (?) Heck, 1979: 199; (?) Christoffersen, 1998: 353. *Thor c. manningi* — Rodríguez, 1980: 170, 171, fig. 49. *Thornanningi* — Young, 1986: 103 (misspelled). *Thor cf. manningi* — Fiedler *et al.*, 2010: 5, fig. 1.

Material examined. Antigua and Barbuda: Male, holotype (prehensile, CL 1.3 mm), USNM 135393, English Harbour, Antigua, from bottom of yacht anchored for several months, coll. D.V. Nicholson, Smithsonian-Bredin Expedition Sta 82-56, 04 April 1956. Panama: 1 ovigerous female (CL 2.5 mm), UF 44457 (photo available), Bocas del Toro (09°13'58.8"N 82°06'43.2"W), colls. M. Leray, F. Michonneau and R. Lasley, 24 May 2016; 1 ovigerous female (CL 1.93 mm), CCDB 6407, Bocas del Toro (09°19.805'N 82°15.087'W), colls. F. Mantelatto *et al.*, 02 August 2011. Brazil: Ceará — 2 males (1 prehensile and 1 male with *appendix masculina*, CL 1.4–1.6 mm), LIMCE-UFC 300, Trairí, Mundaú, colls. PROBIO team, 14 March 2003; 1 ovigerous female (CL 2.0 mm), LIMCE-UFC 320, Paracuru, coll. P.P.G. Pachel, 23 September 2010; 1 male (prehensile) and 4 females (3 ovigerous) (CL 1.2–2.6 mm), LABOMAR 732, São Gonçalo do Amarante, Terminal Portuário do Pecém, coll. PROCAD team, 29 January 2010. Pernambuco — 1 ovigerous female and 1 male with *appendix masculina* (CL 0.9–1.9 mm), DZ/UFRGS 6849, Cabo de Santo Agostinho, Praia de Suape, colls. G.L. Bochini, A.O. Almeida and G.O. Soledade, 26 May 2017; 2 males (1 prehensile and 1 with *appendix masculina*, CL 1.1–1.3 mm), DZ/UFRGS 6850, same location and colls., 26 June 2017; 1 female (CL 1.8 mm), DZ/UFRGS 6851, same location and colls., 23 August 2017; 1 female with breeding dress (CL 1.9 mm), DZ/UFRGS 6852, same location and colls., 28 August 2017; 2 ovigerous females (CL 2.0–2.1 mm), DZ/UFRGS 6853, same location and colls., 29 March 2018; 2 females (CL 2.2–2.4 mm), DZ/UFRGS 6832, same location and colls., 21 March 2019; 2 females (CL 1.8–2.2 mm), DZ/UFRGS 6833, same location and colls., 21 March 2019; 1 male with *appendix masculina* (CL 1.3 mm), DZ/UFRGS 6854, Cabo de Santo Agostinho, Praia do Paraíso, 08°21'29.9"S 34°57'00.9"W, colls. G.L. Bochini, A.O. Almeida and G.O. Soledade,

26 April 2017. São Paulo — 1 male with *appendix masculina* and 5 females (3 ovigerous) (CL 1.1–2.7 mm, one dissected specimen), CCDB 2593, Ubatuba, Praia Itaguá (23°26'59"S 045°01'49"W), coll. F.L. Mantelatto, 17 September 2008; 1 ovigerous female (CL 2.2 mm), CCDB 1850, Ubatuba, Praia Itaguá (23°26'59"S 045°01'49"W), colls. F.L. Mantelatto, I.C. Leone and R.C. Buranelli, 16 September 2010;

3 males with *appendix masculina* and 4 females (3 ovigerous and 1 with breeding dress) (CL 1.8–2.1 mm), CCDB 2737, Ubatuba, Praia Itaguá (23°26'59"S 045°01'49"W), colls. F.L. Mantelatto, R. Robles, M. Terossi, I.C. Leone and N.M. Grilli, 22 February 2011; 1 male with *appendix masculina* (CL 2.5 mm), CCDB 3840, Ilhabela, Praia do Engenho d'Água, colls. F.L. Mantelatto and E.C. Mossolin, 12 July 2006.

