

Universidade Estadual Paulista “Júlio de Mesquita Filho”
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Pós-Graduação em Ciências Biológicas (Zoologia)

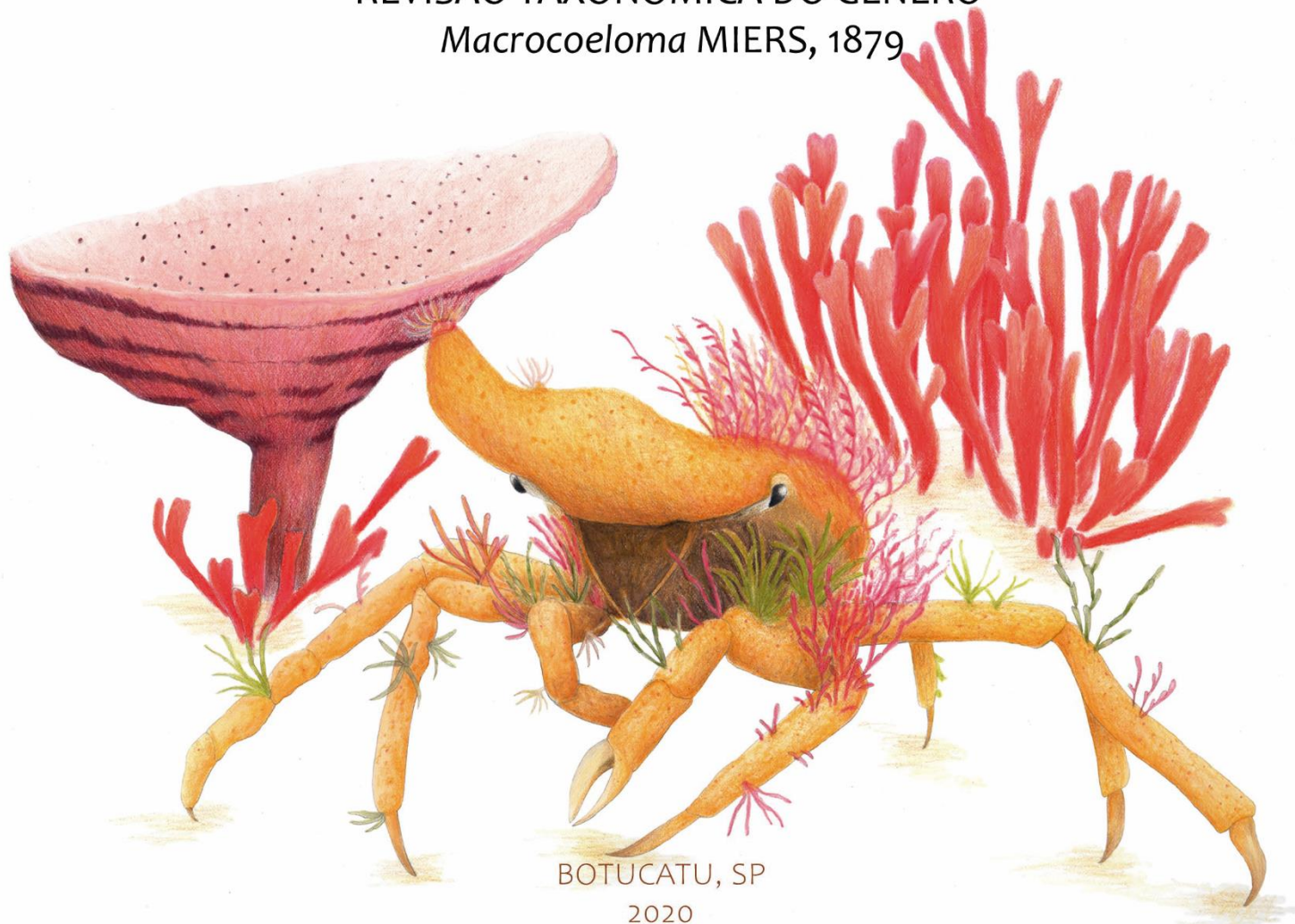
Tese de Doutorado

Jéssica Colavite

PHYLOGENETIC RELATIONS AND
TAXONOMIC REVISION OF THE GENUS
Macrocoeloma MIERS, 1879

(CRUSTACEA: DECAPODA: BRACHYURA)

RELAÇÕES FILOGENÉTICAS E
REVISÃO TAXONÔMICA DO GÊNERO
Macrocoeloma MIERS, 1879



BOTUCATU, SP
2020

JESSICA COLAVITE

**Phylogenetic relationships and taxonomic revision of the genus
Macrocoeloma Miers, 1879 (Crustacea: Decapoda: Brachyura)**

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Orientador: Prof. Dr. William Santana
Coorientadora: Ph.D. Amanda Windsor

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“Let us pick up our books and our pencils, they are
the most powerful weapon.”

Malala Yousafzai

“The ultimate tasking of the systematist is not only
describe the diversity of the living world but also to
contribute to its understanding.”

Ernst Mayr (1969)

Dedico essa tese aos meus pais, Inês e Nilton Colavite, e minha irmã Juliana, por todo amor, dedicação e incentivo. Sem vocês nada disso seria possível!

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LIST OF ABBREVIATIONS

col.: collector;	S: south;
cl.: carapace length;	W: west;
cw.: carapace width;	St.: Saint;
det.: determinator;	sta.: station;
redet.: re-determinator;	EP. eastern Pacific;
F/V: Fishing vessel;	WA. western Atlantic;
R/V: (Research Vessel);	GEDIP: Grupo Executivo do Desenvolvimento da Indústria da Pesca;
Fig. (s): figures;	H.M.S: His or Her Majesty's Ship;
Pl.(s): plates;	IMSWE project: Investigations Marine Shallow Water Ecosystems;
G1: Gonopod 1 = male pleopod 1;	REVIZEE program: Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva;
G2: Gonopod 2 = male pleopod 2;	M.M.S. Minerals Management Service.
m: meters;	
mm: millimeters;	
N: north;	

INSTITUTIONS

AMNH: American Museum of Natural History, New York, USA;

CIASB/ UESC: Coleção de Invertebrados Aquáticos do Sul da Bahia, Universidade Estadual de Santa Cruz, Brazil;

GIC: Grupo de Invetigaciones Carcinologica, Universidad de Oriente, Venezuela;

LSZ: Laboratório de Sistemática Zoológica, Universidade do Sagrado Coração, Bauru, Brazil;

MCZ: Museum of Comparative Zoology, Harvard University, USA;

MNHN: Muséum national d'Histoire naturelle, Paris, France;

MNRJ: Museu Nacional do Rio de Janeiro, Brazil;

MOUFPE: Museu Oceanográfico da Universidade Federal de Pernambuco, Brazil;

MZUSP: Museu de Zoologia da Universidade de São Paulo, Brazil;

NHMLA: Natural History Museum of Los Angeles County, USA—**AHF:** Allan Hancock Foundation;

NHMUK: Natural History Museum United Kingdom, London, UK;

OUM: Oxford University Museum of Natural History, UK;

SMF: Senckenberg Museum of Natural History, Frankfurt, German;

ULLZ: University of Louisiana at Lafayette Zoological Collection;

USNM: National Museum of Natural History, Smithsonian Institution, USA..

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Abstract

The amphi-American genus, *Macrocoeloma* Miers, 1879, is composed of decorator crabs from tropical and subtropical regions. These crabs are found on distinct substrates, including mainly coral reefs and rock. *Macrocoeloma* has undergone several systematic changes in its family status, since the original description until its recent exclusion of Mithracidae. Prior to this study, *Macrocoeloma* was considered *incertae sedis*, due to little knowledge of the relationships between species of the genus and related genera, and its taxonomic revision has been suggested several times in the literature. Thus, in order to address these taxonomic and phylogenetics gaps, this study employed morphological and molecular approaches to reconstruct the phylogenetic relationships of *Macrocoeloma*. We used a combined molecular dataset of a nuclear (18S) and three mitochondrial genes (12S, 16S, COI) using Maximum Likelihood and Bayesian Inference. In addition, the inference of species delimitation was performed with the Poisson tree processes model (PTP), using Maximum Likelihood phylogeny of the mitochondrial COI gene. The taxonomic revision of *Macrocoeloma* was provided with elaborated diagnosis, detailed descriptions and maps of geographic distribution based on examined material. The monophyly of *Macrocoeloma* was demonstrated after exclusion of *Pericera heptacantha* and *P. septemspinosa*. The monotypic genus *Thersandrus* Rathbun, 1897 is a sister group of *Macrocoeloma*, followed by the new genus proposed to accommodate *P. heptacantha* and *P. septemspinosa*. *Macrocoeloma*, *Thersandrus* and the new genus belong to the family Pisidae. The species complex formed by *M. trispinosum* (Latreille, 1825) and *M. nodipes* (Desbonne in Desbonne & Schramm, 1867), despite of the low statistical support, are treated here as two valid species, considering their morphological distinction. The *Macrocoeloma* outlandish record for the Fiji Islands, *M. trigonum* Dana, 1852, is probably a label error, with the location being corrected for Rio de

Janeiro city. The Brazilian morphotype previously identified as *M. trispinosum* (Latreille, 1825) was re-determined as *M. trigonum*, being a valid species with morphological and molecular support. After this study, *Macrocoeloma concavum*, *M. euthecum* and, *M. laevigatum* also had their range of occurrences expanded to the southeastern coast of Brazil.

Key words: Majoidea, Epialtidae, Pisidae, decorator crabs, spider crabs.

Resumo

O gênero anfi-americano *Macrocoeloma* Miers, 1879 é composto por caranguejos decoradores de habitats tropicais e subtropicais. Esses caranguejos são encontrados em substratos distintos, incluindo principalmente recifes de corais e rochas. Esse gênero passou por várias alterações sistemáticas em seu status de família, desde sua descrição original até a sua recente exclusão de Mithracidae. No início deste estudo *Macrocoeloma* era considerado *incertae sedis*, devido ao pouco conhecimento das relações entre as espécies do gênero e outros gêneros relacionados, sendo sua revisão taxonômica sugerida diversas vezes na literatura. Assim, com o objetivo de suprir essas lacunas taxonômicas e filogenéticas, este estudo empregou abordagens morfológicas e moleculares para reconstruir as relações filogenéticas de *Macrocoeloma*. Para isso, utilizamos um conjunto de dados moleculares combinados de um gene nuclear (18S) e três mitocondriais (12S, 16S, COI), usando máxima verossimilhança e inferência bayesiana. Além disso, uma inferência de delimitação de espécies foi realizada com o modelo de Poisson tree processes (PTP), usando a filogenia de máxima verossimilhança do gene mitocondrial COI. Foi realizada a revisão taxonômica de *Macrocoeloma*, com diagnóstico elaborado, descrições detalhadas e mapas de distribuição geográfica com base no material examinado. A monofilia de *Macrocoeloma* foi demonstrada, após exclusão de *Pericera heptacantha* Bell, 1836 e *P. septemspinosa* Stimpson, 1871. O gênero monotípico *Thersandrus* Rathbun, 1897 é o grupo irmão de *Macrocoeloma*, seguido pelo novo gênero criado para acomodar *P. heptacantha* e *P. septemspinosa*. *Macrocoeloma*, *Thersandrus* e o novo gênero pertencem a família Pisidae. O complexo de espécies formado por *M. trispinosum* (Latreille, 1825) e *M. nodipes* (Desbonne em Desbonne & Schramm, 1867), apesar do baixo suporte estatístico, são tratados aqui como espécies válidas com base principalmente na morfologia. O registro duvidoso de *Macrocoeloma* para as Ilhas Fiji, *M.*

trigonum Dana, 1852, após revisão taxonômica mostrou ser um erro de etiquetagem, sendo a localidade corrigida para a cidade do Rio de Janeiro. O morfotipo brasileiro previamente identificado como *M. trispinosum* (Latreille, 1825), foi re-determinado como *M. trigonum*, sendo uma espécie válida, com suporte molecular e morfológico. Após esse estudo, *Macrocoeloma concavum*, *M. euthechum* e *M. laevigatum* tiveram a faixa de ocorrência ampliada para a costa sudeste do Brasil.

Palavras-chave: Majoidea, Epialtidae, Pisidae, caranguejos decoradores, caranguejos-aranha.

INTRODUCTION

Macrocoeloma Miers, 1879 is an amphi-American genus of the superfamily Majoidea Samouelle, 1819, a group commonly known as spider crabs. These crabs are found in distinct substrates in the tropical and subtropical habitats, including primarily coral and rock reefs, but also in rock and broken shell bottoms, ranging from the intertidal zone to about 300 meters deep (Rathbun, 1925; Melo, 1996). According to Ng et al. (2008), this genus is represented by fourteen species. Three of them inhabiting the eastern Pacific, and eleven the western Atlantic oceans and, eight species are found in the Brazilian coast (Garth, 1958; Del Solar et al., 1970; Prahll and Guhl, 1979; Ramos, 1986; Barreto et al., 1993; Melo, 1996; 1998; Marcano and Bolaños, 2001; Coelho-Filho, 2006; Serejo et al., 2006; Moscoso, 2012).

All *Macrocoeloma* species are decorator crabs, attaching materials found in the environment to their body in order to camouflage themselves (personal observation, and Hultgren and Stachowicz, 2009). The adornments consist of sponges, hydroids, algae, and several other groups. These materials are adhered to specialized setae called “hooked setae” that works like a Velcro, being a morphological adaptation of most majoids (Wicksten, 1979, 1993; Hultgren and Stachowicz, 2011). These species are also densely covered by a pubescence that has a velvet aspect when seen macroscopically.

The vibrant colors and the decoration behavior of decorator crabs may have been calling the attention of aquarists, who use them to ornament aquariums. In fact, it is easy to find specimens of Sponge decorator crab [e.g. *Macrocoeloma trispinosum* (Latreille, 1825) and *M. nodipes* (Desbonne in Desbonne & Schramm, 1867)] in fishkeeping websites (personal observation).

The growing trade of coral reef species has been degrading the habitats where *Macrocoeloma* species are found. This fact, alongside with other environmental problems, such

as the introduction of exotic species and the absence of risk assessment, which often occur due to the poor knowledge of reef habitats, evidence the importance of systematics studies that provide data to conserve and regiment trade actions (Calado, 2006).

In 1879, Miers (1879: 665) proposed *Macrocoeloma* to accommodate part of the species previously included in *Pericera* Latreille, 1825. Nowadays, species of *Pericera* are distributed into the genera *Stenocionops* Desmarest, 1823, *Omalacantha* Streets, 1871, *Macrocoeloma*, and *Tiarinia* Dana, 1851. Miers also mentioned the inclusion of *Pericera* [*Pisa*] *trispinosa* (Latreille, 1825) as type species, originally included in *Periceridae* Dana, 1851. He provided a superficial description for *Macrocoeloma*: "...a highly convex carapace and large branchial spines; parallel or almost parallel rostral spines; tubular orbits laterally projected and with broad infraorbital space; the male chelipeds have elongated palm and its dactyls meet or nearly meet when closed". In 1925, Rathbun elaborated the diagnosis of *Macrocoeloma* and provided an identification key to the species described or included after Miers (1879).

In 1958, Garth reviewed the Pacific species of spider crabs following Balss' (1929) classification, which included *Macrocoeloma* in *Macrocoelominae*. However, Garth did not agree with his classification and grouped this subfamily into *Mithracinae*, using the first male gonopods as a primary character.

Until recently, *Mithracinae* MacLeay, 1838 passed through several systematic changes, being sometimes considered as a family or subfamily of *Majoidea*. In 2014 Windsor and Felder proposed a comprehensive molecular phylogeny for the group and elevated it to the family status, suggesting the inclusion of *Pitho* Bell, 1836 and *Hemus* A. Milne-Edwards, 1875 and the exclusion of *Coelocerus* A. Milne-Edwards, 1875, *Cyclocoeloma* Miers, 1880, *Cyphocarcinus* A. Milne-Edwards, 1868, *Leptopisa* Stimpson, 1871, *Macrocoeloma*, *Micippa* Leach, 1817, *Picroceroides* Miers, 1886, *Stenocionops* and *Tiarinia*. As a result of Windsor and Felder (2014) revision, *Macrocoeloma* was considered *incertae sedis* within *Majoidea*.

They suggested that *Macrocoeloma* is close related to other putative pisid crabs, such as *Leptopisa*, *Stenocionops*, *Picroceroides* and *Libinia* Leach, 1825. However, the relationship between these species is poorly known. In fact, the relationships between *Macrocoeloma* species have not been comprehensively studied up until now, making it difficult to assess the taxonomic position to the genus itself.

Previous studies based on larval morphology had no success in establish a taxonomic position for *Macrocoeloma* among majoids. Some authors suggested that *Macrocoeloma* did not belong to or was basal to Mithracidae clade (Yang, 1967; Kurata, 1969; Marques and Pohle, 2003). Yang (1967) described the zoeal stages of *M. diplacanthum* (Stimpson, 1860) and *M. camptocerum* (Stimpson, 1871) by comparing their descriptions to other mithracids. On the other hand, Gore et al. (1982) included *Macrocoeloma* in the Group I proposed by Ingle (1979), which includes *Mithrax* and *Microphrys*, but the definitions of Ingle were clearly plesiomorphic within Majoidea (Marques et al., 2003).

In 2016, Colavite et al. described the first zoeal stage of *M. subparallelum* (Stimpson, 1860) and compared it with *M. camptocerum* and *M. diplacanthum*, described by Yang (1967) and Marques et al. (2013), respectively. The authors suggested that the genus could be recognized through a combination of certain characters: distended forehead with strong underlying muscle bands, one dorsal spine and a distinct, strong spine in the distal article of the endopodite of the third maxilliped. Comparisons to other majoid zoea showed that the presence of this distinct spine in *Macrocoeloma* is similar to other genera within Epialtidae MacLeay, 1838 and Pisidae Dana, 1851, which was congruent with the phylogeny proposed by Windsor and Felder (2014). Based on these previous results, some databases already consider *Macrocoeloma* as Pisinae (see Worms, 2019), but a detailed revision of the group is essential to solve the taxonomic problems involved with the genus.

Macrocoeloma, as well as many genera of Majoidea, has some systematic and nomenclatural problems due to the similarities between the congener species, which causes difficulties in identification. According to Stimpson (1871), *Macrocoeloma* has analogue species in both sides of America, such as: *M. subparallelum* [western Atlantic, WA] and *M. villosum* (Bell, 1836) [eastern Pacific, EP]; *M. septemspinusum* (Stimpson, 1871) [WA] and *M. heptacanthum* (Bell, 1836) [EP]. Rathbun (1901) even observed that there are species with very similar morphology in the WA: *M. concavum* Miers, 1886, *M. euthecum* (Stimpson, 1871) and *M. intermedium* Rathbun, 1901. The eastern Pacific species *Macrocoeloma heptacanthum*, *M. maccullochae* and *M. villosum* are also poorly studied with few specimens deposited in collections. Di Mauro (1982) rediscovered the type material of *Pericera heptacantha* and *Pericera villosa* of Prof. Bell in the Oxford Museum. This material was considered lost for over 50 years and, for this reason, was never compared with specimens in recent collections (Boone 1927; 1930; Rathbun, 1925; Garth 1946, 1958). Garth (1958) suggested that these materials could solve important taxonomic status questions of several pacific species that he had left as undecided (Di Mauro, 1982). One is the *Macrocoeloma villosum*, for which Garth (1958) suggested the possible existence of two distinct species.

Macrocoeloma has another outlandish record in the Fiji Islands, *Macrocoeloma trigonum* Dana, 1852. The original description is the first and only record of occurrence of the species and genus outside the Americas. *Macrocoeloma trigonum* type material was collected during “The United States Exploring Expedition’ between 1938 and 1942. This expedition faced several difficulties, which could have led to a mislabeling of the material, with similar cases reported in the literature (e.g. *Sesarma trapezium* Dana, 1852 synonymous of *Armases rubripes* (Rathbun, 1897) (Abele, 1974); *Acanthonyx simplex* Dana, 1852 junior synonymous of *A. petiverii* H. Milne Edwards, 1834 (Emparanza et al., 2007) and *Galene hawaiiensis* Dana, 1852 junior synonym of *Panopeus herbstii* H. Milne Edwards, 1834 (Ng, Guinot, &

Davie, 2008 footnote in pg.191). Despite of that, *M. trigonum* was never studied and is still considered a valid species (Ng et al., 2008).

Another taxonomic problem is the case between *Macrocoeloma trispinosum* (Latreille, 1825) and *M. nodipes* (Desbonne in Desbonne & Schramm, 1867). These species have a morphological gradient between them, called by Rathbun (1925) as “variety”. She noticed the differences between the specimens deposited at the National Museum of Natural History, Smithsonian Institution (USNM) collections, dividing the two species into three series of specimens. However, she could not divide the series into three different species and decided to consider all *M. trispinosum*, with two subspecies *M. trispinosum trispinosum*, *M. trispinosum nodipes*, which was accepted by several authors (Rathbun, 1925; Wass, 1955; Powers, 1977; Soto, 1980; Williams, 1984; Abele and Kim, 1986; Nizinski, 2003). However, for more than 90 years, some authors alerted for the necessity of a careful revision of this potential complex of species (e.g. Rathbun, 1925; Abele, 1970; Coelho, 1971; Powers, 1977). Identification doubts reflect in the collection labels and species checklists and undermine the distribution of these “subspecies”. Also, the poorly detailed descriptions, and the loss of the type material of *Macrocoeloma trispinosum* and *M. nodipes* are troublesome to split or to synonymize both species.

The absence of type material is not exclusive of these species. The types of five other species of *Macrocoeloma* are considered lost. Some of them are Stimpson's material was most likely destroyed in the Great Chicago Fire in 1871 (Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006). The Stimpson's descriptions are in general short and poorly detailed, and the absence of figures in the original publication allows different interpretations of the morphological characters. In these cases, a neotype specimen is crucial to assure the correct application of the nomenclature through the material comparison.

The lack of a thorough taxonomic revision at the genus level also reflects in the higher taxonomic categories, resulting in a vague definition of several groups of species that leads many authors to divide a family into several subfamilies or to elevate subfamilies to family level, and/or establishing new tribes (Rathbun, 1925; Števcic, 2005; 2011; Ng et al., 2008, De Grave et al., 2009; Guinot, 2012; Windsor and Felder, 2014, Fig. 1). The internal placement of Majoidea groups and the internal relationship between the species is far from resolved (Marques and Pohle, 2003; Hultgren and Stachowicz, 2008; Mahon and Neigel, 2008; Hultgren et al., 2009; Davie et al., 2015b). Hence, there is acute need for an in-depth phylogenetic analysis of the Majoidea at all levels.

Windsor and Felder (2014), were the first to include species of *Macrocoeloma* in molecular phylogenies (Fig. 1), followed by the recent phylogeny published by Colavite et al (2019) (Fig. 2). However, both inferences have no sufficient data to recover the internal relationships of *Macrocoeloma* and the position of this group still *incertae sedis* in Majoidea.

In light of the taxonomic gaps, this study employs morphological and molecular analyses to reconstruct phylogenetic relationships of the genus *Macrocoeloma* and related genera. A taxonomic revision of *Macrocoeloma* is made, with new diagnosis and detailed descriptions, identification key, and distribution based on examined material. Also, lectotypes and neotypes are also designated in order to avoid further nomenclatural problems.

Figure 1. Molecular phylogenetic tree modified from Windsor and Felder (2014). Three used to indicate the position of Mithracidae in Majoidea with representatives of other families of the group. *Macrocoeloma* represented by two species (marked in dark red).

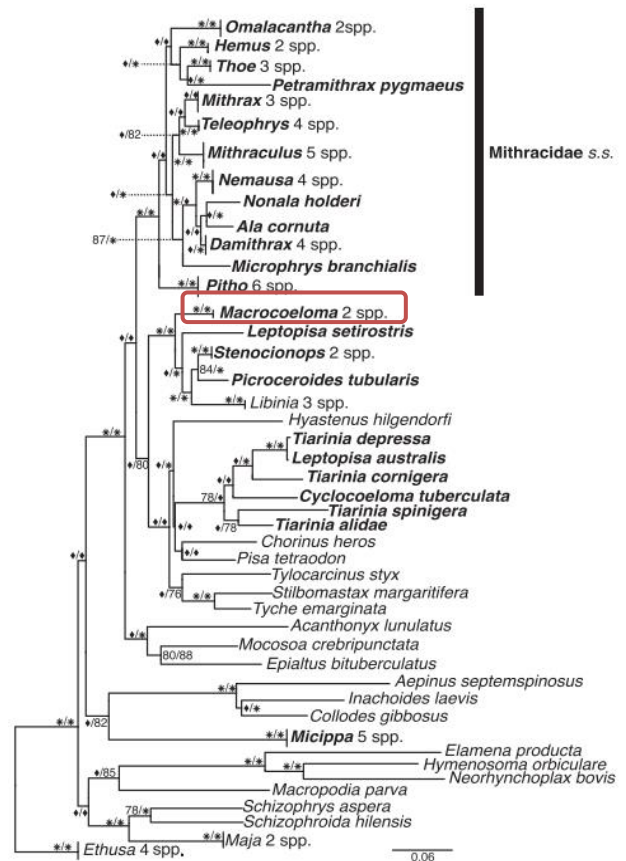
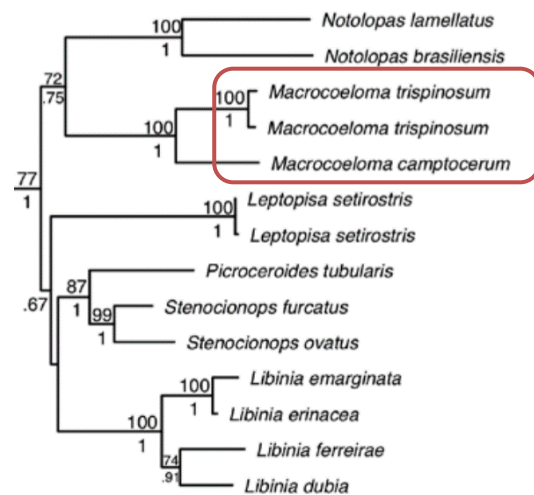


Figure 2. Molecular phylogenetic tree modified from Colavite et al. (2019). Two species of *Macrocoeloma* used in the analyses (marked in dark red).



OBJECTIVES

The main objective of this study is to propose a phylogenetic hypothesis of relationship and the taxonomic revision of *Macrocoeloma* Miers, 1879. Specific aims are: (i) to test the monophyly of *Macrocoeloma* using a multigene approach; (ii) to re-describe in detail the morphology and update the geographic distribution of each species of the genus; (ii) and to assign a taxonomic position of *Macrocoeloma* in Majoidea.

MATERIAL AND METHODS

Material Examined

Specimens of *Macrocoeloma* deposited in the crustaceans collections of the follow Museums were examined: American Museum of Natural History, New York (AMNH); Coleção de Invertebrados Aquáticos do Sul da Bahia, Universidade Estadual de Santa Cruz, Brazil (CIASB/ UESC); Grupo de Invetigaciones Carcinologicas, Universidad de Oriente, Venezuela (GIC); Laboratório de Sistemática Zoológica, Universidade do Sagrado Coração, Bauru (LSZ); Muséum national d'Histoire naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard University (MCZ); Museu Nacional do Rio de Janeiro (MNRJ); Museu Oceanográfico da Universidade Federal de Pernambuco, Brazil (MOUFPE); Museu de Zoologia da Universidade de São Paulo (MZUSP); Natural History Museum of Los Angeles County (NHMLA); National Museum of Natural History, Smithsonian Institution, (USNM). Specimens from the follow collections was examined through photographs: Natural History Museum United Kingdom, Londres (NHMUK); Oxford University Museum of Natural History (OUM); Senckenberg Museum of Natural History, Frankfurt (SMF); University of Louisiana at Lafayette Zoological Collection (ULLZ).

Specimens of all species of *Macrocoeloma* were morphologically examined and the material includes the type material for five nominal species.

When divergences were found between the information on the museum label and the primary description of species, the data of the original publication were kept.

Comparative material.

Cyclocoeloma tuberculata Miers, 1880 – *PHILIPPINES*, Manila, no data, Mitchell, A., 28.viii.2017, Colavite J. det., 1 male (USNM 306881).

Entomonyx spinosus Miers, 1884 – *MOZAMBIQUE*, 50-mile SE of Beira, IIOE–International Indian Ocean Expedition, Anton Bruun R/V, cruise 8, 3 Oct 1964, D.J.G. Griffin det., 62m, 2 males (USNM 135131). *MADAGASCAR*, 65 Mile SW of Cap St. Andre, IIOE–International Indian Ocean Expedition, Anton Bruun R/V, cruise 8, stn. 408D, 15 Oct 1964, 1970, D.J.G. Griffin det., 150-300m, 1 female (USNM 135132).

Laubierinia nodosa (Rathbun, 1916) – *JAPAN*, Shikoku Island, off W. Ashiuzuri Peninsula, sta.21, T. and K. Sakai col., 27-31.iii.1966, T. Sakai det., 300m, 2 females, 1 male (USNM 120726).

Leptopisa setirostris (Stimpson, 1871) – *UNITED STATES*, Off Florida, SOFLA expedition, Suncoaster R/V, 27.vi.1985, BOEM Collections; Southwest Florida Shelf Ecosystem Study col., ix.2017, J. Colavite det., 24m, 1 male (USNM 276592). *BRAZIL*, Rio Doce Project, sta. RD53, Prof. W. Besnard R/V, 1973, 1 male (MZUSP 9123). Paraíba, Algas Project, sta. 89, 1981, 1 female (MZUSP 5903).

Libinia dubia H. Milne Edwards, 1834 – *UNITED STATES*, Florida, Key West, without date, M.J. Rathbun det., 1 male, 2 ovigerous females (USNM 72933). Dunedin, Florida, 1916, M.J. Rathbun det., 1 male (USNM 57841). Florida, Miami, Bear Cut, 20.vi.1953, D. Moore det., 1 male (USNM 1191752). Florida, Everglades National Park, Conchie Channel, R. Manning coll., 17.x.1958, W. Santana det., 1 male (USNM 1191753).

Libinia spinosa H. Milne Edwards in Guérin, 1832–*BRAZIL*, Rio de Janeiro, Cabo de São Tomé, stn. iv, 1 female [old number MZUSP 3414] (MOUFPE 4380). Rio de Janeiro, Almirante Saldanha R/V, stn. 1931 C, 1 female (MOUFPE 4379). Rio de Janeiro, Almirante Saldanha R/V, stn. 2260 A, 2 males (MOUFPE 4381). Rio de Janeiro, Almirante Saldanha R/V, stn. 2258 A, 34°32S:52°06'W, 8 juveniles (MOUFPE 4382).

Leptopisa setirostris (Rathbun, 1892) – *JAMAICA*, Albatross bank, Morant Cay, 17.7347 - 75.65, 29.ii.1884, United States Fish Commission col., 42m, 1 male holotype of *Macrocoeloma tenuirostra* Rathbun, 1892 (USNM 6929).

Rhinocarcinus agassizi (Rathbun, 1894) – *PERU*, Piura, El Alto, 10°00'S- 81°27'W, Anton Brunn R/V, SEBOP Expedition, 9.ix.1966, Smithsonian Oceanographic Sorting Center col., 1815-1860 m, A. Windsor det., 27.iii.2011, 1 male (USNM 1155074).

Stenocionops furcatus (Olivier, 1791) – *BRAZIL*, Rio de Janeiro, Bacia de Campos, Petrobrás, 25. Xi.2010, V.B. Mendonça Jr. coll., 1 female (MZUSP 29838). Rio de Janeiro, Baia da Ilha Grande, i.2007, 1 male (MZUSP 17909). São Paulo, Ubatuba, Projeto Integrado, 14.vi.1995, F. Torres coll., 1 male (MZUSP10839). São Paulo, Ubatuba, Projeto Integrado, stn., 4856, 03. vii.1990, 1 juvenile male (MZUSP 8044).

Stenocionops spinosissimus (Saussure, 1857) – *BRAZIL*, Rio de Janeiro, Prof. W. Besnard R/V, Projeto Sol, stn. 1147, 23°30'S-42°27'W, 08.viii.1970, 136m, 1 female (MZUSP 3982). Rio de Janeiro, Prof. W. Besnard R/V, Projeto Sol, stn. 1147, 23°30'S-42°27'W, 11.vii.1970, 136 m, 1 male (MZUSP 3985).

Thersandrus compressus (Desbonne in Desbonne & Schramm, 1867) – *BELIZE*, west Bay, 1.3m, 9.vi.1985, 1 male; (USNM 1526077). *MARTINIQUE*, Passe du Marin, MARIBENTHOS, stn. AR116, 14° 26' 53.9988'N-60° 54' 4.0068'W, 10.ix.2016, 4m, 1 male (MNHN 2016-4188).

DNA extraction, PCR, and sequencing

To extract the DNA, the samples were obtained from ethanol-preserved muscle tissue of the pereopods or gills. When the dissection was not possible, the whole appendages or specimen was used, using either Total genomic DNA DNeasy Blood and Tissue extraction kit

(Qiagen Catalog No. 69504) or E.Z.N.A.® Tissue DNA kit (Omega Bio-Tek Catalog No. D3396-02).

Partial sequences of the mitochondrial genes 12S rRNA, 16S rRNA, cytochrome C oxidase 1 COI mRNA and the small subunit 18S rRNA nuclear gene were amplified with the following primers respectively: 12SF (Mokady et al., 1994) and 12S1R (Shull et al., 2005), 16SAr/16SBr majoid-specific primers (Hultgren and Stachowicz, 2008), universal primer LCO1490/HCO2198 (Folmer et al., 1994) and 18S A/L, C/Y, O/B (Medlin et al., 1988; Apakupakul et al., 1999) or B/D18s1R, D18s2FD18s2R, D18s3F-D18s3R, D18s4F-D18s4R and D18s5F-A (Bracken et al., 2009).

Each locus used evolve at different rates (Tsang *in* Chu et al., 2015). This is helpful in solving divergences at the species (mitochondrial markers) and family (nuclear makers) level. Mitochondrial loci, 12S and 16S are commonly used for intra-specific crustacean phylogenies (Fratini et al., 2018; Thoma et al., 2009), and have been used to resolve relationships between genera within several brachyuran families (Windsor and Felder, 2014; Shih et al., 2016). The COI gene has also been used as a marker for species identification (Buhay, 2009; Da Silva et al., 2011; Landschoff and Gouws, 2018). The nuclear loci such as a subunit of 18S rRNA have been used in multi-locus datasets (in conjunction with mitochondrial markers) to reconstruct major clades in the Brachyura (Ahyong et al., 2007).

At the Laboratory of Molecular Biology of the MZUSP

Amplification by the Polymerase Chain Reaction (PCR) technique (Ward et al., 2005; Ochoa et al., 2017) was performed in a final volume of 20 µL for 12S/ 16S/ COI and 25 µL for 18S. Reagent volumes and concentrations were composed by 1 µL of total DNA sample. For 12S/ 16S/ COI was used: 0.4 µL of primers ;2 µL of Taq buffer (10X); 0.6 µL of MgCl₂ (50mM); 0.4 µL of dNTPs (10 mM) and 0.2 µL of Taq (PlatinumR *Taq* DNA Polymerase) (5

U/uL), plus 15 μ L of ultrapure water to complete the final volume. For 18S was used: 1.25 μ L of primer (10 mM); 2.5 μ L of Taq buffer (10X); 1 μ L of MgCl₂ (50mM); 1 μ L of dNTPs (10 mM) and 0.5 μ L of Taq (Platinum *Taq* DNA Polymerase) (5 U/uL), plus 16.5 μ L of ultrapure water to complete the final volume. The PCR reactions were performed on Verity (Applied System) thermocycler according to the following schedule: 12S/ 16S: first cycle at 94°C for 2'; 35 cycles of 94°C for 5' during 30", 52°C during 30", and 72°C for 1'; final extension of 72°C for 5'. COI: first cycle at 94°C for 2'; 35 cycles of 94°C for 5' during 30", 48°C during 30", and 72°C for 1'; final extension of 72°C for 5'. 18S: first cycle at 94°C for 2'; 35 cycles of 94°C for 5' during 30", 58°C during 30", and 72°C for 1'; final extension of 72°C for 5'. Each PCR reaction was checked by electrophoresis in agarose at 1%. Only those reactions which had shown a considerable success were purified using ExoSAP-IT™ (Thermo Fisher Scientific Inc) and sent to be sequenced at the Instituto de Biotecnologia da Unesp (IBTEC), Botucatu - SP. Sequencing reactions were performed using 1 μ L of purified PCR product in a 15 μ L reaction containing 5 μ L primer (0.5 pmol/ μ L), sequenced on an ABI 3500 automated DNA (Applied Biosystems) according to the manufacturer's instructions. Sequences were assembled and checked for quality using Geneious 8.0.5 and 9.1.8.

At the Laboratory of Analytical Biology (LAB) of the Smithsonian Institution

Amplification was performed in a total volume of 10 μ L. The PCR mix was composed by 0.1 μ L of 10x Promega Go Taq G2 Hot Start Master Mix (M7833); 0.3 μ L of each primer (10 mM); 0.25 μ L BSA (New England Biolabs B9000S); 6.5 μ L of nuclease-free water and 1 μ L of template DNA. The thermocycler profiles are the same of described above. PCR reaction was checked by electrophoresis in agarose at 1.5%. Only those reactions which had shown successful amplification were purified using ExoSAP (Affymetrix) (0,5 μ L ExoSap enzyme, 1,5 μ L nuclease-free water per reaction). The thermocycle profile for PCR purification was

36°C for 30' followed by 80°C for 20'. Sequencing reactions were performed using 1 µL of purified PCR product in a 10 µL reaction containing 0.5 µL primer, 1.75 µL Big Dye buffer and 0.5 µL Big Dye (Life Technologies). The thermocycler profile consisted of 35 cycles of denaturation (95°C 30"), annealing (50°C 30"), and extension (60°C 4'). The BigDye products were purified with Sephadex G-50 (Sigma-Aldrich) in Millipore Sephadex plates (MAHVN-4550) to remove unincorporated dNTPs, and dried at 95°C for 15 minutes. The purified products were then loaded on an automatic sequencer ABI 3730XL in the Laboratory of Analytical Biology (LAB) at National Museum of Natural History, Smithsonian Institution.

Molecular Data analysis

Sequences generated for this study were combined with those from Windsor and Felder (2014; 2017) and GenBank sequences, in order to place our specimens within the context of *Majoidea* (see Table 1). Taxon information about catalog numbers and GenBank accession number, locality and molecular markers included in the phylogenetic trees are provided in the Table 1. Multiple sequence alignment was performed using the MUSCLE alignment algorithm (Edgar, 2004) for the individual molecular markers, under default parameters; the alignments were visually inspected for any obvious misalignments. The individual datasets were concatenated in Geneious and the perl script PartitionFinder (Lanfear et al., 2016) was run to determine an appropriate model(s) of evolution and partitioning scheme, with the Akaike information criterion (AIC) (Posada and Buckley, 2004). To evaluate the occurrence of substitution saturation of the concatenated matrix the rate of transitions/transversions (Xia and Lemey, 2009) were evaluated in the software DAMBE 5.2.31 (Xia and Xie, 2001). Two methods of phylogenetic inference were applied to our concatenated dataset: maximum likelihood using RAxML version 8.2.12 (Stamatakis, 2014) and Bayesian inference (BI) in MrBayes (v3.2.1) (Huelsenbeck and Ronquist, 2001). All analyses were run on the Hydra

computing cluster at USNM or CIPRES Portal (Miller et al., 2010). In RAxML, the '-f ae' option with 1000 bootstrap replicates was used. Likelihood parameters followed the General Time Reversible (GTR) model with a gamma distribution on the partitioned dataset and RAxML estimated all free parameters. The resulting best tree was used to reflect the phylogeny. Bayesian inference was performed with 10 000 000 generations with a 25% burn-in and sampling every 1000 generations. A mixed model was applied to the partitioned dataset. A 50% majority-rule consensus tree was constructed from the post-burn-in trees. The resulting trees were analyzed and edited FigTree 1.4.4 (Rambaut, 2012).

Species delimitation

Species delimitation analyses, an evolutionary approach based on relative branch lengths was performed using the Poisson tree processes (PTP) model (Zhang et al., 2013) to infer putative species boundaries using phylogenetic placements. PTP model consider the number of substitutions between branching and/or speciation events, by modeling speciation using the number of substitutions instead of the time, as used in coalescence model. The underlying assumption is that each substitution has a small probability of generating a speciation (Zhang et al., 2013). In this analysis, specimens more likely to belong to a single species branch were colored in red and species branches in blue. For the application of PTP model, a reference tree was inferred using RAxML version 8.2.12 (Stamatakis, 2014) for the mtDNA COI gene dataset with 648pb of 39 sequences of *Macrocoeloma* and seven other genera of Pisidae. The analysis was performed at CIPRES Portal (Miller et al., 2010) and PTP at the webserver (<http://species.h-its.org/>). Likelihood parameters followed the General Time Reversible (GTR) model with a gamma distribution. The index of substitution saturation (Iss) of COI matrix was estimated as described by Xia et al. (2003) in the software DAMBE 5.2.31 (Xia and Xie, 2001).

Table 1. Taxa included in the molecular phylogenetic analyses of *Macrocoeloma* Miers, 1879. Catalog number abbreviations: BCBC; Biodiversity of Carrie Bow Cay, Belize; LACM, Los Angeles County Museum; LSZ, Laboratory of Zoological Systematic, UNESP/Botucatu; MPEG, Museu Paraense Emilio Goeldi; MNHN, Muséum National d'Historie Naturelle, Paris; MZUSP; ULLZ, University of Louisiana at Lafayette Zoological Collection; USNM, United States National Museum, Smithsonian Institution. EA= eastern Atlantic; WA= western Atlantic; EP= eastern Pacific; Car. Caribbean Sea; GMx = Gulf of Mexico; N, S, E, or W to indicate north, south, east or west, respectively; –, no sequence.

Taxon name	Collection Locality	Catalog number	Molecular markers Gene bank accession numbers				Authors
			12S	16S	COI	18S	
<i>Macrocoeloma</i>							
<i>Macrocoeloma camptocerum</i>	Sw of GMx	ULL7261	#	#	#	—	Present study
	Sw of GMx	ULLZ6889	KF453110	KF453003	KF452924	KF453173	Windsor, A. M.
<i>Macrocoeloma concavum</i>	Sw of GMx	ULLZ6767	#	#	#	#	Present study
	Atlantic Amazon, Brazil	MPEG1182	#	—	—	—	Present study
<i>Macrocoeloma diplacanthum</i>	Car., Belize	ULLZ11111	#	#	#	—	Present study
	Car., Belize	ULLZ14655	#	#	#	—	Present study
<i>Macrocoeloma euthecum</i>	Sw of GMx, Florida	ULLZ6824	#	#	—	—	Present study
	Sw of GMx	ULLZ7541	#	—	—	—	Present study
	Car., Guadeloupe	MNHN2013-13091	#	—	#	—	Present study
<i>Macrocoeloma laevigatum</i>	Car., Guadeloupe	MNHN2013-5916	#	—	#	—	Present study
	SW of GMx	ULLZ6887	#	#	#	—	Present study
	Car., Guadeloupe	MNHN2013-5134	#	#	#	—	Present study
<i>Macrocoeloma nodipes</i>	WA, USA	ULLZ4571	KF453097	KF453042	KF452911	KF453162	Windsor, A. M.
	N of WA, Ft. Pierce, Florida	ULLZ9904	#	#	—	—	Present study
	N of GMx	ULLZ7862	#	—	—	—	Present study
	Car., Guadeloupe	MNHN 2013-4312	MK309561	MK309574	MK281284	—	Windsor, A. M.

	Car., Bocas del Toro, Panama	ULLZ10763	#	#	—	#	Present study
	Weewee Key, Florida	ULLZ15463	#	#	#	—	Present study
	Car., Panamá	MZUSP33456	—	—	#	#	Present study
	Sw of GMx	ULLZ6802	#	—	#	—	Present study
	Twin Cays, Belize	ULLZ16544	#	#	—	—	Present study
	Bocas del Toro, Panama	ULLZ12024	#	#	#	—	Present study
	Bocas del Toro, Panama	118755075*	—	—	#	—	Present study
<i>Macrocoeloma subparallelum</i>	S of WA, Salvador, BA, Brazil	MZUSP18626	—	—	#	#	Present study
	Car., Carrie Bow Cay, Belize	BCBC424	—	—	#	—	Present study
	Car., Carrie Bow Cay, Belize	BCBC638	—	—	#	—	Present study
	Car., Carrie Bow Cay, Belize	BCBC637	—	—	#	—	Present study
	Car., Carrie Bow Cay, Belize	BCBC425	—	—	#	—	Present study
	Bocas del Toro, Panama	118755129*	—	—	#	—	Present study
	Car., Carrie Bow Cay, Belize	ULLZ12592	#	#	—	—	Present study
	Car., Guadeloupe	MNHN2013-5932	#	—	—	—	Present study
	Car., Guadeloupe	MNHN2013-4961	#	#	#	—	Present study
<i>Macrocoeloma trispinosum</i>	N of GMx	ULLZ13374	—	#	—	—	Present study
	WA, STRI Point, Panama	ULLZ10753	—	#	#	—	Present study
	Car., Guadeloupe	MNHN2013-5951	#	—	#	—	Present study
<i>Macrocoeloma trigonum</i>	S of WA, Ilha das Cabras, SP, Brazil	LSZ 179	#	#	#	#	Present study
	S of WA, Ubatuba, SP, Brazil	MF490094*	—	—	MF490094	—	Mantelatto,F.L. et al.