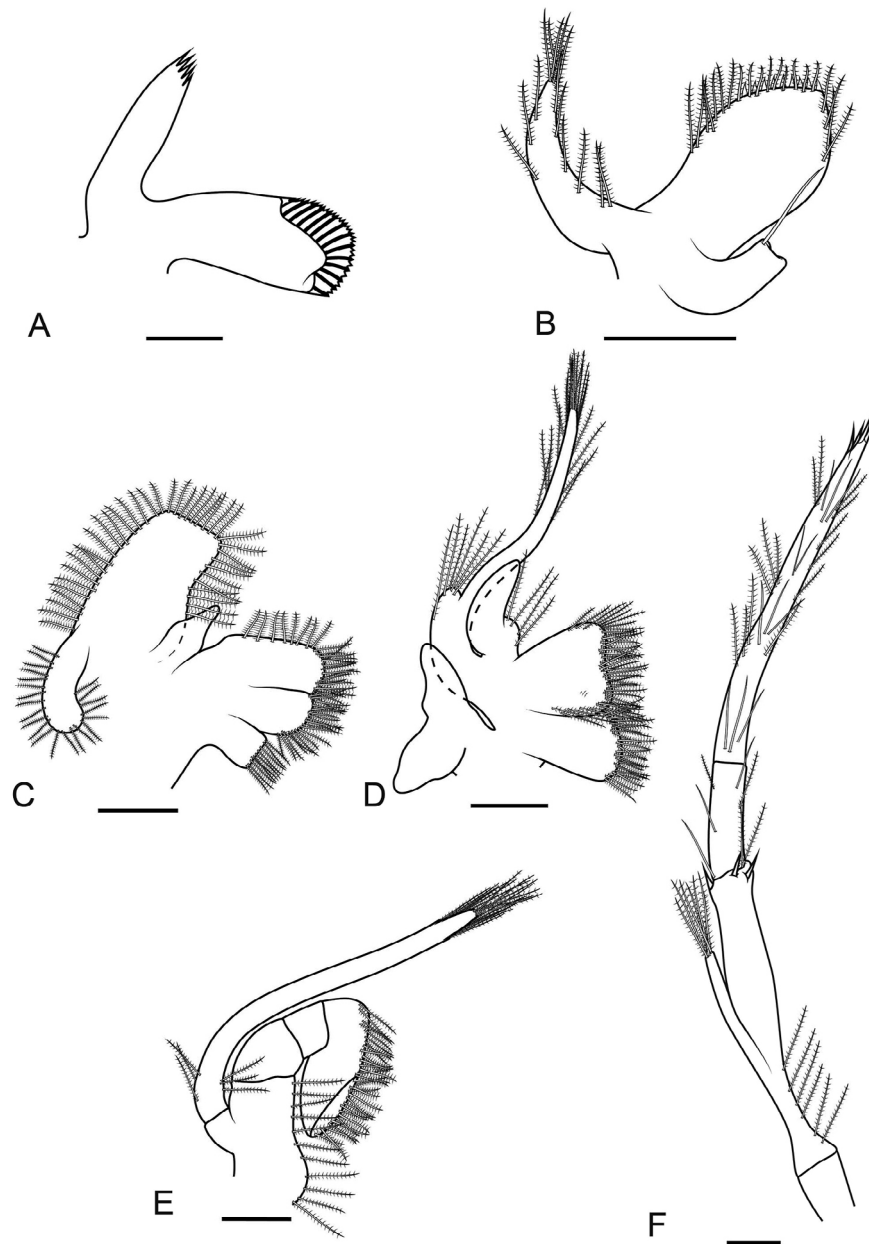


Figure 3. *Thor manningi* Chace, 1972. Brazil, São Paulo. Female (CCDB 2593). **A**, Right mandible, ventral view; **B**, right maxillule, ventral view; **C**, left maxilla, ventral view; **D**, left first maxilliped, ventral view; **E**, left second maxilliped, ventral view; **F**, left third maxilliped, ventral view. Scale bars: 0.25 mm.

Additions to original description provided by Chace (1972). Telson 3 times longer than proximal width, with 3–6 pairs of dorsolateral spiniform setae (frequently 3 or 4 pairs). Acute stylocerite of variable length from reaching distal margin of second article of antennular peduncle to slightly exceeding distal margin of third article of antennular peduncle; inner flagellum overreaching outer flagellum; inner flagellum slender and elongate; outer flagellum stout, with dense row of aesthetascs. Antennal basicerite with two ventral teeth; carpopocerite variable in length, reaching or slightly exceeding half-length of scaphocerite; antennal flagellum long, filiform, articulated slightly broader at base than tip.

Mandible asymmetrical (Fig. 3A), molar process with serrated surface, incisor process with 5–6 teeth, palp absent. Maxillule (Fig. 3B) with distally truncated and undivided endopod, with distal simple seta; endite with upper lacinia broad, with somewhat acute distomedial angle, with numerous plumose setae and 9 spiniform setae; lower lacinia slender, with numerous plumose setae distally. Maxilla (Fig. 3C) with coxal endite distally truncated and bilobed basal endite slightly rounded, numerous plumose setae on both endites; short endopod, distally slender, free of setae; exopod (scaphognathite) well developed, rounded, slender terminal margin, with numerous plumose setae.