	S of WA, Recife, PE, Brazil	R2	—	—	#	—	Present study
<i>Macrocoeloma villosum</i>	S of EP, Ecuador	LACM unnumbered	#	—	—	—	Present study
	S of EP, Ecuador	USNM70942	#	—	—	—	Present study
New genus							
New genus <i>septemspinosa</i> gen. nov., comb. nov.	S of GMx	ULLZ 7552	#	#	#	#	Present study
	Car., Guadeloupe WA, Recife, PE, Brazil	MNHN2013-2682	#	#	#	—	Present study
		R7	—	#	—	—	Present study
Outgroup taxa							
Pisidae							
<i>Libinia dubia</i>	N of WA, Florida	ULLZ10160	KF453077	KF452973	KF452965	—	Windsor,A.M. and Felder,D.L.
<i>Libinia emarginata</i>	N of GMx, Louisiana	ULLZ10344	KF453078	KF452974	KF452896	KF453151	Windsor,A.M. and Felder,D.L.
<i>Libinia erinacea</i>	N of WA, US	ULLZ7747	KF453119	KF453011	KF452932	—	Windsor,A.M. and Felder,D.L.
<i>Libinia ferreirae</i>	S of WA, Ubatuba, SP, Brazil	MF490093*	—	—	MF490093	—	Mantelatto,F.L. et al.
<i>Stenocionops furcatus</i>	S of WA, Ubatuba, SP, Brazil	LSZ 180	#	—	—	#	Present study
	N of WA, US	ULLZ8410	KF453125	KF453017	KF452936	KF453179	Windsor,A.M. and Felder,D.L.
	GMx, South Pulley Ridge	ULLZ6673	—	—	#	#	Present study
<i>Stenocionops ovatus</i>	EP, Panamá	ULLZ9747	KF453142	KF453032	KF452956	KF453190	Windsor,A.M. and Felder,D.L.
<i>Stenocionops spinosissimus</i>	Car., Guadeloupe	MNHN 2013-6792	#	—	#	—	Present study
	Car., Saba Bank, Netherlands Antilles	ULLZ15687	#	#	#	—	Present study
<i>Thersandrus compressus</i>	Car., Belize	ULLZ 17597	#	#	#	—	Present study

	Car., St. Vincent & The Grenadines	ULLZ11045	#	#	—	#	Present study
<i>Leptopisa setirostris</i>	Sw of GMx, Yucatán	ULLZ6798	KF453107	KF453000	KF452921	MK281273	Windsor,A.M. and Felder,D.L.
<i>Pisoides edwardsii</i>	S of EP, Chile	ULLZ9144	—	MK309589	MK281273	MK285647	Windsor,A.M. and Felder,D.L.
<i>Herbstia condyliata</i>	EA, Portugal	EU682845*	—	EU682790	EU682845	—	Hultgren,K.M. and Stachowicz,J.J.
<i>Nibilia antilocapra</i>	SW of GMx	ULLZ7365	—	MK309583	MK281282	MK285646	Windsor,A.M.
<i>Nibilia machala</i>	EP, Ecuador	USNM1462701	—	MK309606	MK281281	—	Windsor,A.M.
<i>Notolopas brasiliensis</i>	S of WA, Ubatuba, SP, Brazil	MF490104*	—	—	MF490104	—	Mantelatto,F.L. et al.
<i>Notolopas lamellatus</i>	EP, Costa Rica	ULLZ8337	—	—	MK281280	—	Present study
<i>Chorinus herus</i>	Car., Belize	ULLZ11199	KF453081	KF452977	KF452900	KF453154	Windsor,A.M. and Felder,D.L.
<i>Pisa tetraodon</i>	EA, Spain	ULLZ11427	KF453084	KF452980	KF452902	KF453157	Windsor,A.M. and Felder,D.L.
Mithracidae							
<i>Mithraculus sculptus</i>	N of WA, Florida	ULLZ8774	GU144526	GU144539	GU144555	—	Windsor,A.M. and Felder,D.L.
<i>Mithraculus forceps</i>	N of GMx, Louisiana	ULLZ4893	KF453098	—	KF452912	—	Windsor,A.M. and Felder,D.L.
<i>Mithrax pleuracanthus</i>	N of WA, Florida	ULLZ5694	GU144537	GU144544	GU144560	—	Windsor,A.M. and Felder,D.L.
<i>Ala cornuta</i>	EP, Panamá	ULLZ9065	KF453126	KF453018	KF452937	KF453181	Windsor,A.M. and Felder,D.L.
<i>Amphithrax aculeatus</i>	Car., Belize	ULLZ9148	KF453131	KF453022	KF452942	KF453186	Windsor,A.M. and Felder,D.L.
Epialtidae							
<i>Acanthonyx lunulatus</i>	EA, Cape Verde Island	ULLZ11713	—	KF452983	KF452903	KF453159	Windsor,A.M. and Felder,D.L.
<i>Acanthonyx petiverii</i>	W of GMx	ULLZ8480	—	MK309588	MK281285	—	Windsor,A.M. and Felder,D.L.
<i>Epialtus bituberculatus</i>	Car., Panamá	ULLZ10757	KF453080	KF452976	KF452898	KF453153	Windsor,A.M. and Felder,D.L.
<i>Hyastenus hilgendorfi</i>	Suez Canal, Egypt	ULLZ12262	KF453092	KF452989	KF452907	—	Windsor,A.M.

<i>Mocosoa crebripunctata</i>	Sw of GMx	ULLZ6821	KF453108	KF453001	KF452922.	KF453171	Windsor,A.M.
Majidae							
<i>Maja brachydactyla</i>	EA, Spain	ULLZ11425	KF453082	KF452978	MK281275	KF453155	Windsor,A.M.
Inachidae							
<i>Macropodia parva</i>	EP, Spain	ULLZ11426	KF453083	KF452979	KF452901	KF453156	Windsor,A.M.
Inachoididae							
<i>Inachoides laevis</i>	EP, Panamá	ULLZ9156	KF453134	KF453025	KF452945	KF453188	Windsor,A.M.
Hymenosomatidae							
<i>Elamena producta</i>	Kaikoura, New Zealand	FJ812337*	FJ812301	FJ812319	FJ812283	FJ812337	Teske,P.R. et al.
<i>Neorhynchoplax bovis</i>	Haga Haga, South Africa	FJ812336*	FJ812300	FJ812318	—	FJ812336	Teske,P.R. et al.

* Genbank number used to name the specimen.

Taxonomy and Morphology

The synonym, type locality, type material, material examined, diagnosis, description, and geographic distribution were included for all species belonging to the genus *Macrocoeloma* Miers, 1879.

The specimens were comparatively analyzed as to the external morphology of juveniles, adults, males, females and ovigerous females. The morphological terminology follows Rathbun (1925), Williams (1984) and Davie et al. (2015a) (Fig. 3, 4, 5, 6). Type material were measured for carapace length (cl), between the anterior extremity of the rostrum to the posterior margin of the carapace; and for carapace width (cw), between the maximal width without lateral spines (Fig. 3).

The specimens were examined using stereomicroscopy Leica MZ125 or Motic K 400 L, and photographed using a Nikon Coolpix L810 and Canon EOS Rebel T6. Gonopods were examined using Leica M165C or Leica MZ16A stereomicroscope and photographed using an attached NIKON D670 or Canon EOS Rebel T6 or JVC KY-F75U digital cameras.

Images were digitally processed with Helicon Focus v. 5.1, Auto-Montage (v5.0), or Adobe Photoshop CS2015 software. Plates were edited using the software Adobe Illustrator CS2015 and Adobe Photoshop CS2015, with the aid of the graphic tablet WACOM-CTL470L. The scale bars are in millimeters (mm) and indicated in the figure legends.

Distribution maps are based on the material examined in this study, including the type locality for each species. In the maps, the yellow star represents the type locality, red circles the distribution and green circles the new range of distribution. The maps were elaborated using the QGIS Desktop 3.10.0 software.

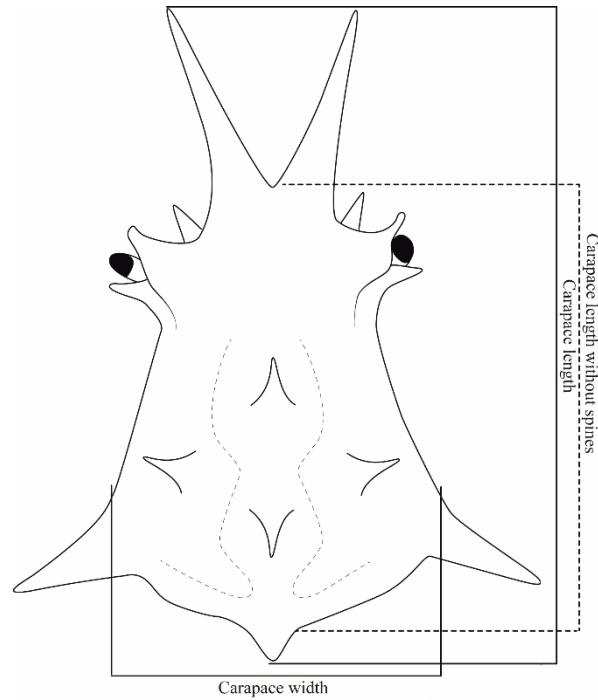


Figure 3. Schematic representation of the carapace of *Macrocoeloma camptoceram* (Stimpson, 1871), with measures of carapace length with and without spines (CL) and carapace width (CW).

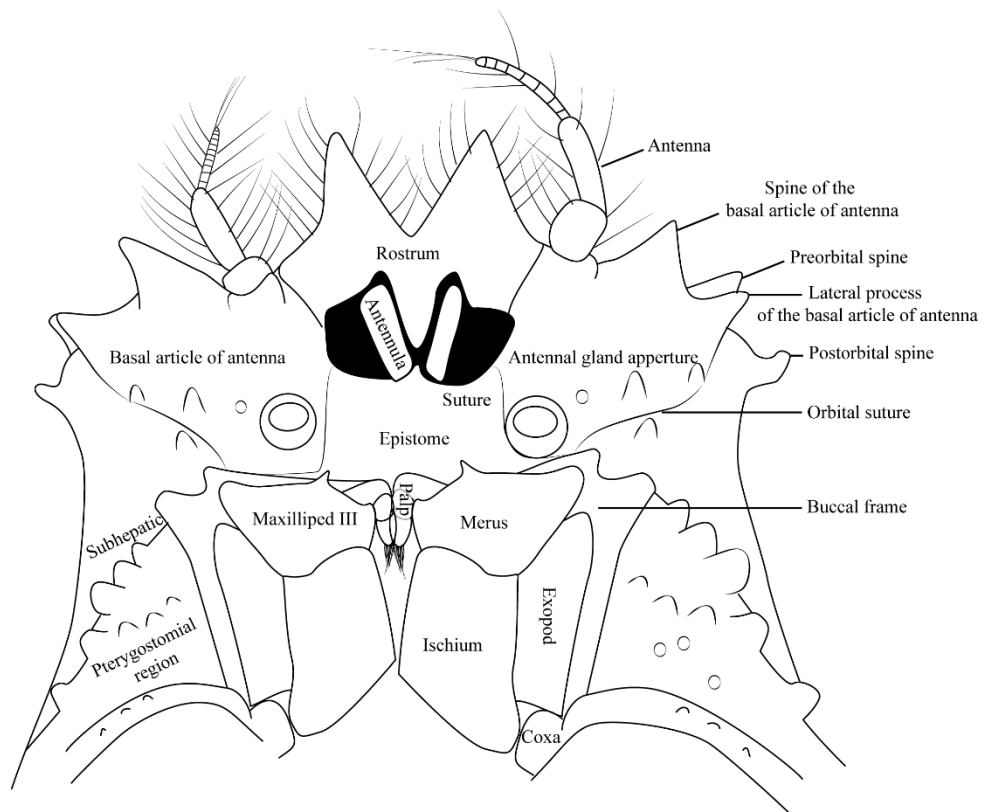


Figure 4. Schematic representation of the frontal region in ventral view of the carapace of *Macrocoeloma concavum* Miers, 1886, with indications of the regions and spines, based on Rathbun (1925), Williams (1984) and Davie et al. (2015a).

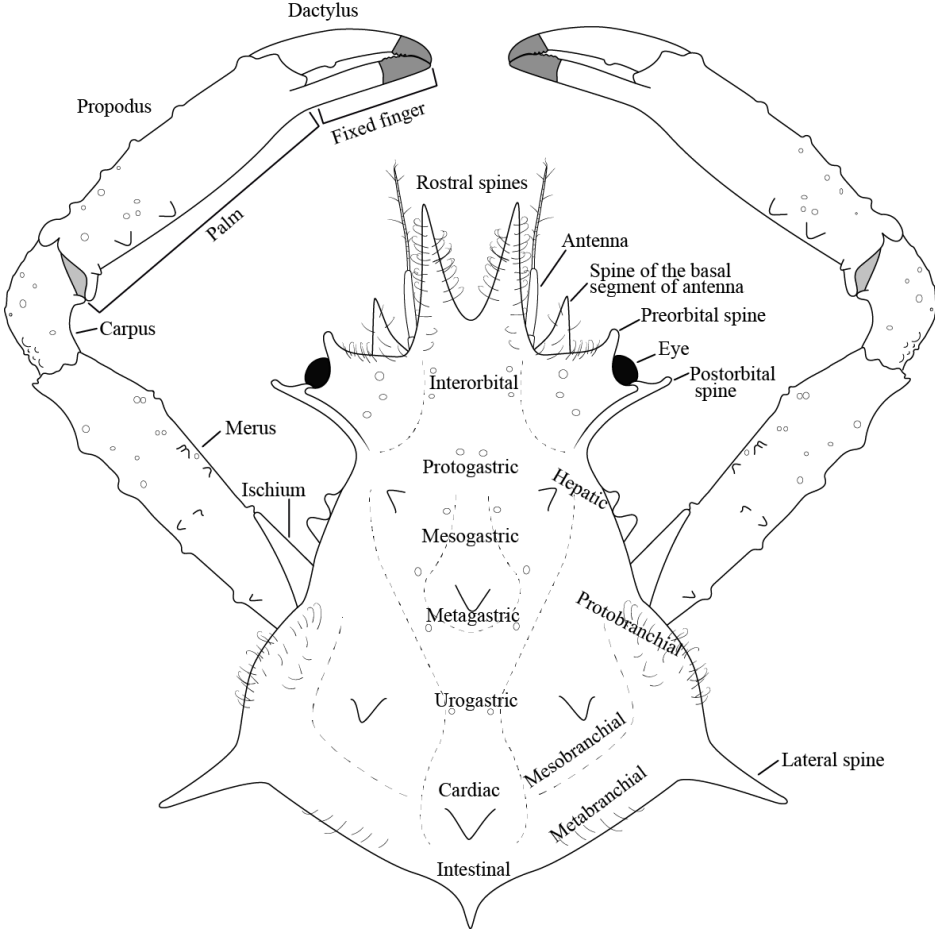


Figure 5. Schematic representation of the dorsal view of the carapace and chelipeds of *Macrocoeloma euthecum* (Stimpson, 1871) with indications of the carapace regions and spines.

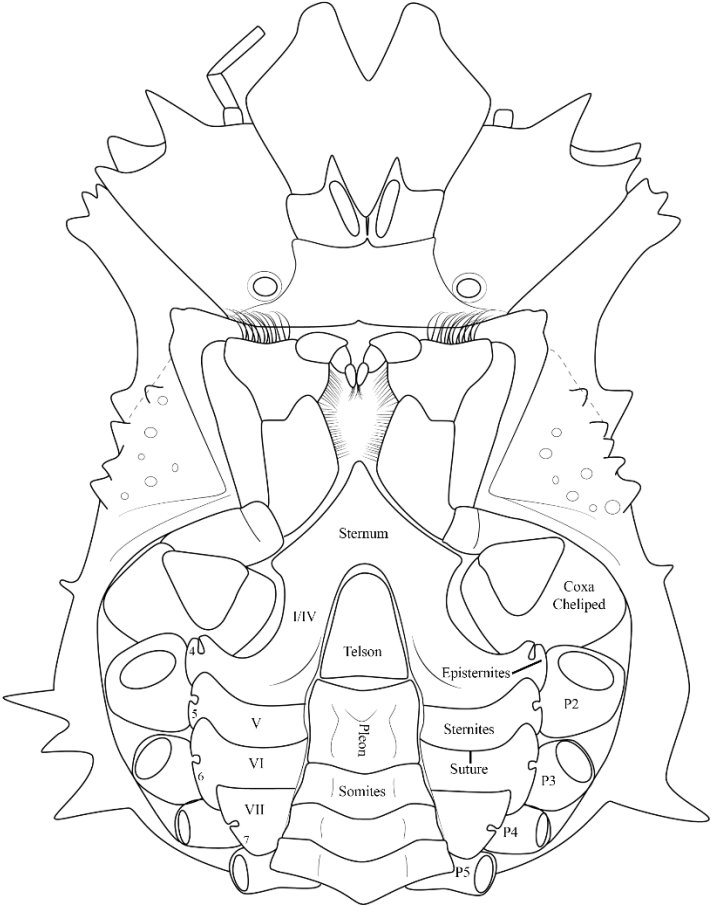


Figure 6. Schematic representation of the ventral view of the carapace of *Macrocoeloma intermedium* Rathbun, 1901, male holotype (USNM 9492), with indications of the sternum, pleon and pereopods.

RESULTS

Molecular phylogeny

In the present study, a multi-gene approach using three mitochondrial (12S, 16S and COI) and one nuclear (18S) loci was adopted to infer the phylogenetic relationships of *Macrocoeloma*.

The trimmed alignments after the primer sequence removal and adjacent regions were as follows: 12S= 436 bp; 16S=501 bp; COI= 651 bp; 18S= 1922pb, with a concatenation of 3511 bp. The alignments of the protein coding gene (COI) contained no stop codons, which indicated the absence of pseudogenes. The best evolutionary model obtained with PartitionFinder (Lanfear et al., 2016) was the General Time Reversible (Tavaré, 1986) plus Gamma (+G) model for among-site rate variation plus Invariable-sites (+I) model (Hasegawa et al., 1985).

No significant substitution saturation, estimated in the software DAMBE 7.2.7 (Xia and Xie, 2001), was observed for the concatenate genes. The data obtained in the test of substitution saturation demonstrate that the transversions and transitions ratios are increasing linearly during the time as expected, demonstrating that the sequences are appropriate for phylogenetic studies (Fig. 7).

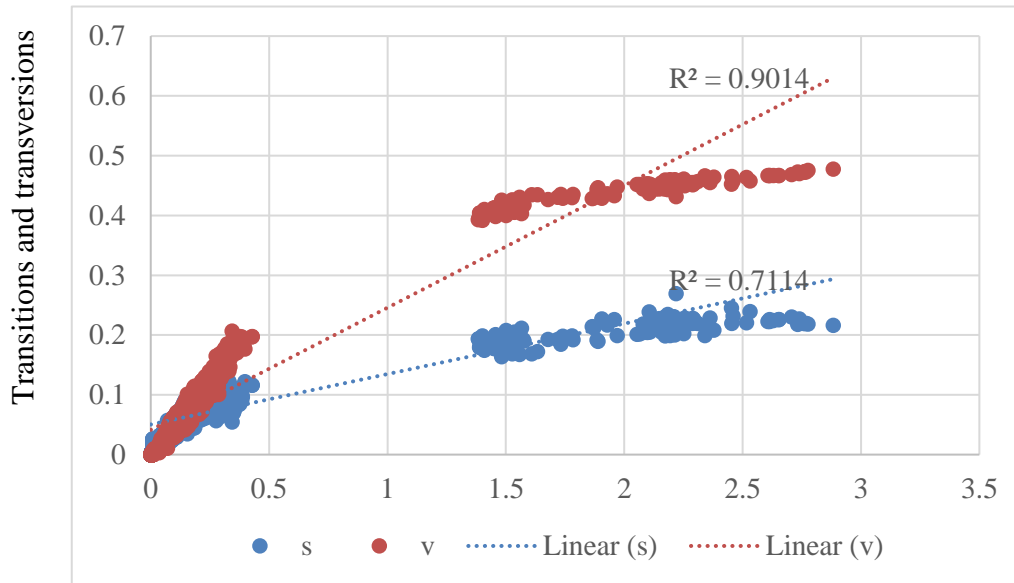


Figure 7. Substitution saturation plot for the concatenate matrix of the genes (COI, 12S, 16S and 18S). The x-axis represents the genetic distance based on the ML-CompositeTN93 (Tamura-Nei, 1993) substitution model and is expected to increase linearly with the divergence time. The y-axis is for the observed proportion of transitions (s) and transversions (v), respectively. R^2 is the value of the linear regression.

For the phylogenetic analyses, at least two of three mitochondrial genes 12S, 16S, COI were successfully amplified and sequenced for the 47 specimens from 10 species of *Macrocoeloma* being: *M. concavum*, *M. camptocerum*, *M. diplacanthum*, *M. euthecum*, *M. laevigatum*, *M. nodipes* and its variety, *M. septemspinusum*, *M. subparallelum*, *M. trigonum*, *M. trispinusum*, and *M. villosum* and for the nuclear gene (18S) the follow species of *Macrocoeloma* were sequenced: *M. camptocerum*, *M. septemspinusum*, *M. subparallelum*, *M. trigonum* and *M. trispinusum*. Unfortunately, no sequences of *M. heptacanthum*, *M. maccullochae* and *M. intermedium* could be generated due the conditions of preservation/fixation of the few specimens deposited in the collections. To present a tree with the phylogenetic position of *Macrocoeloma* within the context of Majoidea, the data generated for this study and sequences deposited in GenBank by Windsor and Felder (2014) and Colavite et al. (2019) were combined, considering at least one representative of each family of Majoidea. In total, thirty-nine sequences of 36 species were included. Of those, two individuals from the superfamily Hymenosomatoidea MacLeay, 1838 [*Neorhynchoplax bovis*

(Barnard, 1946) and *Elamena producta* Kirk, 1878] were used as outgroup (Davie et al., 2015a) (Table 1).

In general, the analyses produced highly supported clades in Maximum Likelihood (ML) than Bayesian Inference (BI) for most genera; the topologies were congruent between Bayesian and Maximum Likelihood analyses in most topologies. All species clades have strong support (>75%/ 0.75 bootstrap/posterior probability) with well support (>60%/ 0.6 bootstrap/posterior probability) among the genera relationship (Fig. 8).

The taxonomic position of *Macrocoeloma* is confirmed here to be in the family Pisidae. The phylogenetic trees places *Macrocoeloma* as close to *Libinia*, *Stenocionops* and *Leptopisa*, which is in agreement with previous molecular phylogenies for these taxa (Windsor and Felder, 2014; Colavite et al., 2019). Here, *Macrocoeloma septemspinosa* is not nested within the highly supported clade (95/0.64) of *Macrocoeloma*. The combined molecular and morphological data warrant erection of a new genus to accommodate both *M. septemspinosa* and *M. heptacanthum*, provisionally treated here as New genus *septemspinosa* gen. nov., comb. nov. and New genus *heptacantha* gen. nov., comb. nov.

analysis *M. villosum* is highly supported (91) as the first species to diverge and *M. diplacanthum* and *M. subparallelum* have low supported as sister species (58), while in BI analysis *M. diplacanthum* the first species to diverge has a support of 0.64 and *M. villosum* and *M. subparallelum* as sister species has high support (0.75). This is the only divergence between the ML and BI trees for *Macrocoeloma*.

The second clade (85/1) is comprised by *M. euthecum*, *M. concavum*, *M. laevigatum*, *camptocerum*, *M. trigonum* and the *M. trispinosum* species complex (*M. trispinosum* and *M. nodipes*). Each of these species is well supported, but the relationships between *M. concavum*, *M. laevigatum*, *M. camptocerum*, *M. trigonum* and the *M. trispinosum* species complex are moderately to poorly supported (59/0.8). *Macrocoeloma euthecum* is the first species to diverge, followed by *M. concavum*, *M. laevigatum*, *M. camptocerum*, *M. trigonum* and the *M. trispinosum* species complex forming a clade with two subclades. The first subclade is well supported (71/1) comprising *M. laevigatum* and *M. concavum* as sister species and the another highly supported clade (98/1) comprising *M. camptocerum*, *M. trigonum* and *M. trispinosum* complex.

The clade of *M. trigonum* and *M. trispinosum* complex is subdivided in three small subclades. *Macrocoeloma trigonum* is not considered here as part of the *Macrocoeloma trispinosum* complex, showing a considerable branch length diverging earlier among species of the *Macrocoeloma trispinosum* complex. *Macrocoeloma trispinosum*, *M. nodipes* and “*M. nodipes* variety” clustered with a high support (91/0.97), but with a very short branch length separating a group of *Macrocoeloma nodipes* specimens and the rest of the specimens of the *Macrocoeloma trispinosum* complex.

Species delimitation based on COI

The species delimitation analyses based on Maximum Likelihood phylogenetic tree of the mtDNA gene COI, using the Poisson tree processes (PTP) model (Zhang et al., 2013), do not present significant substitution saturation, estimated by the software DAMBE 7.2.7 (Xia and Xie, 2001).

The COI tree reflects the recent relationship between the studied species, considering the different rates of evolution of mitochondrial genes being the COI gene considered highly informative at the species level (Tsang in Chu et al., 2015). That may cause the topological incongruence between COI and multi-locus phylogenies, with *Stenocionops* Desmarest, 1823 grouping into the *Macrocoeloma* clade (Fig. 10).

The PTP analysis recovered twenty taxonomic units, seven of which are of *Macrocoeloma* species. Several species of closely related genera were added to test the effectiveness of the species delimitation method (Fig. 10). The resulting tree is very conservative, recovering all morphologically accepted species with the exception of two. The species of *Macrocoeloma trispinosum* complex: *M. nodipes* and *M. trispinosum* as observed in the multi-locus tree grouped in the same clade (Fig. 9). However, two monophyletic lineages could be recovered in the PTP analysis, one for *M. nodipes* and another to *M. trispinosum*.

This analysis showed two putative new species, one putative species belongs to the New genus *septemspinosa* gen. nov., comb. nov. with two distinct lineages and another taxonomic unit correspond to the specimens from the Brazilian coast, identified here as *M. trigonum*. *Macrocoeloma trigonum* is clearly divergent from the clade of the *M. trispinosum* complex (Figure 10), a separation also congruent with the morphological analysis.

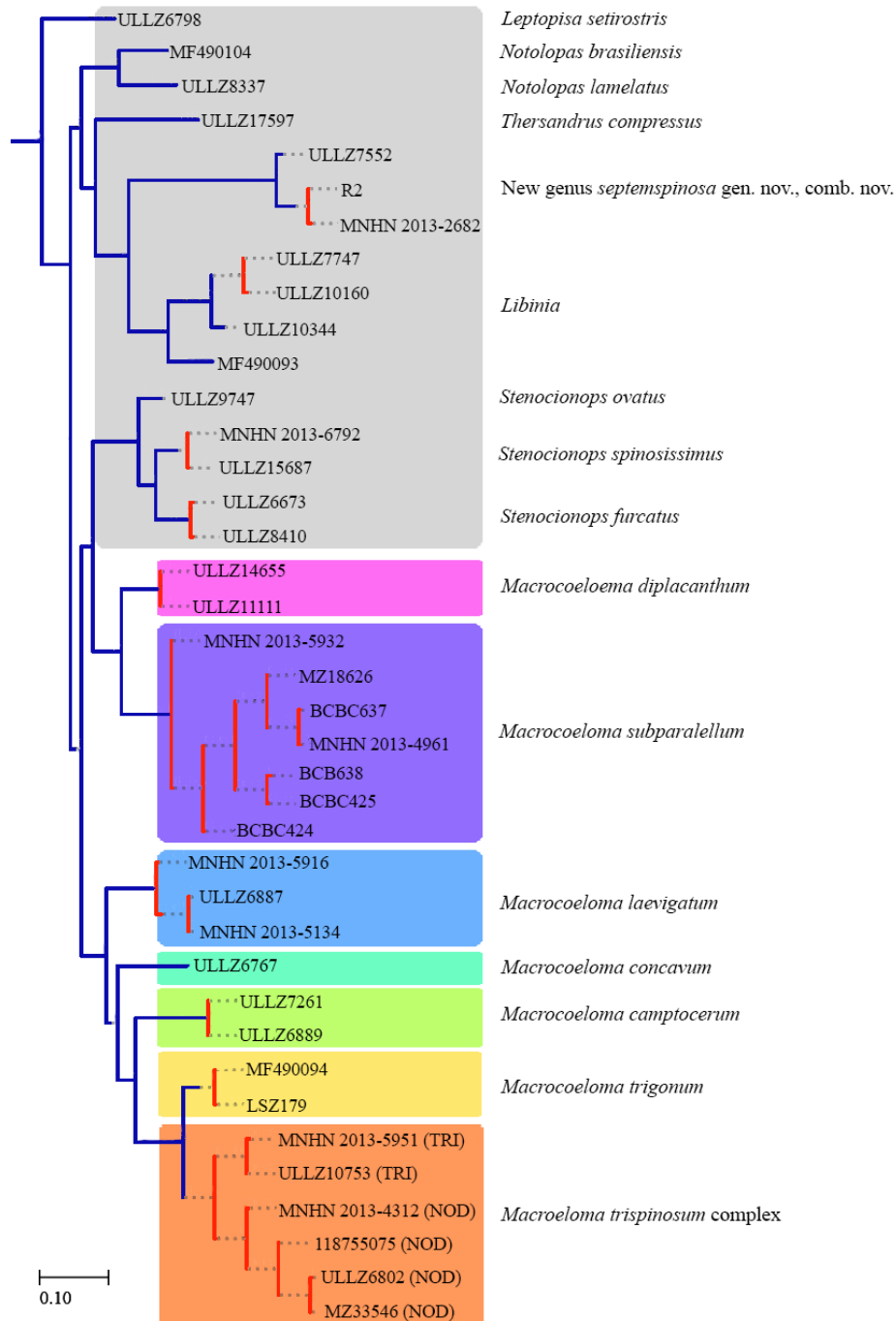


Figure 10. Poisson Tree Processes (PTP) model to infer putative species boundaries on a given phylogenetic input tree mtDNA COI gene. Branches are the Maximum likelihood partition support values from the Poisson Tree Processes (PTP) model given for each species identified by the model. Blue branch indicates separated species. Red branch indicates species at the same lineage. Color of the clades: grey = Pisidae genera; pink = *Macrocoeloma diplacanthum*; purple = *Macrocoeloma subparallelum*; blue = *Macrocoeloma laevigatum*; cyan green = *Macrocoeloma concavum*; green = *Macrocoeloma camptocerum*; yellow = *Macrocoeloma trigonum*; orange = *Macrocoeloma trispinosum* complex. TRI = *trispinosum*; NOD = *nodipes*.

*Taxonomy***Pisidae Dana, 1851**

Emended diagnosis: Rostrum bifid, long or short; orbit always with post-orbital spine or lobe, usually cupped but never concealing eye in dorsal view, sometimes with preorbital spine; carapace triangular, often rounded posteriorly, sometimes with posterior spine (modified from Davie, 2002, Poore, 2004; Feldmann and Schweitzer, 2016).

Remarks. Pisidae Dana, 1851 is currently considered a subfamily of Epialtidae MacLeay, 1838 by recent classifications (e.g. Ng et al., 2008; Davie et al., 2015). Ng et al. (2008) describe the group formed by Pisinae, Tychinae and Epialtinae as one of the most heterogeneous with a “gray line” separating several genera. According to these authors, the character most used in Majoidea classification, the orbits, are poorly developed or absent in some genera of Pisinae and Tychinae. Also, for Davie et al. (2015) in the diagnosis of the family Epialtidae, the absence of the intercalated spine is diagnostic for this family. However, the intercalated spine is present in *Macrocoeloma* and *Stenocionops*, species recently transferred for Pisinae. Recent phylogenies including species of Mithracidae, Epialtidae and Pisidae, showed Pisidae and Mithracidae are distinct monophyletic groups, thus Pisidae can no longer be considered a subfamily of Epialtidae (Windsor and Felder, 2014; Colavite et al., 2019). According to Wicksten in Guinot and Wicksten (2015), the differences between these groups are also observed in the decorating activities, and she recognized Epialtidae and Pisidae as different families. Assignment of *Macrocoeloma* to Pisidae is also consistent with the definition proposed by Davie (2002) and Poore (2004), mainly considering the carapace and rostrum morphology.

Considering the phylogenetic position of the monotypic genus *Thersandrus*, we also suggest the assignment of this species in Pisidae based on the molecular results. Balss (1929) considered *Thersandrus* related to *Cyclocoeloma* based on the basal article of antenna and the orbits closed without an intercalated spine, and placed both in Ophthalmiinae Balss, 1929. In the Windsor and Felder (2014) phylogenetic analysis, *Cyclocoeloma* fitted into *Tiarinia* species, also considered a Pisidae. However, *Cyclocoeloma* was considered *incertae sedis* (Windsor and Felder, 2014).

Thersandrus herein is assigned to the Pisidae based also on morphological characters of the rostrum, carapace shape and orbits with a post orbital lobe.

Identification Key to *Macrocoeloma* Miers, 1879

- 1a. Carapace without lateral branchial spines *Macrocoeloma laevigatum* (Fig. 22)
- 1b. Carapace with lateral branchial spines 3
- 3a. Carapace with two or three spines in line with the lateral spines (lateral, mesobranchial and cardiac spines) 4
- 3b. Carapace with five or more spines in line with the lateral spines (lateral, mesobranchial and cardiac spines) 5
- 4a. Rostral spines convergent from the base *Macrocoeloma maccullochae* (Fig. 24)
- 4b. Rostral spines divergent or parallel 6
- 5a. Rostral spine parallel separate by a U sinus *Macrocoeloma subparallelum* (Fig. 28)
- 5b. Rostral spines base elongated diverging at the tip 7
- 6a. Rostral spines parallel separate by a U sinus 8
- 6b. Rostral spines divergent separate by a V sinus 9
- 7a. Basal article of antenna without spines or tubercles
..... *Macrocoeloma intermedium* (Fig. 20)
- 7b. Basal article of antenna with one or two small spines
..... *Macrocoeloma concavum* (Fig. 14)
- 8a. Orbits tubular laterally projected, lateral spines small and undivided
..... *Macrocoeloma euthecum* (Fig. 18)
- 8b. Orbits not tubular, lateral spines long and bifurcated
..... *Macrocoeloma diplacanthum* (Fig. 16)
- 9a. Posterior half of carapace with deep sulcus *Macrocoeloma villosum* (Fig. 39)
- 9b. Posterior half of carapace smooth or with spines 10
- 10a. Carapace smooth or with small tubercles 11

- 10b. Carapace armed with a spine in the gastric and cardiac regions 12
- 11a. Three tubercles in the gastric region, lateral spines conical
 *Macrocoeloma trispinosum* (Fig. 37)
- 11b. Gastric region smooth, lateral spines laminated or slightly flatted.....
 *Macrocoeloma nodipes* (Fig. 26)
- 12a. Mesobranchial region with two spines, lateral spines conical
 *Macrocoeloma camptocerum* (Fig. 12)
- 12b. Mesobranchial region smooth, lateral spines almost continuing the boarder of the carapace
 *Macrocoeloma trigonum* (Fig. 32)

***Macrocoeloma* Miers, 1879**

Pericera Latreille, 1828:699 (*pro parte*) – Latreille, 1829: 58; 1834: 166; H. Milne Edwards, 1834: 336.

Macrocoeloma Miers, 1879: 665 [type species: *Pisa trispinosa* Latreille, 1825 accepted as *Macrocoeloma trispinosum* (Latreille, 1825) by original designation].

Emended diagnosis: Cephalothorax and appendages fully covered by short, velvet-like pubescence. Carapace pyriform or subtriangular with interorbital region depressed medially. Rostral spines well developed, bifurcated and parallel. Eyes completely protected in orbits when retracted; preorbital, postorbital and one or two projections of the basal article of antenna forming a functional, laterally projected protective hood around the eyes. Basal article of antenna enlarged, latero-distally armed with one or two projected spines; mobile portion of antenna sometimes concealed by rostral spines, sometimes visible in dorsal view. Palm of adult male chelipeds enlarged, fingers arched, meeting at tip. Ambulatory legs shorter than chelipeds. Thoracic sternal somite IV with lateral margins very concave.

Included species: *Macrocoeloma camptocerum* (Stimpson, 1871) [*Pericera*] [WA]; *Macrocoeloma concavum* Miers, 1886 [WA]; *Macrocoeloma diplacanthum* (Stimpson, 1860) [*Pericera*] [WA]; *Macrocoeloma euthecum* (Stimpson, 1871) [*Pericera*] [WA]; *Macrocoeloma intermedium* Rathbun, 1901 [WA]; *Macrocoeloma laevigatum* (Stimpson, 1860) [*Pericera*] [WA]; *Macrocoeloma maccullochae* Garth, 1940 [EP]; *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867) [*Pericera*] [WA]; *Macrocoeloma subparallelum* (Stimpson, 1860) [*Pericera*] [WA]; *Macrocoeloma trispinosum* (Latreille, 1825) [*Pisa*] [WA]; *Macrocoeloma trigonum* (Dana, 1851) [WA]; *Macrocoeloma villosum* (Bell, 1836) [*Pericera*] [EP].

Remarks. Two species originally described as *Macrocoeloma* and after revision, was transferred to another genera. For example, *Macrocoeloma nummifer* Alcock, 1895 (pg. pl. IV, Fig. 4) was described from material collected in India, based on two specimens no longer existent. In its original description, Alcock affirmed that this species is closely allied to *Macrocoeloma concavum* and *Entomonyx spinosus* Miers, 1884. According to Balss (1929), *M. nummifer* is a junior synonym of *E. spinosus*, and stated that this species does not belong to *Macrocoeloma*, due to the antennal projection interacting with the orbits, absent in *Macrocoeloma* species. *Entomonyx spinosus* was transferred to the genus *Acanthophrys* A. Milne-Edwards, 1865, an arrangement followed by Sakai (1938:309). However, Griffin (1966a) did not agree with Balls arguments to place *Entomonyx* into *Acanthophrys* and re-erected the monotypic genus *Entomonyx* to accommodate *Entomonyx spinosus* (see Griffin, 1966a:10). We examined the specimens identified by Griffin as *E. spinosus* and compared with the description and figures of Alcock (1895), and we agree that *Macrocoeloma nummifer* Alcock, 1895 does not belongs to *Macrocoeloma*, considering also its occurrence in the Indo Pacific Ocean. Unfortunately, we could not sequence the examined material.

Macrocoeloma tenuirostra Rathbun, 1892 was considered a junior synonym of *Leptopisa setirostris* (Stimpson, 1871) by Rathbun (1901). The comparisons between the holotypes of *M. tenuirostra* (USNM 6929) and *L. setirostris* (USNM 216592) led us to maintain the synonymy proposed by Rathbun (1901).

***Macrocoeloma camptocerum* (Stimpson, 1871)**

(Figure 12 A-F)

Pericera camptocera Stimpson, 1871 (1870): 112 [type locality: United States, Florida, off Key West, 3.7 to 9.2 m; type material: non-extant] – A. Milne-Edwards, 1873: 57, pl. 5.

Pericera diacantha A. Milne-Edwards, 1875: 57, pl. 15, f. 3-3c (*P. dicantha* by error) [type locality: Isla Mujeres (not Majores); 21.9 m; type material: holotype MCZ 1919].

Macrocoeloma camptocera – Miers, 1886: 79-80; Rathbun, 1892, 249, pl. 33 fig. 2.

Macrocoeloma diacantha – Miers, 1886: 80.

Macrocoeloma diacanthum – Rathbun 1898a: 576; Rathbun, 1901: 74.

Macrocoeloma camptocerum – Rathbun, 1898b: 257; 1921: 87; 1925, 469, pl. 174, fig. 4, pl. 270, fig. 2; Wass, 1955: 168; Williams, 1965: 264, fig. 244, 245k; Williams, 1984: 326, fig. 262, 275m; Abele and Kim, 1986: 45, fig. 519 e, f; Powers, 1977: 50; Nizinski, 2003: 130; Coelho-Filho, 2006; Coelho et al., 2008: 21; Ng et al., 2008: 119; Alves et al., 2012: 54.

Type Material. neotype, male, cl. 38.6 mm, cw. 23.9 mm; *UNITED STATES*, Florida, North Key section, R/V Fish Hawk., sta.7207, 28°57'30"N– 82°58'00"W, 9.xii.1901 (USMN 46883).

Material examined. *UNITED STATES*, North Carolina, 35°20'30"N–75°21'36"W, 23m, 18.viii.1980, Duke University for MMS IS04 col., P. Krikorian det., 22.xii.1980, 1 juvenile (USNM 220809). North Carolina, 33°33'30"N–77°25'00"W, 18.v.1981, Duke University for BLM MS04 col./det., 34m, 2 ovigerous female (USNM 202857). North Carolina, 33°32'48"N–77°24'18"W, Duke University for BLM MS04 col./det., 18.v.1981, 32m, 1 ovigerous female (USNM 202859). North Carolina, 33°31'41"N–77°24'30"W, 18.v.1981,

Duke University for BLM MS04 col./det., 29m, 1 ovigerous female (USNM 202858). North Carolina, 33°31'24"N–77°24'00"W, 19.v.1981, Duke University for BLM MS04, 30m, 1 ovigerous female (USNM 202860). North Carolina, 33°31'24"N–77°24'42"W, 12.viii.1981, Duke University col./det., 28 m, 1 ovigerous female (USNM 202863). North Carolina, 33°31'12"N–77°24'00"W, 19.v.1981, Duke University for BLM MS04 col./det., 29m, 2 males (USNM 202861). North Carolina, 33°30'42"N–77°23'42"W, 12.viii.1981, Duke University col./det., 28 m, 1 ovigerous female, 1 male (USNM 202862). North Carolina, 33°30'36"N–77°24'42"W, 28m, Duke University for BLM MS04, 12.viii.1981, 1 juvenile female (USNM 202864). Beaufort Harbor, R/V Fish Hawk, sta. 7942, 6.ix.1913, M. J. Rathbun det., 6.4m, 1 juvenile female (USNM 51023). Beaufort Harbor, R/V Fish Hawk, sta. D8211, 11.viii.1914, M. J. Rathbun det., 27.4m, 1 ovigerous female (USNM 51028). South Carolina, R/V Dolphin, 32°50'12"N–78°36'36"W, 21.ix.1979, E. Wenner det., 35m, 1 male (USNM 188335). South Carolina, R/V Dolphin, 32°42'N–79°45'W, 23.x.1973, 1979, E. Wenner det., 11m., 1 juvenile female (USNM 186450). South Carolina, 32°30'54"N–79°42'54"W, 16.xii.1983, South Carolina Marine Research col., 18m, 1 ovigerous female (USNM 224121). South Carolina, 32°29'36"N–76°42'30"W, 22.i.1980, South Carolina Marine Research for MMS IS01, 03.vii.1980, ELW det., 19m, 1 male (USNM 220810). South Carolina, 32°29'36"N–79°09'30"W, 10.iii.1981, Continental Shelf Associates, 27.viii.1985, M. Dorigi, det., 18m, 1 male (USNM 232313). South Carolina, 32°29'24"N–79°42'30"W, 26.ii.1981, South Carolina Marine Research IS01 col., 1985, M. Dorigi det., 17 m., 1 male (USNM 232305). South Carolina, 32°29'18"N–79°42'30"W, 26.ii.1981, South Carolina Marine Research col., 1985, M. Dorigi det., 17 m., 1 ovigerous female, 1 male (USNM 232306). South Carolina, 32°28'48"N–79°42'06"W, R/V Dolphin, 07.iv.1979, 1979, E. Wenner det., 18m., 1 male (USNM 188429). South Carolina, 32°24'42"N–79°49'36"W, 21.ix.1983, South Carolina Marine Research for ST02, 19m, 1 juvenile (USNM 224120). Georgia, 31°45'N–80°28'W,

24.ii.1977, Texas Instruments 4C col., 11.xi.1979, B. Boothe det., 16m, 1 male (USNM 174087). Georgia, 31°41'00"N–80°20'36"W, 29.iv.1981, Georgia Marine Research MS02 col., 24.vi.1985, M. Dojiri det., 27m, 1 ovigerous female (USNM 232310). Georgia, 31°23'42"N–80°53'00"W, 28.iv.1981, Georgia Marine Research IS02 col., 21.vi.1985, M. Dojiri det., 16m, 1 ovigerous female, 1 male (USNM 232311). Georgia, 31°23'36"N–80°52'42"W, 23. x.1981, Georgia Marine Research IS02, 19.vi.1895, M. Dojiri det., 17 m., 1 juvenile female (USNM 232312). Georgia, 31°23'24"N–80°53'00"W, 27.iv.1981, Georgia Marine Research IS02 col., 18.vi.1985, M. Dojiri det., 16m, 2 males (USNM 232309). Georgia, 31°23'24"N–80°53'00", 27.iv.1981, Georgia Marine Research IS02, 12.iv.1895, M. Dojiri det., 16 m., 1 ovigerous female (USNM 232308). Georgia, 31°23'12"N–80°53'00"W, 05.iii.1981, Georgia Marine Research IS02 col., 24.vi.1895, M. Dojiri det., 17 m., 1 male (USNM 232307). Florida, off Fort Walton, 3-4.vi.1947, Frank Lyman col., 28.viii.2017, J. Colavite det., 25.6-27.4 m, 1 ovigerous female, 1 male (USNM 1278765). Florida, 30°23'N–80°51'W, 28.ii.1977, Texas Instruments 6C col., ii.1978, K. Shaw det., 26m, 1 male (USNM 174255). Florida, MAFLA Expedition, R/V Java Seal, 29°47'59"N–86°09'29"W, 21.x.1977, 48m, 1 juvenile (USNM 1085599). Florida, Northwest end Saint Martin Reef, 28°50'00"N–83°00'00"W, 1887, 1 male, 1 female (USNM 13043). Florida, North Key section, R/V Fish Hawk., sta.7207, 28°57'30"N– 82°58'00"W, 9.xii.1901, 5.4 m, 15.5°C, 2 males, 2 females (USMN 46883). Florida, Off. Rt. Martmo Key Reef, 28°56'N–82°55'W, 3.iv.1887, L.G.F. Mases col., 5.7m, 2 ovigerous female (USNM 13046). Florida, R/V Fish Hawk, sta. 24, 28°19'30"N–83°01'00"W, i. 1902, 1.9m, 1 male (USNM 46887). Florida, R/V Silver Bay, sta. 60, 27°11'N–82°33'W, 5.4 m, 17.vii.1957, F. A Chance det., 1 male (USNM 101582). Florida, 26°46'01"N–82°06'04"W, 08.xii.1982, Continental Shelf Associates col., 16m, 2 females, 1 male (USNM 270586). Florida, 26°46'01"N–82°06'04"W, 19m, 02.vi.1983, Continental Shelf Associates col., 1 juvenile female (USNM 271469). Florida, 26°46'01"N–82°06'04"W, 14.xii.1982, Continental

Shelf Associates col., 19m, 1 juvenile (USNM 270594). Florida, 26°46'01"N–82°06'04"W, 07.xii.1982, Continental Shelf Associates col., 19m, 1 juvenile (USNM 270595). Florida, 26°46'01"N–82°06'04"W, 15.xii.1982, Continental Shelf Associates col., 19m, 1 juvenile female (USNM 270593). Florida, 26°46'01"N–82°06'04"W, 15.xii.1982, Continental Shelf Associates col., 19m, 2 females (USNM 270596). Florida, 26°46'01"N–82°06'04"W, 02.vi.1983, Continental Shelf Associates col., 19m, 1 ovigerous female (USNM 270600). Florida, 26°46'01"N–82°06'04"W, 15.xii.1982, Continental Shelf Associates col., 19m, 1 male (USNM 270592). Florida, 26°46'01"N–82°06'04"W, 14.xii.1982, Continental Shelf Associates col., 19m, 1 juvenile female (USNM 270599). Florida, 26°46'01"N–82°06'04"W, 07.xii.1982, Continental Shelf Associates col., R. Lemaitre det., 19m, 3 females, 2 males (USNM 270597). Florida, 26°46'01"N–82°06'04"W, 19m, 07.xii.1982, Continental Shelf Associates col., 1 male (USNM 270598). Florida, Cape Florida, i.1925, John W. Mills col., 07.ix.2017, J. Colavite det., 4 females, 2 juvenile females, 3 males (USNM 76553). Florida, 26°45'46"N–82°43'07"W, 28.x.1980, Continental Shelf Associates col., R. Lemaitre det., 24m, 1 male (USNM 273373). Florida, 26°45'46"N–82°43'07"W, 28.x.1980, Continental Shelf Associates for BLM/ MMS col., R. Lemaitre det., 24m, 1 male, 3 juvenile females (USNM 242761). Florida, 26°45'46"N–82°43'07"W, 28.x.1980, Continental Shelf Associates for BLM/ MMS col., R. Lemaitre det., 24m, 2 juvenile females, 1 juvenile male (USNM 242762). Florida, 26°45'46"N–82°43'07"W, 28.x.1980, Continental Shelf Associates for BLM/ MMS col., R. Lemaitre det., 24m, 1 male (USNM 242760). Florida, 26°45'46"N–82°43'07"W, 28.x.1980, Continental Shelf Associates for BLM/ MMS col., R. Lemaitre det., 24m, 1 male (USNM 229837). Florida, 26°45'46"N–82°43'07"W, 24m, 02.ii.1982, Continental Shelf Associates col., 1 ovigerous female (USNM 273441). Florida, 26°45'46"N–82°43'07"W, 02.v.1981, Continental Shelf Associates, R. Lemaitre det., 24 m, 1 ovigerous female (USNM 236998). Florida, 26°45'46"N–82°48'07"W, 02.ii.1982, Continental

Shelf Associates, R. Lemaitre det., 24 m, 1 male, 2 juvenile females (USNM 241040). Florida, 26°45'46"N–82°48'07"W, 02.ii.1982, Continental Shelf Associates, R. Lemaitre det., 24 m, 1 male, 1 juvenile male (USNM 238305). Florida, 26°45'46"N–82°43'07"W, 29.vii.1981, Continental Shelf Associates, R. Lemaitre det., 24m, 2 juvenile females (USNM 238306). Florida, 26°45'46"N–82°48'07"W, 28.x.1980, Continental Shelf Associates, R. Lemaitre det., 24 m, 1 juvenile female (USNM 241003). Florida, 26°45'46"N–82°43'07"W, 28.x.1980, Continental Shelf Associates for BLM/ MMS col., R. Lemaitre det., 24m, 1 juvenile female (USNM 242766). Okaloosa, 8 mi east of Destin, x.1941, T.G. McGinty col., F.A. Chace det., 25.6 m, 1 male (MCZ 12007). Florida, Anclote Section, U. S. Fish Commission, sta. 7106, 22.86m, 1 juvenile female (USNM 25595). Florida, Sanibel Island, 26.440359°N–82.113705°W, iii.1938, F.A. Chace Jr. col. det., 0.54-11 m, 13 males, 7 females, 7 ovigerous females (MCZ 10191). Florida, 26°17'52"N–82°12'37"W, 05.xii.1982, Continental Shelf Associates col., 13m, 1 male (USNM 270579). Florida, 26°17'52"N–82°12'37"W, 31.v.1983, Continental Shelf Associates col., 13m, 1 ovigerous female (USNM 270576). Florida, 26°17'52"N–82°12'37"W, 31.v.1983, Continental Shelf Associates col., R. Lemaitre det., 13m, 1 male (USNM 270577). Florida, 26°17'52"N–82°12'37"W, 05.xii.1982, Continental Shelf Associates col., 13m, 1 juvenile female (USNM 270578). Florida, 26°17'52"N–82°12'37"W, 05.xii.1982, Continental Shelf Associates col., 13m, 2 males (USNM 270581). Florida, 26°16'49"N–82°44'01"W, 19.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 30.4m, 1 ovigerous female, 1 male (USNM 241041). Florida, R/V Suncoaster, 26°16'59"N–82°43'40"W, 01.vi.1985, LGL/ESE col., T. Czapla det. 32m, 1 female (USNM 276587). Florida, 25°45'56"N–82°09'21"W, 19.6m, 29.vii.1981, Continental Shelf Associates, R. Lemaitre det., 1 juvenile female (USNM 238304). Florida, 25°45'56"N–82°09'21"W, 19.6m, 28.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 2 males, 1 female (USNM 273206). Florida,

25°45'56"N–82°09'21"W, 08.xi.1980, Continental Shelf Associates, R. Lemaitre det., 19.6 m, 1 male (USNM 236984). Florida, 25°45'56"N–82°09'21"W, 28.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 19.6m, 1 ovigerous female (USNM 274473). Florida, 25°45'56"N–82°09'21"W, 08.xi.1980, Continental Shelf Associates for BLM/ MMS col., R. Lemaitre det., 19.6m, 1 female, 2 males (USNM 236991). Florida, 25°45'56"N–82°09'21"W, 28.iv.1981, Continental Shelf Associates, R. Lemaitre det., 19.6m, 1 ovigerous female (USNM 241000). Florida, 25°45'56"N–82°09'21"W, 08.xi.1980, Continental Shelf Associates, R. Lemaitre det., 19.6m, 2 males (USNM 241002). Florida, 25°45'56"N–82°09'21"W, 08.xi.1980, Continental Shelf Associates, R. Lemaitre det., 19.6m, 1 male (USNM 241001). Florida, 25°45'56"N–82°09'21"W, 08.xi.1980, Continental Shelf Associates, R. Lemaitre det., 19.6m, 1 juvenile female (USNM 239999). Florida, 25°45'56"N–82°09'21"W, 08.xi.1980, Continental Shelf Associates, R. Lemaitre det., 19.6m, 2 juvenile females, 1 male (USNM 241013). Florida, 25°17'22"N–82°09'00"W, 18.xi.1980, Continental Shelf Associates, R. Lemaitre det., 22.5m, 1 juvenile female (USNM 241004). Florida, R/V Suncoaster, 25°45'50"N–82°06'06"W, 08.xii.1983, LGL/ESE col., T. Czaplá det., 20m, 1 juvenile male (USNM 276586). Florida, 25°17'48"N–81°39'48"W, 04.vi.1983, Continental Shelf Associates col., 14m, 1 male (USNM 270591). Florida, 25°17'48"N–81°39'39"W, 09.xii.1982, Continental Shelf Associates col., R. Lemaitre det., 14m, 1 male (USNM 271422). Florida, 25°17'48"N–81°39'48"W, 04.vi.1983, Continental Shelf Associates col., 14m, 1 male (USNM 271421). Florida, 25°17'40"N–81°48'00"W, 03.vi.1983, Continental Shelf Associates col., 16m, 1 female (USNM 270590). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 1 male (USNM 270583). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 2 males, 1 female (USNM 270582). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 1 male, 2 females (USNM 270582). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 1 male, 2 females (USNM 270582). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 1 male, 2 females (USNM 270582).

Shelf Associates col., 16m, 1 juvenile (USNM 270589). Florida, 25°17'40"N–81°48'00"W, 11.xii.1982, Continental Shelf Associates col., 16m, 1 female (USNM 270588). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 1 male (USNM 270587). Florida, 25°17'40"N–81°48'00"W, 08.xii.1982, Continental Shelf Associates col., 16m, 1 male (USNM 270584). Florida, R/V Suncoaster, 25°17'32"N–81°39'49"W, 15.viii.1984, LGL/ESE col., T. Czapla det., 13m, 2 males, 2 females (USNM 274776). Florida, R/V Suncoaster, 25°17'32"N–81°39'49"W, 15.viii.1984, LGL/ESE col., T. Czapla det., 13 m, 2 males (USNM 274786). Florida, R/V Suncoaster, 25°17'32"N–81°39'49"W, 15.viii.1984, LGL/ESE col., T. Czapla det., 13m, 1 male (USNM 274833). Florida, R/V Suncoaster, 25°17'24"N–82°08'59"W, 11.xii.1983, LGL/ESE col., T. Czapla det. 24m, 1 ovigerous female (USNM 274791). Florida, 25°17'22"N–82°09'00"W, 18.xi.1980, Continental Shelf Associates, R. Lemaitre det., 22.5m, 3 males (USNM 241005). Florida, 25°17'22"N–82°09'00"W, Continental Shelf Associates, 18.xi.1980, R. Lemaitre det., 22.5m, 1 juvenile female (USNM 242945). Florida, R/V Suncoaster, 25°17'24"N–82°08'59"W, LGL/ESE for MMS, 11.xii.1983, T. Czapla det., 24m, 1 female (USNM 274791). Florida, Off Northwest Channel, R/V Fish Hawk, sta. 7292, 24°44'50"N–81°55'50"W, 24.ii.1902, M. J. Rathbun det., 18.74m, 1 ovigerous female (USNM 46890). Off Northwest Channel, R/V Fish Hawk, sta. 7295, 24°42'30"N–81°56'28"W, 24.ii.1902, M. J. Rathbun det., 9.6 m, 1 male (USNM 46891). Florida, Off Northwest channel, R/V Fish Hawk, sta.7293, 24°42'30"N–81°55'52"W, 24.ii.1902, M. J. Rathbun det., 13.25m, 1 juvenile male (USNM 46949). Florida, Off Key West Florida, Key West Light to East Channel Bar Buoy, R/V Fish Hawk, sta. 7278, 71°53'W to Beacon "A" 74°46'W, 13.ii.1902, 9.6 m, 1 ovigerous female (USNM 46889). Florida, Indian Key, H. Hemphill col., 1 female (USNM 15140). Florida, Off Key West, sta. 44, 1 mile from Light, State of Iowa University col., 26.vi.1893, 1 male (USNM 69080). Florida, Key West, R/V Albatross, 1885, Fish Commission col., M. J. Rathbun, 1 male

(USNM 15141). Florida, Cape Florida, i.1925, John W. Mills col., 07.ix.2017, J. Colavite det., 1 male (USNM 1278772). Florida, Pepperfish Key, R/V Fish Hawk, sta. 160, 21.xi.1901, M. J. Rathbun det., 11.43m, 1 juvenile male (USNM 46945). Florida, Deadman's Bay, R/V Fish Hawk, sta. 7201, 6.xii.1901, M. J. Rathbun det., 16.4 m, 1 juvenile male (USNM 46946). Florida, Saint Martin, R/V Fish Hawk, sta. 7225, 17.i.1902, M. J. Rathbun det., 12.8 m, 1 juvenile male (USNM 46947). Florida, Anclote, R/V Fish Hawk, sta. 7244, 24.i.1902, M. J. Rathbun det., 12.34m, 1 juvenile female (USNM 46948). Florida, North of Knights Key Channel, R/V Fish Hawk, sta. 7417, 2 miles NE by East of Basin Bank, 22.i.1903, M. J. Rathbun det., 15.54m, 1 male (USNM 46950). Florida, Hawk Channel, R/V Fish Hawk, sta. 7464, 1.12 miles East by South of West end of Lower Metacumbe, 18.ii.1903, M. J. Rathbun det., 5.4 m, 1 juvenile female (USNM 46951). Florida, Hawk Channel, R/V Fish Hawk, sta. 7466, 1.5 miles East of Tea Table Key, 19.ii.1903, M. J. Rathbun det., 4.5m, 1 juvenile female (USNM 46952). Florida, off Cape Sable, R/V Fish Hawk, sta. 7351, 25°09'45"N–81°18'35"W, 5.9 m, 16.xii.1902, M. J. Rathbun det., 2 females (USNM 46892). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7352, 25°09'52"N–81°21'53"W 16.xii.1902, M. J. Rathbun det., 6.7m, 1 juvenile female, 1 male (USNM 46893). Florida, North Key, R/V Fish Hawk, sta. 7211, 25°06'30"N–81°12'25"W, 9.xii.1901, M. J. Rathbun det., 14.6 m, 1 juvenile female (USNM 46894). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7360, 25°07'05"N–81°25'50"W, 18.xii.1902, M. J. Rathbun det., 8.2m, 1 male (USNM 46895). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7361, 25°07'10"N–81°29'00"W, 18.xii.1902, M. J. Rathbun det., 9.1 m, 1 female (USNM 46896). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7369, 25°00'30"N–81°12'20"W, 19.xii.1902, M. J. Rathbun det., 3.6 m, 1 juvenile female (USNM 46897). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7370, 25°00'40"N–81°15'37"W, 19.xii.1902, M. J. Rathbun det., 4.5m, 1 female, 2 juvenile females (USNM 46898). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7372, 25°00'55"N–81°22'15"W, 19.xii.1902, 7.3 m, 1 male, 1 ovigerous females (USNM

46899). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7373, 25°01'00"N–81°25'30"W, 19.xii.1902, M. J. Rathbun det., 8.2m, 1 male (USNM 46900). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7375, 24°58'05"N–81°28'30"W, 19.xii.1902, M. J. Rathbun det., 9.1 m, 2 males, 1 juvenile female (USNM 46901). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7390, 22.xii.1902, M. J. Rathbun det., 8.68m, 1 male, 2 females (USNM 46902). Florida, Pigeon Key Lake, R/V Fish Hawk, sta. 7409, 1.5 miles NW of Knights Key, 07.i.1903, M. J. Rathbun det., 19.2m, 1 female, 1 male (USNM 46903). Florida, North of Knights Key Channel, R/V Fish Hawk, sta. 7412, 3 miles NE of East Bahia Honda Key, 22.i.1903, 1 female (USNM 46904). Florida, Hawk Channel, R/V Fish Hawk, sta. 7426, 1.75 miles South, 0.75 East of Pigeon Key, 27.i.1903, 5.4 m, 1 ovigerous female (USNM 46905). Florida, Hawk Channel, R/V Fish Hawk, sta. 7427, 3.12 miles North, 0.75 East of Sombrero Light, 27.i.1903, 21 m, 1 ovigerous female (USNM 46906). Florida, Hawk Channel, 1-mile North NW, 0.5 West of East Washerwoman Key, R/V Fish Hawk, sta. 7428, 27.i.1903, 4.8m, 1 ovigerous female (USNM 46907). Florida, Hawk Channel, 0.5-mile SE. by South of SE end of Duck Key, R/V Fish Hawk, sta. 7429, 27.i.1903, 4.2m, 1 ovigerous female, 3 females (USNM 46908). Florida, Hawk Channel, 1.25 miles S. by West of SE point Long Key, R/V Fish Hawk, sta. 7463, 18.ii.1903, 4.5m, 1 juvenile female, 1 male (USNM 46909). Florida, Hawk Channel, R/V Fish Hawk, sta. 7469, 0.25 miles SW, by south of Basin Hill Beacon, 19.ii.1903, 3.6 m, 1 ovigerous female, 1 juvenile female, 1 male (USNM 46910). Florida, Card Sound, Hawk Channel, R/V Fish Hawk, sta. 7493, 10.iii.1903, 3m, 2 ovigerous female, 1 male (USNM 46912). Off Cape Sable, R/V Fish Hawk, sta. 7429, 17.xii.1902, 1 juvenile female (USNM 46913). Florida, Pepperfish Key, R/V Fish Hawk, sta. 7161, 21.xi.1901, 14.6 m, 1 ovigerous female (USNM 46880). Florida, Pepperfish Key, R/V Fish Hawk, sta. 7165, 21.xi.1901, 13.2m, 1 male (USNM 46881). Florida, Aucilla, R/V Fish Hawk, sta. 7195, 05.xii.1901, 19.2m, 1 female (USNM 46882). Florida, Saint Martin, R/V Fish Hawk, sta. 7218, 15.i.1902, 19.2m, 1 juvenile female (USNM 46885). Florida, Saint

Martin, R/V Fish Hawk, sta. 7219, 15.i.1902, 16.4 m, 1 male (USNM 46886). Florida, Anclote, R/V Fish Hawk, sta. 7239, 24.i.1902, 11.43m, 1 male (USNM 46887). Florida, Highland Section, R/V Fish Hawk, 27°49'30"N–83°02'45"W, sta. 7256, 20.i.1902, 14m, 1 male (USNM 46888). Florida, Key West, R/V Fish Hawk, sta. 7278, 13.ii.1902, 16.4 m, 1 ovigerous female (USNM 46889). Florida, Cedar keys, ii.1887, U.S. Navy, Bache, Lieut. J. F. Moser col., 2 females, 1 male (USNM 15138). *MEXICO*, Yucatán, off Isla Mujeres, 1832-1872, W. Stimpson col., 1875, A. Milne-Edwards det., 21.9m, 1 male holotype of *Pericera diacantha* (MCZ 1919). off Isla Contoy, Yucatan, 21.495181°N–86.794478° W, weed rocks, 1873, W. Stimpson col., 1875, A. Milne-Edwards det., 12-114.6 m, 2 juveniles females (MCZ 1920 *Pericera diacantha*).

Diagnosis. Four pointed parallel spines (one mesial metagastric, one mesial cardiac and one metabranchial each side). Lateral spines conical, long and acute, slightly directed backward.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae interspersed mainly in rostral, gastric, lateral branchial region. Rostrum long, longer than half of interorbital length, bifurcated, divergent from base, ending in acute tip. Interorbital region depressed medially. Four acute spines (one mesial metagastric, one mesial cardiac and one metabranchial in each side). Intestinal spine present. Lateral spines conical, long, acute, slightly directed backward. Eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine pointed forward, as long as postorbital spine, a long tuft of seta in posterior face of postorbital spine. Antennular fossae wider than long, with smooth margins. Interantennular septum elongated, slightly compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, antennal gland opening near suture line. Spine of basal article of

antenna slender, slightly curved upward. Antennal flagella long, between antennal spine and rostral spines, almost exceeding rostral spines, visible in dorsal view.

Epistome narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth. Buccal field sub-rectangular, longer than wide, narrower at posterior edge with smooth anterolateral angles. Third maxillipeds covering completely buccal field. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by prominent groove, with one tubercle on border medially.

Males chelipeds equal, longer than legs, more robust in adults. Ischium smooth, merus armed with 3-4 dorsal tubercles in line with a tuft of long setae in each tubercle, with a tubercle at distal margin of merus; carpus and propodus smooth. Dactylus very arched in adult males, leaving a small gap between fingers, fixed finger less arched than dactylus. Fixed and movable fingers distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males, distal half with black or dark brown color in fixed specimens. Females with shorter, slender chelipeds. Ischium, merus, carpus and propodus with less tubercles than males, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tips.

Thoracic sternum I-IV fused, broadly triangular, smooth, anterior half strongly declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Sterno-pleonal cavity fully fitted to telson or leaving a small gap in anterior margin. Sternites with smooth surface in male and females, sternite IV deeply concave laterally. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, slender, parallel, distinctly curved sub-distally, with a torsion in apical margin, bilobed apex. Mesial lobe elongated, acute and curved toward to mesial line; lateral lobe circling apical plate; apical plate with an aperture surrounded with several small setae. Lateral margin smooth. Sternal suture present. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Pink with dark pink veins in frontal regions and orbits, tips of the rostral and lateral spines white [Photo by Arthur Anker, Florida, 19.i.2009].

Type locality: United States, North Key section, 28°57'30"N–82°58'00"W, 5.4 m.

Geographic distribution: western Atlantic: United States (from Beaufort Harbor, North Carolina, Alligator Harbor to Florida) (Fig. 11)

Remarks. The type material of *Pericera camptocera* was probably destroyed in the Great Chicago Fire in 1871 (Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006). The male specimen, USMN 46883 (Fig. 12) is designated herein as neotype, considering the status of preservation and resemblance between of the specimen and the original description. The neotype is close to the original type locality, due to the absence of well-preserved specimens from Key West being North Key section the type locality (cf. ICZN art.75 and 76).

Pericera diacantha A. Milne-Edwards, 1875 [in A. Milne-Edwards, 1873-1880] was synonymized to *M. camptocerum* considering the morphological comparison between the holotype of *P. diacantha* (MCZ 1919) and the juvenile specimen (MCZ 1926), also determined by A. Milne Edwards as *P. diacantha* with our examined material.

Macrocoeloma camptocerum is the species that shares more morphological characters with *P. diacantha* material: (i) the shape and direction of the rostral spines, straight and divergent in *P. diacantha* and *M. camptocerum* than *M. trispinosum*; (ii) and the antero-lateral border of the mouth frame unarmed in *P. diacantha* and *M. camptocerum* than *M. trispinosum*. However, the mesobranchial spines are poorly developed in *P. diacantha* material, this fact could be easily explained by the great variation in size and shape of the carapace spines (variations were observed even in sequences of specimens from the same locality).

For example: (i) the rostral spines could be very large and acute (Fig. 12E) or short and thick (USNM 15139), straight or very divergent; (ii) the mesobranchial spines could be shorter in size than the gastric and cardiac spines, usually in small specimens (Fig. 12C); (iii) lateral spines could be directed: forward (USNM 46884), laterally straight (USNM 270597 ovigerous female), upwards (Fig. 12E), and the most common slightly directed backward (Fig. 12 A,C)

No specimens from the Brazilian coast were found, the material examined in the zoological collections identified as *M. camptocerum* revealed are all misidentifications. Thus, the occurrence of this species in Brazil is in doubt.

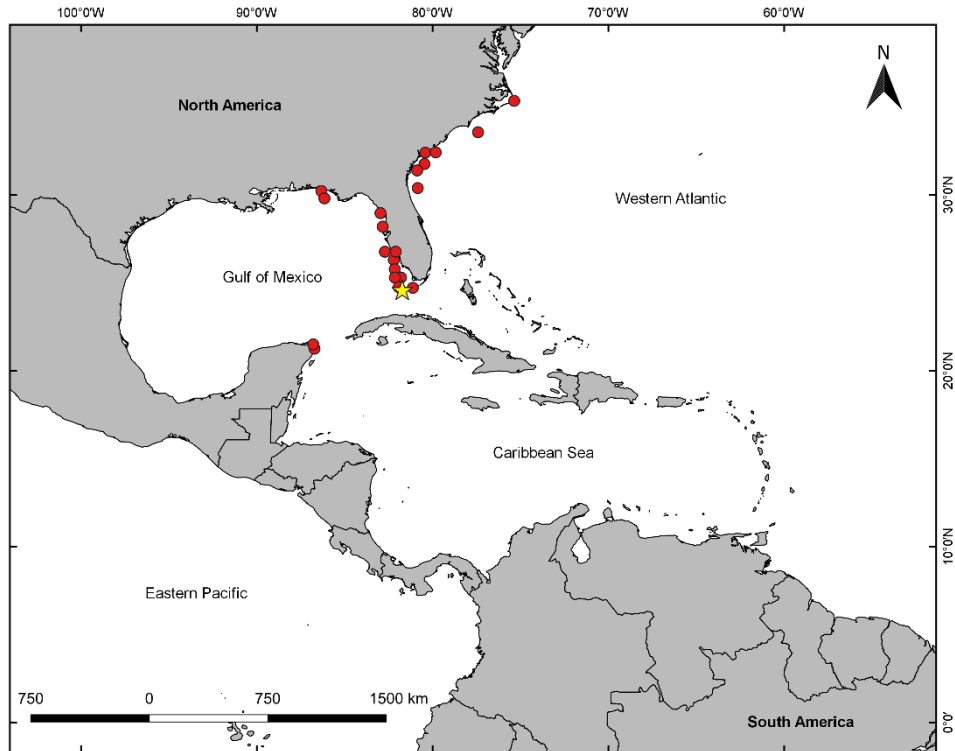


Figure 11. *Macrocoeloma camptocerum* (Stimpson, 1871). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

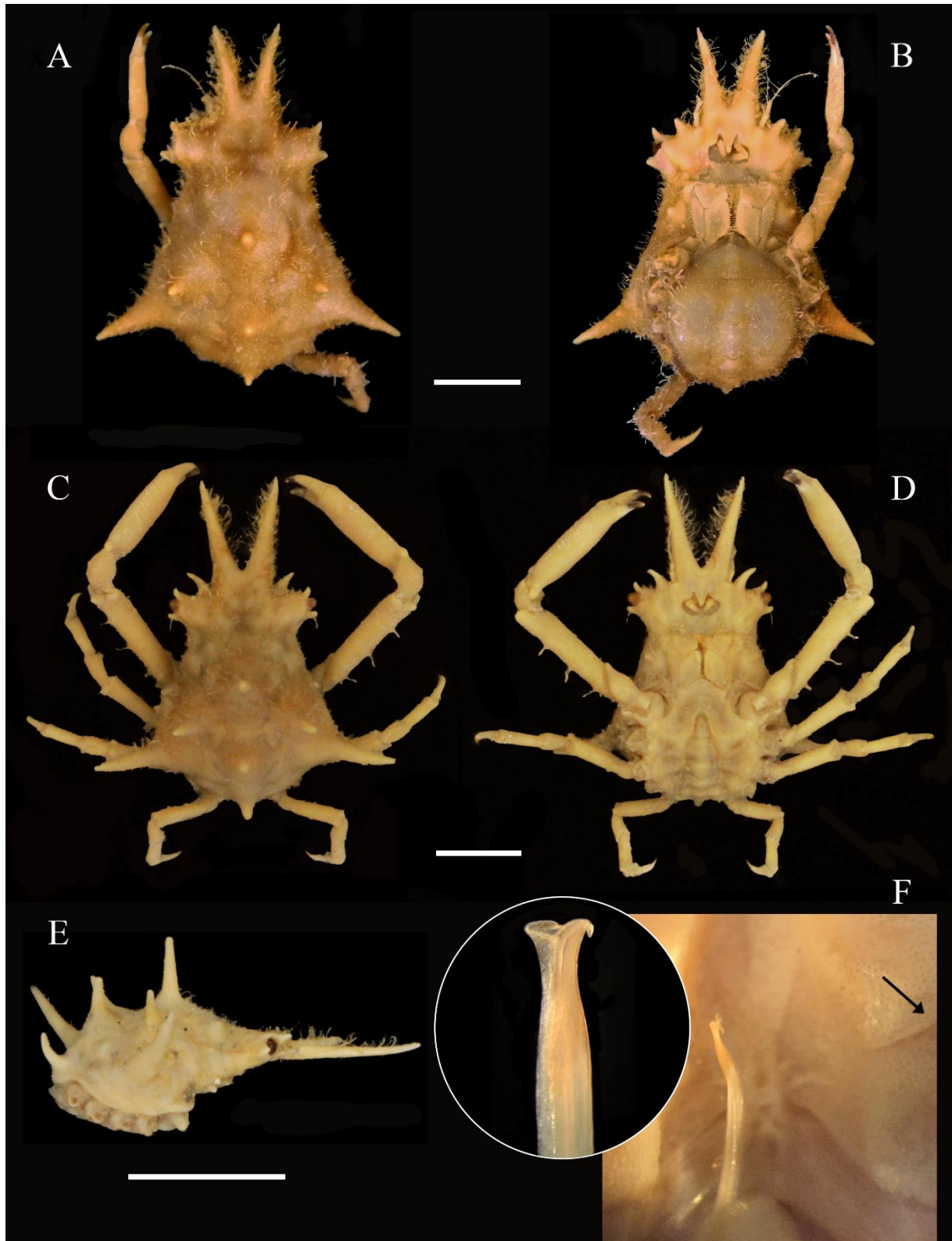


Figure 12. *Macrocoeloma camptocerum* (Stimpson, 1871). A–B, female (USNM 46883). C–D, male neotype, cl. 38.6 mm, cw. 23.9 mm (USNM 46883). E, male (USNM 46901). F, sternopleonal cavity with first gonopod in place, pleonal view of the first gonopod in the detail (USNM 46883). A, C, Habitus; B, D, ventral view; E, lateral view of cephalothorax. Note the thoracic sternal suture IV-V (black arrows) (F). Scale bars A-B 5mm, C-E 10 mm.

***Macrocoeloma concavum* Miers, 1886**

(Figure 14 A-F)

Macrocoeloma concava Miers, 1886: 81, pl. 10, fig. 2-2B [type locality: Brazil, Archipelago Fernando de Noronha and Bahia; type material: cotypes, 1 male and 4 juveniles (NHMUK 1254223) and 1 female (NHMUK 1254223)].

Macrocoeloma eutheca [not *Macrocoeloma euthecum* (Stimpson, 1871)] – Aurivillius, 1889: 55, pl. 2, fig. 1.

Macrocoeloma concavum – Rathbun, 1899: 576; 1901: 75; 1925: 487, pl. 170, fig.3, pl. 171, fig. 3; Moreira, 1901: 64, 136; Coelho, 1971:141; Coelho and Ramos, 1972: 218; Fausto-Filho, 1974: 19; Melo, 1996: 216, fig. 1; Melo, 1998: 463; Almeida et al., 2007: 15; Alves et al.: 2008, 58; Ng et al., 2008: 119; Alves et al., 2012: 54; Lira et al., 2013: 50, fig. 1; Carmona-Suárez and Poupin, 2016: 358, fig.5B.

Type material. Lectotype, male; *BRAZIL*, Pernambuco, Archipelago Fernando de Noronha, HMS Challenger exp., 1884 (NHMUK 1254223). 2 males and 2 females juveniles paralectotype; *BRAZIL*, Pernambuco, Archipelago Fernando de Noronha, HMS Challenger exp., 1884 (NHMUK 1254223). Adult female paralectotype; *BRAZIL*, Bahia, in shallow water, HMS Challenger exp., 1884 (NHMUK1254219) (by present designation).

Material examined. *PUERTO RICO*, Vieques, 10 mi off Culebrita lighthouse, Puerto Rico expedition, sta. 6091, 10.ii.1899, M. J. Rathbun det., 27.4 m, 26°C, 1 female (USNM 24214). Vieques, 10.75 mi off Point Mula lighthouse, Puerto Rico expedition, sta. 6095, 1899, M. J. Rathbun det., 22.8m, 27°C, 1 male (USNM 24221). *MARTINIQUE*, Campagne, IGMAR3, sta. 417, 14°43,65'N–60°52,06'W, 14.ix.1994, IFREMER col., 1 female juvenile (MZUSP 17296). *VENEZUELA*, Costa de Falcon, UTM 378365 and 1358259, 27.iv.2007, 1 female (GIC040).

BRAZIL, Atlantic Amazon, Piatam Oceano, leg 1, stn. 307, 26.10.2008, Santana W. det., 2 males, 1 female (MPEG1182). Maranhão, R/V Almirante Saldanha, sta. 1732A, 02°13' S–41°51'W, 30.x.1967, 30.i.2019, J. Colavite det., 1 female (MZUSP 39067). Paraíba, Off Cape Saint Roque, R/V Albatross, sta. 2758, 6°59'30"S–34°47'00"W, 1887–88, US. Fish Commission col., 36.5m, 1 female (USNM 21934). Paraíba, Projeto Algas, sta. 54-C, 12.ii.1981, G. Melo col., 14.vii.2015, W. Santana det., 1 juvenile (MZUSP 11790). Paraíba, Projeto Algas, sta. 85-B, 4.vi.1981, 22.xii.1983, L.E.A Bezerra det., 1 male (MZUSP 5937). Paraíba, Projeto Algas, sta. 3-A, 7°34'S–34°39'W, 22.i.1981, iv.2008, L.E.A Bezerra, det., 1 female (MZUSP 5934 broken). Bahia, Ilhéus, Ilhéus Coast, 31.xi.2004, A. O. Almeida det., 2 males (CIASB M.2017. 0122.UESC). Bahia, Ilhéus Coast, 14°42'41"S–38°55'05"W, 31.i.2004, R.R. Cavalcante col., A. O Almeida det., 1 ovigerous female (CIASB M.2017. 0121.UESC). Espírito Santo, Archipelago of Trindade and Martin Vaz, TAAF MD55/BRESIL 1987, sta. 27/ DC47, 20°41' S–32°12'60"W, 19.v.1987, 94-105m, 1 male (MZUSP 21329). Espírito Santo, Archipelago of Trindade and Martin Vaz, REVIZEE Benthos, R/V Astro Garoupa, sta. 44, 20°37'49"S–40°01'29"W, 14.vi.2002, 54m, 1 male (MNRJ 17095). Espírito Santo, Archipelago of Trindade and Martin Vaz, REVIZEE Benthos, R/V Astro Garoupa, sta.42, 20°44'28"S–31°50'03"W, 11.vii.2001, 80-90m, 1 male, 1 male juvenile (MNRJ 16500). Espírito Santo, Canopus, sta. 84, 19.xii.1965, P.A. Coelho det., 1 female (MZUSP 8980).

Diagnosis. Two or three small tubercles in the base of orbits. One protogastric spines each side, one small mesial spine in mesogastric region. Four spines in the mesial line. Branchial region inflated with one mesobranchial spine each side. Four spines of the basal article of antenna.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae interspersed mainly in rostral and branchial regions.

Rostrum short, approximately one-third of interorbital length or less, bifurcated, broad, divergent from base, straight or with a convex lateral, ending in acute tip. Interorbital region slightly depressed medially. 2-3 small tubercles on dorsal margin of orbital base. One protogastric spines each side, one small mesial spine in mesogastric region (three small accessory tubercles). Four spines in mesial line (one metogastric, one urogastric, one cardiac spine). Intestinal spine pointed up. Branchial region inflated with one mesobranchial spine each side. Lateral spines longest, conical, acute. Hepatic region slightly depressed. Eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine straight forward, blunt, crenulated, postorbital spine longer than preorbital, slightly curved upward with a small tubercle in ventral margin. Antennular fossae wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles wider than long, fused to epistome, suture between antenna and epistome visible, antennal gland opening near suture line. Four spines of basal article of antenna, two proximal spines small on boarder of suture; mesial spine acute, shorter than distal spine, distal spine very acute, directed toward lateral, mesial and distal visible in dorsal. Antennal flagella longer than rostral spines, visible in dorsal view.

Epistome narrower than antennular fossae at anterior edge, margin smooth. Molt line with a row of spines, from pterygostomial to branchiostegal region (pterygostomial region with three tubercles on boarder medially and 4-6 small mesial tubercles; two branchiostegal spines). Buccal field sub-rectangular, wider than long, narrower at posterior edge, anterolateral margin crenulated. Third maxillipeds covering buccal frame, with a small gap between ischia and meri. Anterolateral angle of merus elongated. Exopod long, nearly reaching antero-lateral margin of merus.

Males chelipeds equal, longer than legs, more robust in adults. Ischium, carpus and propodus granulated, merus armed with 4-5 blunt spines in dorsal face and a row of tubercles

in other faces. Dactylus, arched in adult, leaving a small gap between fingers. Fixed and movable fingers distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males, distal half with black or dark brown color in fixed specimens. Females cheliped, longer than legs, slender. Ischium, carpus and propodus smooth, merus armed with 4-5 small blunt spines in dorsal face and a row of tubercles in other faces. Dactylus slightly arched without gap.

Walking legs short, slender, cylindrical, covered with long simple setae. P2 longest, reaching propodus of cheliped. P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth, anterior half declivous, forming a carina along margin of sterno-pleonal cavity in males. Telson fully fitted to sterno-pleonal cavity, anterior margin smooth. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon. One tubercle delimits the sterno-pleonal cavity laterally (lateral swellings) at level of thoracic sternites VII.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, somites I-IV with a mesial spine progressively, apex rounded. Female pleon markedly arched, somite I with a mesial blunt spine, with row of short setae on margin. Female telson transversally oval or triangular.

G1 longer than thoracic sternal suture IV-V, slender, straight, dorsal-ventrally compressed, slightly curved inwards sub-distally, parallels, unilobed apex, Lateral lobe prominent, membranous, acute in apical edge; apical plate with aperture in pleonal view. Sternal suture present. G2 slender, straight, short (one fifth of G1 length) and cylindric.

Color in life: Yellowish-brown, tips of finger of chelipeds black (Miers, 1886)

Type locality: Brazil, Archipelago of Fernando de Noronha.

Geographic distribution: western Atlantic: Puerto Rico, Martinique, Guadeloupe and Brazil (Maranhão, Recife, Espírito Santo, including the Archipelago of Fernando de Noronha and Archipelago of Trindade and Martin Vaz) (Fig.13)

Remarks. Miers (1886) original description designated seven specimens as cotypes of *Macrocoeloma concavum*. The description is based in an adult male (including the measurements), an adult female from Bahia, Brazil, and another four juvenile specimens (two male and two females) from Archipelago Fernando de Noronha, Brazil.

After that, Rathbun (1925) mentioned that the type was deposited in the British Museum and Fernando de Noronha, Brazil is the type locality, but she did not provide the catalog number of the lectotype and paralectotypes. Checking the Natural History Museum of United Kingdom online database info, we found that there are two lots of *Macrocoeloma concavum* from the H.M.S Challenger deposited in the collection: one from Bahia (NHMUK 1254219) and one from Archipelago Fernando de Noronha (NHMUK 1254223).

The adult male from Fernando de Noronha is designated here as lectotype of *M. concavum* (NHMUK 1254223), based in the original description of the male and illustration data. The juveniles from the same locality and catalog number was designated as a paralectotypes (NHMUK 1254223), as well as the adult female from Bahia, Brazil (NHMUK 1254219) (cf. ICZN art.75 and 76).

Macrocoeloma eutheca of Aurivillius (1889) was reidentified here as *M. concavum* due to the similarities of the description and illustration of both species. For example: (i) rostral spines flatted in Aurivillius (1889) specimen as in *M. concavum* [vs. U-shaped in *M. euthecum* (Stimpson, 1871)]; (ii) Aurivillius (1889) specimen presented a spine in the urogastric region

as in *M. concavum* [vs. *M. euthecum* without spines in the urogastric region]; (iii) Aurivillius' specimen has the region behind the orbits less constricted as observed in *M. concavum* [vs. very constricted in *M. euthecum*]; (iv) branchial lateral spines are shorter in Aurivillius' specimen than in *M. euthecum*.

The examined material revealed the existence of two morphotypes of *M. concavum*: the first morphotype has the rostral spines longer and the anterior region narrowest. The spines of the carapace and branchiostegal region are prominent, as the type material drawn by Miers (1886). This is the most common morphotypes (Fig. 14 A-D). The second morphotype has the carapace blunter, the dorsal spines are shorter and the rostral spines are reduced, resembling the specimen illustrated by Aurivillius (1889) as *M. eutheca* (USNM 24214) (Fig. 14 E).

The range of distribution of *M. concavum* is expanded in the Brazilian coast, before recorded until Bahia state, currently occurring until the Espírito Santo State, including the islands of Trindade and Martin Vaz. This species inhabiting bottoms of calcareous algae and shells, from shallow waters to 105 m (Fig. 13).

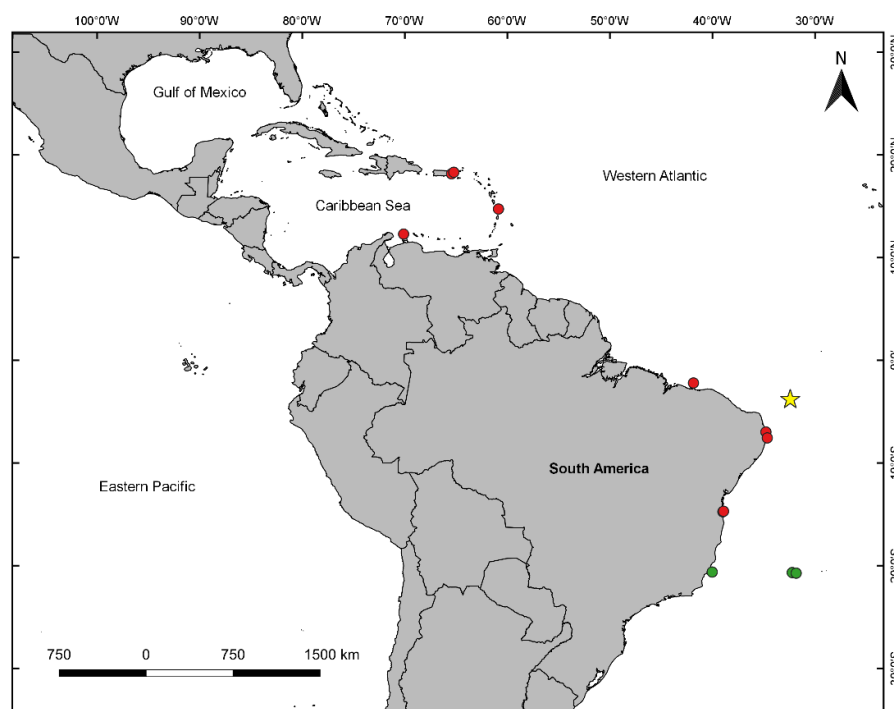


Figure 13. *Macrocoeloma concavum* Miers, 1886. Geographic distribution. Red circles = distribution based on examined material. Green circle = new record. Yellow star = type locality.

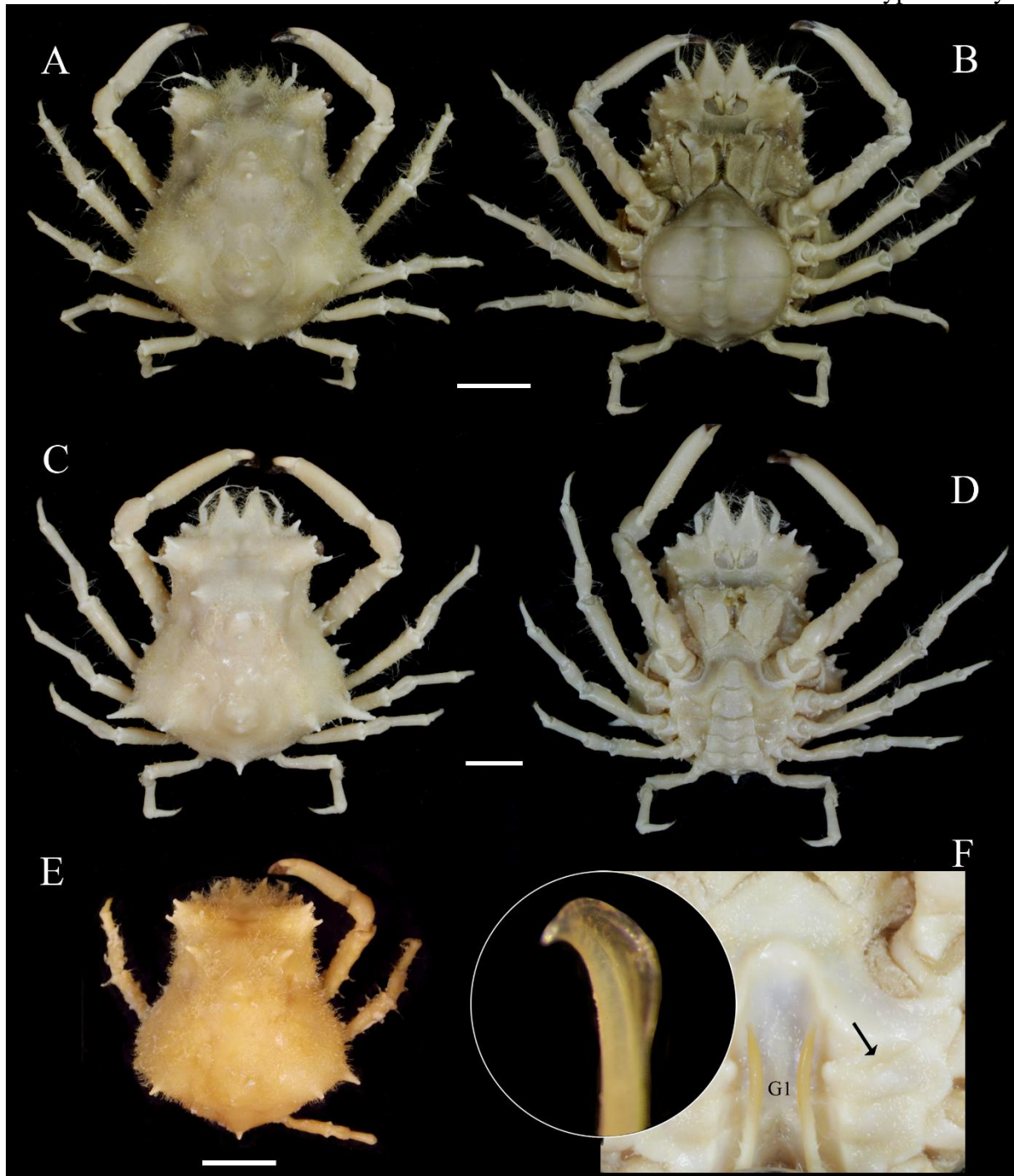


Figure 14. *Macrocoeloma concavum* Miers, 1886. A–B, female (MPEG 1182). C–D, male (MPEG 1182). E, female (USNM 24214). F, sterno-pleonal cavity with first gonopod in place, pleonal view of the first gonopod in the detail (USNM 1278783). A, C, E, habitus; B, D, ventral view. Note the thoracic sternal suture IV-V (black arrows) in F. Scale bars A, B, E 10 mm, C–D 05 mm.