First maxilliped (Fig. 3D) with coxal and basal endites similar in length, covered by numerous plumose setae; distal margin of coxal endite slightly rounded; distal margin of basal endite slightly concave on median region and rounded on tips; undivided endopod, slightly more slender distally, with some plumose setae on proximal region; exopod well developed and undivided, with some plumose setae on proximal region and numerous plumose setae on distal region; proximal and distal lobes of large epipod similar in width. Second maxilliped (Fig. 3E) with protopodite with plumose setae; endopod with 4 articles, merus 5 times as long as dactylus, carpus 3 times as long as dactylus, propodus 12 times as long as dactylus, propodus and dactylus with numerous plumose setae; long, slender, undivided exopod, some plumose setae on proximal region and numerous plumose setae on distal region; podobranch on epipod. Third maxilliped (Fig. 3F) overreaching antennular

peduncle; antepenultimate article 0.9 times as long as ultimate article, proximal region with some plumose setae, distal region unarmed or with 1 papillose seta and 0, 1, 2, or 3 spiniform setae, with variable positions; penultimate article 0.3 times as long as ultimate article, with some simple and plumose setae; ultimate article with many simple and plumose setae, tip with 7 or 8 spiniform setae; exopod not reaching distal margin of antepenultimate article, with tuft of plumose setae on tip.

Pereopods without epipods. First pereopod of variable length, not reaching or exceeding half-length of scaphocerite; ischium with 1 or 2 spiniform setae on distal flexor region; merus with 1 or 2, rarely 3, spiniform setae on flexor proximal region; chela slender, fingers 0.6 times as long as palm, both with short setae on cutting edge and tufts of setae on lateral margin. Second pereopod, ischium with 2 or 3 simple and long setae on proximal flexor region; carpus subdivided into 6 articles, length ratio of carpal articles from proximal to distal 2:2:4:2.5:1:2; chela slender, fingers 0.8 times as long as palm, both with tufts of setae on lateral margin. Third pereopod, merus with 1 to 4 lateral spiniform setae on distal region, rarely unarmed or with 5 or 6 spiniform setae, tuft of setae on distal dorsal region; carpus with tip of dorsal region projected anteriorly; flexor region of propodus with 8 to 13 spiniform setae, distal setae paired; dactylus 0.2 times as long as propodus, distally biunguiculate with 2 or 3 spiniform setae on flexor margin in non-prehensile pereopod (females and non-functional males); absence or presence of 1 spiniform seta on prehensile pereopod (functional males). Fourth pereopod, merus with 1 to 3 spiniform setae on distal region, rarely 4, tuft setae on distal dorsal region; carpus with tip of dorsal region projected anteriorly; flexor region of propodus with 8 to 12 spiniform setae, distal setae paired; dactylus 0.2 times as long as propodus, distally biunguiculate with 2 or 3, rarely 1 or 4, spiniform setae on flexor margin. Fifth pereopod, merus unarmed or with 1 spiniform seta on distal region, tuft of setae on distal dorsal region; carpus with tip of dorsal region projected anteriorly; flexor region of propodus with 8 to 12 spiniform setae, distal setae paired, some specimens with tuft of simple setae on distal region of flexor margin; dactylus 0.2 times as long as propodus, distally biunguiculate with 2 or 3, rarely 1 or 4, spiniform setae on flexor margin.

Type locality. Antigua and Barbuda, Antigua, English Harbour.

Distribution. Western Atlantic — USA (North Carolina, Florida), Bermuda, Mexico (Veracruz, Yucatán, Campeche, Quintana Roo), Cuba, Puerto Rico, British Virgin Islands, Anguilla, Saint Kitts and Nevis, Antigua and Barbuda, Guadeloupe, Dominica, Martinique, Saint Lucia, Grenada, Trinidad and Tobago, Curaçao, Honduras, Panama, Venezuela, Brazil (Seamounts of North Chain, Fernando de Noronha, Trindade Island, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Bahia, São Paulo). Central Atlantic — Ascension Island (Chace, 1972; Birkeland *et al.*, 1976; Markham and McDermott, 1980; Rodríguez, 1980; Gore, 1981; Carvacho, 1982; Martínez Iglesias, 1986; Young, 1986; Manning and Chace, 1990; Markham *et al.*, 1990; Duarte and Nalesso, 1996; Hernández-Aguilera *et al.*, 1996; Álvarez *et al.*, 1999; Coelho Filho, 2006; De Grave *et al.*, 2006; Almeida *et al.*, 2008; 2012; Fielder *et al.*, 2010; Tavares *et al.*, 2017). Although Chace (1972) reported *T. manningi* from the Pacific coast of Mexico (Islas Tres Marias), those specimens were *Thor algicola* Wicksten, 1987 (see Wicksten, 1987).