***Macrocoeloma diplacanthum* (Stimpson, 1860)**

(Figure 16 A-F)

Pericera diplacantha Stimpson, 1860: 183 [type locality: United States Virgin Islands, Saint Thomas; type material: non-extant].

Pericera diplacantha – A. Milne-Edwards, 1873: 55, pl. 13, fig. 2a; Desbonne and Schramm, 1867: 16, pl. 5, figs. 16-18.

Macrocoeloma diplacantha – Miers, 1886: 79; Rathbun, 1892: 250; Young, 1900: 77.

Macrocoeloma diplacanthum – Rathbun, 1901: 74; 1898b: 257; 1925: 478, pl. 169, fig. 1 pl. 269, 1-3; 1933: 36; Powers, 1977: 51; Rodríguez, 1980: 291, pl. 28; Abele and Kim, 1986: 45, fig. 519a; Coen and Heck Jr, 1983, 215; Keith, 1985; Marcano and Bolaños, 2001: 79; Ng et al., 2008: 119; Alves et al., 2012: 54; Carmona-Suárez and Poupin, 2016: 358, fig. 5C-D.

Material examined. *UNITED STATES*, Florida, South of Long Key Tortugas, 05. Viii. 1924, W. L. Schmitt col., M. J. Rathbun det., 2 ovigerous female (USNM 72871). Florida, Key west, 1885, H. Hemphill col. 1 ovigerous female (USNM 9365). *BAHAMAS*, Bimini, 1-2, xi, 1948, A. S. Pearse col., F. A. Chace Jr. det., 2 males (USNM 88676). Near Cat Cay, Chaplin Bahamas Expedition, sta. 547, 25°32'N–79°17'W, no col. date, 27.x.2014, W. Santana det., 1 male (USNM 1256375). *PUERTO RICO*, Ponce reef, 1.ii.1899, U.S. Fish Commission col., M. J. Rathbun det., 1 juvenile (USNM 24015). Culebra, 11.ii.1899, U.S. Fish Commission col., M. J. Rathbun det., 1 male (USNM 24119). Punta Arenas, Mayaguez, sta. 133, 5.4 m, under coral rocks. 27. X. 1945, W. G. Hewatt col., F. A. Chace Jr. det., 1 ovigerous female (USNM 82160). *BELIZE*, Lagoon, Carrie bow cay, Stann Creek district, iv.1974, IMSWE project col, 1975, F. A. Chace Jr. det., 7.3 m, 1 juvenile female (USNM 184060). Ensenada Honda, Culebra Island, Steamer R/V Fish Hawk, 9.ii.1899, M.J. Rathbun det., 1 juvenile female [old number USNM

24093] (MCZ 12201). *ANGUILLA*, Half Moon Bay, Bode Sta. 7, 17.v.1958, J. Colavite det., 1 male (USNM1462699). *UNITED STATES VIRGIN ISLANDS*, Saint Thomas, R/V Albatross, 17-24.i.1884; 1 male (USNM 16182). *JAMAICA*, Montego Bay Point, 25. vi. 1910, E. A. Andrews col., 1 female (USNM 43013). Montego Bay, Bathing beach, 19.vii.1910, E. A. Andrews col. 1 male (USNM 43012). *GUADELOUPE*, KARUBENTHOS 2012, sta. GD49, 16°13'37.3188"N–61°32'23.0388"W, 21.v.2012, 1 ovigerous female (MNHN IU-2013-6755). *COLOMBIA*, Old Providence Island, Archipelago of San Andrés, R/V Albatross, 4-9.iv.1884, 1 juvenile (USNM 9136). Old province Island, 6.viii, 1938 W. L. Schmitt col., M.J. Rathbun det., 1 ovigerous female (USNM 77835). *PANAMA*, Colon, Playa Blanca, Expedition Panama oil Spill Project, 09°34'48"N–79°40'12"W, 23.ix.1986, STRI for MMS col., 1 ovigerous female (USNM 262197). Buenaventura bay, Mangote Island, Expedition Panama oil Spill Project, 09°34'48"N–79°40'12"W, 09.iv.1987, STRI for MMS col., 1 male (USNM 262191). *VENEZUELA*, Isla Tortuga, 13.iv.1959, stn. A22-39, J. S. Garth col., J. Colavite det., 3-10m, 4 males, 2 females (NHMLA-AHF 39296).

Diagnosis. Rostrum long, divergent from basis with U-shape. Carapace regions well delimited with four prominent tubercles. Lateral spines as two spines fused medially, bifurcated on tips, slightly directed backward. Spine of basal article of antenna brief, no visible in dorsal view. Antennal flagella no visible in dorsal view.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae arranged in two rolls since from rostral spines to lateral spines. Rostrum longer than interorbital length, bifurcated, divergent from base with U-shape distance between spines, acute. Interorbital region slightly depressed medially. Carapace regions well delimited with four prominent tubercles (one mesial metagastric, one lateral

mesobranchial each side and one mesial cardiac). Intestinal spine short. Lateral spines as two spines fused medially, bifurcated on tips, slightly directed backward. Orbital region prominent, eyes completely protect in orbit when retracted, ocular peduncle no visible when not retracted. Preorbital spine blunt, brief, as long as postorbital spine, postorbital spine blunts with a tubercle compounding ventral margin of orbit. Antennular fossae wider than long, with smooth margins. Interantennular septum broad in base, elongated, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna brief, acute, no or barely visible in dorsal view. Antennal flagella shorter than rostral spines, behind posterior margin of rostrum, no visible in dorsal view.

Epistome shorter and narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth. Subhepatic region with one tubercle each side, visible in dorsal view. Buccal field sub-rectangular, wider than length, narrower at posterior edge, anterolateral angles expanded. Third maxillipeds completely covering buccal frame. Ischium sculpted medially. Exopod long, nearly reaching distal margin of merus, slightly inflated, separated from subhepatic region by groove, smooth.

Males chelipeds equal, much longer than legs, robust in adults. Ischium smooth, merus armed with four spines in dorsal face with few sparsely tubercles, carpus and propodus with sparse tubercles, propodus with four prominent tubercles in dorsal face. Dactylus distinctly shorter than palm, arched in adult, leaving a small gap between fingers. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with light brown color in fixed specimens. Females cheliped shorter and slender. Ischium, merus, carpus and propodus as tuberculated as males, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest, no reaching carpus of chelipeds in males, progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half strongly declivous in ventral view with two distinct depressions, forming a carina along margin of sterno-pleonal cavity in males. Thoracic sternites V-VII with one strong, transverse ridge each, forming a depression between sternites in males. Telson fully fitted to sterno-pleonal cavity. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, slender, parallels, distinctly curved sub-distally, with a torsion in distal margin, with bilobed apex. Mesial lobe longest, acute in tip, strongly curved down and towards sternal margin; lateral lobe, short, spinulated, continuing apical plate; apical plate with aperture in pleonal view. Distal lobe prominent. Sternal suture present. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Brown and dark green (Carmona-Suárez and Poupin, 2016, fig. 5C, D).

Type locality: United States Virgin Islands, Saint Thomas.

Geographic distribution: western Atlantic: United States (from Florida), Bahamas, Cuba, Jamaica, Puerto Rico, Antilles, Panama. Colombia and Venezuela (Fig. 15).

Remarks. The type material of *Macrocoeloma diplacanthum* was originally deposited at the USNM collections by Stimpson. However, the material is considered lost, probably taken by Stimpson when he moved and was probably destroyed in the Great Chicago Fire in 1871 (Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006).

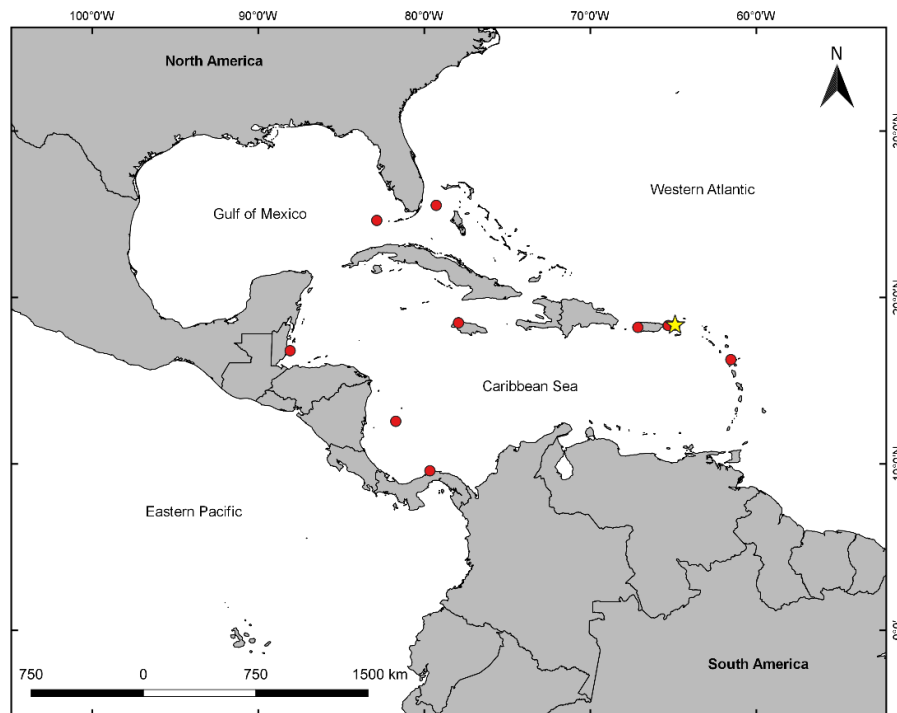


Figure 15. *Macrocoeloma diplacanthum* (Stimpson, 1860). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

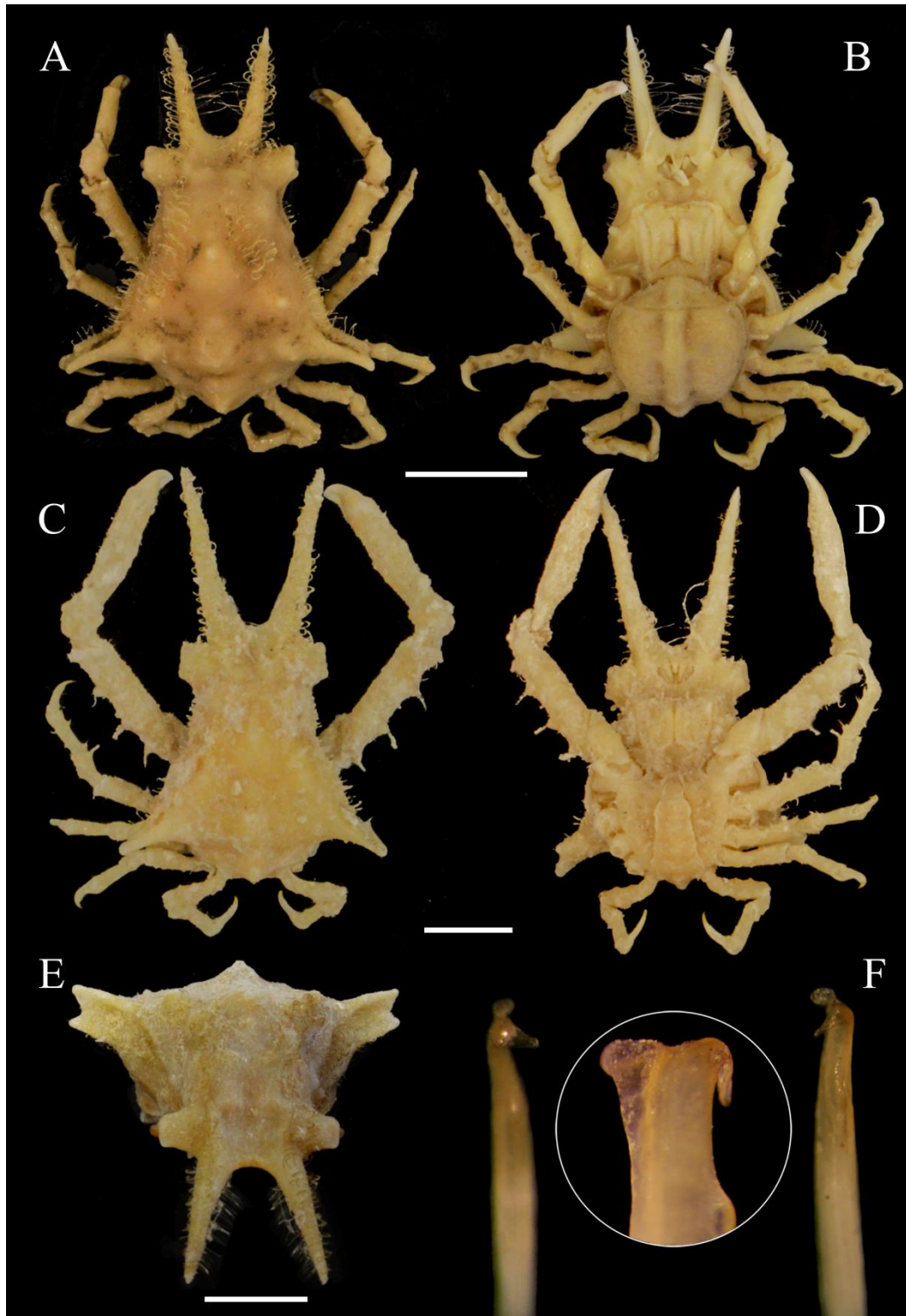


Figure 16. *Macrocoeloma diplacanthum* (Stimpson, 1860). A–B, female (USNM 8216). C–D, male (USNM 88676). E, female (USNM 262497). F, first gonopod in pleonal position, apex in pleonal view in detail. (USNM 1256378). A, C, habitus; B, D, ventral view; E, frontal view. Scale bars A, B, E 10 mm, C–D 05 mm.

***Macrocoeloma euthecum* (Stimpson, 1871)**

(Figure 17 A-D, 19 A-F)

Pericera eutheca Stimpson, 1871 (1870): 112 [Type locality: United States, Florida, Off French reef, 27.4 m, and west of Tortugas; 67.7m; type material: not extant] – A. Milne-Edwards, 1873: 58, 200, pl. 15A, fig. 1-1c.

Macrocoeloma eutheca – Miers, 1886: 82; Rathbun, 1892:251; 1898b: 257; 1925: 484, text-fig, 137, pl. 170, fig. 1, pl. 171, Fig. 1; 1921: 87; 1933: 37; 1930, Boone, 1930: 105, pl. 32, fig. B; Coelho, 1971: 141; Coelho Ramos, 1972: 218; Power, 1977: 51; Williams, 1984: 327, fig. 263, 275k; Abele and Kim, 1986: 45, fig. 519 b, c; Melo, 1996: 217. fig. 1; 1998: 463; Nizinski, 2003: 130; Coelho et al., 2008: 21; Ng et al., 2008: 119; Alves et al., 2012: 54; Carmona-Suárez and Poupin, 2016: 358, fig. 5E.

Type Material. Neotype, female, cl. 14 mm, cw. 9 mm; *UNITED STATES*, off Dry Tortugas, 24°24'N–83°16'W, 65.8 m, xii.1877-i.1878, USCSS Blake Expeditions col., A. Milne-Edwards det. (MCZ 8204).

Material examined. North Atlantic Ocean, Dolphin R/V, sta.781103, MARMAP, 1974, gift, 1 male (USNM 188428). *UNITED STATES*, off North Carolina, 33°48'48"N–76°34'24"W, 04.iii.1981. Duke University for BLM 0S05 col., P. Krikorian det., 1981, 64m, 1 ovigerous female (USNM 202856). off North Carolina, 33°48'48"N–76°34'24"W, 03.iii.1981, Duke University for BLM0S05 col., P. Krikorian det., 62m, 2 males (USNM 202855). North Carolina, 33°48'06"N–76°34'42"W, 03iii.1981. Duke University for MMS 0S05 col., P. Krikorian det., 1981, 77m, 1 ovigerous female (USNM 220812). Gulf of Mexico, R/V Oregon, sta. 727, 28°44'N–85°01'W, 16.xii.1952, 1953, F.A. Chace Jr. det., 54.8 m, 1 ovigerous female (USNM 94463). Florida, Straits of Florida, SE of Miami, R/V Silver bay, sta. 2351, 25°32'N–

80°04'W, 24.x.1960, viii.1960, D.J.G. Griffin and H.B. Roberts det., 65.8 m, 4 males, 1 ovigerous female (USNM 1736375). Florida, Miami, no date, J.B. Henderson col., 54.8 m, 1 male, 1 ovigerous female (USNM 46932). Florida, Off Key west, Sand Key Light bearing North, 109.7 m, sta.24, State University Iowa Expedition, 1 male (USNM 69086). Florida, 26°16'43"N–83°46'49"W, 06.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 77m, 1 male (USNM 241037). Gulf of Mexico, 25°16'53"N–83°37'47"W, 08.ii.1982, R. Lemaitre det., 70m, 1 male (USNM 241039). Gulf of Mexico, 25°16'55"N–83°37'47"W, 05.iii.1984, LGL/ESE for MMS col., T. Czapla det., 74m, 1 male (USNM 274754). Gulf of Mexico, 26°16'43"N–83°46'49"W, 06.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 77m, 1 female (USNM 273460). Gulf of Mexico, 25°16'53"N–83°37'47"W, 01.viii.1981, Continental Shelf Associates col., R. Lemaitre det., 70m, 1 male, 1 ovigerous female (USNM 273433). Gulf of Mexico, 25°16'53"N–83°37'47"W, 08.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 70m, 1 ovigerous female (USNM 241038). Gulf of Mexico, 25°16'55"N–83°37'47"W, 05.iii.1984, LGL/ESE for MMS col., T. Czapla det., 74m, 1 ovigerous female (USNM 274784). Gulf of Mexico, 25°16'53"N–83°37'47"W, 01.viii.1981, Continental Shelf Associates col., R. Lemaitre det., 70m, 1 male (USNM 273203). Gulf of Mexico, 25°16'53"N–83°37'47"W, 01.viii.1981, Continental Shelf Associates col., R. Lemaitre det., 70m, 1 female, 2 ovigerous female (USNM 273341). Gulf of Mexico, 24°47'46"N–83°08'01"W, 08.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 1 ovigerous female (USNM 236988). Gulf of Mexico, 24°47'25"N–83°51'09"W, 25.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 76.1m, 1 male (USNM 273200). Florida, off Dry Tortugas, 24°24'N–83°16'W, 65.8 m, xii.1877-i.1878, USCSS Blake Expeditions col., A. Milne Edwards det., 1 female (MCZ 8204 illustrated by A. Milne-Edwards). *BAHAMAS*, Bahamas bank, 18.v.1893, State University of Iowa col., 1 juvenile (USNM 20020). *ANTIGUA AND BARBUDA*, West by North of Telegraph station, Barbados-Antigua Expedition, sta.66,

1.vi.1918, M. J. Rathbun det., 54.8–128m, 1 female (USNM 72901). *UNITED STATES VIRGIN ISLANDS*, Saint Croix, off Frederiksted, sta. 132, 17°37'55"N–64°54'20"W, 213.9m, 5.i.1879, USCSS Blake Expeditions col., A. Milne Edwards det., 1 ovigerous female (MCZ 2850). *VENEZUELA*, 125-mile northeast of Macaibo, R/V Oregon, sta. 4400, 12°37'N–70°45'W, 26.ix.1963, 27.x.2014, W. Santana det., 97m, 1 ovigerous female (USNM 1256369). 50 miles northeast of Caracas, R/V Oregon, sta.4466, 10°44'N–66°09'W, 17.x.1963, 23.x.2014, W. Santana det., 73m, 1 male, 1 ovigerous female (USNM 1256348). *BRAZIL*, Amapá, Cape Orange, R/V Almirante Saldanha, sta. 2014, G. Melo det., 29.i.1987, 1 male (MZUSP 8521). Maranhão, R/V Almirante Saldanha, sta. 1732A, 02°13' S–41°51'W, 03.ii.1987, G. Melo det., 1 female, 1 male (MZUSP 8525). Maranhão, R/V Almirante Saldanha, sta. 1732A, 02°13' S–41°51'W, 30.x.1967, P.A. Coelho det., 1 juvenile male (MZUSP 7201). Bahia, off Salvador, REVIZEE Benthos, R/V Astro Garoupa, sta. 1R4, 13°04'18"S–38°23'38"W, 23.vi.2002, 91m, 1 male, 1 female (MNRJ 17092). off Espírito Santo, REVIZEE Benthos, R/V Astro Garoupa, sta. 44, 20°37'49"S–40°01'29"W, 14.vi.2002, 54m, 1 ovigerous female (MNRJ 17078). off Rio de Janeiro, REVIZEE Benthos, R/V Astro Garoupa, sta. 1R1, 21°38'57"S–40°10'47"W, vi.2002, 100-180m, 1 ovigerous female (MNRJ 17078).

Diagnosis. Rostrum short, divergent from the base with U-shape sinus, acute, little divergent at the tip. Orbital region very prominent and hepatic region very constricted.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae interspersed mainly in orbits, protogastric, protobranchial, metabranchial and cardiac regions and with few short sparsely tubercles. Rostrum short, approximately one third of interorbital length, bifurcated, divergent from base with U-shape sinus, acute, little divergent at the tip. Interorbital region slightly depressed

medially. One lateral protogastric each side, one mesial metogastric, one lateral mesobranchial each side and one mesial cardiac. Intestinal spine short. Branchial region inflated with one lateral spine each side, conical, long and acute, slightly directed backward. Orbital region very prominent, directed obliquely forward and upwards, eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine directed upwards, shorter than postorbital spine, posterior margin of preorbital spine forming a small spine. One projection of basal article of antenna closing orbital sinus on ventral margin. Antennal flagella longer than rostral spines, visible in dorsal view.

Antennular fossae distinctly wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Basal article of antenna with two spines; one proximal spine short than distal spine, directed towards the orbits, no visible in dorsal view; one distal spine between preorbital spine and rostral spine, directed forward, visible in dorsal view.

Epistome narrower than antennular fossae, at anterior edge, slightly depressed posteriorly, anterior margin smooth. Hepatic region very constricted, subhepatic with one small tubercle near antennal gland. Buccal field sub-rectangular, wider than length, narrower at posterior edge, anterolateral angles expanded and crenulated. Third maxillipeds covering buccal frame, leaving a gap between ischia. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by groove, with three small mesial tubercles and two blunt spines on border medially, visible in dorsal view.

Males chelipeds equal, much longer than legs, robust in adults. Ischium smooth; merus armed with 4 longitudinal rows of tubercles longer in dorsal face, carpus and propodus granulated with small tubercles, propodus with at least four prominent tubercles in dorsal face.

Dactylus arched in adult, distinctly shorter than palm, leaving a small gap between fingers. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with dark brown color in fixed specimens. Females with shorter than male, slender, dactylus arched without gap.

Walking legs short, slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tip.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Telson is fully fitted to cavity sterno-pleonal, anterior margin smooth. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, straight proximally and medially, distinctly curved inwards sub-distally after mesial process, with bilobed apex. Sternal suture present. Lobes lateral and mesial elongated, both curved toward to mesial line, forming a semicircle; mesial lobe acute; apical plate with aperture covered with small spines in pleonal view. Lateral margin smooth. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Red to dark orange; eggs vivid orange (USNM 1462741) (Boone, 1930).

Type locality: United States, Florida, off Dry Tortugas, 24°24'N–83°16'W, 65.8 m.

Geographic distribution: western Atlantic: United States (from North Carolina), Gulf of Mexico, Bahamas, Guadeloupe, Barbados, Guyana and in Brazil from the state of Amapá to Rio de Janeiro (Fig. 18)

Remarks. The type material of *Pericera eutheca* Stimpson, 1871, as most of the species described by Stimpson, was probably destroyed in the Great Chicago Fire in 1871 (Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006). Thus, the specimen illustrated by A. Milne-Edwards (1873: pl. 15A, fig. 1-1c) was designated here as neotype (MCZ 8204) of *Pericera eutheca* (Fig. 17). This specimen was elected considering that the first illustration of this species in the literature is based on it and the material was collected in the same locality of the Stimpson's specimen (cf. ICZN art.75 and 76).

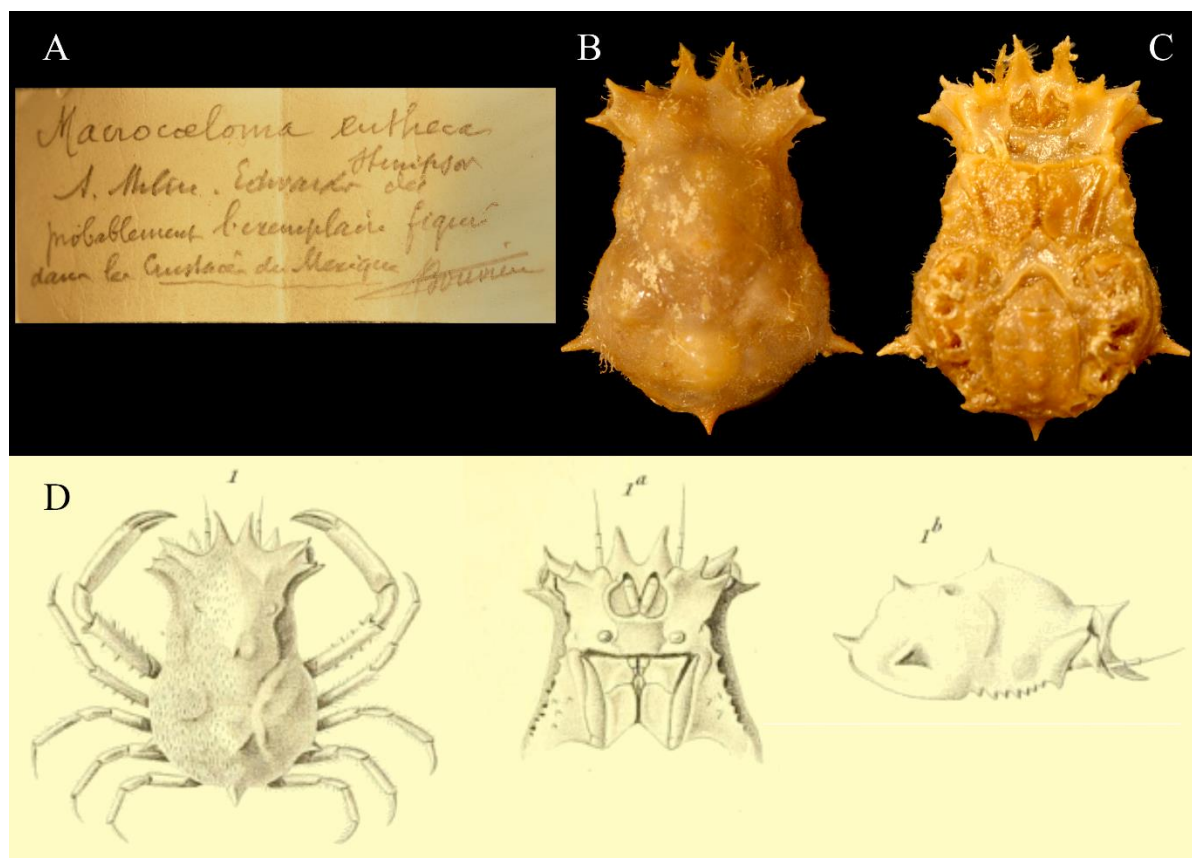


Figure 17. Neotype of *Pericera eutheca* Stimpson, 1871. A. Museum label. B, Dorsal view; C, ventral view of 1 female neotype, cl. 14 mm, cw. 9 mm (MCZ 8204). D. Illustration extracted of A. Milne-Edwards (1873: plate 15A, fig. 1-1c), female; 1, dorsal view; a, ventral view of front; b, lateral view; c, proportions.

The epithet of this species is corrected here in accordance to the genus gender (neuter) being *Macrocoeloma euthecum* the correct combination (cf. ICZN art. 31.2).

Macrocoeloma euthecum showed a great variation in the shape and length of the rostral spines. This variation was noticed between specimens of the same sex and between males and females, for example, there are specimens with: (i) short rostral spines, with a V-shape, divergent from the base (USNM 188428 male); specimens with (ii) long rostral spines with approximately one half of interorbital length (NHMLA-AHF 45018 male); or specimens with (iii) a very short rostral spines, with less than one fourth of the interorbital length (NHMLA-AHF 45018 female; USNM 202855 female; USNM 220812; Fig. 19 A, B, E). The difference in size seems to be a sexual dimorphism, more notable mainly in large specimens. However, the rostrum is a good character to distinguish *M. euthecum* to the other species of the genus.

The range distribution of *Macrocoeloma euthecum* was expanded in the Brazilian coast current recorded to Rio de Janeiro State. This species inhabiting sand and shell bottoms, from shallow waters to 180m of deep (Melo, 1996).

Boone (1930) detailed the habitat of *M. euthecum*, and provided a very detailed description of its decorative behavior. In this study, specimens from Florida, USA were observed in situ, and have its preference to camouflage tested in laboratory, this study observed the preference of orange sponge instead other kinds of sponges available.

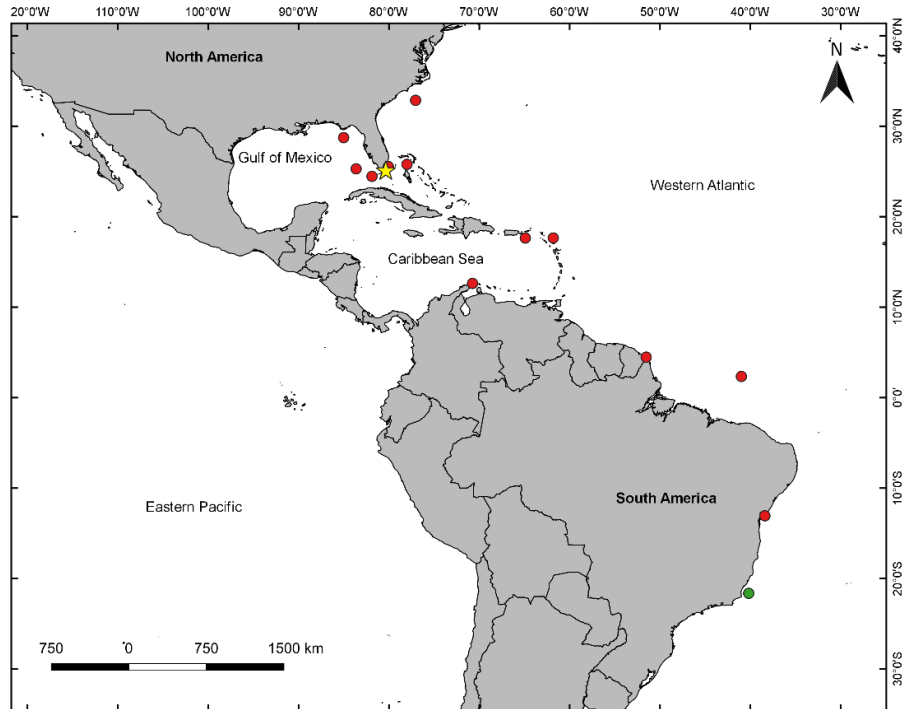


Figure 18. *Macrocoeloma euthecum* (Stimpson, 1860). Geographic distribution. Red circles = distribution based on examined material. Green circle = new record. Yellow star = type locality.

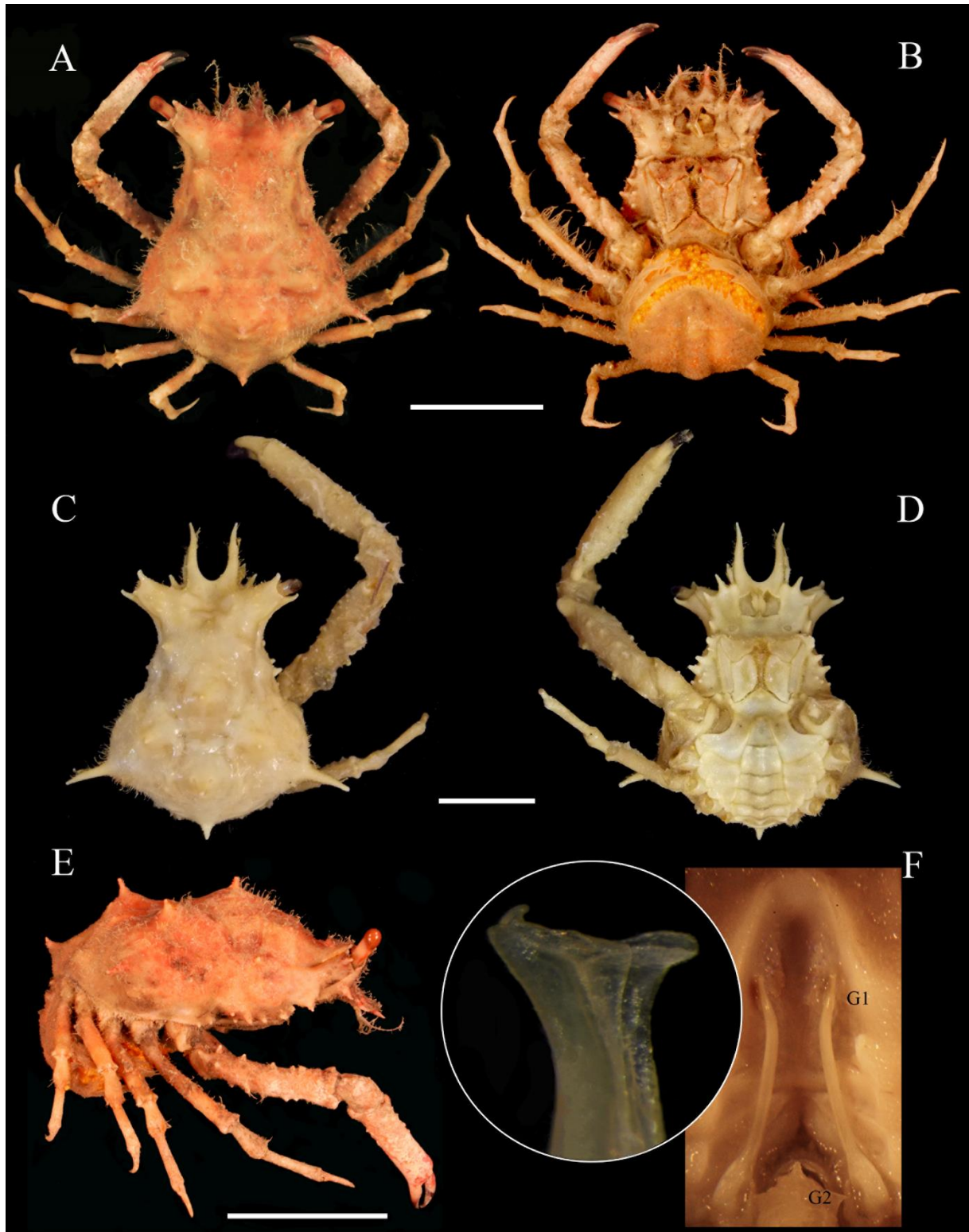


Figure 19. *Macrocoeloma euthecum* (Stimpson, 1860). A–B, female (USNM 1462741). C–D, male (USMN 202855). E, female (USNM 1462741). F, sterno-pleonal cavity with first (G1) and second (G2) gonopods in place, pleonal view in the detail. (USNM 1256348). A, C, habitus; B, D, ventral view; E, lateral view. Scale bars 10 mm.

***Macrocoeloma intermedium* Rathbun, 1901**

(Figure 21 A-F)

Macrocoeloma eutheca – Rathbun 1892: 251 [not *Pericera eutheca* Stimpson, 1871].

Macrocoeloma intermedium Rathbun, 1901: 75 [type locality: Cuba, off Havana, 298 m; type material: holotype male (USNM 9492)] – Rathbun, 1921: 87; Powers, 1977: 51; Vélez, 1977: 136, fig. 27; Ramos, 1986: 91, pl.5, fig. 13; Marcano and Bolaños, 2001: 80; Ng et al., 2008: 119; Carmona-Suárez and Poupin, 2016: 359.

Type material. Holotype, male, cl. 24 mm, cw. 16 mm; *CUBA*, off Havana, R/V Albatross, sta. 2323, 23°10'51"N–82°19'03"W, 17.i. 1885, M. J. Rathbun det. (USNM 9492).

Material examined. *BAHAMAS*, Bahamas Bank, S. U. I. Bahamas expedition col., 18. V. 1893, M. J. Rathbun det. 1 juvenile (USNM 72861). *CUBA*, off Havana, R/V Albatross, sta. 2323, 23°10'51"N–82°19'03"W, 17.i. 1885, M. J. Rathbun det., 298 m, 1 male holotype (USNM 9492). 23°10'36"N–82°20'20"W, 1.v.1884, sta. 2168, M. J. Rathbun det., 223m; 1 juvenile female (USNM 7756). *PANAMA*, Near Colon, Panama, R/V Albatross, sta. 2146, 9°32'00"W–79°54'30"W, 2.iv.1884, 62m, 1 juvenile male (USNM 7780). *COLOMBIA*, Santa Marta, 29.06.1975, M. Vélez det, 1 female (SMF 9093).

Diagnosis. Rostrum short, divergent and broad from base, with convex laterals. Protobranchial region smooth. Lateral spines conical, slightly longer than intestinal spine, acute, directed backward.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae interspersed mainly in frontal and branchial regions.

Rostrum short, approximately a quarter of interorbital length, bifurcated, divergent and broad from base with convex laterals, ending in acute tip. Interorbital region slightly depressed medially. Three mesial spines: one metagastric, one cardiac, one intestinal. Branchial region inflated. Lateral spines of branchial region, conical, slightly longer than intestinal spine, acute, slightly directed backward. Hepatic region with one small tubercle. Orbital region prominent, eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine pointed forward, as long as postorbital spine with crenulations on boarder, posterior margin of preorbital spine forming a small spine. Antennular fossae distinctly wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna very acute, directed forward, reaching the third article of antenna, visible in dorsal view; proximal boarder of basal article of antenna acute, compounding the orbits. Antennal flagella longer than rostral spine, straight, visible in dorsal view.

Epistome broader than antennular fossae, slightly depressed posteriorly, anterior margin smooth. Buccal field sub-rectangular, wider than long, narrower at posterior edge. Third maxillipeds covering buccal frame, leaving a gap between ischia and meri. Anterolateral angle of merus elongated. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by groove, with five tubercles on border medially and sparsely mesial granules.

Males chelipeds equal, longer than legs, more robust in adults. Ischium smooth; merus armed with four small spines in dorsal face; carpus and propodus granulated with small sparsely tubercles. Dactylus arched in adult, distinctly shorter than palm, leaving a small gap between fingers. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger

males; distal half with light brown color in fixed specimens. Females chelipeds shorter and slender, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally, corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Telson fully fitted to cavity sterno-pleonal, anterior margin smooth. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, slender, parallels, slightly curved inwards sub-distally, cylindrical, sharp apex. Apical plate with an aperture. Distal lobe prominent. Sternal suture present. G2 slender, straight, very short (one sixth of G1 length) and cylindrical.

Color in life: No data available.

Type locality: Cuba, off Havana, 23°10'51"N–82°19'03"W, 298m.

Geographic distribution: western Atlantic: United States (From Florida Straits), Bermuda, Cuba, Panamá; Bahamas, Guadeloupe, Colombia and Los Roques Venezuela. (Fig. 18)

Remarks. Rathbun (1892) identified three specimens (USNM 9402, USNM 7780, USNM 7756 see examined material) as *Macrocoeloma euthecum*, however, she mentioned differences between these specimens and Stimpson's description of *M. euthecum*. After that, in 1901,

Rathbun, in the remarks of *Macrocoeloma concavum* presented morphological characters to separate three close allied species of *Macrocoeloma* from the West Indies, *M. concavum*, *M. euthecum* and *M. intermedium*. It was the first time that the name *M. intermedium* appears in the literature, the author also mentioned that this species was based on the same specimens from *M. euthecum* description of Rathbun (1892). The holotype was also designated in a footnote in the pg. 75 of Rathbun (1901), under the catalog number USNM 9492 (Fig. 6, 21).

The holotype of *M. intermedium* is the biggest specimen of the examined material, although this specimen show morphological variations or injuries, for example: (i) the lateral spines is broken and two adjacent small spines can be observed, in the branchial region; (ii) the gastric and hepatic spines are very reduced like a tubercles, (iii) the left cheliped was in process of regeneration, since it is much smaller than the right cheliped; (iv) the telson is broke and not fully fitted to the sterno-pleonal cavity (Fig. 19 C, D, F).

Macrocoeloma intermedium is often misidentified as its congener *M. concavum*, as mentioned above, due to the similar morphology. However, they can be easy distinguish by the follow characters: (i) protobranchial region without spines in *M. intermedium* (vs. one protobranchial spine each side in *M. concavum*); (ii) region between the orbits is narrower in *M. intermedium* than in *M. concavum*; (iii) basal article of antenna no present spines or tubercles in postero-mesial region in *M. intermedium* (vs. a small spine in same level of orbital fissure and antennal gland in *M. concavum*) (see Fig. 13, 19 C, D).

Joseph Poupin (museum label data) corrected the identification of specimen considered the first record of *M. concavum* to Guadeloupe (MNHM IU 2013-5916), to *M. laevigatum* (see Carmona-Suárez and Poupin, 2016) and considered the specimen MNHM IU 2013-4767 as the first record of *M. intermedium* to Guadeloupe, unfortunately this specimen was not examined in this study.