Variations. The variations in the length of structures or number of spiniform setae of the pereopods did not show any relation with geographic distribution. The number of spiniform setae on the distal region of the merus of the third and fourth pereopods and on the telson dorsolateral surface may vary on each side of the body of the same specimen.

Genetic data

Final matrices with 520 bp (16S) and 570 bp (COI) were used in the analyses. The best-fitting substitution model for the 16S was TPM3uf+G, with nucleotide frequencies of A = 0.3623, C = 0.1030, G = 0.1797, and T = 0.3550, and gamma distribution = 0.3070. For COI, the best-fitting substitution model was TPM1uf+G, with nucleotide frequencies of A = 0.2894, C = 0.1585, G = 0.1535, and T = 0.3986, and gamma distribution = 0.2240.

We obtained almost the same topology for the phylogeny using the ML and BI analyses. Thus, we selected the ML tree as the basis for discussions,

showing bootstrap supporting values, but also including posterior probabilities (expressed as a percentage) for BI analyses (Fig. 4). Both trees recovered *T. manningi* and *T. paulae* sp. nov. as two separate lineages with high support values. The *T. manningi* clade included specimens from Brazil (Pernambuco and São Paulo), Panama, and Puerto Rico; and *T. paulae* sp. nov. included only specimens from Panama. For the 16S gene, *T. manningi* and *T. paulae* sp. nov. were recovered as sister group (Fig. 4A), whereas for COI gene, *T. paulae* sp. nov. was included in a clade with specimens from *T. amboinensis* complex and *T. hainanensis*, being *T. manningi* sister group of this huge clade (Fig. 4B).

The genetic distance analysis corroborated the phylogenetic reconstruction results. The intraspecific variation of both genes was null for *T. manningi* and *T. paulae* sp. nov. In contrast, the values of interspecific variation between these two species were high (16S: 20 %, COI: 23 %). Such values are similar or even higher when these species are compared to different lineages of the *T. amboinensis* complex (*T. manningi* - 16S: 18–19 %, COI: 13–17 %; *T. paulae* sp. nov. - 16S: 20–22 %, COI: 14–15 %) and *T. hainanensis* (*T. manningi* - COI: 22 %; *T. paulae* sp. nov. - COI: 22 %).

DISCUSSION

This study describes a new species from Panama Atlantic coast (previously identified as *T. manningi*) and provides remarks on *T. manningi*, including material from Brazil. The phylogenetic analysis (ML and BI) separating two distinct clades with high support values for both analyzed genes, the presence of a supraorbital prominence in *T. manningi* (versus absent or vestigial in the new species), and the pterygostomial margin rounded and unarmed in *T. manningi* (versus angular with one tooth in the new species) showed that these species are clearly separated, based on molecular and morphological data. Moreover, the proximal tooth on the dorsolateral margin of the stylocerite is more developed in the new species than in *T. manningi*.

Thor paulae sp. nov. is the seventeenth species described for the genus (Tab. 1). The new species can be separated from the other four Atlantic species. The new species differs from *T. dobkini*, *T. floridanus*, and *T. manningi* by the absence or presence of a vestigial

supraorbital tooth (*versus* presence of a prominence in the other three species) and by the pterygostomial margin angular with one tooth (*versus* rounded and unarmed in the other three species) (see Fig. 1A, and Chace, 1972, figs. 57a, 58a, 59a, 60a). Otherwise, *T. paulae* sp. nov. shares these characters (supraorbital tooth absent and pterygostomial margin angular with one tooth) with *T. dicaprio* (see Anker and Baeza, 2021). However, *T. paulae* sp. nov. differs from the

latter species in morphology (3 dorsolateral setae on telson *versus* 4 in *T. dicaprio*; Fig. 1I; Anker and Baeza, 2021, fig. 1D), by genetics (Fig. 4; 22 % for COI), and by coloration since the new species does not have the “sexy shrimp pattern” as *T. dicaprio* and other lineages of the *T. amboinensis* complex (see Anker and Baeza, 2021; photos of *T. paulae* sp. nov. are available at <http://specifyportal.flmnh.ufl.edu/iz/>, UF 44518 and UF 44393).

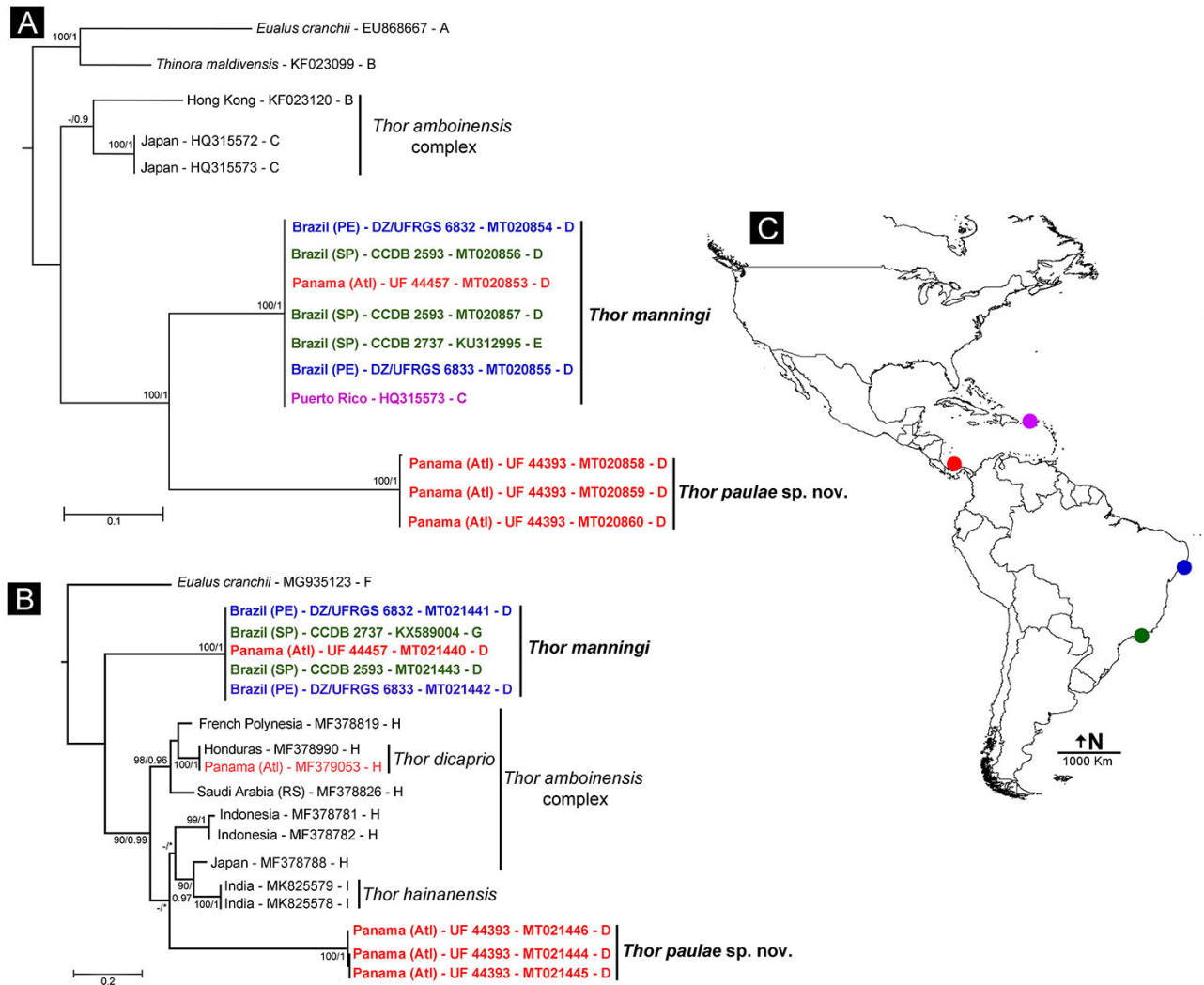


Figure 4. Maximum Likelihood phylogenetic trees based on 16S mt (A) and Cytochrome Oxidase subunit I (B) genes. Numbers on branches represent bootstraps/posterior probabilities (Maximum Likelihood/Bayesian Inference), numbers < 90 %/0.90 are not shown. Colors correspond to localities in the map (C). Localities - Atl: Atlantic; PE: Pernambuco; RS: Red Sea; SP: São Paulo. Collections - CCDB: Coleção de Crustáceos do Departamento de Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Brazil; DZ/UFRGS: Coleção de Crustáceos do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Brazil; UF: Florida Museum of Natural History, USA. References - A: Bracken *et al.* (2009 as *Thoralus cranchii*); B: De Grave *et al.* (2014); C: Fiedler *et al.* (2010 as *Thor cf. manningi*); D: present study; E: Terossi *et al.* (2018); F: D.K.G. Lundin (unpublished data); G: Terossi *et al.* (2017); H: Titus *et al.* (2018); I: Madhavan *et al.* (2019). Bold represents species analyzed in this study. * Represent nodes in the clades not recovered by one of the analyzes (inconsistencies).