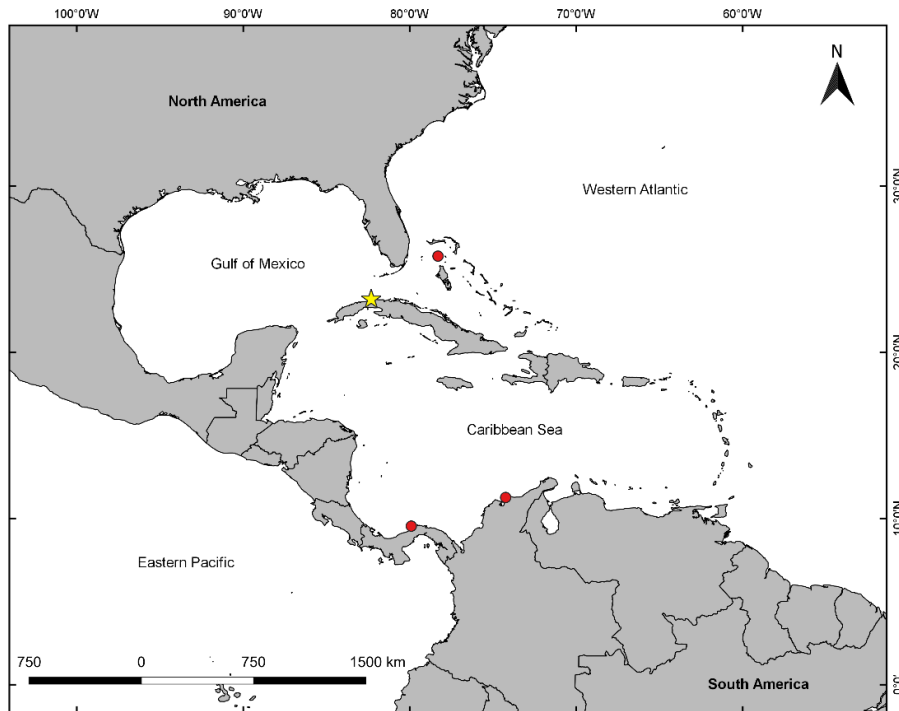


Figure 20. *Macrocoeloma intermedium* Rathbun, 1901. Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

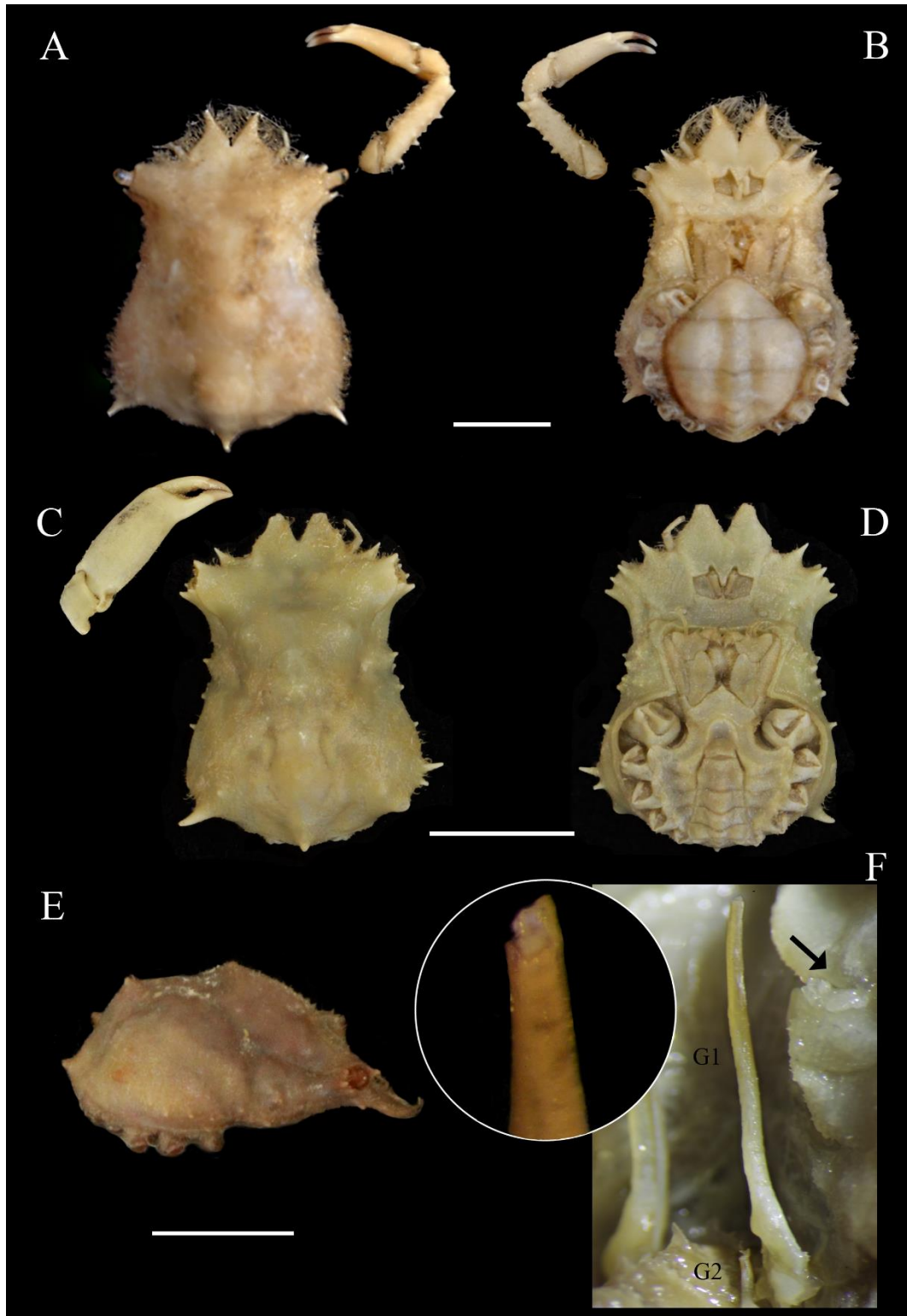


Figure 21. *Macrocoeloma intermedium* Rathbun, 1901. A–B, female (SMF 9093). C–D, male holotype, cl. 24 mm, cw. 16 mm (USNM 9492). E, male (USNM 7780). F, sterno-pleonal cavity with first (G1) and second (G2) gonopods in place, pleonal view of the apex in the detail. (USNM 9492). A, C, habitus; B, D, ventral view; E, lateral view. Scale bars A–D, 10 mm; E, 0.5mm.

***Macrocoeloma laevigatum* (Stimpson, 1860)**

(Figure 23 A-F)

Pericera laevigata Stimpson, 1860: 181 [type locality: United States Virgin Islands, Saint Thomas; type material: non-extant].

Pericera laevigata – A. Milne-Edwards, 1873: 56, pl. 15, figs. 1-1e.

Pericera curvicorna Desbonne in Desbonne & Schramm, 1867, p.14, pl.5, fig. 19 [type locality: Moule, Guadeloupe; type material: non-extant].

Macrocoeloma laevigata – Miers, 1886: 80; Young, 1900: 77.

Macrocoeloma laevigatum – Rathbun, 1925: 483, pl. 169, figs. 2, 3; 1933: 36; Coelho, 1971: 141; Coelho and Ramos, 1972: 217; Powers, 1977: 51; Abele and Kim, 1986: 45, fig. 519d; Melo, 1996: 218, fig. 1; 1998: 463; Almeida et al., 2007: 28; Coelho et al., 2008: 21; Ng et al., 2008: 119; Alves et al., 2012: 54; Carmona-Suárez and Poupin, 2016: 359, fig. 5F.

Material examined. *UNITED STATES*, Florida, Miami, Biscayne Bay, iii-iv.1937, H. L. Clark col., F.A. Chace Jr. det., 1 male (MCZ 9681). Hawk Channel, R/V Fish Hawk, sta.7429, 27.i.1903, 4.2m, 1 male (USNM 46933). *BAHAMAS*, off Whale Cay, 9.vii.1904, F.A. Chace Jr. det., 23.7 m, 1 female (MCZ 8927). *CUBA*, Bahia Honda, 2.vii.1914, M. J. Rathbun col./det., 1 female (USNM 48673). Varadero, iv.1927, among weed on ocean reef, shallow water, Melbourne Ward col., M. J. Rathbun det., 1 female (USNM 79169). Tomas Barrera Expedition, Between Cape San Antonio and Cape Cajon, sta. 12-315, 22.v.1914, Henderson and Bartsch col., M. J. Rathbun id., 3.6-22m, 2 juveniles (USNM 48740). *JAMAICA*, Port Antonia, no data, J. E. Querdess col., Institute of Jamaica don., 1 male (USNM 21235). *GADELOUPE*, KARUBENTHOS 2012 Expedition, sta. D63, 16°10'32.88"N– 61°9'11.4012"W, 26.v.2012, 1 male (MNHN 2013-5134). Ilet du Gosier, KARUBENTHOS 2012 Expedition, sta. GS03, Jéssica Colavite (2020) Phylogenetic relations and taxonomic review of the genus *Macrocoeloma* Miers, 1879.

16°11'47.7996"N–61°29'39.9012"W, 03.v.2012, 1 male (MNHN 2013-5932). îlot Caret, KARUBENTHOS 2012 Expedition, sta. GR43, 16°21'15.7788"N–61°37'47.28"W, 23.v.2012, 1 male (MNHN 2013-5916). *MARTINIQUE*, Champagne, IGMAR3, sta. 427, 14°35.02'N–60°48.30'W, 16.ix.1994, IFREMER col., 28.viii.2008, W. Santana and F. Faria det., 1 male (MZUSP 17299). Champagne, IGMAR3, sta. 427, 14°35.02'N–60°48.30'W, IFREMER col., 16.ix.1994, 1 male (MZUSP 17295). *BRAZIL*, Pernambuco, Archipelago of Fernando de Noronha, Boldró, 27.x.1985, S. Rodrigues col., 15.iii.2016, J. Colavite, 1 male (MZUSP 7241). Pernambuco, Projeto Algas, sta. 35B, 26.iii.1981, F. Torres det., 22.vi.1995, 1 juvenile (MZUSP 6440). Pernambuco, Projeto Algas, sta. 33B, 27.iii.1981, 21. xii. 1983, G. Melo det., 1 female (MZUSP 5940). Pernambuco, Projeto Algas, sta. 34C, 27.iii.1981, P.A. Coelho det., 1 male (MZUSP 5982). Pernambuco, Projeto Algas, sta. 75C, 22.v.1981, P.A. Coelho det., 1 juvenile (MZUSP 5979). Bahia, Salvador, iv.2006, W. Santana, F. Faria, R. Jhonsson col., 1 male (LSZ 183). off Espírito Santo, REVIZEE Benthos, R/V Astro Garoupa, sta. 5, 20°37'49"S–40°01'29"W, 14.vi.2002, 54m, 1 male, 1 ovigerous female (MNRJ 16245).

Diagnosis. Carapace convex, with small tubercles or elevations. Branchial region inflated without lateral spines. Rostrum short pointing downwards, divergent from base, ending in acute tip.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform, convex, with long hooked setae interspersed mainly in rostrum, orbits, protogastric, hepatic and branchial regions, forming two rows from rostral spines to lateral spines. Rostrum short pointing downwards, approximately half of interorbital distance, bifurcated, divergent from base, ending in acute tip. Carapace without spines with small tubercles or elevations: one lateral protogastric tubercle, one mesial metogastric, one mesial

cardiac, one mesial intestinal. Branchial region inflated without lateral spines. Orbital region prominent, eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital and postorbital spines directed laterally forward, blunt, similar in length. Antennular fossae distinctly wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome with suture visible, suture line near antennal gland, with two tubercles aligned. Proximal boarder of basal article of antenna projected compounding orbits, as long as anterolateral spine, no visible in dorsal view; distal spine of basal article of antenna cylindrical, curved towards lateral, visible in dorsal view. Antennal flagella longer than rostral spines, visible in dorsal view.

Epistome as width as antennular fossae at anterior edge, slightly depressed posteriorly, smooth. Subhepatic region smooth. Buccal field sub-rectangular, wider than long, narrower at posterior edge with a tubercle in anterolateral angles. Third maxillipeds covering buccal frame, leaving a gap between ischia. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by groove, with three tubercles on border medially.

Males chelipeds equal, longer than legs, more robust in adults. Ischium smooth, merus armed with two rows with six spines or tubercles in dorsal face, carpus with four tubercles, propodus with small sparsely tubercles. Dactylus slightly arched in adult, distinctly shorter than palm, leaving a small gap between fingers. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with dark brown color in fixed specimens. Females chelipeds shorter and slender. Ischium, merus, carpus and propodus with short tubercles than males, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Telson fully fitted to cavity sterno-pleonal, anterior margin smooth. Sternite VIII concealed by pleon. Thoracic sternites with smooth surface in male and females.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, parallels, slightly curved inwards sub-distally, acute apex with a membrane in lateral margin in distal portion. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Brownish to orange with darker stains on chelipeds and other pereopods. (based on database photos of the specimens MNHN 2016-10114, MNHN 2013-5134, MNHN 2016-10390 from Martinique).

Type locality: United States Virgin Island, Saint Thomas.

Geographic distribution: western Atlantic: United States (from Florida), Cuba, Jamaica, Saint Thomas, Guadeloupe, Martinique and Brazil (from Pará to Espírito Santo, including the Archipelago of Fernando de Noronha) (Fig. 22)

Remarks. The type material of *Pericera laevigata* Stimpson, 1860 was probably destroyed in the Great Chicago Fire in 1871 (Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006). Unfortunately, no material from Saint Thomas, the type locality, Island was examined in this study. However, good and freshly preserved specimens

were examined through photos, from localities close to the type locality place. These specimens are deposited in the crustacean collection of Muséum national d'Histoire naturelle, Paris (MNHN). However, considering its potential for neotype designation, we opted to postpone this decision until a better evaluation of the specimens can be performed.

Hartnoll (1965) studied modifications in male chelipeds due to the sexual maturity of *M. trispinosum* from Jamaica. These growth modifications was observed in all species of *Macrocoeloma* studied here. However, in the examined specimens of *M. laevigatum* these changes can be noted only in large individuals with equivalent carapace length. For instance, the male specimen (MNHN IU 2013-5916) does not present the growth tooth and the dactylus teeth cover three-quarter of the dactylus leaving only a quite small final gap. In the male specimen (MNHN IU 2013-5134) the gap is much larger and more open between the fingers of the cheliped, the propodus is more inflated and the growth tooth can be observed, both specimens are from Guadeloupe.

The range of distribution of *M. laevigatum* is expanded in the Brazilian coast, currently occurring until from the state of Pará to Espírito Santo (Fig. 22). This species inhabits sand, rock, and algae bottoms, from shallow waters to 54 m of deep.

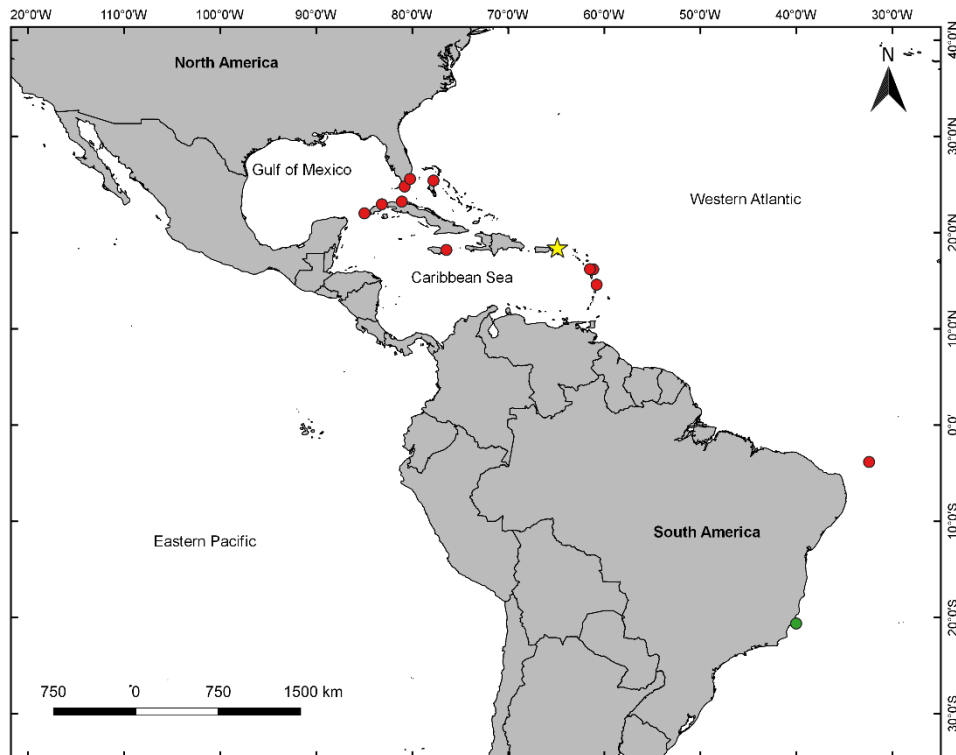


Figure 22. *Macrocoeloma laevigatum* (Stimpson, 1860). Geographic distribution. Red circles = distribution based on examined material. Green circle = new record. Yellow star = type locality.

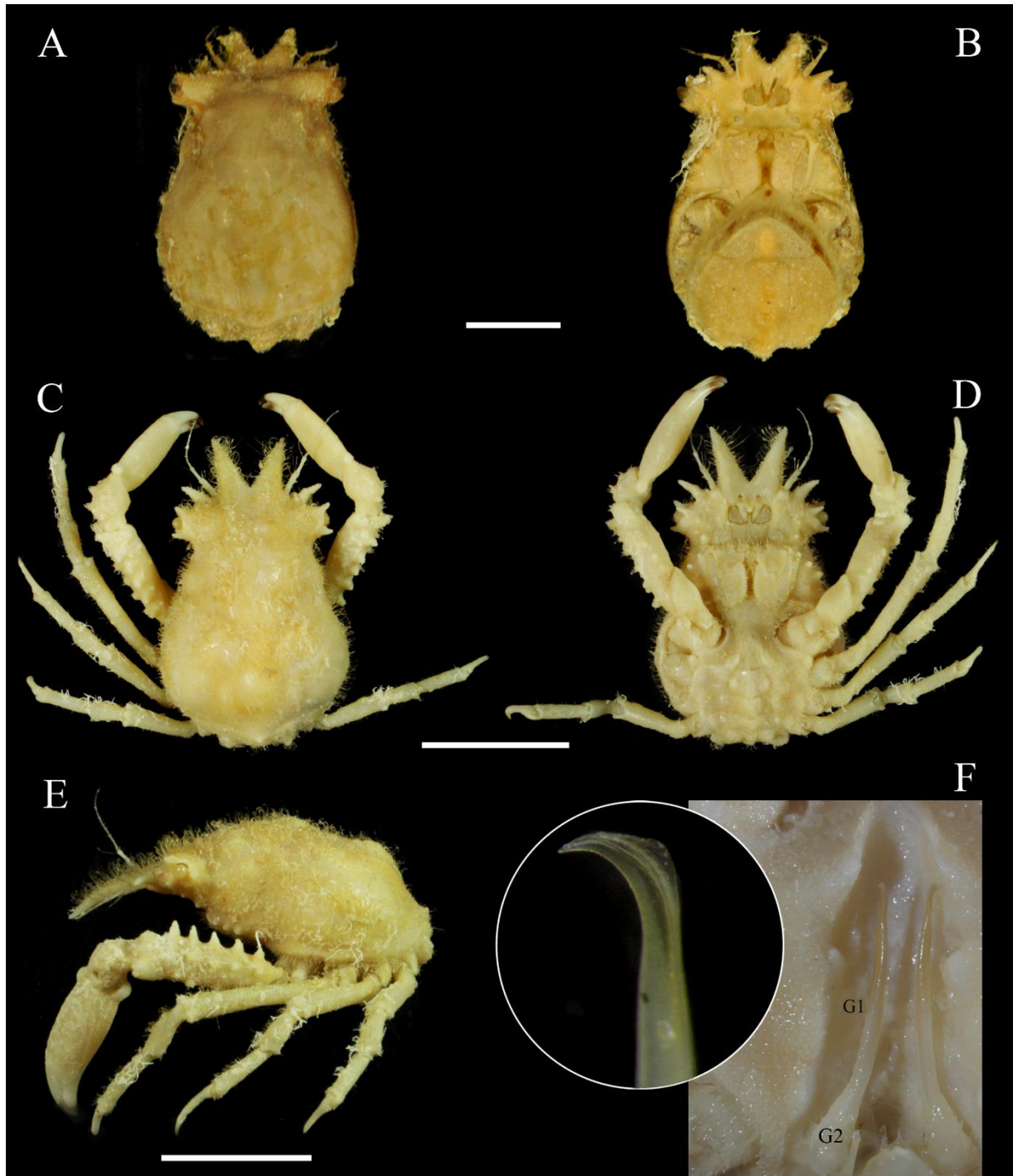


Figure 23. *Macrocoeloma laevigatum* (Stimpson, 1860). A–B, female (MZUSP 5940). C–E, male, (USNM 46933). F, sterno-pleonal cavity with first (G1) and second (G2) gonopods in place, pleonal view of the apex in the detail (MNHN IU 2013-5134). A, C, habitus; B, D, ventral view; E, lateral view. Scale bars 10 mm.

***Macrocoeloma maccullochae* Garth, 1940**

(Figure 25 A-F)

Macrocoeloma maccullochae Garth, 1940: 65, pl.16, figs. 1-4 [type locality: Mexico, Isabel Island, 18.28 to 32.91 m; type material: male holotype (NHMLAC-AHF 372)]. – Garth, 1958: 413, pl. Y, fig.1, pl. 46, fig. 1; 1959: 120; Chirichigno, 1970: 75; del Solar et al., 1970: 34; Kameya et al., 1998: 99; Hendrickx, 1995: 132; ,1999: 172, fig. 79, pl. 7B; Ng et al., 2008: 119; Moscoso, 2012: 119.

Macrocoeloma villosum [not *Macrocoeloma villosum* (Bell, 1836)] – Prahl and Guhl, 1979:188, fig.18.

Type material. Holotype, male, cl. 31.3 mm, cw. 20 mm; *MEXICO*, Isabel Island, Allan Hancock Pacific Expedition, R/V Velero III, sta. 747-37, 2.iv.1937, W. Schmitt col., 1940, J. S. Garth det., 18-32 m (NHMLAC-AHF 372). Paratypes, 1 ovigerous female, 1 male, 1 juvenile male; sta. 870-38, 8.iii.1938, 18-27 m (NHMLAC-AHF 38218). 1 male, 1 female, sta. 870-38, 8.iii.1938, 18-27 m (USNM 78787).

Material examined. *MEXICO*, Maria Magdalena Island, Tres Marias Island, 9.v.1939, sta. 970-39, 5.4 m, 1 ovigerous female (NHMLAC-AHF 39162). Manzanillo, sta. 184 D-2, 22.xi.1937, 1 male (NHMLAC-AHF 37237). *COSTA RICA*, Port Parker, Velero III, sta. 468-35, 09.ii.1935, 1 female (NHMLAC-468-35). Port Parker, R/V Zaca, sta. 203-D-2, 20.i.1938, 1959, Garth det., 18.28 m, 1 male (NHMLAC-AHF 38104). Port Parker, R/V Zaca, sta. 203-D-4, 22.i.1938, 1959, Garth det., 12.8 m, old number AMNH 38104, 1 juvenile, broken (NHMLAC-AHF 38104). Port Parker, R/V Zaca, sta. 203 D-5, 22.i.1938, 5.4 m, 1959, Garth det., 1 juvenile male (NHMLAC-AHF 38104). *COLOMBIA*, La Vigía, Nariño, 6.vi.1978, 10 m, 2 ovigerous female, 1 male (CERBMcr-UV 78048).

Diagnosis: Rostrum bifurcated, convergent from the base, acute, slightly divergent at the tip. Interorbital region slightly depressed medially. One lateral protogastric tubercle, one mesial metagastric spine, one lateral mesobranchial spines or tubercle, one mesial cardiac spine.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae interspersed mainly in rostral region, protobranchial, metabranchial and cardiac regions. Rostrum slightly shorter than interorbital length, bifurcated, convergent from base, acute, slightly divergent at the tips. Interorbital region slightly depressed medially. One lateral protogastric tubercle, one mesial metagastric spine, one lateral mesobranchial spines or tubercle, one mesial cardiac spine. Intestinal spine present. Branchial region inflated. Lateral spines of branchial region conical, long, slightly directed backward. Orbital region prominent, eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine directed forward and upward, as long as postorbital spine, both acute. Antennular fossae distinctly wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna between preorbital spine and rostral spine, straight, directed forward, no reaching the third article of antenna, visible in dorsal view. Antennal flagella shorter than rostral spines, visible in dorsal view.

Epistome narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth. Subhepatic region constricted. Buccal field sub-rectangular, wider than long, narrower at posterior edge, anterolateral angles expanded. Third maxillipeds completely covering buccal frame. Exopod long, nearly reaching distal margin of

merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by groove, with two tubercles on border medially.

Males chelipeds equal, longer than legs, robust in adults. Ischium smooth; merus armed with two rows with four spines or tubercles in dorsal and ventral faces, dorsal face spines longest; carpus and propodus with small sparsely tubercles. Dactylus arched in adult males, distinctly shorter than palm, leaving a small gap between fingers. Cutting edges with sub-equal teeth in distal quarter, one distinct proximal tooth in larger males; distal quarter with dark brown color in fixed specimens. Females with shorter, slender, chelipeds. Ischium, merus, carpus and propodus with less tubercles than males, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tip.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Sterno-pleonal cavity longer than telson, leaving a gap between pleon and cavity, anterior margin smooth. Sternites with smooth surface in male and females. Sternite VIII visible.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, slender, slightly tapered, parallels, with bilobed apex. Mesial lobe long, slender, curved upward; apical plate with several small setae or spines; lateral lobe stout with an acute tip, curved downward. Sternal suture present. Lateral margin smooth. G2 slender, straight, very short (one fifth of G1 length).

Color in life: No data available.

Type locality: Mexico, Isabel Island, 21°54'10"N–105°53'15"W, 18-32m.

Geographic distribution: eastern Pacific: Isabel Island, Mexico; Playa Blanca Costa Rica; Santa Elena Bay, Ecuador, Colombia (Fig. 24)

Remarks. The register book of the Allan Hancock Foundation (AHF) was lost, and some samples are still without a new collection number, for these specimens we maintained the AHF numbers that used the vessel station as collection number, in order to provide an easier comparison with the literature reference.

Although we did not have direct access to the material identified as *Macrocoeloma villosum* by Prah1 and Guhl (1979) deposited at the Crustacean Collection of the Universidad del Valle (CERBMcr-UV 78048), the good photos provided were sufficient to assign that the specimens described and illustrated by Prah1 and Guhl (1979) are *M. maccullochae*.

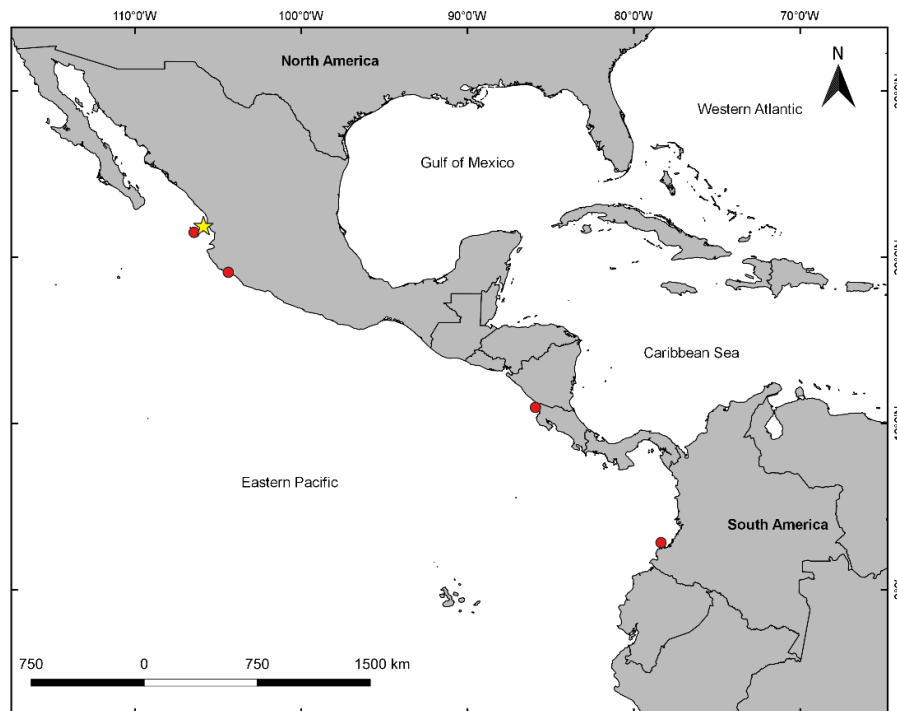


Figure 24. *Macrocoeloma maccullochae* Garth, 1940. Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

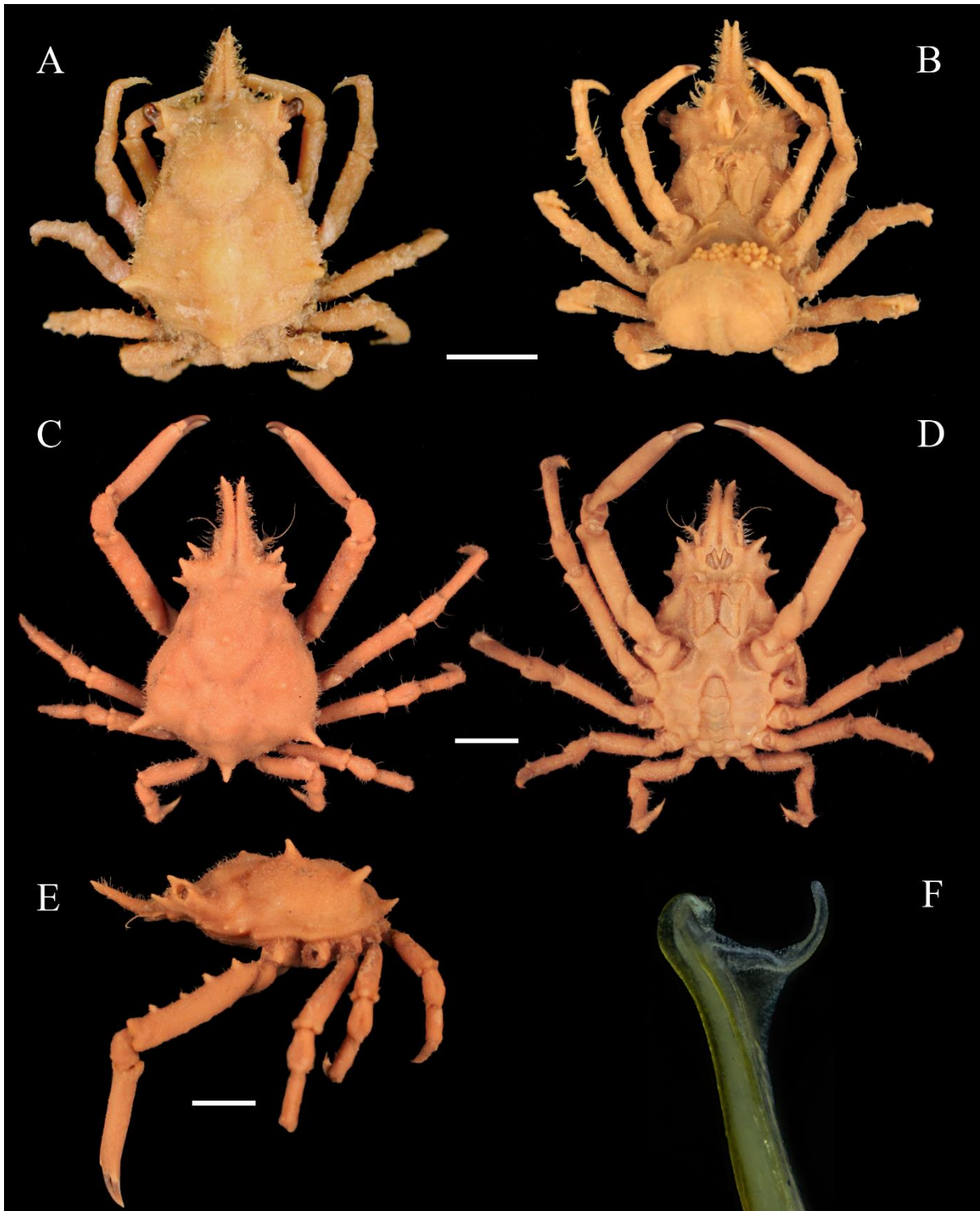


Figure 25. *Macrocoeloma maccullochae* Garth, 1940. A–B, female (NHMLAC-AHF 39162). C–E, male, (USNM 37237). F, distal half of first gonopod of holotype, sternal view (NHMLAC-AHF 372). A, C, habitus; B, D, ventral view; E, lateral view of cephalothorax; F, Apex of the first gonopod sternal. Scale bars A–B, 10 mm; C–E, 05 mm.

***Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867)**

(Figure 27 A,B; 28 A-F; 29 B, C)

Pericera nodipes Desbonne in Desbonne & Schramm, 1867: 15, pl. 5, fig. 13 [Type locality: Guadeloupe; non-extant].

Macrocoeloma trispinosum nodipes – Rathbun, 1927: 87; 1925: 468, pl. 166, fig. 2; pl. 168, fig. 2; Wass, 1955: 168; Williams, 1965: 264; 1984: 328, fig. 264, 275l; Powers, 1977: 53; Soto; 1980 (archive without page number); Keith, 1985: 256, fig. 4A, Abele and Kim, 1986: 46, fig. 517d; Nizinski, 2003: 130.

Macrocoeloma trispinosum variety – Rathbun: 1925p. 468, Pl.168, Fig. 1; 1933; 36; Powers, 1977: 53; Abele and Kim, 1986: 46, fig. 517 c, Williams: 1984: 328.

Macrocoeloma nodipes – Abele, 1970:108; Coelho et al., 2008: 21; Ng et al., 2008: 119; Alves et al., 2012: 54; Carmona-Suárez and Poupin, 2016: 359, fig. 5G.

Type Material. Neotype, male, cl. 40.63 mm, cw. 35.17 mm; *GRENADA*, Grand Anse Bay, 12°01'45.19"N–61°45'21.29"W, 11.x.2012, LRL Simone; AP Dornellas, VS Amaral cols., 27.xi.2019, Colavite, J. det. (MZUSP 40162).

Material examined. *UNITED STATES*, South Carolina, 33°14'54"N–78°24'48"W, R/V Dolphin, 24m, 27.ix.1979, E. Wenner det., 3 ovigerous females, 2 males (USNM 188433). South Carolina, 32°29'36"N–79°41'48", R/V Dolphin, 16m, 28.vii.1979, Continental Shelf Associates col., 27.ix.2017, J. Colavite redet., 1 male (USNM 188430). Georgia, 31°40'54"N–80°19'06", 19.ix.1979, Continental Shelf Associates col., 27.ix.2017, J. Colavite redet., 27m, 1 male (USNM 188430). Florida, vi.1859, G.W. Wunderman col., 5.iii.2018, J. Colavite det., 4 ovigerous female, 1 male (MCZ 75760). Florida, Aucilla section, R/V Fish Hawk, sta. 7193, 29°44'09"N–84°05'30"W, 09.xii.1901, 12.8 m, 1 male (USNM 46915).

Florida, R/V Fish Hawk, sta. 7152, 29°39'30"N–83°53'10"W, 13.7 m, 07.xi.1901, 1 female (USNM 46914). Suez of Mexico, 29°28'N–84°03'W, R/V Oregon, sta. 902, 9.iii.1954, S. Springer col., F.A. Chace Jr. det., 20–22m, 1 male (USNM 96390). Florida, North Key section, R/V Fish Hawk, sta. 7208, 28°55'30"N–83°02'00"W, 09.xii.1901, 7.3 m, 2 juvenile females (USNM 46916). Florida, North Key section, R/V Fish Hawk, sta. 7209, 28°52'45"N–83°07'00"W, 10.5 m, 09.xii.1901, 1 male (USNM 46917). Florida, North Key section, R/V Fish Hawk, sta. 7211, 28°47'55"N–83°16'30"W, 09.xii.1901, 14.6 m, 1 female (USNM 46918). Florida, Saint Martin section, R/V Fish Hawk, sta. 7226, 28°41'00"N–83°15'15"W, 17.i.1902, 15.5 m, 1 male (USNM 47920). Florida, Anclote Section, R/V Fish Hawk, sta. 7231, 28°08'30"N–83°10'00"W, 23.i.1902, M. J. Rathbun det., 13.5°C, 18.28 m, 1 male (USNM 46921). Florida, Highland, R/V Fish Hawk, sta. 7253, 28.i.1902, 23.7 m, 1 juvenile male (USNM 46954). Florida, Cedar keys, ii.1887, R/V S.S. Bache, U.S.N., U.S.C., Lient. J. F. Moser col., 1 male (USNM 15137). Suez of Mexico, 28°09'N–82°50'W, R/V Silver Bay, sta. 54, 16.4 m, 16.vii.1957, F. A. Chace det., 2 males, 1 female (USNM 101584). Florida, Anclote Section, R/V Fish Hawk, sta. 7231, 28°08'30"N–83°10'00"W, 23.i.1902, 18.28 m, 1 male (USNM 46921). Florida, Charlotte Harbor, 26°33'00"N–83°10'00"W, R/V Fish Hawk, sta. 7123, 214.6 m, 2.iv.1901, 1 male, 1 female (USNM 25594). Florida, 26°16'49"N–82°44'01"W, SOFLA expedition, sta. 07, 6.xi.1980, Continental Shelf Associates For BLM/MMS col., R. Lemaitre det., 1 ovigerous female (USNM 242771). Florida, 26°16'49"N–82°44'01"W, 06.xi.1980, Continental Shelf Associates col., R. Lemaitre det., 30.4m, 1 male (USNM 236985). Suez of Mexico, 26°09'N–82°10'W, R/V Oregon, sta.251, 16.4m, 24.i.1951, F. A. Chace det., 1 male (USNM 92379). Florida, 25.2878 N–82.8694 W, 18.x.1980, Continental Shelf Associates for BLM/MMS col., R. Lemaitre det., 44.2m, 1 male (USNM 239988). Florida, R/V Suncoaster, 25°45'50"N–82°06'0"W, 08.xii.1983, LGL/ESE for MMS col., T. Czapla det., 20m, 1 male

(USNM 244832). 25°17'16"N–82°52'10", 31.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 44.2m, 1 male (USNM 241032). Florida, Off Cape Sable, East end of Sawyer Key, 0.75 miles West, R/V Fish Hawk, sta. 7390, 22. xii.1902, 8.68 m, 1 male, 1 juvenile female (USNM 46930). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7351, 25°09'45"N–81°18'35"W, 17.xii.1902, 5.9 m, 3 males, 2 females (USNM 46922). Florida, Off Cable Sable, R/V Fish Hawk, sta. 7370, 25°00'40"N–81°15'37"W, 19.xii.1902, 4.5 m, 1 male (USNM 46927). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7372, 25°00'55"N–81°22'15"W, 19.xii.1902, 7.3 m, 1 male, 1 ovigerous female (USNM 46928). Florida, Off Sanibel Island, bell buoy off Sanibel, Id. Light, Northeast, 10-2.5 miles, R/V Fish Hawk, sta.9, 8.68-12.8m, 1.i.1913, 1 ovigerous female (USNM 50979). Florida, 4 miles West Sanitel, West coast of Florida, sta.43, 07.xii.1935, Bass Biol. Lab. col., M. J. Rathbun det., 1 juvenile (USNM 72907). Florida, eastern Dry Rocks, 1884, Edward Palmer col., 1 male (USNM 9280). Florida, Tortugas, East side Bird Key Harbor, 8.viii.1924, W.L. Schmitt col., 18.28m, M. J. Rathbun det., 2 males (USNM 72894). Florida, Tortugas, sta. 12,15,32, 23.vi.1932, W.L. Schmitt col., 18.28m, M. J. Rathbun det., 1 ovigerous female (USNM 72888). Florida, Tortugas, in channel West of White Shoal, sta. 10, 22.vi.1932, W.L. Schmitt col., M. J. Rathbun det., 1 ovigerous female (USNM 72893). Florida, Tortugas, Between red buoys, head of channel East of White Shoal and Black channel buoy, sta. 37, 07.vii.1932, W.L. Schmitt col., M. J. Rathbun det., 1 male (USNM 72887). Florida, Ragged Keys, 25.iii.1948, F.M. Bayer and M.H. Boehme col, F.A. Chace Jr. det, 2 females (USNM 1278768). Florida, Soldier Keys, 10.x.1960, F. M. Bayer col. det., 2 males (USNM 107240). *BERMUDA*, sta. 1264, 1932, H. S. Richards col., 1 ovigerous female (USNM 75565). Bermuda Oceanographic Expedition, 4.vii.1934, W. Beebe col., 2 juvenile females (AMNH 16069). *BAHAMAS*, Cat cay, R/V Oregon, 11 m, 10.xi.1954, F. A. Chace det., 1 female (USNM 98442). *CUBA*, Reef Lavesos Italianos, opposite Cayo Lavessos, Tomas Barrera Expedition, sta. 14, 2.vi, 1914, Henderson

and Bartsch col., 1 ovigerous female (USNM 48678). Bahia Honda Expedition, R/V Blake, 1878, A. Agassiz col., A. Milne-Edwards det., 1 male (MCZ 2778). *JAMAICA*, Port Antonio, iii.1909, H. L. Clark col., F.A. Chace det., 1 juvenile female (MCZ 8917). *PUERTO RICO*, Ensenada Honda, Culebra Island, R/V Fish Hawk, 9.ii.1899, 1 juvenile (USNM 24217). *WEST INDIES*, 24.v.1929, The Brooklyn Institute of Arts and Sciences col., Lee Boone det., 3 male, 1 immature (AMNH 6120). *GUADELOUPE*, ilet du Gosier, W, KARUBENTHOS 2012 Expedition, sta. GB01, 16°11'47.7996"N–61°29'39.9012"W, 1 juvenile female (MNHN IU-2013-2682). *COLOMBIA*, Cartagena, Isla Rosario, Casumba Beach (northside), 23.x.1992, R. Lemaitre, D. Felder, S. Rodrigues col., A. Windsor det., 0-0.5m, 1 ovigerous female (USNM 1437415). *VENEZUELA*, Isla de Tortuga, 27.viii.2010, R. López col., 2 males, 1 female (GIC 314). Isla Margarita, Bajo Cambuyo, 28.vii.2007, 1 male (GIC1800). Isla Margarita, Laguna Las Marites, 11.v.1989, 1 female (GIC110). Isla Margarita, Laguna Las Marites, 27.iv.1989, Hernández E. col., 1 female (GIC unnumbered). Pier de Comando, Boca del Río, 21.iv.2004, 1 female, 1 juvenile female, 1 male (GIC129). Bajo de Piedras, 01.vii.1999, 1 female (GIC unnumbered). Pier Boca del Rio, 21.vi.2004, 1 female (LSZ007). Bajo de Piedras, 01.vii.1999, S. Marcelo col., 1 male (LSZ007). Bajo de Piedras, 8 males, 7 females (USNM 101585). *PANAMA*, Isla Colón, Punta Caracol, sta.3, 27.iv.2015, A. Anker, J. Luque, T. Kaji, J. Vicente col., 2019, J. Colavite det., under and in rubble, 0.5-2m, 1 male (MZUSP 33456).

Variety. *UNITED STATES*, off Louisiana, Ewing Bank, R/V Oregon, sta. 1416, 28°06'N–91°02'W, 21.ix.1955, 1956, F. A. Chace det., 53 m, 1 male, 1 female (USNM 99739). Florida, Saint Martin' S section, R/V Fish Hawk, sta. 7216, 28°26'30"N–83°08'00"W, 15.i.1902, 13.9 °C, 18.28 m, 1 male (USNM 46919). Cape Florida, off Marco Island, R/V Oregon, sta.1215, 25°45'N–82°03'W, 19.xi.1954, F. A. Chace det., 18.28 m, 1 ovigerous female (USNM 99497). Florida, Off Cape Sable, R/V Fish Hawk, sta. 7360, 25°00'30"N–81°12'20"W, 19.xii.1902, 21 m, 1 female (USNM 46926). Florida, Biscayne Bay,

21.iii.1930, Edward J. Brown col., M.J. Rathbun det., 1 ovigerous female (USNM 64916). Cape Florida, Biscayne, i.1925, John W. Mills col., M. J. Rathbun det., 8 females, 6 males (USNM 76552). Florida, Cape Sable, sta. 73364, 18.x.1902, U. S. Fish Commission col., M. J. Rathbun det., 6.8 m, 1 ovigerous female (USNM 46925). Florida, Miami, 18.2-73.15 m, no date, J. B. Henderson col., 1 male (USNM 49085). Florida, North of Knights Key Channel, 6 miles North, Northeast 0.5 East of East Bahia Honda Key, R/V Fish Hawk, sta. 7414, 22.i.1903, 3.35m, 1 male (USNM 46931). Florida, Dry Tortugas, Bird Key Reef, 20.vi.1925, W. L. Schmitt col., M. J. Rathbun det., 1 male (USNM 72932). Florida, Abt Opposite, East of sta. 8 Red buoy, Tortuga, sta.13, 26.vi.1931, W. L. Schmitt col., M. J. Rathbun det., 18.28 m, 1 female (USNM 72930). Florida, White Shoals, sta.15, 17.vii.1924, W. L. Schmitt col., M. J. Rathbun det., 2 juvenile females (USNM 71934). Florida, White Shoal, sta. 17-18, 25.vi.1932, W. L. Schmitt col., M. J. Rathbun det., 1 juvenile male (USNM 72940). Florida, White Shoal, sta.18, 17.vii.1924, W. L. Schmitt col., M. J. Rathbun det., 1 juvenile male (USNM 71937). Florida, White Shoals, Tortugas, sta.22, 19.vii.1924, W. L. Schmitt col., M. J. Rathbun det., 2 females (USNM 72914). White Shoals, sta. 25, 19.vii.1924, W. L. Schmitt col., M. J. Rathbun det., 1 female (USNM 72936). Florida, White Shoals, sta. 27, 17.vii.1924, W. L. Schmitt col., M. J. Rathbun det., 1 juvenile male (USNM 72935). Florida, White Shoals, Tortugas, sta. 35-37, 20.vii.1924, W. L. Schmitt col., M. J. Rathbun det., 1 juvenile (USNM 72938). Florida, sta. 46, 09.viii.1930, W. L. Schmitt col., M. J. Rathbun det., 1 juvenile female (USNM 72939). Florida, 3 miles North of Loggerhead Key, 17-25.vi, Taylor and Dexter col., M. J. Rathbun det., 18.2-82.3 m, 3 juveniles (USNM 72941). Florida, West of Loggerhead Key, off dock and North of lighthouse pier, 3.viii.1924, Taylor and Dexter col., M. J. Rathbun det., 14.6-9.1 m, 1 female (USNM 72942). Florida, North of Loggerhead Key, 17-25.vi, Taylor and Dexter col., M. J. Rathbun det., 18.28-82.3 m, 1 ovigerous female (USNM 72921). Florida, North of Loggerhead Key, Tortugas, 06.viii.1924, Taylor and Dexter col., M. J. Rathbun det., 36.5-54.8 m, 2 females

(USNM 72922). Florida, Channel haul, East side Loggerhead, Tortugas, sta. 47, 08.viii.1930, W. L. Schmitt col., M. J. Rathbun det., 18.28-20.11 m, 1 male (USNM 72913). Florida, Off send middle Key, 07.viii.1924, W. L. Schmitt col., M. J. Rathbun det., 18.28 m, 1 female (USNM 72915). Florida, Bush Key reef, 19.vi.1925, Dexter col., M. J. Rathbun det., 1 male (USNM 72912). West of Loggerhead Key, off dock, North of lighthouse pier, 03.viii.1924, W. L. Schmitt col., M. J. Rathbun det., 5-14.6 m, 1 female (USNM 72918). Florida, Down Channel, 16.vii.1930, W. L. Schmitt col., M. J. Rathbun det., 18.2-20.1 m, 1 male (USNM 72920). Florida, 21.vi.1931, W. L. Schmitt col., M. J. Rathbun det., 10.9-56.6 m, 1 female (USNM 72919). Florida, Bird Key reef, 19.vi.1932, Dexter and W. L. Schmitt col., M. J. Rathbun det., 1 ovigerous female (USNM 72859). Florida, Fort Jefferson, sta. 28, 22.vii.1930, W. L. Schmitt col., M. J. Rathbun det., 1 juvenile female (USNM 72943). Florida, Cape Florida, iv.1858, Wurdemann col., A. Milne Edwards det., 1 female (MCZ 8207). Florida reef, M.J. Rathbun det., 1 juvenile male (MCZ 1918). off Suez of Mexico, R/V Silver Bay, sta. 60, 27°11'N–82°33'W, 17.vii.1957, U.S Fish and Wildlife col., 1957, F.A Chace Jr. det., 5.4 m, 1 male (USNM 101583). Florida, Key West, 1885, Henry Hemphill col., 1 male, 1 ovigerous female (USNM 9279). *BAHAMAS*, Bimini, sta.28, 22.x.1948, A.S. Pearse col./det., 1 juvenile (USNM 88675). Nassau, Lyford Cay, 25°02'33"N–71°31'W, vii-viii.1961, W. Schmitt col., 28.x.2014, W. Santana det., 1 male (USNM 1256383). Green turtle Cay, E. A. Andrews, 2 females (USNM 20704). Bahama Banks, 15.v.1893, S. U. I. Bahama Expedition col., M. J. Rathbun det., 1 female, 1 juvenile female (USNM 72903). *HAITI*, 1927, W. Beebe col., 1 juvenile female (AMNH 10819). *PUERTO RICO*, La Parguera, i.1974, R. Komuniecki col. det., 15.iv.1999, D.G. Smith don., 4 males, 2 females, 1 ovigerous female (MCZ 17565). *JAMAICA*, 8 miles East of Montego Bay, 20.vii.1920, Chas. B. Wilson Expedition col., 1 male, 1 juvenile female (USNM 43015). *BELIZE*, Spanish Key, University of Iowa State don., vii.1906, 1 ovigerous female, 1 female (USNM 72908). Stann Creak, Pelicans Cays,

16°49'50"N–88°06'17"W, 5.vii.2014, McKeon, S.; Windsor, A. M.; Weber, C. M.; Harris, S.; Yockachonis, T.; Jones, M. S.; Boehm cols., A. M Windsor det., 1 male (USNM 1439035). Twin Cay' S, 16°46'N–88°03'W, 28.iv.1983, D. L. Felder, R. B. Manning cols., 24.x.2014, W. Santana det., 1 male (USNM 1256355). *SANTA LUCIA*, R/V Oregon, Cruise 92, sta. 5058, 14°02'N–61°00'W, 29.ix.1964, viii.1970, 9-23.7 m, 1 ovigerous female (USNM 1278788). *COLOMBIA*, off Santa Marta, R/V Oregon, Cruise 92, sta. 4850, 11°04.1'N–74°23'W, 18.v.1964, viii.1970, D.J.G. Griffin det., 18.2-19.2 m, 1 male (USNM 1278770).

Diagnosis. Carapace oblong with gastric, cardiac, protobranchial region well-delimited (four inflated regions), without spines. Cardiac region slightly depressed. Lateral spines laminate or flatted, slightly directed backward.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace triangulated, oblong, with long hooked setae, arranged mainly in rostral and lateral branchial region. Rostrum short, approximately one-third of interorbital length, bifurcated, parallel from the base slightly diverging at the tip, tips acute. Interorbital region slightly depressed medially. Gastric, cardiac, protobranchial region well-delimited (four inflated regions). Cardiac region slightly depressed. Intestinal spine curved upward, blunt. Lateral spines laminate, slightly directed backward. Eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine blunt, pointed forward as long as postorbital spine, postorbital spine blunt. Antennular fossae distinctly wider than long, with smooth margins. Interantennular septum elongated, slightly compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna, cylindrical, pointed towards laterally; lateral boarder of basal article of antenna, compounding ventral

margin of orbits. Antennal flagella short, almost reaching the tip of rostral spine, visible in dorsal view.

Epistome narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth. Subhepatic region with one tubercle aligned with antennal gland. Buccal field sub-rectangular, longer than wide, narrower at posterior edge, anterolateral angles expanded forming a small tubercle in large specimens. Third maxillipeds completely covering buccal frame. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, inflated, separated from subhepatic region by prominent groove, with one tubercle on border medially.

Males chelipeds equal, longer than legs, robust in adults. Ischium, carpus and propodus with small sparsely tubercles, merus armed with small sparsely tubercles and 3-4 tubercles in dorsal face. Dactylus arched in adult, leaving a gap between fingers. Fixed and movable fingers distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males, distal half with light brown color in fixed specimens. Females with shorter, slender, Ischium, merus, carpus and propodus with small tubercles than males, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tip.

Thoracic sternum I-IV fused, broadly triangular, smooth, anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Thoracic sternum V-VII with one strong, transverse ridge each, forming a depression between sternites in males. Telson fully fitted to sterno-pleonal cavity. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, parallel, with bilobed apex. Sternal suture present. One thin lamella continuing from sternal suture to the tip; apical plate with aperture in pleonal view; lateral lobe elongated covered with small spines in distal boarder. Lateral margin smooth with setae sparsely. G2 slender, straight, very short (one fifth of G1 length).

Type locality: Grenada, Grand Anse Bay, 12°01'45.19"N–61°45'21.29"W, 5-10m.

Geographic distribution: western Atlantic: United States (North Carolina to Florida), Bermuda, Bahamas, Puerto Rico, Jamaica, West Indies, Lesser Antilles, Colombia, Venezuela and Brazil (Archipelago Fernando de Noronha) (Fig. 26).

Remarks: In 1867, Schramm published the Desbonne's manuscript of Crustaceans from Guadeloupe after his death. Desbonne described hundreds of species of crabs from the island, but the major part was synonym to other species already published, most of them, species previously described by Stimpson (1860). These synonyms were established by Schramm in the same publication (1867). For example, *Pericera vilpini* junior synonym of *Pericera subparallela* and *Pericera curvicorna* junior synonym of *Pericera laevigata*.

Schramm (1874: 342) in the ratification of the names of the Desbonne manuscript (1867), also mentioned that *Pericera nodipes* is the same species of *P. trispinosa*. However, this fact is not mentioned in the subsequent literature and *Macrocoeloma nodipes* is still being considered as a valid species. In Desbonne's description of *Pericera nodipes*, the lateral spines

are described as obtuse (1867: pl. 5, fig. 13), while the lateral spines are conical in *M. trispinosum*. The specimens from Desbonne's collection were sent to the "1867 International Exposition in Paris" (Schramm, 1867), but the type material was not found at the MNHN-Paris (see Carmona-Suarez and Poupin, 2016: 359 remarks).

Rathbun (1925) noticed the presence of a gradient variation between *M. trispinosum* and *M. nodipes* in the USNM collection and divided the specimens of the collection into three series. She named this group as "trispinosum-diacathum" in allusion to the species *Macrocoeloma trispinosum* and *Pericera diacantha* A. Milne Edwards, 1875, considered synonyms. However, we reassign here the synonym of *P. diacantha* to *Macrocoeloma camptocerum* [detailed in *Macrocoeloma camptocerum* (Stimpson, 1871)].

Rathbun (1925) distinguish the species by the: (i) the lateral spines (ii) carapace shape (iii) spines or tubercles in the carapace. The series one of Rathbun's called as *trispinosum*, has the typical morphology of *Macrocoeloma trispinosum*, illustrated and described by Latreille (1825), with: (i) lateral spines narrow, conical, laterally projected; (ii) carapace constricted behind the orbits; (iii) three well distinct tubercles in the gastric region (Fig. 29 A).

The series two named as "variety", is considered an intermediated form between *trispinosum* and *nodipes* and it is the most abundant morphotype at the USNM collection (see examined material of *M. nodipes*). "Variety" has: (i) the lateral spines wider and more laminate than in the first group; (ii) carapace less narrow behind the orbits; (iii) four tubercles in the gastric region are lower than in the first group or absent, mesial gastric, mesial cardiac and lateral branchial regions are inflated. This group resembles *Pericera trispinosum* illustrated by Von Martens (1872, Pl. 4, figs 4a-c) (p.s. Von Martens mentioned the figs 4a-d as *Pericera trispinosum*, but the illustrations 4 b-d resembles *Macrocoeloma diplacathum*) (Fig. 29B).

The third series, *nodipes*, is the species named by Desbonne (1867) and the second most abundant in collections. *Macrocoeloma nodipes* has: (i) the lateral spine broader and more

obtuse than both anterior series, with the margins almost contiguous with the margin of the carapace; (ii) carapace slightly, or not at all, constricted behind the orbits; (iii) dorsal margin smooth (Fig. 29 C).

Despite of those differences, Rathbun (1925) could not divide these series into different species and considered *M. trispinosum trispinosum* and *M. trispinosum nodipes*, as subspecies. Abele (1970) was the first author, after Rathbun, to treat *M. nodipes* as a distinct species again and drew attention to the necessity of a careful revision of this species complex and mentioned that would be highly improbable that the all species occur in sympatry. He also mentioned that, if *M. nodipes* were raised to the status of a full species, “variety” would require reevaluation as its subspecies or species status. However, in a follow-up publication, Abele and Kim (1986), considered both *M. nodipes* as subspecies of *M. trispinosum*.

According to the characters illustrated and described in this study, the morphological gradient between *Macrocoeloma nodipes* and *M. trispinosum*, called ‘variety’, shares more similarities with *M. nodipes* and should be considered part of this species. During the exam of samples with several specimens from the same locality and dredge, we observed specimens of both morphologies, “*M. nodipes*” and “variety” (e.g. USNM 76552; 101585; 188533), being variety more frequent in juveniles or no well-developed specimens, and *M. nodipes* frequent noticed in well-developed adults.

A neotype is herein designated to *Pericera nodipes* Desbonne in Desbonne & Schramm, 1867. Unfortunately, no adult specimens from the type locality, Guadeloupe, was examined in this study, thus, an adult male from Grenade, also a Caribbean Island was designated as neotype considering the status of preservation and resemblance between of the specimen selected (MZUSP 40162) and the original description (cf. ICZN art.75.3.6. and 76.3).

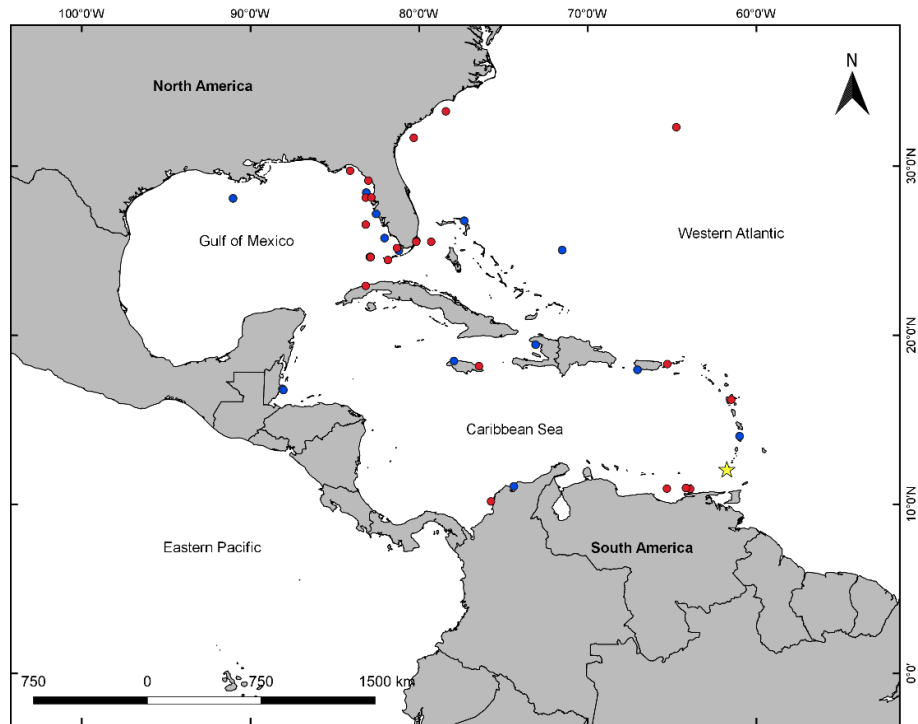


Fig. 26. *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867) Geographic distribution. Red circles = distribution based on examined material. Blue circles = distribution based on examined material of 'variety'. Yellow star = type locality.



Figure 27. *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867). A–B, male neotype, cl. 40.63 mm, cw. 35.17 mm (MZUSP 40162). A, Habitus; B, ventral view. Scale bars 10 mm.

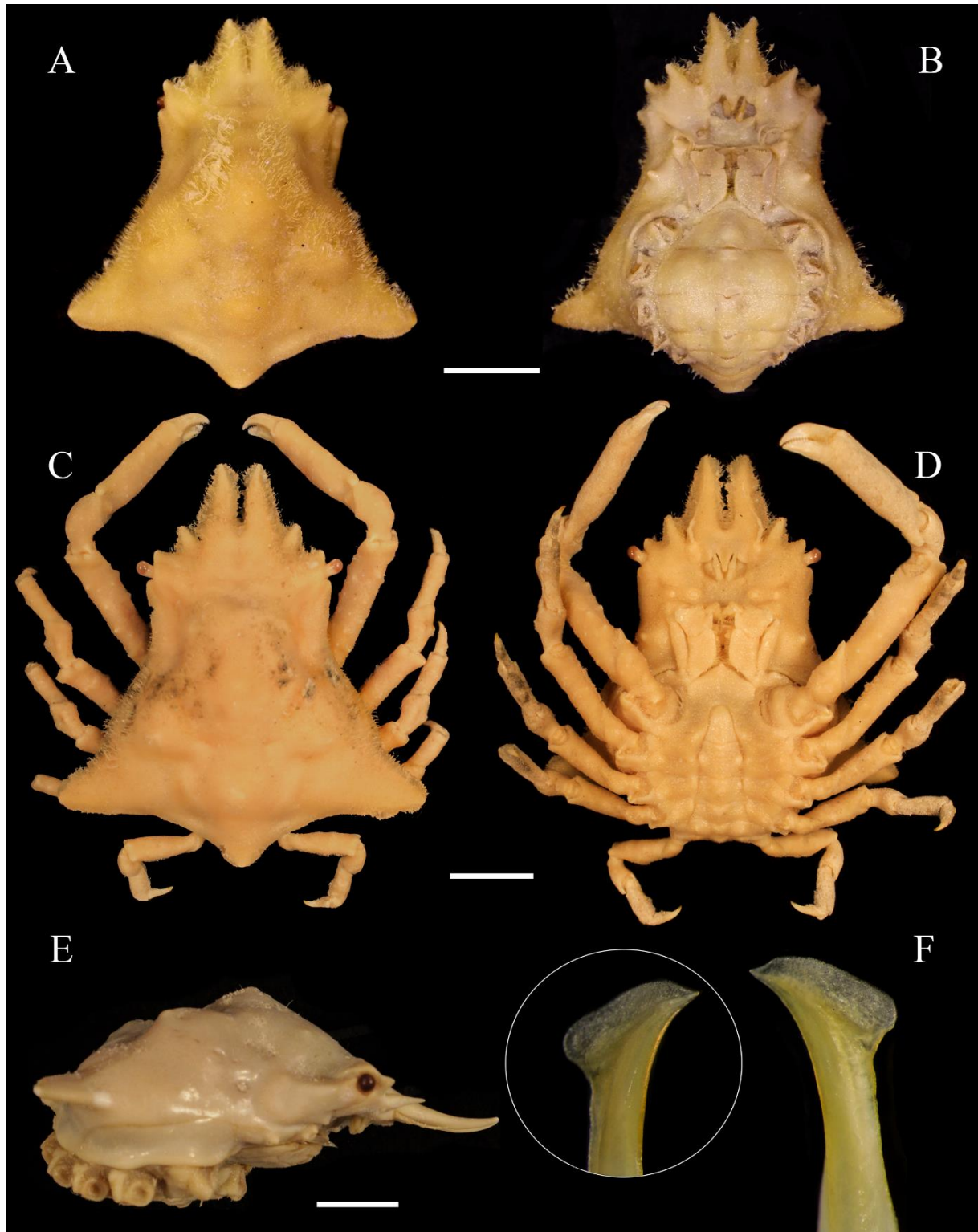


Figure 28. *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867). A–B, female (USNM 188422). C–D, male (USNM 10740). E, male (USNM 270615). F, distal half of first gonopod, pleonal view, apex sternal view in the detail. (USNM 188433). A, C, Habitus; B, D, ventral view; E, lateral view of cephalothorax. Scale bars 10 mm.

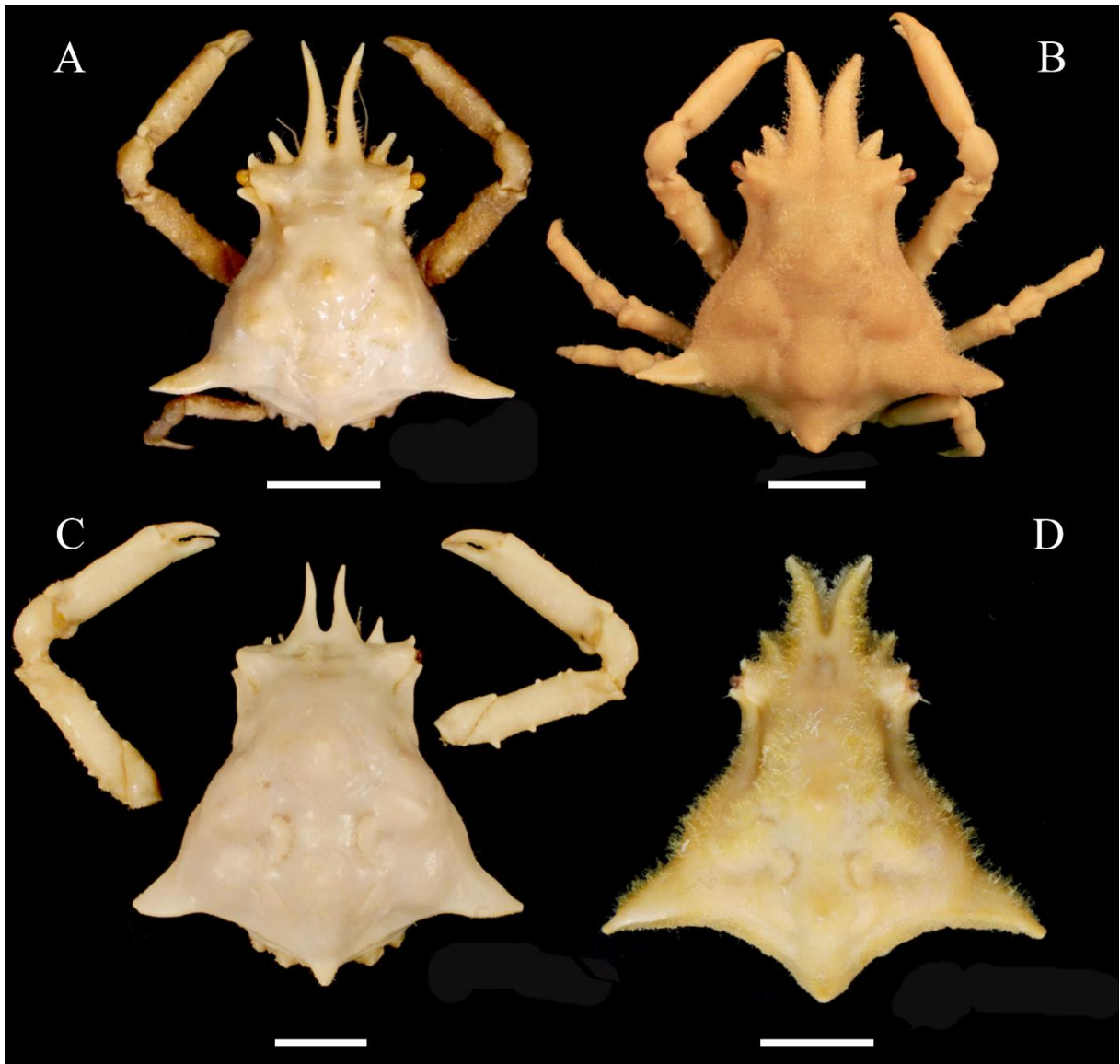


Figure 29. Species of *Macrocoeloma trispinosum* complex, habitus dorsal view. A, *Macrocoeloma trispinosum* (Latreille, 1825) (USNM 17959); B, *Macrocoeloma nodipes* “variety” (USNM 43015); C, *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867) (USNM 270615); D, *Macrocoeloma trigonum* (Dana, 1851) (MZUSP 17903). Scale bars 10 mm.

***Macrocoeloma subparallelum* (Stimpson, 1860)**

(Figure 31 A-H)

Pericera subparallela Stimpson, 1860: 182 [type locality: United States Virgin Islands, Saint Thomas; type material: cotypes, 1 male and 1 juvenile female].

Pericera vilpini Desbonne in Desbonne & Schramm, 1867: 12, pl. 5, fig. 14-15 [type locality: Guadeloupe; type material: non-extant].

Pericera subparallela – A. Milne-Edwards, 1873: 54, pl. 13, figs. 3-3d; Vérril, 1901: 17.

Macrocoeloma subparellela – Miers, 1886: 79; Young, 1900: 76.

Pericera trispinosa – Gundlach and Torralbas, 1900, 365, fig. 121 G.

Macrocoeloma subparallelum – Rathbun, 1901: 74; 1921: 87; 1925: 478, pl. 169, fig. 1, pl. 269, figs. 1-3; 1933:36; Vérril, 1908; 415, pl. 22, fig. 3a, c, d; Coelho, 1971: 141; Coelho and Ramos, 1972: 217; Fausto-Filho, 1974: 18; Powers, 1977: 52; Rodríguez, 1980: 292, fig. 66; Abele and Kim, 1986: 46, fig. 517f; Melo, 1996: 220, fig. 1; 1998: 464; Marcano and Bolaños, 2001: 80; Alves et al., 2008: 59; Ng et al., 2008: 119; Alves et al., 2012: 54; Carmona-Suárez and Poupin, 2016: 359, fig. 5H.

Type material. Lectotype, male, soft shell, cl. 13.98 mm, cw. 9.90 mm; *UNITED STATES VIRGIN ISLANDS*, St. Thomas, 18.345591° N–64.923613° W, no date, A. H. Riise col., 1860, W. Stimpson det., (MCZ 1243). Paralectotype, 1 juvenile female, cl. 13.9 mm, cw. 10.91 mm; same location data (MCZ 1227) (by present designation).

Material examined. *BERMUDA*, Castle Harbor, 3.6 m, vi.1936, F. A. Chace Jr., 1 female (MCZ 9214). North shore of St. George Island, no date, M. D. Burkenroad col., F.A. Chace det., 1 male (MCZ 9293). vii.1936, L.H. Kleinholz col., F.A. Chace Jr. det., 1 male (MCZ 9451). *UNITED STATES*, Florida, no date, M. R. Rathbun det., 1 male. (USNM 16054). R/V

Oregon, 10.xi.1954, F.A. Chace det., 1 male, 1 female (USNM 98441). *BAHAMAS*, Cat cay, Cat Island, Camperdown, 4 mi East Arthurs Town, 28.vii.1935, W.J. Clench col., F.A. Chace det., 1 male (MCZ 9552). Cay Sal Bank, Cay Sal, 23°42'N– 80°24'W, 2.iii.1960, 28.x.2014, W. Santana det., 1 juvenile female (USNM 1256388). *CUBA*, Between Cape San Antonio and Cape Cajon, sta. 12 col 315, 24.v.1914, Tomas Barrera Expedition, Henderson and Bartsch. col., M. J. Rathbun det., 4-22m, 1 juvenile (USNM 48741). vicinity of Guantanamo bay, S. R. Exp. Expedition, sta. 227, 24, iv.1937, Paul Bartsch col., 15.viii.2017, J. Colavite redet., 1 male (USNM 76503). Cabanas, Tomas Barrera Expedition, sta. 16, 8-9.vi.1914, M. J. Rathbun det., 1 male (USNM 48666). *HAITI*, no verbatim date data, David Friedrich Weinland col., 1 juvenile female (MCZ 323). *PUERTO RICO*, Guánica Bay, R/V Steamer Fish Hawk, on coral reef, 28.i.1899, M.J. Rathbun det., 1 male (USNM 24139). Playa de la Ponce Reef, R/V Steamer Fish Hawk 01.ii.1899, M. J. Rathbun det., 1 male (USNM 24140). Ponce, R/V Steamer Fish Hawk, 1899, M.J. Rathbun det., 1 male (USNM 24141). Smithsonian-Hartford Expedition, 29.iii.1937, W. L. Schmitt col., M. J. Rathbun det., 2 males, 1 female (USNM 75127), Fajardo, R/V Fish Hawk, 17.ii.1899, 2 males, 1 female (USNM 24200). Mona Island, H. A. Beatty, 11. viii-03.ix.1944, W. L. Schmitt det., 1 male, 5 juveniles (USNM 80497). *BRITISH VIRGIN ISLANDS*, Tortola, West End, Long Bay Hotel beach, iii.1981, C. Kessler and M. Sibble col., 06.ii.2018, J. Colavite det. 1 male (MCZ 75786). *UNITED STATES VIRGIN ISLANDS*, *St. Thomas*, Smithsonian-Hartford Expedition, 4.iii.1937, W.L. Schmitt col., 15. vii. 2017, J. Colavite redet., 1 ovigerous female (USNM75209). 17-24.i.1884. R/V Albatross, 1 female (USNM 16183). *St. Croix*, Prosperity Bay, sta. 179, H. A. Beatty col., M. J. Rathbun det., 1 male (USNM 75473). Salt River reefs, sta. 157, no date, H. A. Beatty col., M. J. Rathbun det., 1 juvenile (USNM 75477). *BELIZE*, Twin Cays, rubble, 28.v.2012, R. Lemaitre and D. Felder col., R. Lemaitre det., 1m, 1 female and 1 juvenile (USNM 1207733), Lagoon, Carrie bow cay, Stann Creek district, 27.iv.1974, IMSWE project col., 1975, Chace det., 18.28 m, 1 female

(USNM 184061). East side of South Water Cay, sta. I MSWE-AC-CBC-156 J. Norris #21, 29.iv.1977, J. Norris col. 0,5-1m, reef flat rock, 1 male, with four color slides (USNM 1278764). Stann Creek, Pelican Cays, back reef lagoon, 16°48'08"N– 88°04'52"W, 11.vi.2014, S. McKeon, A. Windsor, C. Weber, D. Harris, T. Yockachois col., 28.viii.2017, J. Colavite det., 1m, 1male (USNM 1439342). Stann Creek, Pelican Cays, back reef lagoon, 16°48'08"N– 88°04'52"W, 11.vi.2014, S. McKeon, A. Windsor, C. Weber, D. Harris, T. Yockachois col., 28.viii.2017, J. Colavite det., 1m, 1 juvenile (USNM 1439189). Stann Creek, Pelican Cays, back reef lagoon, 16°48'08"N– 88°04'52"W, 11.vi.2014, S. McKeon, A. Windsor, C. Weber, D. Harris, T. Yockachois col., 28.viii.2017, J. Colavite det., 1m, 1 juvenile (USNM 1441482). *ANTIGUA*, Pelican Island, Barbados-Antigua Expedition, 11.v. 1918, M. J. Rathbun det., tide pools, 1 female (USNM 72865). Pelican Island, Barbados-Antigua Expedition, 1918, M. J. Rathbun det., shallow water, 1 female (USNM 72864). Pelican Island, 03.ix.1937, Elisabeth Deichmann col., F.A. Chace det., 1 male (MCZ 10017). *DOMINICA*, 1992, 28.x.2014, W. Santana det., 1 ovigerous female (USNM 1256378). *BARBADOS*, Barbados-Antigua Expedition, sta. 25565, 1918, 1 female (USNM 72882). Off Sam Lord's Castle, Barbados-Antigua Expedition, 1918, C.C. Nutting col., M.J. Rathbun det., 5-7m, 1 female (USNM 72902). Bathsheba, Barbados-Antigua Expedition, 1918, M. J. Rathbun det., 1 female (USNM 58011). *GRENADA*, Grand Anse Bay, 12°01'45.19"N–61°45'21.29"W, 11.x.2012, Simone LRL; Dornellas, AP, Amaral VS cols., 27.xi.2019, Colavite, J. det., 5-10m, 1 male (MZUSP 40163). *TRINIDAD* and *TOBAGO*, *Tobago*, Pigeon Point, 17-19.viii.1937, E. Deichmann col., F.A. Chace Jr det., 1 male (MCZ 9927). *COLOMBIA*, *Old Providence Island*, Archipelago of San Andrés, R/V Albatross, 4-9.iv.1884, M.J. Rathbun det., 1 female (USNM 16184). Archipelago of San Andrés, Presidential Cruise, sta. 30, 6.viii.1938, W. L. Schmitt col., M. J. Rathbun det. 1 juvenile (USNM 77842). *BONAIRE*, Vista Alegre, R/V Velero III, sta. A46-39, 23.iv.1939, Garth det. 1 juvenile male, 1 female, 1 ovigerous female (NHMLA-AHF

39297). *BRAZIL*, Pontal do Cabo, 17.ix.2001, *Sargassum* sp., 1 juvenile (MZUSP 15455). Praia do Piloto, vii.1974, 15.i.1987, G. Melo det., 1 female (MZUSP 8285). Praia do Piloto, vii.1971, Equipe CEZ col., 15.i.1987, G. Melo det. 1 male (MZUSP 8284). *Rio Grande do Norte*, Praia de Búzios, Nísia Floresta, 10.ii.2009, W. Santana, A. Pinheiro, col./det., 22.v.2009, 1 male (MZUSP 20539). *Alagoas*, Pajuçara, Maceió, ii.1993, 01.ii.2002, G. Melo det., 1 female (MZUSP 15264). Praia Paripueira, 01.ii.1983, M. Christoffersen col., P. A. Coelho det. 1 male (MZUSP 5980). *Bahia*, Itapoã, Salvador, 7.vii.1971, 5.vi.1974, G. Melo det., 1 male (MZUSP 3990). Porto da Barra, Salvador, left, 24.iv.2006, R. Bispo, R. Jhonsson, W. Santana, F. Faria col., iv.2008, G. Melo det. 3 females (MZUSP 18626). *Espírito Santo*, Aracruz, 17.iii.1992, 1 juvenile (MZUSP 32460). Santa Cruz, 18.vii.1970, 15.i.1987, G. Melo det., 1 male (MZUSP 8283),

Diagnosis. Rostrum as long as interorbital length, bifurcated, base elongated, parallel with U-shape distance, acute at the tip. Seven spines in posterior region aligned between lateral spines.

Description: Cephalothorax and appendages densely covered with short, velvet-like pubescence. Carapace pyriform with long and robust hooked setae arranged in two rows from rostral spines and orbital region to branchial spines. Rostrum as long as interorbital length, bifurcated, base elongated, parallel with U-shape distance, acute. Interorbital region slightly depressed medially. Hepatic region inflated with one very small tubercle. One mesial metagastric sharp tubercle, one mesial urogastric tubercles, one lateral mesobranchial tubercle, one mesial intestinal blunt spine. Seven spines in posterior region aligned between lateral spines (one lateral branchial longest. laminated; one lateral-mesial metabranchial; one shortest metabranchial; one mesial cardiac). Branchial region inflated. Orbital region prominent, eyes

completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine blunt, directed upwards, longer than postorbital. Postorbital spine blunt.

Antennular fossae wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna curved directed towards lateral, visible in dorsal view; proximal lateral border of basal article of antenna compounding ventral margin of orbits. Antennal flagella, straight, behind rostrum, shorter than rostral spines.

Epistome narrower than antennular fossae at anterior edge, anterior margin smooth. Subhepatic region smooth. Buccal field sub-rectangular, wider than long, narrower at posterior edge, anterolateral angles smooth. Third maxillipeds covering completely buccal frame. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, inflated, separated from subhepatic region by groove, with one spine on border medially.

Males chelipeds equal, longer than legs, more robust in adults covered with hooked setae. Ischium smooth; merus armed sparsely tubercles, two rows of three blunt spines in dorsal face, one blunt spine on distal border; carpus armed with 3-4 blunt spines, propodus granulated, with two prominent tubercles in dorsal face. Dactylus arched in adult, distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with dark brown color in fixed specimens. Females chelipeds shorter, slender. Ischium, merus, carpus and propodus with less tubercles than males, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half declivous in ventral view, forming two lateral depressions and a carina along margin of sterno-pleonal cavity

in males. Thoracic sternites V-VII with one strong, transverse ridge each, forming a depression between sternites in males. Telson fully fitted to sterno-pleonal cavity, anterior margin smooth. Sternites with smooth surface in male and females. Sternite VIII no visible.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming a longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, parallels, slightly curved in proximal half, with a torsion in distal half, bilobed apex. Lateral lobe long, curved downwards and toward the pleon, apical plate wider, mesial lobe short and curved upwards; with a distinct projection on distal half. Lateral margin smooth. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Light brown to dark green, dactylus of walking legs dark brown brindle (based on database photos of the specimens MNHN IU 2016-10111; MNHN IU 2016-10137; MNHN IU 2016-10275).

Type locality: The United States Virgin Islands, St. Thomas, 18.345591° N–64.923613° W.

Geographic distribution: western Atlantic: Bermuda, United States (from Florida), Cuba, Haiti, Puerto Rico, Caribbean Island, Belize, Colombia (Archipelago of San Andrés), Curaçao and Brazil (from Amapá to Espírito Santo, including the Archipelago of Fernando de Noronha) (Fig. 30)

Remarks. The type material of *Pericera subparallela* was originally deposited in the USNM collections, two cotypes, a male and a juvenile female, designated by Stimpson (1860). Currently, the specimens are deposited in the Crustacean collection of the Museum of

Comparative Zoology of the Harvard University. A post molt soft male (MCZ 1243, Fig. 31 E) is designated as lectotype; the other specimen is a juvenile female designated here as paralectotype (MCZ 1227). It is one of few type materials from the Prof. Stimpson descriptions that are still preserved.

Morphological variations observed in *Macrocoeloma subparallelum* include: (i) urogastric tubercle in some juvenile specimens not visible, including the type material; (ii) preorbital spine as long as the postorbital in small specimens; (iii) some specimens examined presented a sculpted region between the row of branchial spines and the carapace distal edge, surrounding the intestinal spine (e. g. NHMLA-AHF 39299; USNM 24200; USNM 72902).

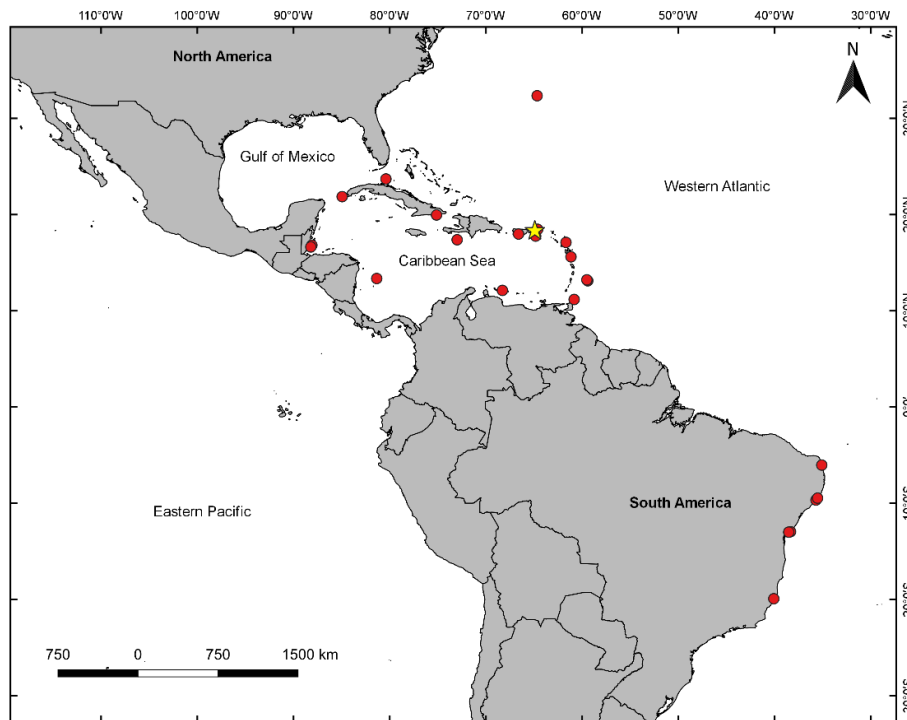


Figure 30. *Macrocoeloma subparallelum* (Stimpson, 1860). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

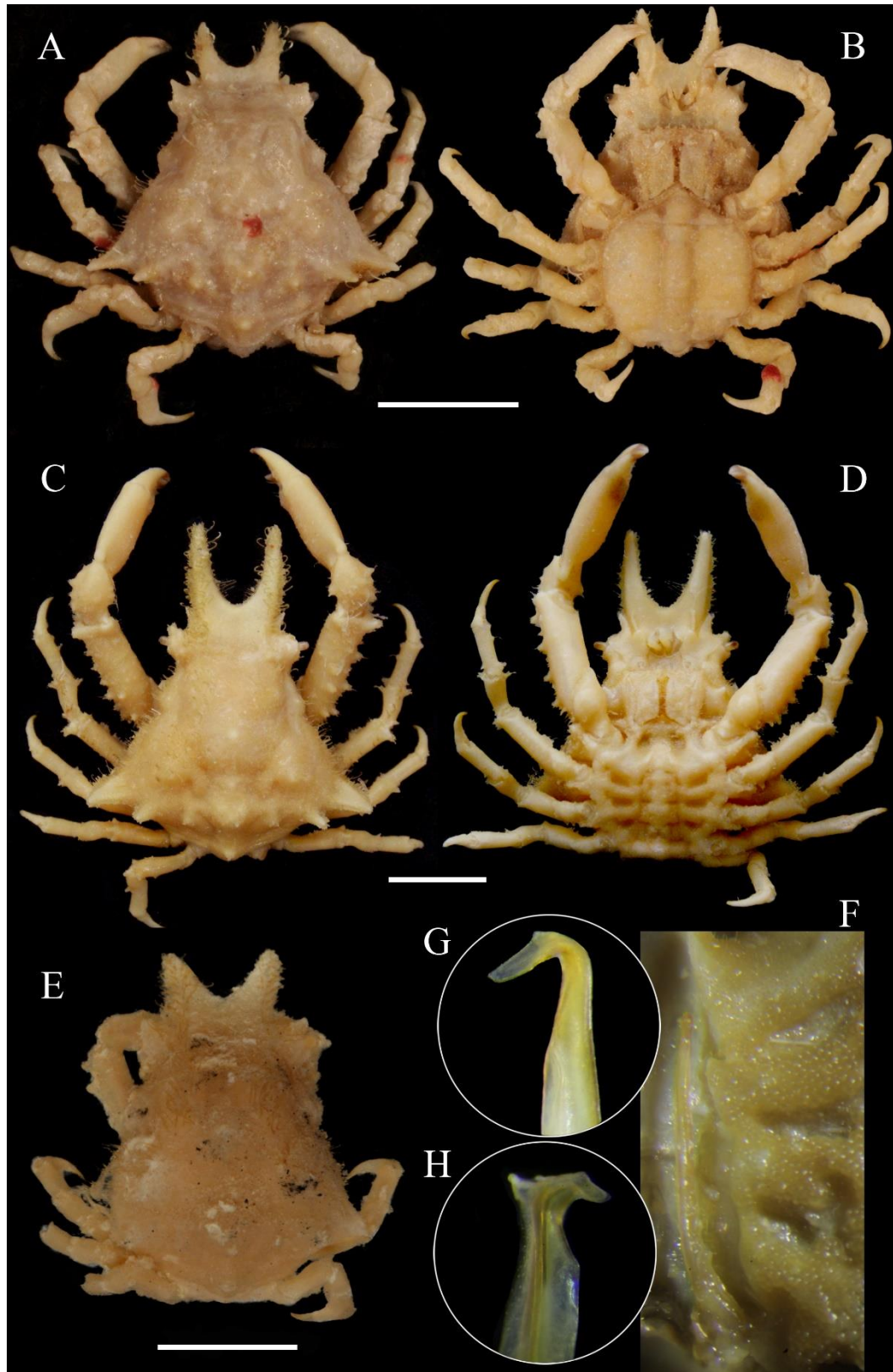


Figure 31. *Macrocoeloma subparallelum* (Stimpson, 1860). A–B, female (USNM 1256378). C–D, male, (MOUPE 15490). E, male lectotype, cl. 13.98 mm, cw.9.90 mm (MCZ 1243). F sterno-pleonal cavity with first (G1) and second (G2) gonopods in place; G, G1 lateral view in detail; H, G1 apex in detail (USNM 48666). A, C, habitus; B, D, ventral view; E, frontal view. Scale bars 10 mm.

***Macrocoeloma trigonum* (Dana, 1851)**

(Figure 29 D, 34 A-B, 35 A-F)

Pericera trigona Dana 1851:271 [type locality: Brazil, Rio de Janeiro; type material: female, non-extant].

Pericera trigona – Dana, 1852: 108; Dana, 1855: (atlas) pl. 3, Fig. .4 a-d.1

Macrocoeloma trispinosum – Moreira, 1901: 64, 136; Coelho, 1971: 141; Coelho e Ramos: 1972, 217; Fausto-Filho, 1974: 19; Melo: 1996, 221, fig. 1; 1998: 464; Melo and Veloso, 2005: 799; Alves et al., 2008: 59; Coelho et al., 2008: 21; Alves et al., 2012: 55.

Macrocoeloma trigona – Ng et al., 2008: 119.

Material examined. BRAZIL, Pernambuco, Archipelago of Fernando de Noronha, 1876-1877, R. Rathbun Expedition, 1 female (USNM 19961). Rio Grande do Norte, Rocas Atoll, R/V Almirante Saldanha, sta. 1662-A, 03°50' S–33°45'W (Rocks), 09.x.1967, H. R. Costa det., 1 juvenile (MZUSP 8610). Ceará, 120 miles off Fortaleza, R/V Canopus, viii.2005, Coltro, J. col., 1 female (MZUSP 16944). Paraíba, R/V Albatross, sta. 2758, 06°59'30"S–34°47'00"W, 16.xi.1887, 36.57m, 1 ovigerous female (USNM 21931). Paraíba, Projeto Algas, sta. 86 D, 06°33' S–34°47'W, 04.vi.1981, 21.xii.1983, G. Melo det., 26m, 1 female (MZUSP 5908). Bahia, REVIZEE Benthos, R/V Astro Garoupa, sta. 7, 16°07'30"S–38°10'52"W, 30.vi.2001, 40m, 2 juveniles (MNRJ 16253). Espírito Santo, Archipelago of Trindade and Martin Vaz, REVIZEE Benthos, R/V Astro Garoupa, sta. 42, 20°44'28"S–31°50'03"W, 11.vii.2001, 80-90 m, 1 juvenile female (MNRJ 16499). Espírito Santo, licentiate area by LO. 246/2008, 20.51791 S–40.28422 W, subarea 10, i.2014, W. Santana det., 1 male (MZUSP 21802). Rio de Janeiro, Baía da Ilha Grande, i.2007, iii.2007, G. Melo det., 2 females (MZUSP 17903). Rio de Janeiro, Praia Forno, Búzios, 17.ii.1998, A. Carvalho col., J. M. Braga det., 1 female (MZUSP 19021). Rio de Janeiro, Arraial do Cabo, Prainha, 18.ix.1993, C.S. Serejo, C. Etcheverria col., 1 male

(MNRJ 5740). São Paulo, Ilha Bela, São Sebastião, x.1925, H. Luederwaldt col., 2019, J. Colavite det., 1 male (USNM 1278769). São Paulo, São Sebastião, 15.xii.1961, S. Rodrigues col., 02.iv.1985, G. Melo det., 1 female (MZUSP 6464). São Paulo, Baraqueçaba Beach, São Sebastião, A. Reigada col., 07.iii.1987, G. Melo det., 1 male (MZUSP 8650). Rio Grande do Sul, Prof. W. Besnard R/V, GEDIP, sta. 1464, 6.iii.1971, 16.xii.1982, G. Melo det., 1 juvenile female (MZUSP 5288).

Diagnosis. Spine of basal article of antenna flat, straight towards laterally. Gastric and cardiac region well-delimited with one mesial spine each. Intestinal spine curved upward. Lateral spines continuing carapace line, forming an arch with distal area of metabranchial region, tips slightly directed backward.

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace triangular with long hooked setae interspersed mainly in rostral, gastric and lateral branchial region. Rostrum short, approximately half of interorbital length, bifurcated, parallel, divergent in the tip, acute. Interorbital region depressed medially. Gastric and cardiac region well-delimited with one mesial spine each. Intestinal spine curved upward. Lateral spines continuing carapace line, forming an arch with distal area of metabranchial region, tips slightly directed backward. Eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine blunt, pointed forward as long as postorbital spine, postorbital spine blunt. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna flat, straight towards laterally. Antennular fossae wider than long, with smooth margins. Interantennular septum elongated, slightly compressed laterally, forming distinct lobe ventrally directed. Antennal flagella short with two third of rostral spine, point laterally, visible in dorsal view

Epistome narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth. Subhepatic region with one tubercle aligned with antennal gland. Buccal field sub-rectangular, longer than wide, narrower at posterior edge with one tubercle in anterolateral angles. Third maxillipeds covering buccal frame, leaving a gap between ischium and merus. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, with one mesial tubercle.

Males chelipeds equal, longer than legs, robust in adults. Ischium smooth; merus armed with 4 dorsal tubercles; carpus with sparsely tubercles; propodus smooth. Dactylus arched in adult, leaving a gap between fingers. fixed finger slightly arched on tip. Fixed and movable finger distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males, distal half with light brown color in fixed specimens. Females with shorter, slender, propodus sculpted by distinct sulcus in lateral, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tip.