Table 1. Species of the genus *Thor* Kingsley, 1878, distribution (underlined type locality) and comparison of some morphological characters.

Species	Distribution	Supraorbital tooth or prominence	Pterygostomial margin	Tooth on dorsolateral margin of the stylocerite proximally	Pairs of setae on telson (dorsolateral; posterior)	References
<i>Thor algicola</i> Wicksten, 1987	Northeastern Pacific: Mexico (<u>Sonora</u> and southwestern), Panama	absent	rounded	distinct	(4–5; 3)	Wicksten (1987); Ayón-Parente <i>et al.</i> (2016) and references therein
<i>Thor amboinensis</i> (de Man, 1888 [in de Man, 1887–1888])	Circumtropical: Red Sea, widely distributed in Indo-West Pacific (Indonesia, <u>Ambon</u>) and eastern Pacific	absent	angular	distinct	(4; 4)	de Man (1888 as <i>Hippolyte amboinensis</i>); Titus <i>et al.</i> (2018); Anker and Baeza (2021)
<i>Thor cocoensis</i> Wicksten and Vargas, 2001	Eastern Pacific: Mexico (Jalisco), Costa Rica (<u>Isla del Coco</u>), Ecuador (Galápagos)	absent	angular	distinct	(3–4; 3)	Wicksten and Vargas (2001); Ayón-Parente <i>et al.</i> (2016)
<i>Thor cordelli</i> Wicksten, 1996	Eastern Pacific: Mexico (Rocas Alijos, <u>Clarion Island</u> , Baja California), Colombia	strong tooth	angular	distinct	(3–5; 2–3)	Wicksten (1996); Ayón-Parente <i>et al.</i> , (2016) and references therein
<i>Thor dicaprio</i> Anker and Baeza, 2021	Western Atlantic: Bermuda, USA (Florida, Texas), Mexico (Quintana Roo), Bahamas, Cuba, Cayman Islands, US Virgin Islands, Antigua, <u>Saint Martin</u> , Guadeloupe, Dominica, Martinique, Barbados, Bonaire, Curaçao, Trinidad and Tobago, Belize, Honduras, Panama, Colombia, Brazil (North Chain, Fernando de Noronha Chain, Trindade e Martim Vaz)	absent	angular	distinct	(4; 3–4)	Anker and Baeza (2021) and references therein
<i>Thor dobkini</i> Chace, 1972	Western Atlantic: USA (North Carolina, South Carolina, <u>Florida</u> , Louisiana), Mexico (Quintana Roo), Cuba	prominence	rounded	distinct	(3–5; 3–4)	Chace (1972); Felder <i>et al.</i> (2009) and references therein
<i>Thor floridanus</i> Kingsley, 1878	Western Atlantic: USA (North Carolina, <u>Florida</u>), Gulf of Mexico, Mexico (Quintana Roo), Costa Rica	prominence	rounded	distinct	(3; 3)	Kingsley (1878); Chace (1972); Felder <i>et al.</i> (2009) and references therein
<i>Thor hainanensis</i> Xu and Li, 2014	Indo-West Pacific: China (<u>Hainan Island</u>), India	absent	angular	indistinct	(3–5; 3)	Xu and Li (2014; 2015); Madhavan <i>et al.</i> (2019)
<i>Thor intermedius</i> Holthuis, 1947	Indo-West Pacific: Indonesia (<u>Misool</u>)	absent	rounded	distinct	(1; 4)	Holthuis (1947); Chace (1997)
<i>Thor leptochelus</i> (Xu and Li, 2015)	Northwestern Pacific: China (<u>Xisha Islands</u>) and Japan (Ryukyu Archipelago)	strong tooth	angular	absent or indistinct	(3; 3)	Xu and Li (2015 as <i>Thinora leptochelus</i>); Komai <i>et al.</i> (2015)

Table 1. Cont.