Thoracic sternum I-IV fused, broadly triangular, smooth, anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Sterno-pleonal cavity as long as telson, telson is fully fitted to cavity, anterior margin smooth. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male Telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, parallel, with distal torsion, bilobed apex. Sternal suture present. One distinct lamella continuing sternal suture to middle of apical plate; apical plate with an aperture in pleonal view; lateral lobe elongated covered with small

spines in distal boarder. Lateral margin smooth with sparsely setae. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Dark orange to red (Fig.34)

Type locality: Brazil, Rio de Janeiro.

Geographic distribution: Brazil: Ceará, Rio Grande do Norte, Recife, Espírito Santo, Rio de Janeiro, São Paulo and Rio Grande do Sul (including Archipelago of Fernando de Noronha, Rocas Atoll and Archipelago of Trindade and Martin Vaz) (Fig. 33).

Remarks. Coelho (1971) in his notes about the majoids from Brazil, observed that the reexam of *M. trispinosum* and the total area of occurrence could be proving the existence of three valid species and included the specimens from Brazil in the typical group of *M. trispinosum*, based on Rathbun identification of specimens from Paraíba and Bahia. These two specimens deposited at the USNM collection, one very small ovigerous female (USNM 21931[Paraíba]) identified as *M. trispinosum* and an adult male with the rostrum and lateral spines broken (USNM 19961[Fernando de Noronha]) included in *M. nodipes*, were the only material of *M. trispinosum* from Brazil examined by Rathbun (1925). However, during this study the reexam of the specimens from Brazil, identified as *Macrocoeloma trispinosum*, revealed to be the morphologically different of *M. nodipes* and *M. trispinosum* from North Atlantic and Caribbean Sea.

The Brazilian morphotype is characterized by: (i) lateral spines are less broad than *M. nodipes* and their margin continuing the margin of the carapace; (ii) carapace constricted behind the orbits; (iii) one mesial gastric and one mesial cardiac spine (Fig. 35). No significative

variations were noticed in this group, such as occurs in *M. nodipes* (variety) (see *Macrocoeloma nodipes* Remarks).

Beside those specimens deposited in USNM collection mentioned above, another adult male from Ilha Bela, São Sebastião-SP (USNM 1278769), was identified at USNM collection. This specimen collected in 1925 and donated by Hermann Luederwaldt, was found at the unidentified material. It is the only specimen in good conditions deposited in the collections outside the Brazil examined by me, despite of that, the other specimens of USNM collection have the diagnostic characters of this species.

The similarities between the specimens collected in the Brazilian coast and the illustrations and description of Dana (1855: pl. 3, fig. 4)(Fig. 32) of *Macrocoeloma trigonum* called our attention. *Pericera trigona* Dana, 1852 was described based on Fiji Islands material collected during the United States Exploring Expedition, being the first and unique record of the genus outside the Americas.

The United States Exploring Expedition is one of the most important expeditions that had scientific, economic, political and diplomatic objectives, commended by the Captain Charles Wilkes. Scientist and artist were invited to participate of the travel, between those the mineralogist, James Dwight Dana. The expedition collected forty tons of plants, animal and mineral specimens, organized later in collections that were the foundation of what became the Smithsonian Institution, Washington-DC (Viola and Margolis, 1985). Dana was responsible to wrote the crustacean report, illustrated by 61 plates, and described 230 new species, most of them invalid nowadays (Dana, 1852).

The expedition started from the port of Norfolk, Virginia in 1838, finishing the trip in 1842, being Rio de Janeiro the first pier off the United States. The expedition pass thought many problems during the voyage, which may have caused errors in the labeling of the material,

which may lead Dana to describe the species as being from the Fiji Islands, being this locality is probably a mistake (see Dana, 1852:1).

Similar cases were related in literature including species occurring in the Brazilian coast, for example: *Sesarma trapezium* Dana, 1852 synonymous of *Armases rubripes* (Rathbun, 1897) (Abele, 1974); *Acanthonyx simplex* Dana, 1852 junior synonymous of *A. petiverii* H. Milne Edwards, 1834 (Emparanza et al., 2007) and *Galene hawaiiensis* Dana, 1852 junior synonym of *Panopeus herbstii* H. Milne Edwards, 1834 (Ng et al., 2008 footnote in pg.191).

Considering that this species still valid in the literature (Ng et al., 2008) and despite of its type material is considered lost for a long time, the facts presented above are sufficient to recognize the specimens from the Brazilian coast, belongs to *M. trigonum*, wrongly called as *Macrocoeloma trispinosum* or *M. nodipes* (see *Macrocoeloma trispinosum* Remarks). Thereby, based on evidences presented above, we corrected here the original type locality of *Pericera trigona* to the Rio de Janeiro city and a neotype will be designated to a specimen from the same locality (cf. ICZN art.76A.2). Considering the recommendations of The International Code of Zoological Nomenclature (cf. ICZN art.75A), that topotypical specimens should be preferred to neotype designation, we will elect a suitable specimen in future.

The epithet of this species is corrected here in accordance to the genus gender (neuter) being *Macrocoeloma trigonum* the correct combination (cf. ICZN art. 31.2).

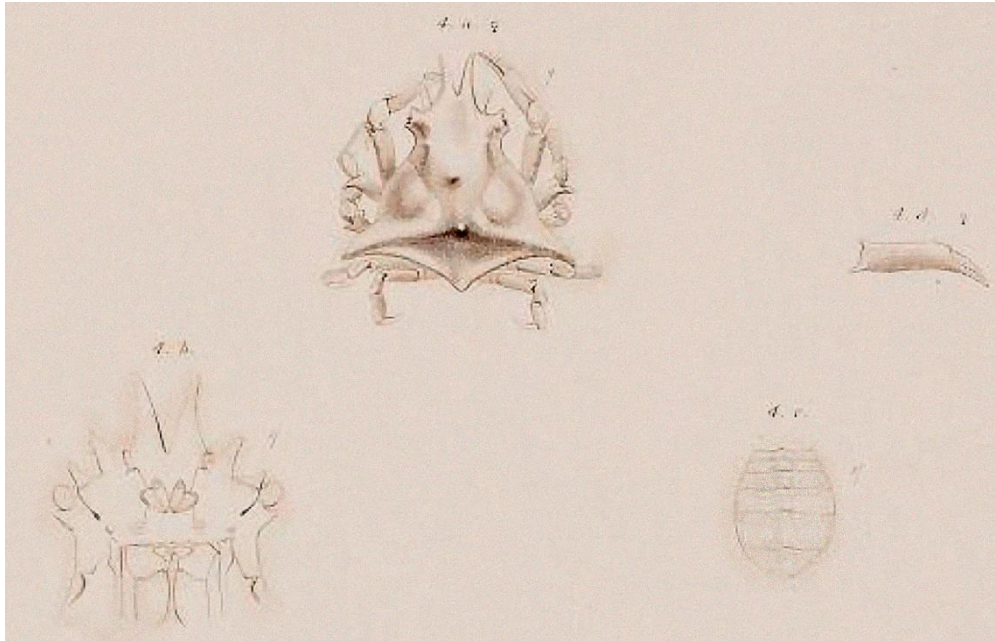


Figure 32. *Pericera trigona* Dana, 1852. Illustration extracted of Dana (1855); plate 3; fig. 4 a, female, dorsal view; b, ventral view of front; c, pleonal view; d, cheliped.



Figure 33. *Macrocoeloma trigonum* (Dana, 1852). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

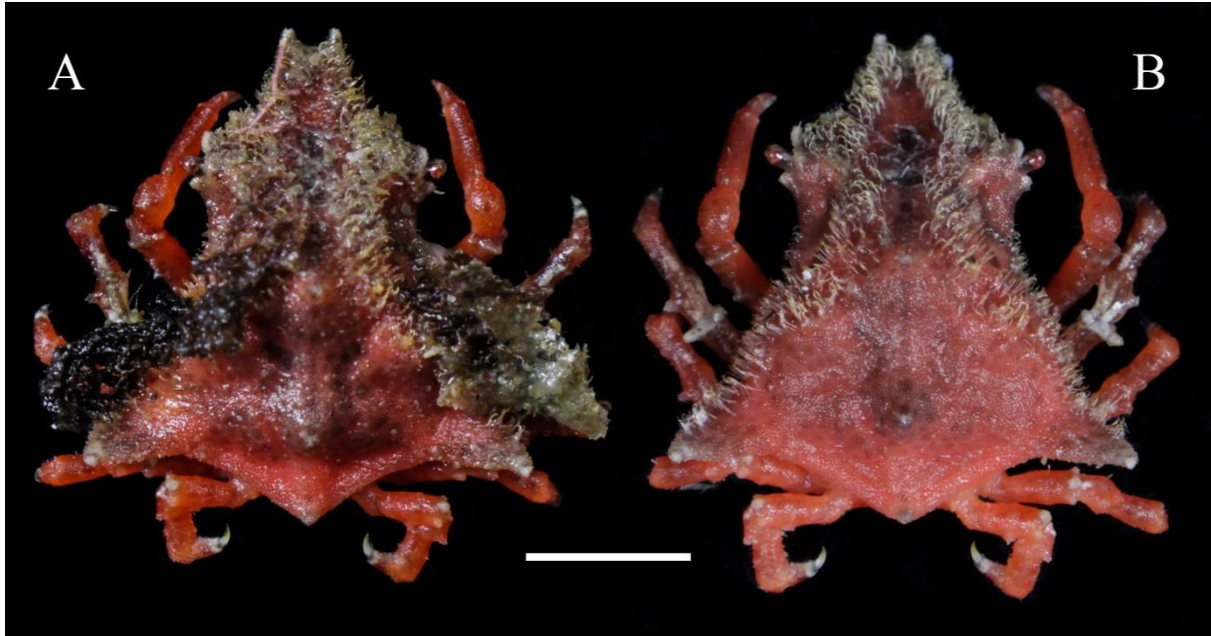


Figure 34. A, B, Habitus, dorsal view of *Macrocoeloma trigonum* (Dana, 1851) (LSZ179). A, Crab decorated with sponges for camouflage; B, Color in life. Scale bars: 10 mm.

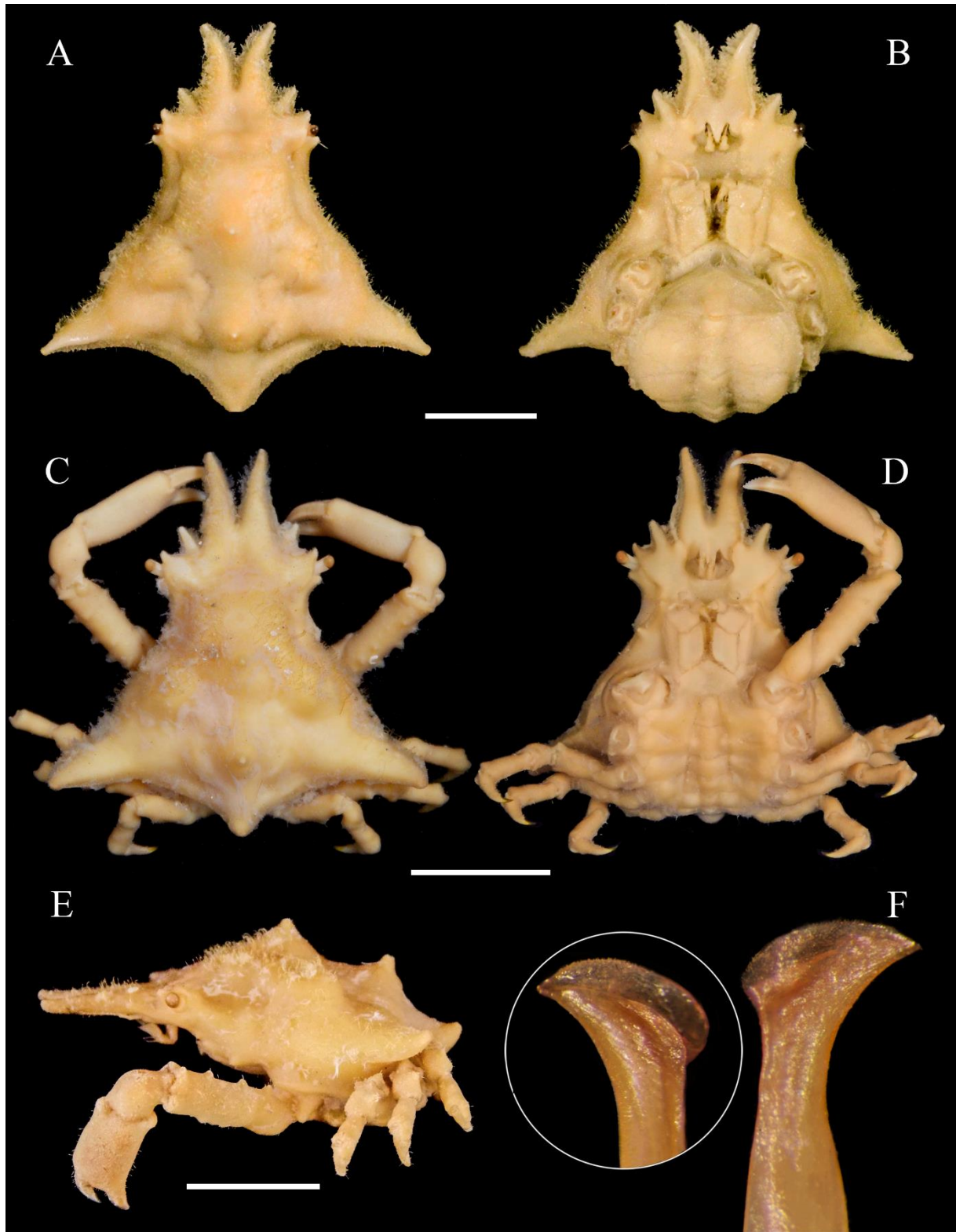


Figure 35. *Macrocoeloma trigonum* (Dana, 1852). A–B, female (MZUSP 16944). C–E, male (MZUSP 8650). F, distal half of first gonopod pleonal view, sternal view in the detail (USNM 1278769). A, C, Habitus; B, D, ventral view; E, lateral view of cephalothorax. Scale bars 10 mm.

***Macrocoeloma trispinosum* (Latreille, 1825)**

(Figure 29 A, 37 A-F)

Cancer 9 Browne, 1756: 422, pl. 48 (not 46) fig.2 [type locality: Jamaica; type material: non-extant].

Pisa trispinosa Latreille, 1825: 142 [type locality: Nouvelle Hollande? by error; non-extant].

Pericera trispinosa – Latreille, 1834: pl. 10.2, fig.3-3a; H. Milne Edwards, 1834: 336; Lucas, 1840:135; Guérin-Méneville, 1843:09, pl. 8, f. 3-3a.; Gibbes, 1850: 172; Saussure, 1858: 426; Stimpson, 1871: 112; Von Martens, 1872: 84, pl.4, figs.4a,4c; A. Milne-Edwards; 1873: 52, pl. 15, fig. 2; Aurivillius, 1889: 55, pl.2, fig.2; Ives, 1891: 178.

Macrocoeloma trispinosa – Miers, 1879: 665; Miers, 1886: 79-80; Kingsley, 1879: 387; Young, 1900: 75.

Macrocoeloma trispinosum – Rathbun, 1892: 249; 1898a: 576; 1898b: 256; 1899: 576; 1901: 74; 1925: 466, text-fig. 132, pl. 166, fig. 1, pl. 167, figs. 1-2; Moreira, 1901: 64, 136; Verril, 1908: 414, fig. 44; Hay and Shore, 1918: 457, pl. 38, fig. 11; Boone, 1930: 108, pl. 33, figs A-D; Williams, 1965, 263, fig. 243, 245j; 1984: 328, figs. 264, 275l; Abele, 1970: 108; Felder, 1973: 53, pl. 87, fig. 9; Powers, 1977: 52; Vélez, 1977: 134; fig. 26; Abele and Kim, 1986: 46, fig. 517 a, b, c; Coelho, 1971: 141; Coelho e Ramos: 1972, 217; Fausto-Filho, 1974: 19; Melo: 1996, 221, fig. 1; 1998: 464; Marcano e Bolaños, 2001: 79; Melo and Veloso, 2005: 799; Alves et al., 2008: 59; Coelho et al., 2008: 21; Ng et al., 2008: 119; Alves et al., 2012: 55; Carmona-Suárez and Poupin, 2016: 358, fig.5I-J.

Macrocoeloma trispinosum trispinosum – Wass, 1955:168; Abele and Kim, 1986: 46, fig. 516a-c; Nizinski, 2003: 130.

Type material. Neotype, male, cl. 33.45 mm, cw. 28.6 mm; *JAMAICA*, Kingston Harbor, 1893, R.P. Bigelow col., M. J. Rathbun det. (USNM 17959)

Material examined. *UNITED STATES*, Florida, Off Cape Sable, sta. 7356, 18.xii.1902, 21.03m, 1 male (USNM 46923). Bahia Honda, 1893, State University of Iowa Bahamas Expedition col., M. J. Rathbun det., 1 juvenile female (USNM 72955). *BAHAMAS*, off Whale Cay, 9.vii.1904, F.A. Chace Jr. det., 23.77m, 1 ovigerous female (MCZ 8928). *CUBA*, Esperanza, Tomas Barrera Expedition, sta. 1+2, 11.v.1914, M. J. Rathbun det., 1 male, 1 ovigerous female (USNM 48652). off Varadero, Cárdenas Bay, Matanzas, 24.i.1957, W. L. Schmitt col., 1957, F.A Chace det., 3.6-4.5 m 1 male, 1 ovigerous female (USNM 99928). Cabanas, Tomas Barrera Expedition, 8-9.vi.1914, Henderson and Bartsch col., M. J. Rathbun det., 1 female (USNM 48660). Siguaneya Bay, Smithsonian-Roebbing Exploring Expedition, sta. 124, S. R. P. Rarsch col., J. Colavite det., 21.9-47.5 m, 1 male, 1 ovigerous female, 2 juveniles (USNM 76480). *JAMAICA*, T. H. Morgan Collection, 1 male, 1 ovigerous female (USNM 17202). Bague Island, Montego Bay, 23.vi.1919, 1 male (USNM 43026). Bague Island, Montego Bay, 2.vii.1910, E. A. Andrews, 1 male, 1 ovigerous female (USNM 43016). Bague Island, Montego Bay, 6.vii.1910, E. A. Andrews col., 2 ovigerous female (USNM 43028). Bague Island, Montego Bay, 2.vii.1910, E. A. Andrews col., 1 male (USNM 43027). Kingston Harbor, v-vi.1896, F. S. Conant det., 1 male, 1 ovigerous female (USNM 19584). Kingston Harbor, 1893, R.P. Bigelow col., M. J. Rathbun det., 1 male (USNM 17959). Kingston Harbor, 1893, R.P. Bigelow col., M. J. Rathbun det., 1 ovigerous female (USNM 17958). *PUERTO RICO*, off Boca Prieta, Fanduco Cay, Steamer R/V Fish Hawk, sta. 6075, 25.i.1899, U.S. Fish Commission col., 15.5 m, 1 female (USNM 24092). South West of Parguera, Laurell reef, 13.viii.1964, K.B. Sandved col., 1.5 m, 2 males, 2 females, 1 ovigerous female (USNM 1278771). *UNITED STATES VIRGIN ISLANDS*, St. Thomas, S. R. Shoemaker col., 1915, M.

J. Rathbun det., 1 ovigerous female, 1 female, 2 males (USNM 50954). Gregerie Channel, between Water Island and St. Thomas, sta. 7, 7.vii. 1915; M. J. Rathbun det., 0.9-5 m, 1 ovigerous female, 1 juvenile female (USNM 50956). *ANTIGUA*, English Harbor, Antigua-Barbados Expedition, 1918, University of Iowa State col., M. J. Rathbun det., 1 ovigerous female (USNM 72956). *GUADELOUPE*, La faille?. vi.1948, A. Quested col., F.A Chace Jr. det., 1 male (USNM 89589). KUBENTHOS 2012, sta. GR39, 16°18.02'N–61°33.03'W, 20.v.2012, MNHN col., 1 male (MNHN 2013-5951). *SANTA LUCIA*, Port Castries, R/V Albatross, 30.xi.1887, M. J. Rathbun det., 1 male (USNM 21930). *PANAMA*, Caledonia Bay, sta. A2-39, 3.vi.1939, J. Garth det., 1.8-12.8 m, 1 ovigerous female (AHF 39291). *CURAÇAO*, U. S. Fish Commission, R/V Albatross, 10-18.ii.1884, 1 male, 1 female, 1 ovigerous female (USNM 16181).

Diagnosis. Hepatic region constricts with lateral spines of branchial region acute, cylindrical, slightly directed backward. Gastric region well-delimited with tree distinct tubercles (two lateral protogastric, one mesial metagastric).

Description: Cephalothorax and appendages fully covered with short, velvet-like pubescence. Carapace pyriform with long hooked setae interspersed mainly in rostral, gastric, lateral and branchial regions. Rostrum with approximately two-thirds of interorbital length, bifurcated, straight, ending in acute tip. Interorbital region depressed medially. Gastric region well-delimited with tree tubercles (two lateral protogastric, one mesial metagastric). Intestinal spine curved upward. Lateral spines of branchial region acute, cylindrical, slightly directed backward. Eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine blunt, pointed forward and upward, as long as postorbital spine, postorbital spine blunt. Antennular fossae distinctly wider than long, with smooth margins. Interantennular

septum elongated, slightly compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of basal article of antenna cylindrical, straight towards lateral. Antennal flagella shorter than rostral spine, straight, visible in dorsal view.

Epistome narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth. Buccal field sub-rectangular, longer than wide, narrower at posterior edge, anterolateral angles expanded. Third maxillipeds covering buccal frame, with a small gap between meri. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by groove, with one tubercle on border medially.

Male chelipeds equal, longer than legs, densely covered by pubescence, more robust in adults. Ischium, merus, carpus and propodus with small sparse tubercles. Dactylus arched in adult males, distinctly shorter than palm, leaving a small gap between fingers. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with light brown color in fixed specimens. Females with shorter, slender chelipeds. Ischium, merus, carpus and propodus with less tubercles than males, dactylus slightly arched without gap.

Walking legs slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth, covered by pubescence; anterior half declivous in ventral view, forming a carina along margin of sterno-pleonal cavity in males. Thoracic sternites V-VII with one strong, transverse ridge each, forming a depression between sternites in males. Sterno-pleonal cavity fully fitted to cavity or leaving a small gap in anterior margin. Sternites with smooth surface in males and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, parallel, with bilobed apex. Sternal suture present. One thin lamella continuing from sternal suture to the tip; apical plate with aperture in pleonal view; lateral lobe elongated covered with small spines in distal boarder. Lateral margin smooth with setae sparsely. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Setae yellowish or reddish brown (Rathbun, 1925)

Type Locality: Jamaica, Kingston Harbor.

Geographic distribution: western Atlantic, from North Carolina to Colombia, Caribe (Fig. 36).

Remarks. Latreille (1825) originally described the type locality of *Pisa trispinosa* as “Nouvelle Hollande? Péron et Lesueur”. However, Latreille cited the collectors name, probably meaning the Expedition of François Péron (1816) to Australia, called “New Holland”. Rathbun (1925) considered this location an error, since this species has a distribution restricted to western Atlantic. However, Nouvelle Hollande was also a name used for some Dutch colonies, as the Caribbean Island: Tobago, Sint Eustatius, St. Martin’s and Saba, as observed by Boone (1930). In the same publication, Latreille (1825) also described *Pisa bicornuta*= *Omalacantha bicornuta* (another western Atlantic species) from same type locality than *Pisa trispinosa*=*Macrocoeloma trispinosum*, this fact reinforced a possible mistake considering the

current recorders for both. Years later, Latreille (1834) changed *Pisa trispinosa* to *Pericera*, a new combination that only appeared in the plate caption (pl. 10.2, fig.3-3a). Taking into account the absence of the type material, an inaccurate type locality and the poorly detailed original description, only the illustration of Latreille (1834) well detailed to help the identification of *M. trispinosum*. This have caused confusions in the identification with other species, such as *M. nodipes*, a species several times considered a subspecies or even a junior synonym of *M. trispinosum* (Rathbun, 1925; Wass, 1955; Williams, 1965; 1984; Powers, 1977; Soto; 1980; Keith, 1985; Abele and Kim, 1986; Nizinski, 2003). Latreille (1834) replace *Pisa trispinosa* to *Pericera*, the new combination only appeared in the plate legend (pl. 10.2, fig.3-3a).

Due the impossibility to designate a topotypical specimen as neotype of *Pericera trispinosa*, take into account the problems detailed above, we designated a male (USNM 17959) from Jamaica (cf. ICZN art.75 and 76.3), based on the fidelity of the Latreille (1825) description and draws, material preservation and the locality that seems to have more abundance of this species, based on examined material.

We followed the morphological characters preestablish by Rathbun (1925) to distinguish: (i) the lateral spines, shape and direction; (ii) carapace shape and (iii) spines or tubercles in the carapace, we were able to separated our own groups. All the material examined by Rathbun (1925) were reevaluated and more specimens were included. Any other distinguish characters was observed, even in the first gonopods.

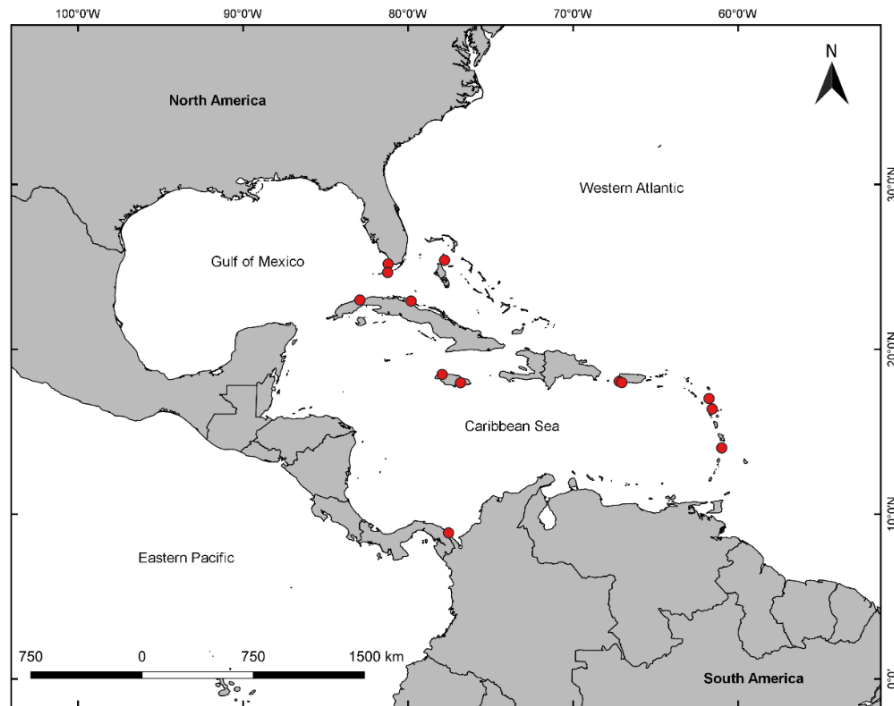


Figure 36. *Macrocoeloma trispinosum* (Latreille, 1825). Geographic distribution. Red circles = distribution based on examined material.

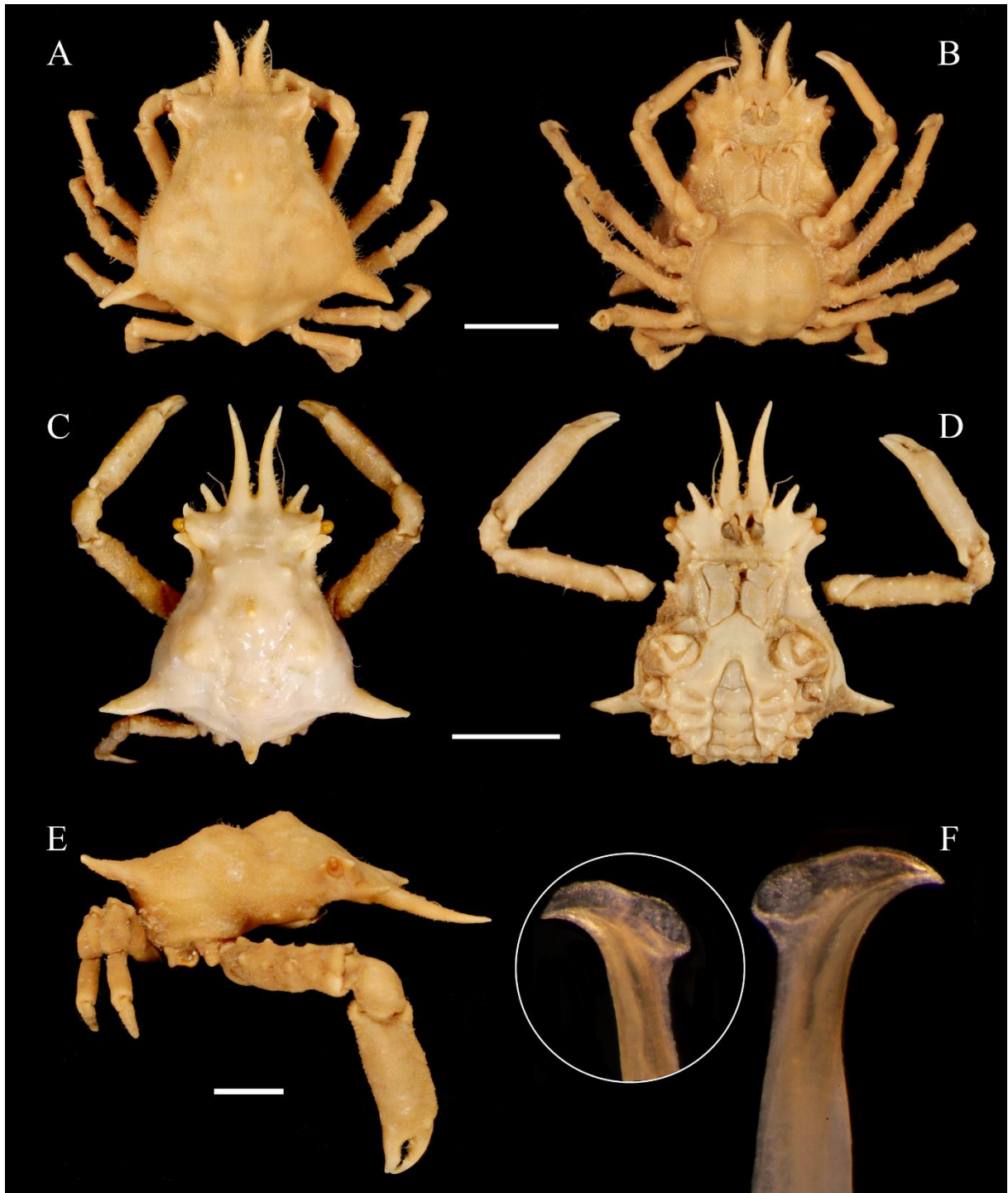


Figure 37. *Macrocoeloma trispinosum* (Latreille, 1825). A–B, female (USNM 43028). C–D, male neotype, cl. 33.45 mm, cw. 28.6 mm (USNM 17959). E, male (USNM 21930). F, distal half of first gonopod sternal view, pleonal view in the detail (USNM 43027). A, C, habitus; B, D, ventral view; E, lateral view. Scale bars 10 mm.

***Macrocoeloma villosum* (Bell, 1836)**

(Figure 39 A-G)

Pericera villosa Bell, 1836: 173 [type locality: Ecuador, Guayaquil Bay; type materials: syntypes: 1 male (OUM 13761), 1 female (OUM 13762)].– Bell 1836b: 59, pl. 12, figs. 4, 4k-n; H. Milne Edwards, 1837: 140; A. Milne-Edwards, 1873: 59; Nobili, 1901: 30.

Pericera fossata Stimpson, 1860: 181 [type locality: Cape San Lucas, Mexico; type material: non-extant]. – A. Milne-Edwards, 1873: 53; Bouvier, 1895: 7.

Macrocoeloma villosa – Miers, 1886: 79.

Macrocoeloma villosum – Rathbun, 1910: 574; 1925: 482, pl. 269, figs. 4-7, text-fig. 135; Crane, 1937: 63, pl. 3, fig. 12; Garth, 1958: 417, pl. Y, fig. 5; pl. 46, fig. 2; del Solar, 1970: 34; Di Mauro, 1981: 169.

Type material. Lectotype, male, cl. 36 mm, cw 36 mm; *ECUADOR*, Guayaquil Bay (OUM 13761). Paralectotype, 1 juvenile female, cl. 21 mm, cw 18 mm; same location data (OUM 13762) (Fig. 39 E, F) (by present designation).

Material examined. *MEXICO*, Santa Inez Bay, Baja California, Templeton Crocker Expedition, R/V Zaca, iv.1936, J. Crane det., 1 juvenile male (AMNH 13390). Gulf of California, Agua Verde Bay, R/V Velero III, sta. 1099-40, 25°31'05"N–111°02'30"W, 12.ii.1940, J. Garth det., 1 male (NHMLA-AHF 40300). *ECUADOR*, Manta Bay, Allan Hancock Pacific Expeditions, R/V Velero III, sta. 400-35, 0°56'30"S–80°44'18"W, 19.i.1935, Garth det., 1 male (NHMLA-AHF 6980). West of Manta, Allan Hancock Pacific Expeditions, R/V Velero III, sta. 403-35, 0°56'43"S–80°44'43"W, 20.i.1935, J. Garth det., 1 male (NHMLA-403-35). West of Manta, Allan Hancock Pacific Expeditions R/V Velero III, sta. 403-35, 0°56'43"S–80°44'43"W 20.i.1935, 1 male (NHMLA-AHF 6908). Salinas, Walter

Rathbone Bacon traveling Scholarship Expedition, sta. 1, 2, 3, 12-14. ix. 1926, W. L. Schmitt col., M. J. Rathbun det., 3 males, 1 female (USNM 70942). Off Anconcito, Northwest side, Intertidal, 2°19.5'N–80°54.0'W, 6.iii.1970, 70-11, James H. McLean col., 18.i.2018, J. Colavite det., 2 juvenile females (NHMLA unnumbered). *PERU*, Piura, Punta Sal (4°0'S), rock bottom, 11.xi.1950, Koepke col., 1 ovigerous female (SMF 2239).

Diagnosis: Carapace subtriangulate with anterior region slightly down. Eyes diminutive. Lateral spines long, blunt, slightly curved forward. Posterior half of carapace, sternum and pleon deep sculpted.

Description. Cephalothorax and appendages fully and densely covered with short, velvet-like pubescence. Carapace subtriangulate, anterior region slightly down with hooked setae interspersed in two rows from rostral region to antero-lateral spines. Rostrum broad, base slightly elongated, bifurcated, divergent, as long as interorbital length. Lateral spines long, blunt, slightly curved forward. Gastric region elongated. Branchial, cardiac, intestinal regions well defined separated by deep sunken areas. Hepatic and subhepatic region broad. Eyes diminutive, completely protect in orbit when retracted, ocular peduncle not visible. Preorbital spine blunt, straight forward, longer than postorbital; postorbital spine diminutive as a small tubercle. Antennular fossae distinctly wider than long, with smooth margins. Interantennular septum elongated, compressed laterally, forming distinct lobe ventrally directed. First, second antennal articles fused to epistome, with suture visible, antennal gland opening near suture line. Spine of anterolateral angle of basal article of antenna strong, directed forward acute at the tip, reaching considerably beyond preorbital spine and lodged in orbital hiatus; posterolateral boarder elongated compounding ventral margin of orbit. Antennal flagella shorter than rostral spines, no visible in dorsal view with a long seta in a third article of flagellum.

Epistome narrower than antennular fossae at anterior edge, slightly depressed posteriorly, anterior margin smooth, posterior margin depressed. Buccal field subrectangular, anterolateral angles smooth. Third maxillipeds completely covering buccal frame. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by groove, smooth.

Males chelipeds equal, longer than legs, more robust in adults. Ischium, merus, carpus, propodus smooth. Dactylus distinctly shorter than palm, slightly arched in adult, leaving a small gap between fingers, inconspicuous carina on lateral face of dactylus. Cutting edges with subequal teeth in distal half, one distinct proximal tooth in larger males; distal half with light brown color in fixed specimens. Females with shorter, slender chelipeds, dactylus slightly arched without gap.

Walking legs short, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally with corneous tip.

Thoracic sternites I-IV fused, broadly triangular, smooth; anterior half declivous, forming two lateral depressions and a carina along anterolateral margin of telson. Thoracic sternites V-VII with one strong, transverse ridge each, forming a depression between sternites in males. Sterno-pleonal cavity as long as telson, telson is fully fitted to cavity, anterior smooth margin. Sternites with smooth surface in male and females. Sternite VIII concealed by pleon.

Pleonal somites I-VI, sculpted, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, with apex rounded. Female pleon markedly arched, with row of setae on margin. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, parallels, with bilobed apex. Lateral margin elongated with acute apex; mesial lobe short than lateral, surrounding aperture with several small spines. Sternal suture present. Lateral margin smooth. G2 slender, straight, very short (one fifth of G1 length).

Color in life: Male is brown red, the latter color predominating of the outer surface, that of the female is a darker brown without any admixture of red (Bell, 1836b), and dark buff, inclining to brownish, to *Pericera fossata* (Stimpson, 1860). Schmitt (1927), in his notes about the four specimens from Guayaquil (USNM 70942) related “Carapace and legs orange; chelae and their carpi and basal half of propodi blackish clove brown; distal half of dactyli dirty, but still uniform white”.

Type locality: Ecuador, Guayaquil Bay.

Geographic distribution: eastern Pacific: Mexico, Gulf of California, Ecuador to Playa Marcora, Punta Sal, Peru (Fig. 38)

Remarks. Bell (1836b) designated three specimens as the type material of *Pericera villosa*, an adult male and an immature female deposited in the Bell’s Museum, and an adult female deposited in the Museum of the Zoological Society (London), currently the Natural History Museum of United Kingdom (ACRONIMO). The syntypes were collected by Mr. Cuming in the Guayaquil bay, Ecuador, on sandy mud, at the depth of eleven fathoms (approximately 20.1m). This material was treated as nonexistent in the literature (Rathbun, 1925; Garth, 1958 pg. 5), as well as the material of *Pericera heptacantha* described by Bell in the same publication. Many years later, Di Mauro (1982) found several the types of Prof. Bell in the dry crustacean collection of Oxford University Museum (OUM), including an adult male (OUM 13761, Fig. 39 E) and an immature female (OUM 13762, Fig. 39 F), the syntypes of *Pericera villosa*. Unfortunately, the adult female sent to the Museum of the Zoological Society (London) is still lost. Considering the existence of the type material, the adult male of syntype series is here

designated as lectotype (OUM 13761) and the juvenile female as paralectotype (OUM 13762) of *Macrocoeloma villosum*.

Stimpson (1860) described *Pericera fossata* with the outline of anterolateral margin concave, and the dorsal surface and the rostral spines less divergent as the main differences between *P. fossata* and *Macrocoeloma villosum*. Miers (1886) synonymized *P. fossata* to *M. villosum* without any justification. Rathbun (1925) did not have any material of *P. fossata* to examine, but agreed with the synonym. Crane (1937) recorded a young male from Santa Inez point with cl. 9.6 mm (AMNH 13390), the northern record of a specimen similar to *P. fossata*. She observed differences between this specimen and the original description of *M. villosum*, such as the postero-lateral spines directed backward instead forward and the carapace slightly vermiculated. However, the previously known specimens were much bigger than that one.

Garth (1958) examined several specimens of this species and compared the material from Mexico and Ecuador. He observed that, if the characters of the specimens from Mexico (rostrum elongated and lateral spines placed more posteriorly) described by Stimpson to *P. fossata* were observed in more specimens, the validity of *P. fossata* should be reevaluated. He also called attention to the disjointed distribution of both morphotypes, *P. fossata* (Gulf of Mexico) and *Macrocoeloma villosum* (Ecuador) (see *Macrocoeloma villosum* remarks in Garth, 1958, pg. 418).

The fact of few specimens of *M. villosum* deposited in collections in the world makes difficult the evaluation of the validity of this species by the previous authors.

After the re-discovery of Bell's types (Di Mauro, 1982), the examination of the photos of *M. villosum* type material showed that the paralectotype, a juvenile female (OUM 13762, Fig. 39F) resembles the juveniles from Mexico of *P. fossata* Stimpson, 1860, and the adult male lectotype resembles much of the Ecuadorian morphotype, suggesting that the morphotypes are, in fact,

different ontogenetic stages. Thus, we maintain *Pericera fossata* Stimpson, 1860 as junior synonymy of *Macrocoeloma villosum* (Bell, 1836b).

Others ontogenetic variations observed are: (i) the posterior region of the carapace is more sculpted in adults, shaped like a swollen rhombus (similar to what is observed in *Oxypleurodon* Miers, 1885), but not “vermiculated” and (ii) the lateral spines of branchial region directed outward in young specimens, and can be noticed in the Fig. 39, the difference between the adults A, C, E and the juvenile F.

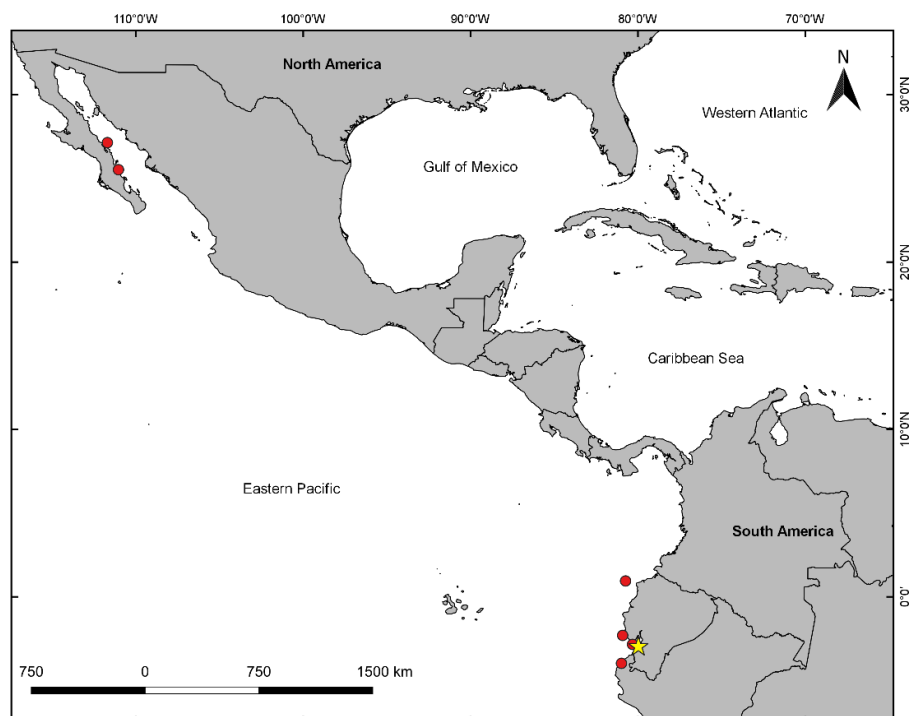


Figure 38. *Macrocoeloma villosum* (Bell, 1836). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

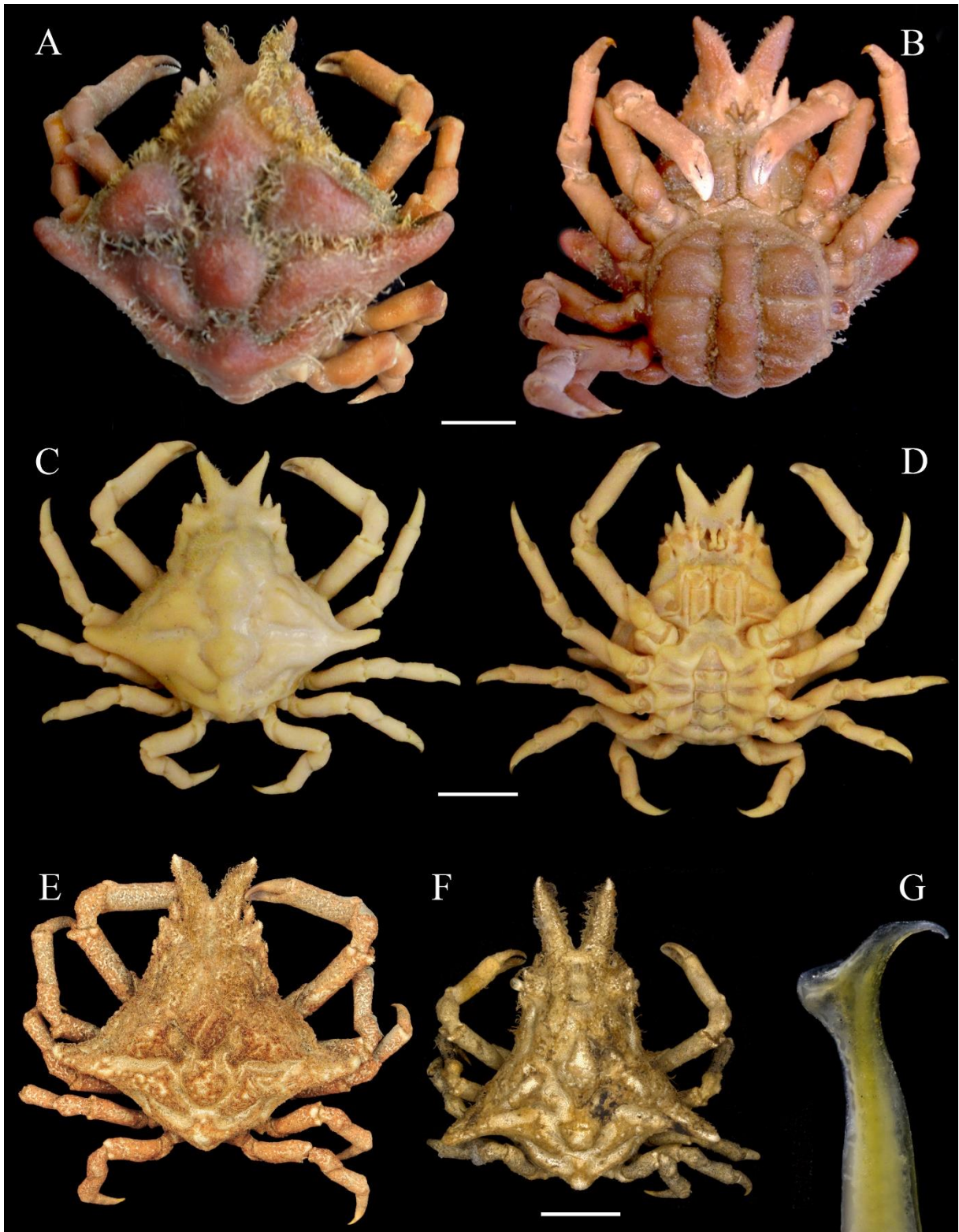


Figure 39. *Macrocoeloma villosum* (Bell, 1836). A–B, female (SMF 239). C–D, male, (USNM 70942). E, male lectotype (OUM 13761); cl. 36 mm, cw 36 mm. F, female paralectotype (OUM 13762); cl. 21 mm, cw 18 mm. G. distal half of first gonopod, pleonal view (NHMLA-AHF 6908). A, C, E, F habitus; B, D, ventral view. Scale bars A–E, 10 mm; F, 05 mm.