Species	Distribution	Supraorbital tooth or prominence	Pterygostomial margin	Tooth on dorsolateral margin of the stylocerite proximally	Pairs of setae on telson (dorsolateral; posterior)	References
<i>Thor manningi</i> Chace, 1972	Western Atlantic: USA (North Carolina, Florida), Bermudas, Mexico (Veracruz, Yucatán, Campeche, Quintana Roo), Cuba, Puerto Rico, British Virgin Islands, Anguilla, Saint Kitts and Nevis, <u>Antigua</u> and Barbuda, Guadeloupe, Dominica, Martinique, Saint Lucia, Grenada, Trinidad and Tobago, Curacao, Honduras, Panama, Venezuela, Brazil (Seamounts of North Chain, Fernando de Noronha, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Bahia, São Paulo, and Trindade Island). Central Atlantic: Ascension Island	prominence	rounded	distinct	(3–6; 3)	Chace (1972); present study and references herein
<i>Thor marguitae</i> Bruce, 1978	Pacific: Australia (<u>Queensland</u>) and Japan (Okinawa Island)	absent	angular	distinct	(3; 3)	Bruce (1978); Komai <i>et al.</i> (2015)
<i>Thor paschalis</i> (Heller, 1861)	Indo-West Pacific: Probably <u>Red Sea</u> to Japan, the Philippines, Indonesia, and the Mariana Islands.	absent	rounded	absent	(not reported; 3)	Heller (1861 as <i>Hippolyte paschalis</i>); Holthuis (1947); Chace (1997)
<i>Thor paulae</i> sp. nov.	Western Atlantic: Panama (<u>Bocas del Toro</u>)	absent or vestigial	angular	distinct	(3; 3)	Present study
<i>Thor singularis</i> Xu and Li, 2015	Northwestern Pacific: China (<u>Hainan Island</u>)	absent	angular	indistinct	(4; 3)	Xu and Li (2015)
<i>Thor spinipes</i> Bruce, 1983	Pacific: Australia (<u>Northern Territory</u>)	strong tooth	rounded	distinct	(3; 3)	Bruce (1983)
<i>Thor spinosus</i> Boone, 1935	Indo-West Pacific: Kenya, Seychelle Islands, Ryukyu Islands, Indonesia (<u>Bali</u>).	strong tooth	rounded	unknown	(3; 4)	Boone (1935); Bruce (1976); Chace (1997)

Thor paulae sp. nov. is morphologically similar to the Pacific *Thor cocoensis* Wicksten and Vargas, 2001 and *Thor marguitae* Bruce, 1978 (Tab. 1) regarding the following characters (Bruce, 1978; Wicksten and Vargas, 2001; this study): supraorbital tooth absent or vestigial, pterygostomial margin angular, telson bearing 3 pairs of dorsolateral spiniform setae (sometimes 4 in *T. cocoensis*) and 3 pairs of setae on posterior margin, antennular stylocerite with a proximal tooth on dorsolateral margin, pereopods without epipod, and merus of the first pereopod with some spiniform setae on the flexor proximal region (not described for *T. cocoensis* by Wicksten and Vargas, 2001, but illustrated in their fig. 4A). Nonetheless, the new species can be distinguished from *T. cocoensis* by the third carpal article of the second pereopod being longest (*versus* sixth carpal article the longest in *T. cocoensis*) and by the rostrum dorsal dentition (4 to 5 in *T. paulae* sp. nov. *versus* 1 to 2 in *T. cocoensis*) (Wicksten and Vargas, 2001; this study). The new species can be separated from *T. marguitae* by the chela of the first pereopod not tapering or strongly compressed (*versus* tapering and clearly compressed in *T. marguitae*) (Bruce, 1978; this study).

The new species is currently restricted to Bocas del Toro, Panama. One of us (FLM) has collected some individuals previously identified as *Thor* sp. in the STRI vicinities during a taxonomic field activity in August 2011. The material was deposited in the Zoological Collection of the University of Louisiana, Lafayette (ULLZ) and recently moved to USNM. The identity of this material should be checked in the future since we were not able to do so at the moment due to pandemic restrictions. With the new species, four species of *Thor* have been reported from the Panama Atlantic coast: *T. dicaprio*, *T. floridanus*, *T. manningi*, and *T. paulae* sp. nov. (De Grave and Anker, 2017; Anker and Baeza, 2021; this study). However, the records of *T. floridanus* by Heck (1977; 1979) could actually refer to *T. manningi* (see De Grave and Anker, 2017). Our molecular analysis has confirmed the occurrence of at least three species on the Panama Atlantic coast: *T. dicaprio*, *T. manningi*, and *T. paulae* sp. nov. (Fig. 4).

As the new species material has been previously identified as *T. manningi*, we analyzed specimens of

T. manningi from Antigua and Barbuda (holotype), Panama, and Brazil, and added more detail to the original description provided by Chace (1972), mainly regarding mouthparts and pereopods. We provide below some comparative observations on this species: the Atlantic *T. dobkini*, *T. manningi*, and *T. floridanus* differ from all other species of the genus by having a small supraorbital prominence; four species have a strong supraorbital tooth (see Tab. 1) and a supraorbital prominence or tooth is absent in the remaining ten species (Tab. 1).

Thor manningi can be separated from *T. dobkini* by the distal half of flexor margin of merus of first pereopod unarmed (*versus* armed with 1 or 2 setae in *T. dobkini*) (Chace, 1972). Chace (1972) mentioned spines (= spiniform setae) on the proximal half of the flexor margin of the merus of the first pereopod in some specimens of *T. manningi* and *T. floridanus*. These setae were also observed in *T. manningi*.

Chace (1972) mentioned that *T. manningi* could be separated from *T. floridanus* based on the number of spinules (= spiniform setae) on the dactylus of the fourth and fifth pereopods (3, sometimes 2 or 4, in *T. manningi* *versus* and 4 or 5, rarely 3 or 6, in *T. floridanus*). However, such characters must be analyzed with caution, considering the possibility of overlap. In this study, only a large female of *T. manningi* was found with 4 spiniform setae on the dactylus of the fourth and fifth pereopods, which agrees with Chace's (1972) report that this condition was rare in the species. Specimens from Brazil have been included in the analysis of *T. manningi*, expanding the knowledge on the variation of some characters. Analyzing more specimens of *T. floridanus* is recommended in order to find characters for more precise separation between these closely related species.

Finally, this study included all species with available sequences in a phylogenetic analysis (*i.e.*, only five of the 17 described species), which is not enough to recover and discuss the phylogeny of the genus. Despite this unfavorable scenario, two considerations can be made: *T. amboinensis* complex is not monophyletic and the hypothesis proposed by Anker and Baeza (2021) that *T. hainanensis* "possibly representing one of the clades in Titus *et al.* (2018)" is refuted because here we included the five clades of Titus *et al.* (2018) and

T. hainanensis is clearly separate from them. More studies on the phylogenetic relationships of this genus need to be conducted.

Identification key to *Thor* species worldwide

Remarks on the proposed key: Xu and Li (2015) mentioned an indistinct tooth on the proximal

dorsolateral margin of the stylocerite of *T. leptochelus* (as *Thinora leptochelus* Xu and Li, 2015) while Komai *et al.* (2015) reported no trace of this tooth; Anker and Baeza (2021), when describing *T. dicaprio*, did not report morphological differences between the species and other *T. amboinensis* lineages, instead only genetics, geography and coloration.

- | | | |
|------|--|---------------------------|
| 1a. | Strong supraorbital tooth present (see Bruce, 1983: fig. 2A–C) | 2 |
| 1b. | Supraorbital tooth reduced to prominence (see Chace, 1972: fig. 59a) or absent (Fig. 1A) | 5 |
| 2a. | Posterior margin of telson bearing acute median tooth (see Wicksten, 1996: fig. 1O) | 3 |
| 2b. | Posterior margin of telson without acute median tooth (Fig. 1I) | 4 |
| 3a. | Posterior margin of telson with 2 pairs of simple setae laterally and 2 pairs of plumose setae centrally (see Bruce, 1976: fig. 20A) | <i>T. spinosus</i> |
| 3b. | Posterior margin of telson with 2–3 pairs of simple setae (see Wicksten, 1996: fig. 1O) | <i>T. cordelli</i> |
| 4a. | Stylocerite with distinct tooth on proximal dorsolateral margin (Fig. 1C) | <i>T. spinipes</i> |
| 4b. | Stylocerite with indistinct tooth or without tooth on proximal dorsolateral margin (see Xu and Li, 2015: fig. 7D) | <i>T. leptochelus</i> |
| 5a. | Pterygostomial margin angular (Fig. 1A) | 6 |
| 5b. | Pterygostomial margin rounded (see Chace, 1972: fig. 59a) | 12 |
| 6a. | First pereopod with epipod (see Xu and Li, 2015: fig. 35E) | 7 |
| 6b. | First pereopod without epipod | 8 |
| 7a. | Second pereopod with epipod (see Xu and Li, 2015: fig. 35F) | <i>T. singularis</i> |
| 7b. | Second pereopod without epipod | <i>T. hainanensis</i> |
| 8a. | First pereopod with chela tapering and clearly compressed (see Bruce, 1978: fig. 4A) | <i>T. marguitae</i> |
| 8b. | First pereopod with chela not tapering or strongly compressed (Fig. 1G) | 9 |
| 9a. | Second pereopod with sixth carpal article longest (see Wicksten and Vargas, 2001: fig. 4B) | <i>T. cocoensis</i> |
| 9b. | Second pereopod with third carpal article longest (Fig. 1H) | 10 |
| 10a. | Telson with 3 pairs of dorsolateral spiniform setae (Fig. 1I); absence of “sexy shrimp pattern” coloration | <i>T. paulae</i> sp. nov. |
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| 11b. | Without red-white banding of the antennal flagella (see Anker and Baeza, 2021: figs. 7–9); Indo-West Pacific, eastern Pacific and eastern Atlantic | <i>T. amboinensis</i> |
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