New genus

Type species. *Pericera septemspinosa* Stimpson, 1871, by present designation. Gender feminine.

Included species. _____ *septemspinosa* (Stimpson, 1871) **gen. nov., comb. nov.**, and _____ *heptacantha* (Bell, 1836) **gen. nov., comb. nov.**

Diagnosis. Carapace sub globose, covered by short velvet pubescence interspaced by dense lines of long, hooked and simple setae in all carapace regions. Carapace armed with strong spines including seven sharp spines on posterior half: one short mesial metagastric, four long, strong, conical lateral spines (two in each branchial region), aligned a with one cardiac spine, and one intestinal spine; lateral spines longest, slightly upward directed. Pterygostomial region with strong spines visible in dorsal view. Rostrum bifurcated, base elongated and fused, diverging abruptly forming a Y-shape, ending in acute tips. Preorbital spine strong, acute, upward directed; postorbital spine short, acute. Basal article of antenna with three spines and one tubercle, not visible in dorsal view. Cheliped long, merus armed with short spines or tubercles, granulated. P2 shorter than cheliped, dactylus much shorter than propodus. Thoracic sternal somite IV with lateral margins straight. Sternite VIII concealed by pleon in males. Male and female pleon with six somites not fused plus telson. Male telson tight-fitting into sternopleonal cavity, distinctly triangular. G1 slender, straight, with bilobed apex. G2 slender, straight, tapering distally, very short (one fifth the length of G1).

_____ *heptacantha* (Bell, 1836) gen. nov., comb. nov.

(Figure 40 A-B)

Pericera heptacantha Bell, 1836: 173 [type locality: Puerto Potrero, Central America, 23.7 m; type material: syntypes, 1 male (non-extant), 1 female (OUM 13764)].

Pericera heptacantha – Bell 1836b, p.61, pl.12, figs 6, 6r-u; White 1847: 10; A. Milne-Edwards 1873: 55.

Macrocoeloma heptacantha – Miers 1886: 79, 81.

Macrocoeloma heptacanthum – Rathbun 1898a: 576; 1925: 473, pl. 17,3, fig. 1; pl. 269, fig. 8-11, text-figs 133, 134; Garth 1958: 415; Di Mauro 1982: 170; Ng et al., 2008: 119.

Type material. Lectotype, female, cl. 35 mm, cw. 43 mm; *COSTA RICA*, Central America, Puerto Potrero, 23.7 m; Hugh Cuming col. (OUM 13764) (Fig. 41), by present designation.

Material examined. *MEXICO*, Off Cape San Lucas, R/V Albatross, sta. 2829, 22°52'00"N–109°55'00"W, RKY, temperature 74.1°F, 1.v.1888, M. J. Rathbun det., 56.6m, 1 juvenile female (USNM 21933 illustrated). *COSTA RICA*, Guanacaste, Puerto Potrero, Hugh Cuming col., 23.7 m, 1 female (OUM 13764 Lectotype). *PANAMA*, Panama Bay, R/V Albatross, sta. 2798, 8° 10'30"N–78°50'30"W, 5.iii.1888, M. J. Rathbun det., 114.6 m, 1 juvenile female (USNM 21932).

Description based on the female lectotype (male characters modified from Bell 1836b): Cephalothorax and appendages slightly covered with short, velvet-like pubescence. Carapace sub globose wider than long, convex, with long lines of hooked and simple setae in all carapace regions. Rostrum short, less than one third of interorbital length, bifurcated, base elongated and fused, diverging abruptly forming a Y-shape, ending in acute tips. Interorbital region slightly

depressed medially. Hepatic region broad. One metagastric spine. Four long, strong, conical lateral spines (two in each branchial region), aligned to one cardiac spine. One short intestinal spine. Orbital region very prominent, eyes completely protected when retracted, ocular peduncle visible when not retracted. Preorbital spine directed upward, slightly curved on the tip, longer than postorbital spine, ventral margin of preorbital spine with a small crenulation; postorbital spine curved upwards.

Antennular fossae wider than long, margins smooth. Interantennular septum elongate, laterally compressed, forming distinct ventrally directed lobe. First and second antennal articles fused to epistome, with suture between antenna and epistome visible, antennal gland opening near suture line. Basal article of antenna with two spines, not visible in dorsal view: proximal spine smallest. Antennal flagella longer than rostral spines, behind rostrum in dorsal view.

Epistome anterior margin narrower than antennular fossae, smooth, posterior margin slightly depressed. Buccal field sub-rectangular, narrower at posterior edge with one acute spine in anterolateral angle aligned with antennal spines. Third maxillipeds covering buccal frame, leaving a small gap between ischia. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by marked groove, with one long, strong spine slightly curved upward on medial margin, visible in dorsal view.

Male chelipeds equal, longer than legs; covered with sparse granulation, unarmed. Dactylus arched in adult males, leaving a small gap between fingers, distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with light brown color in fixed specimens. Walking legs short, slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved and covered with short setae. (Male description based on Bell 1836b)

Female chelipeds equal, longer than legs, slender and smooth. Dactylus arched in adult, shorter than palm, sub-equal teeth in distal half. Walking legs, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally, with corneous tips.

Thoracic sternites I-IV fused, broadly triangular, smooth, anterior half declivous in ventral view. Telson fully fitted to cavity, anterior margin smooth (Male description based on Bell 1836b).

Female pleonal somites I–VI markedly arched, telson free, with a row of setae on margin and one small spine in first somite. Telson transversally oval. Male pleon rather prominent, pleonal somites I-VI, telson free, somite II with a mesial tubercle. Somite III with slightly elevations. Somite VI longest, with a mesial tubercle and a small projection each side. Female telson transversally oval.

Color in life: Light brown, covered with darker hair, first pair of pereopods reddish (Bell, 1936).

Type locality: Costa Rica, Central America, Puerto Potrero, on sand at the deep of 23.7 m.

Geographic distribution: eastern Pacific: Mexico (from Cape San Lucas), Costa Rica and Panamá (Fig. 40).

Remarks. Appendix 2.

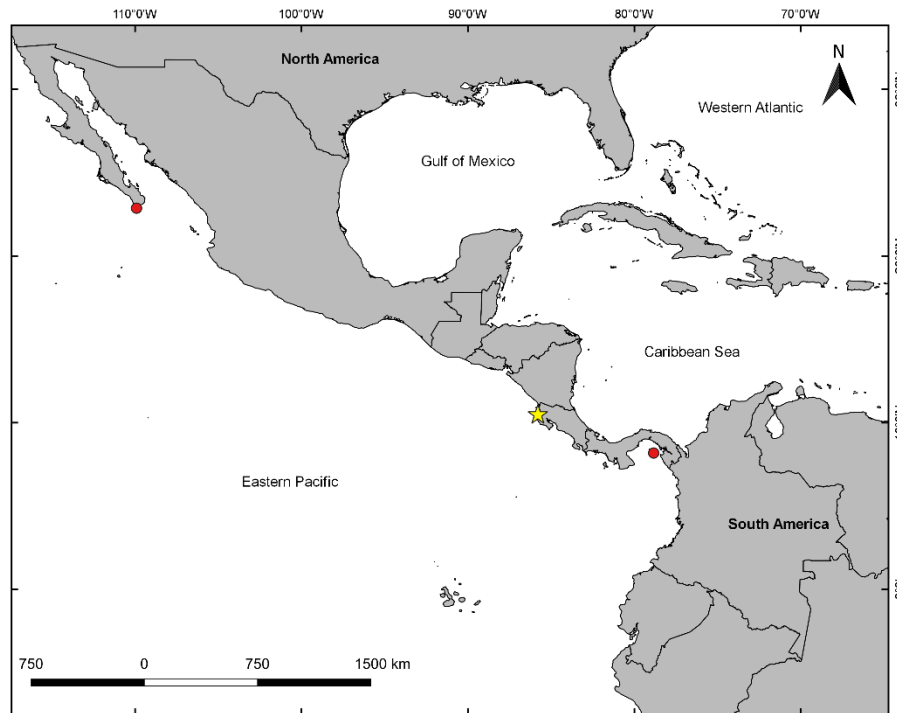


Figure 40. *_____ heptacantha* (Bell, 1836). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.



Figure 41. *_____ heptacantha* (Bell, 1836). A–B, female lectotype, cl. 35 mm, cw. 43 mm (OUM 13764). A, habitus; B, ventral view. Scale bar: 10 mm.

_____ *septemspinosa* (Stimpson, 1871) gen. nov., comb. nov.

(Figure 43 A-F)

Pericera septemspinosa Stimpson, 1870 (1871): 113 [type locality: West of Tortugas; 65m, type material: non-extant].

Pericera septemspinosa – A. Milne-Edwards 1873: 59, 200, pl. 15A, fig. 2; Miers, 1886: 80; Rathbun, 1892: 250; 1898b: 257; 1899: 576; Gundlach and Torralbas, 1900: 365, fig. 366G.

Macrocoeloma septemspinusum – Moreira 1901: 64, 136; Rathbun 1925: 477, pl. 173, figs 2-3; Coelho 1971:142; Coelho and Ramos 1972: 218; Soto 1980 (digital document); Powers 1977: 52; Takeda and Okutani 1983: 141; Abele and Kim 1986: 45, fig. 521A; Melo 1996: 219, fig. 1; 1998: 464; Coelho-Filho 2006: 19; Almeida et al., 2007: 15; Alves et al., 2008: 58; Ng et al., 2008: 119; Alves et al., 2012: 54.

Type material. Neotype, male, cl. 31 mm, cw. 35 mm; *UNITED STATES*, Florida, West of Sarasota, R/V Oregon, sta. 4088, 27°44'N–83°45'W; 4.xii.1962, National Marine Fisheries Service col.; 27 Oct. 2014, W. Santana det. (USNM 1256361) (Fig. 43)

Material examined. *UNITED STATES*, North Carolina, 33°48'06"N–76°34'42"W, 03.iii.1981, Duke Univ. for MMS col., 1981, P. Krikorian det., 77m, 1 male (USNM 220811). South Carolina, East of Cape Romain, R/V Albatross, sta. 2311, 32°55'00"N–77°54'00"W, 5.i.1885, U.S. fish commission col., 59.1°F, 114.4m, 1 male, 1 juvenile female (USNM 15127). Florida, West of Sarasota, R/V Oregon, sta. 4088, 27°44'N–83°45'W, 4.xii.1962, National Marine Fisheries Service col, 27.x.2014, W. Santana det., 1 male (USNM 1256361). Gulf of Mexico, Southwest of Cape San Blas, R/V Albatross, sta. 2373, 29°14'00"N–85°29'15"W, 07.ii.1886, 45.7 m, 1 juvenile female (USNM 15132). Southwest of Cape San Blas, R/V

Albatross, sta. 2370, 29°18'15"N– 85°32'00"W, 07.ii.1886, U.S. fish commission col., M. J. Rathbun det., 45.7 m, 1 juvenile female, 1 male (USNM 15130). Southwest of Cape San Blas, R/V Albatross, sta. 2372, 29°15'30"N– 85°29'30"W, 07.ii.1886, U.S. fish commission col., M. J. Rathbun det., 49.4m, 2 females (USNM 15131). Suez of Mexico, R/V Oregon, sta. 892, 28°55'N, 85°07'W, 07.iii.1954, Fish and Wildlife col., 21.iv.1954, F. A. Chace Jr det., 53m, 1 male (USNM 96389). off Apalachicola Bay, R/V Indian Seal, 28°49'59"N–85°37'02"W, 031.i.1978, col., R. Lemaitre det., 177m, 1 male (USNM 1085620). South of Dog Island, R/V Albatross, sta. 2407, 28°47'30"N–84°37'00"W, 07.ii.1886, U.S. fish commission col., M. J. Rathbun det., 43.8m, 1 male (USNM 15135). South of sta. George Island, R/V Albatross, sta. 2406, 28°46'00"N–84°49'00"W, 15.iii.1885, 47.5m, 3 juvenile females (USNM 15134). South of Cape Saint George, R/V Albatross, sta. 2405, 28°45'00"N–85°02'00"W, 15.iii.1885, 54.8 m, 3 juvenile females (USNM 15133). *Gulf of Mexico*, 26°45'52"N–83°21'26"W, 18.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 50.2m, 1 female (USNM 273379). 26°45'52"N–83°21'26"W, 01.v.1981, Continental Shelf Associates col., R. Lemaitre det., 50.2m, 1 male (USNM 241012). 26°45'52"N–83°21'26"W, 01.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 50.2m, 1 male (USNM 241027). 26°45'52"N–83°21'26"W, 01.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 50.2m, 1 male (USNM 241028). 26°45'52"N–83°21'26"W, 18.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 50.2 m, 1 male (USNM 274440). 26°45'52"N–83°21'26"W, 01.v.1981, Continental Shelf Associates col., R. Lemaitre det., 50.2 m, 1 male, 1 juvenile female (USNM 236995). 26°45'52"N–83°21'26"W, 29.x.1980, Continental Shelf col., R. Lemaitre det., 50.2m, 1 juvenile female (USNM 242767). 26°16'50"N– 83°23'49"W, 05.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 55.5m, 1 male (USNM 241026). 26°16'50"N–83°23'49"W, 19.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 55.5 m, 1 male, 2 females (USNM 273381). 26°16'50"N–83°23'49"W, 05.ii.1982, Continental Shelf Associates col., R.

Lemaitre det., 55.5m, 1 female, 1 male (USNM 241024). 26°16'50"N–83°23'49"W, 19.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 55.5m, 1 juvenile female (USNM 241025). 26°16'50"N–83°23'49"W, 05.xi.1980, Continental Shelf Associates col., R. Lemaitre det., 55.5 m, 1 ovigerous female (USNM 242946). 26°16'50"N–83°23'49"W, 05.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 55.5 m, 1 juvenile female (USNM 274721). 26°16'50"N–83°23'49"W, 04.v.1981, Continental Shelf Associates col., R. Lemaitre det., 55.5 m, 1 male (USNM 236992). 26°16'50"N–83°23'49"W, 05.xi.1980, Continental Shelf Associates col., R. Lemaitre det., 55.5 m, 1 male, 1 ovigerous female (USNM 229838). 26°16'44"N–83°42'49"W, 03.xi.1980, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 1 male (USNM 236994). 26°16'44"N–83°42'49"W, 30.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 1 male (USNM 241006). 26°16'44"N–83°42'49"W, 03.ix.1980, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 1 juvenile female (USNM 241007). 26°16'44"N–83°42'49"W, 03.ix.1980, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 1 male (USNM 241008). 26°16'44"N–83°42'49"W, 30.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 1 male (USNM 236987). 26°16'44"N–83°42'49"W, 30.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 1 male (USNM 229839). 26°16'44"N–83°42'49"W, 30.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 71.3 m, 2 males (USNM 236986). 26°16'44"N–83°42'49"W, 30.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 71.3m, 1 male (USNM 241009). 26°16'43"N–83°46'49"W, 04.xi.1980, Continental Shelf Associates col., R. Lemaitre det., 77 m, 1 juvenile female (USNM 236989). 26°16'43"N–83°46'49"W, 24.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 77 m, 1 male (USNM 241029). 26°16'43"N–83°46'49"W, 06.ii.1982, Continental Shelf Associates col., R. Lemaitre det., 77 m, 1 female (USNM 273382). 26°16'43"N–83°46'49"W, 04.xi.1980, Continental Shelf Associates col., R. Lemaitre det., 77m, 1 female (USNM 241010). 25°45'35"N–83°20'14"W,

24.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 58.5 m, 1 male (USNM 242947). 25°45'35"N–83°20'14"W, 29.iii.1981, Continental Shelf Associates col., R. Lemaitre det., 58.5m, 1 male (USNM 229835). R/V Silver Bay, 25°32'N– 80°04'W, 24.x.1960, viii.1970, D. J. G. Griffin det., 65.8 m, 1 male (USNM 1278767). 25°17'16"N–82°52'10"W, 31.vii.1981, Continental Shelf Associates col., R. Lemaitre det., 44.2 m, 1 juvenile female (USNM 274435). 24°47'46"N–83°08'01"W, 24.iv.1981, Continental Shelf Associates col., R. Lemaitre det., 53.5m, 1 male (USNM 241011). Florida, off Dry Tortugas, 24°34'N–83°16'W, xii.1877-i.1878, USS Blake Expeditions col., A. Milne-Edwards det., 65.8 m, 1 female (MCZ 8206). Florida, Off Sand Key, Sand Key Lighthouse, sta. 24, 19.vi.1893, State Univ. Iowa Expedition, 109.7 m, 4 females, 2 juvenile males (USNM 68821). Florida, off Key West, R/V Albatross, 24°25'45"N–81°46'45"W, sta. 2317, 15.i.1885, U.S. fish commission col., 75°F, 82.3 m, 1 male, 1 female (USNM 15128). Florida, off Key West, R/V Albatross, sta. 2318, 24°25'45"N–81°46'00"W, 15.i.1885, U.S. fish commission col., 75°F, 82.3 m, 1 male, 1 female (USNM 15129). Off Key West, Sand key Light bearing West Northwest, Key West Light bearing North, State Univ. Iowa Expedition, sta. 24, 19.vi.1893, M. J. Rathbun det., 109.7 m, 1 male (USNM 75724). Florida, between Cedar Keys and Delta of Mississippi, R/ V Albatross, sta. 2369-2374, ii.1885, 46-48m, 1 juvenile (USNM 46957). Off Key West, Sand key Light bearing W. NW., Key West Light bearing N., State Univ. Iowa Expedition col., sta. 24, 19.vi.1893, M. J. Rathbun det., 109.7 m, 1 male (USNM 68926). Sand Key Light bearing North, State Univ. Iowa Bahamas Expedition col., sta. 28, 19.vi.1893, M. J. Rathbun det., 109.7 m, 1 male (USNM 72863). Sand Key Light bearing Northwest by North, Key West Light North 0.5mile East, 91.4-109.7m, 1 male, 1 juvenile female (USNM 68913). Florida, Pompano, 23.v.1949, 1 male (AMNH 10961). *BAHAMAS*, Bahamas Bank, 18.v.1893, State Univ. Iowa Bahamas Expedition col., 1 juvenile female (USNM 72862). *COLOMBIA*, 2 miles Southwest of Cape La Vela, 8.iv.1939, Garth col., 17.i.2018, J. Colavite redet., 1 male (AHF 39295). 2

miles off Bahia Honda, R/V Velero III, sta. A15-39, 8.iv.1939, Garth det., 9-18.28 m, 1 juvenile female (AHF 39292). *VENEZUELA*, 7 miles of Tortugas Island, R/V Velero III, sta. A43-39, 21.iv.1939, Garth det., 73-75m, 1 juvenile male (AHF 39293). 125 miles northeast of Macaibo, 12°37'N–70°45'W, R/V Oregon, sta. 4400, 26.ix.1963, 27.x.2014, W. Santana det., 97m, 1 male (USNM 1256370). 50 miles northeast of Caracas, 10°44'N–66°09'W, R/V Oregon, sta.4466, 17.x.1963, 23.x.2014, W. Santana det., 73m, 1 male (USNM 1256347). *FRENCH GUIANA*, Guiana 2014 Expedition, R/V Hermano Gines, 6°17'58.2"N–52°13'18.5952"W, 08.viii.2014, 95-97m, 1 ovigerous female (MNHN IU 2013-2682). *BRAZIL*, Bahia, Ilhéus, Costa de Ilhéus, 28.xi.2004, A. O. Almeida det., 1 ovigerous female (CIASB M. 2017.0084. UESC).

Description: Cephalothorax and appendages slightly covered with short, velvet-like pubescence. Carapace sub globose wider than long, convex, with long lines of hooked and simple setae in all carapace regions, more densely in rostral and lateral spines. Rostrum with half of interorbital length, bifurcated, base elongated and fused, diverging abruptly forming a Y-shape, ending in acute tips. Interorbital region slightly depressed medially. Hepatic region broad. One metagastric spine. Four long, strong, conical lateral spines (two in each branchial region), aligned to one cardiac spine. One short intestinal spine. Orbital region very prominent, eyes completely protect in orbit when retracted, ocular peduncle visible when not retracted. Preorbital spine acute, directed upwards, tip curved, longer than postorbital spine, ventral margin of preorbital spine with a small crenulation; postorbital spine curved upwards.

Antennular fossae wider than long, margins smooth. Interantennular septum elongated, compressed laterally, forming distinct, ventrally directed lobe. First and second antennal articles fused to epistome, suture between antenna and epistome visible, antennal gland opening near

suture line. Basal article of antenna with three spines and one tubercle, not visible in dorsal view. Antennal flagella longer than rostral spines, behind rostrum in dorsal view.

Epistome anterior margin narrower than antennular fossae, smooth. Buccal field sub-quadrate, narrower at posterior edge with acute spine at anterolateral angle aligned with antennal spines. Third maxillipeds completely covering buccal field. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by marked groove, one long, strong spine slightly curved upward on medial margin, visible in dorsal view.

Male chelipeds equal, longer than ambulatory pereopods, more robust in adults. Ischium, merus, carpus and propodus articles granulate. Ischium with one prominent tubercle laterodistally. Merus with one spine on proximal half, one on distal margin. Carpus with four tubercles sparsely distributed. Dactylus arched in adult males, a small gap between fingers, distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with dark brown color in fixed specimens. Females with shorter, slender, chelipeds. Ischium, merus, carpus and propodus with smaller tubercles than males, dactylus slightly arched, without gap between fingers.

Walking legs short, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. P2 Merus with distinct spine in distolateral margin. Dactylus slightly curved, shorter than propodus, smooth ventrally, with corneous tip.

Thoracic sternites I-IV fused, broadly triangular, smooth, anterior half declivous in ventral view, forming a carina along the sterno-pleonal cavity margin. Thoracic sternal somite IV with lateral margins straight. Telson fully fitted to cavity, anterior margin smooth. Sternite VIII concealed by pleon. Episternites IV and V forming a continuing line with the sternite, slightly downward directed

Pleonal somites I-VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, apex rounded. Female pleon markedly arched, with row of setae marginally. Female telson transversally oval.

G1 longer than thoracic sternal suture IV-V, stout, straight, parallel, with a torsion in distal half, apex bilobed. Mesial lobe short, with tip curved upward; lateral lobe long, slightly arched, ending in an acute tip. Lateral margin smooth. G2 slender, straight, very short (one fifth of G1 length), a distomesial process.

Color in life: Carapace light brown; cephalothorax ventral, pleon and legs pinkish to purple.

Type locality: United States, Florida, West of Sarasota, 27°44'N–83°45'W.

Geographic distribution: western Atlantic: United States (from North Carolina); Gulf of Mexico; Bahamas; Venezuela and Brazil (from Ceará to Bahia) (Fig. 42)

Remarks. Appendix 2.

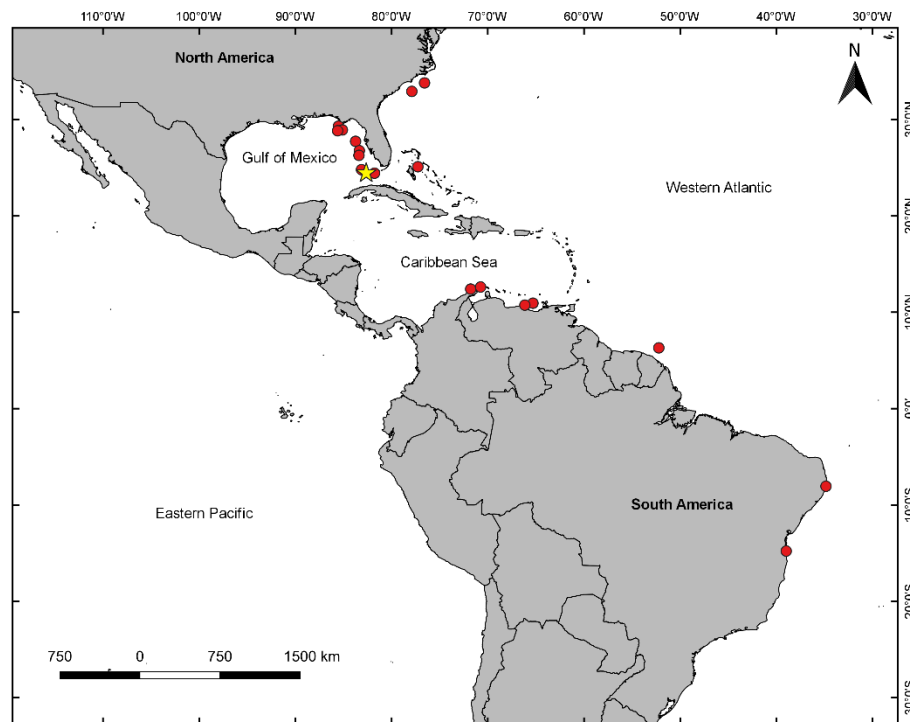


Figure 42. *Macrocoeloma septemspinosa* (Stimpson, 1871). Geographic distribution. Red circles = distribution based on examined material. Yellow star = type locality.

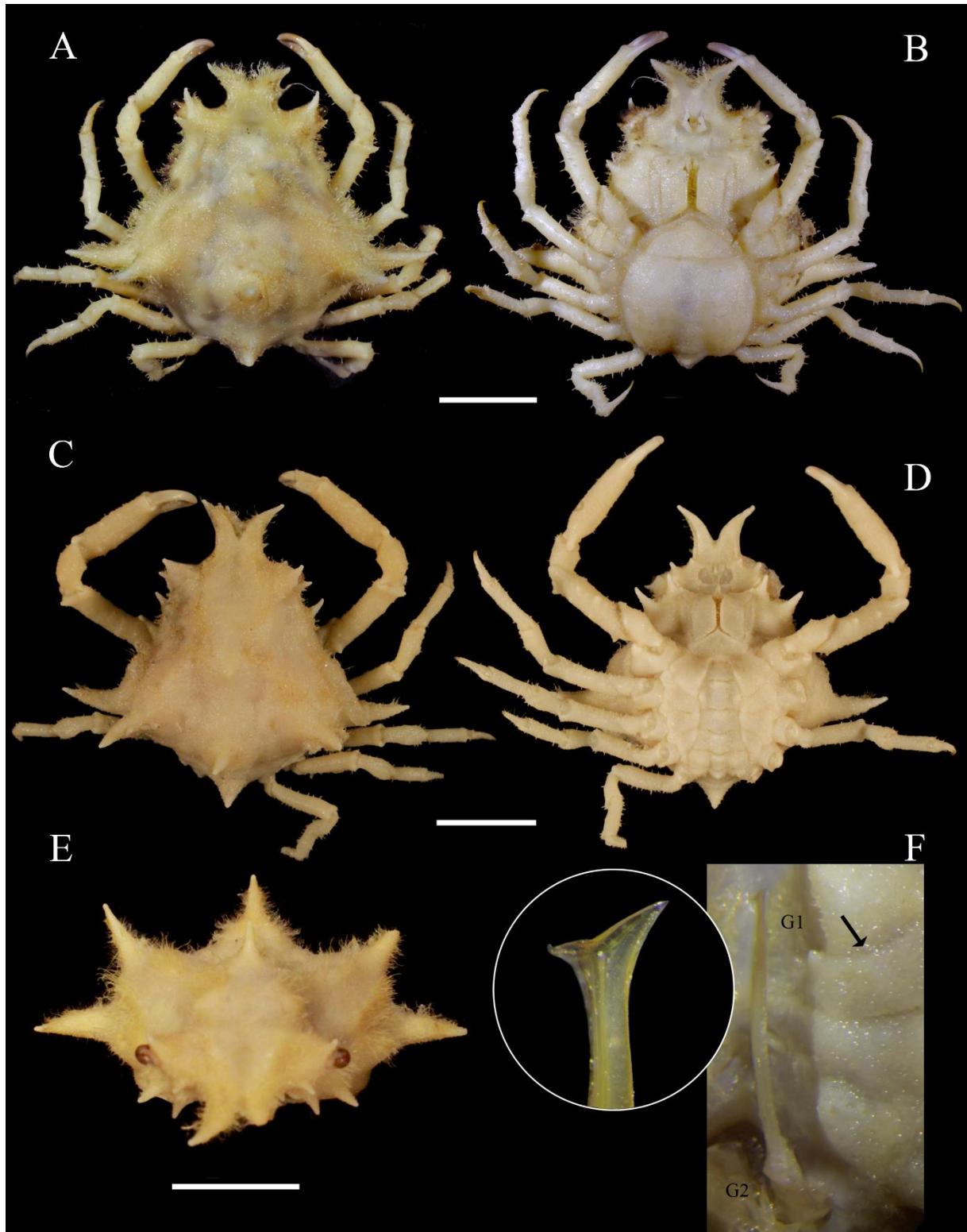


Figure 43. *Macrocoeloma septemspinosa* (Stimpson, 1871). A–B, female (MNHN IU 2013-32682). C–D, male neotype, cl. 31 mm, cw. 35 mm (USNM 1256361). E, male (USNM 241030). F, sternopleonal cavity with first (G1) and second (G2) gonopods in place (USNM 1256361). A, C, habitus; B, D, ventral view; E, frontal view; F, sternopleonal cavity with first (G1) and second (G2) gonopods in place; pleonal view of the apex in the detail. Note the thoracic sternal suture IV-V (black arrows) (F). Scale bars 10 mm

DISCUSSION

This study is the first to take an integrative approach combining molecular and morphological analyses to understand the phylogenetic relationships and to propose the taxonomic revision of *Macrocoeloma* Miers, 1879. The taxonomic treatment presented here was based on biological collections, including the typological series of most of them. Other closely related genera were also examined and morphologically compared with *Macrocoeloma*. Along the study of museum collections, fieldwork was also carried out in São Paulo state areas of known occurrence of *Macrocoeloma* in order to obtain fresh tissue sample for molecular analysis.

Despite of our efforts, few specimens were obtained during field collections, potentially explained by low abundance of this species in situ, low temperature tolerance of larvae and intensification of fishing and tourism in areas where these species were usually found (Alves et al., 2012; Rebolledo and Collin, 2018). The difficulty of obtaining samples is not exclusive to the Brazilian coast, some species of *Macrocoeloma* are rare and/or had few old specimens deposited in biological collections. The scarcity of material and the age of these rare specimens made the extraction of high-quality DNA difficult or impossible and limited morphological comparisons.

In the present study, was possible to observe geographic gaps in sampling of *Macrocoeloma*, mainly in the north region of South America (from Guiana to the state of Pará in Brazil). This area is an important area of transition of fauna, from the Caribbean Sea to the south Atlantic waters, along with the known influence of the Amazon River plum on species distributions (Leão and Dominguez, 2000). Another under sampled area evidenced here is the southeast Pacific coast. Material from these localities are scarce and old, and most often them fixed in formaldehyde, hampering the extraction of DNA samples. Fortunately, we had success

in amplifying some very old tissue samples, for example for *M. villosum* (USNM 70942), which was collected in 1926. However, sequence-quality tissues of some species of *Macrocoeloma* were unavailable for inclusion in our molecular analyses, including New genus *heptacantha* n. gen. n. comb., *M. intermedium* and *M. maccullochae* (Fig. 8)

A multi-gene approach was adopted to infer the phylogenetic relationships and the placement of *Macrocoeloma*, since this group was previously considered *incerta sedis* among the majoid crabs (Windsor and Felder, 2014). For that, several Majoidea genera were included in the analyses to test the monophyly of *Macrocoeloma*, and to ensure a family position for the genus. Based on Guinot (2011), two hymenosomatoid crabs was included as outgroup. Hymenosomatoidea was recently elevated to superfamily status, and despite of the debate about the relationships and placement of this group, there is a strong evidence that Hymenosomatoidea forms a unique lineage deeply rooted in Eubrachyura (Guinot, 2011; Davie et al., 2015a, b).

The four loci chosen here evolve at different rates, addressing both high-level systematics and species delimitation, considering the different time scale of both events. The nuclear ribosomal gene 18S rRNA is highly conserved and has been used to resolve deep branches in the animal tree of life (Aguinaldo et al., 1997). Mitochondrial DNA is the most commonly used in phylogenetic studies for the past three decades, showing more recent information (Ahyong et al., 2007; Hultgren, 2008; Windsor and Felder, 2014; Colavite et al., 2019). The cytochrome c oxidase subunit I (COI) is considered an ideal tool to species discrimination, being proposed as a standard marker for DNA barcoding (Hebert et al., 2003). Another mitochondrial ribosomal gene has become standard marker to brachyuran phylogenies, 16SrRNA (Schubart et al., 2000) as well the 12SrRNA (Mokady, 1994). Although, the high substitution rate in mitochondrial genes provides good resolution in recent speciation events, it also results in mutational saturation and consequently homoplasy in analyses of higher order

systematics. In this regard, besides the addition of the nuclear gene markers in our phylogenetic reconstruction, we also tested the saturation rates in order to ensure the reliability of the data generated.

Our molecular phylogenetic hypothesis is congruent with previous studies among *Macrocoeloma* relationships and larval morphology comparisons (Marques and Pohle, 2003; Windsor and Felder, 2014; Colavite et al., 2016–Appendix 1). The results show this genus related to Pisidae genera: *Leptopisa*, *Stenocionops*, and *Libinia* confirming its position in Pisidae (Fig. 8). Interestingly, *Thersandrus compressus*, the only species of the monotypic genus *Thersandrus*, which until this study has been classified within the family Majidae, groups as sister to *Macrocoeloma* with good statistical support (Fig. 8, 9). This genus nested between *Macrocoeloma* spp. and the New genus *septemspinosa* gen. nov., comb. nov. (detailed in the Appendix 2).

In order to understand the phylogenetic relationships among *Macrocoeloma*, all species of the genus were morphologically and most of them molecularly compared (see exceptions above). The present results demonstrated that *Macrocoeloma septemspinosa* does not belong to *Macrocoeloma* and a new genus was erected to accommodate New genus *septemspinosa* gen. nov., comb. nov. and New genus *heptacantha* gen. nov., comb. nov. New genus *heptacantha* gen. nov., comb. nov. is morphologically very similar to the New genus *septemspinosa* gen. nov., comb. nov., which led us to transfer it to the New genus. The mainly characters that separate *Macrocoeloma* and this New genus are: (i) the shape of the carapace and rostrum; the antennal and pterygostomial spines; and (ii) the shape of the thoracic sternum and the male first gonopods.

Thersandrus compressus also presented several morphological differences from *Macrocoeloma*, which prevent us to synonymize these genera. *Thersandrus compressus* and *Macrocoeloma* exhibit camouflaging behavior, however, *T. compressus* does not actively

decorate the carapace. This species has crypsis behavior consisting of matching their body to the environment in shape or color, being extremely morphologically adapted to live on algal fronds. Examples of this adaptation are: the setae have a felt-like texture, the legs are flattened, and the carapace color matching the inhabited green algae (Guinot and Wicksten, 2015). Thus, we suggested that *Thersandrus* could be better fitted in the Pisidae based on the molecular results (Fig. 8)

Internal relationships of Macrocoeloma

The species of *Macrocoeloma* can be distinguished by a pyriform or subtriangular carapace, orbits prominently laterally projected, and well-developed rostral spines that are usually armed by lateral spines. These small crabs, are rarely larger than five centimeters in carapace width. Unlike the uniform gonopod morphology observed between species in the closely related genera of *Stenocionops* and *Libinia*, the first gonopod of *Macrocoeloma* presented great variation, being useful for species identification. However, members of the *M. trispinosum* species complex do not exhibit variation in gonopod morphology.

Macrocoeloma is a well-supported monophyletic group, with twelve species distributed in the eastern Pacific and western Atlantic. Our results revealed that this genus is divided in two lineages. A subclade including the only eastern Pacific species with molecular data retrieved in the molecular analysis, *M. villosum*. This species is well supported as basal to the western Atlantic species *M. subparallelum* and *M. diplacanthum*. Morphologically, these three species share more similarities among them than with others, being this result congruent with the molecular analysis. The three species have the anterior half of the sternites I-IV is declivous with a depressed area between the sternites IV-VII and the pleon. The rostrum long and separated by a U-shape sinus is shared by *Macrocoeloma diplacanthum* and *M. subparallelum*.

Macrocoeloma subparallelum and *M. villosum* have depressed areas in the postero-dorsal region posterior of the carapace, after the cardiac spine.

The other subclade is composed exclusively by western Atlantic species. The first species to diverge in this clade is *M. euthecum*, followed by two inner clades. One clade comprising *M. laevigatum* and *M. concavum* and another with *M. camptocerum*, *M. trigonum* and the *M. trispinosum* complex. These groups are also morphologically congruent (see Remarks section of these species) (Fig. 9).

Macrocoeloma intermedium was not sequenced here but, based on morphology this species is very similar to *M. euthecum* and *M. concavum* (see Remarks of *M. intermedium* above), and probably should nest closed to one of these species. *Macrocoeloma euthecum*, *M. concavum*, *M. laevigatum* and *M. intermedium* share some similarities such as the carapace more pyriform and short rostral spines, and the orbits very prominent. *Macrocoeloma euthecum*, *M. concavum* and *M. intermedium* present tubular orbits with crenulations in the orbital spines, and the lateral spines is reduced, being diminutive in *M. intermedium*. *Macrocoeloma laevigatum* is the only species of the genus without lateral spines. Our phylogenetic hypothesis points that the absence of this character is probably a derived condition (Fig. 9)

The Pacific *Macrocoeloma maccullochae*, which was also unavailable for inclusion in the molecular analyses, is likely close or basal to *M. trispinosum*. This species has the most distinct rostral spine of this genus, being similar to *Leptopisa setirostris* and *Stenocionops angustus* (Lockington, 1877). However, this species presents the lateral spines characteristics of *Macrocoeloma* and is very similar to *M. trispinosum* in the general shape of the carapace and orbits leading us to maintain *Macrocoeloma maccullochae* in this genus.

Macrocoeloma trispinosum complex

The species *Macrocoeloma trispinosum*, *M. nodipes* and *M. trigonum* are morphologically similar, having been previously considered synonyms and/or subspecies by several authors (e.g. Schramm, 1874; Rathbun, 1925; Rathbun, 1925; Wass, 1955; Powers, 1977; Soto, 1980; Williams, 1984; Abele and Kim, 1986; Nizinski, 2003). However, these species are morphologically distinguishable by the carapace shape and the presence or absence of spines and tubercles in different regions of the carapace (see Remarks of *M. trispinosum*, *M. nodipes* and *M. trigonum*).

Macrocoeloma trispinosum and *M. nodipes* showed consistent morphological differences, most evident in larger adults. However, the existence of a morphological gradient between them, called “variety,” culminated in the synonym of both species. After the morphological exam of the ontogenetic series with well-developed adults from the same locality (e.g. USNM 76552; USNM 101585) and a vast material in the biological collections, we can affirm that “variety” can be fitted in the morphological gradient observed in *M. nodipes*.

These species, *M. trispinosum* and *M. nodipes*, have a sympatric distribution in the Gulf of Mexico and the Caribbean Sea, with *M. trispinosum* being more common in the north western Atlantic and *M. nodipes* in the Caribbean Sea (Fig. 44). The other species, *Macrocoeloma trigonum* only is found in the Brazilian coast (Fig. 44).

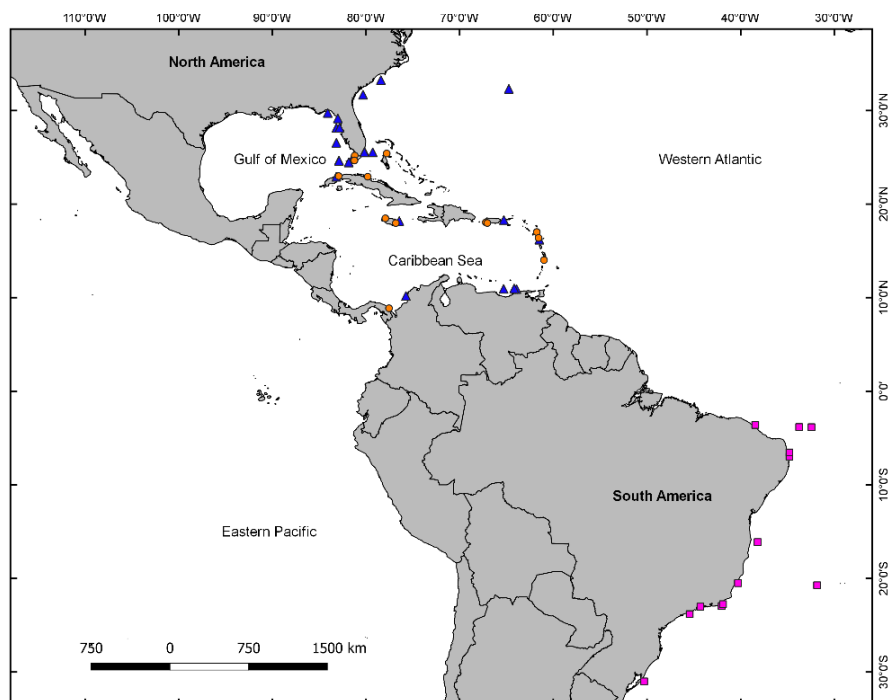


Figure 44. Distribution of species of *Macrocoeloma trispinosum* complex based on examined material. Blue triangle: *Macrocoeloma trispinosum* (Latreille, 1825). Orange circle: *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867). Pink square: *Macrocoeloma trigonum* (Dana, 1852).

The taxonomic revision revealed that what was previously considered the Brazilian morphotype resembles the outlandish species *M. trigonum*, described by Dana to Fiji Islands. The corrected type locality is probably Rio de Janeiro and no Fiji. Also, *Macrocoeloma trigonum* has the most distinct morphology when compared to *M. trispinosum* and *M. nodipes*.

Our phylogenetic analyses, in combination with the species delimitation estimation based on single gene (mtDNA COI), supported the existence of two taxonomic lineages, *M. trispinosum* and *M. trigonum*. In the multi-gene tree, *M. trigonum* showed a short branch length from the clade formed by *M. trispinosum* and *M. nodipes*, more evident in PTP estimation. These results, allied to the disjoint distribution corroborates to the validity of *M. trigonum* (Fig. 8, 9, 10). A clear separation between *M. trispinosum* and *M. nodipes* could not be retrieved in the multi-gene tree, probably due to the incomplete lineage sorting (Knowles and Carstens, 2007). However, different monophyletic lineages can be noticed in both trees (Fig. 9, 10), being clearer the separation in the COI tree (Fig. 10). According Zang et al. (2018), signals of lineage

separation can be detected despite the lack of monophyletic gene trees, being the hypothesis of monophyly a priori hidden in single-locus methods, as PTP. Despite the ambiguous molecular results, we opted to recognize *Macrocoeloma nodipes* as a valid species, considering that this group represents a phenetically distinguishable and diagnosable group supported by a monophyletic lineage in COI analysis.

Conflicts between morphological and molecular data are not rare and the discordance of the approaches used in delimitation of species as *M. trispinosum* and *M. nodipes* can be observed in the literature for several other groups (e.g. Knowles and Carstens, 2007; Astrin et al., 2012).

Other information is helpful in the separation of *M. trispinosum* and *M. nodipes*. The decoration materials used by *M. trispinosum* and *M. nodipes* in the specimens studied here are also distinct, and may suggest that these species inhabit different niches, which could form a geographic and ecological barrier (Sites and Marshall, 2003). Additionally, reports from the literature indicate that the temperature and the short larval development can also have influence in these species' dispersion. For instance, larvae of *Macrocoeloma trispinosum* from Panama showed a low tolerance to higher temperatures, around 35°C with completely mortality at 37°C (Rebolledo and Collin, 2018). However, considering that both species are frequently misidentified in literature, a revision of the female specimens used could help to insure the identity of these larvae as *Macrocoeloma trispinosum*.

Keeping these species as separate and clarifying the characters to diagnose both is helpful in further studies. We expect that future studies analyzing other DNA loci or the whole genomes of individuals at sample sizes equivalent to ours, or population level studies using other species delimitation tools, will be able to understand the dynamics of the dispersion of these species and the possible hybridization of the populations in Caribbean Sea.

CONCLUSIONS

The phylogenetic analyses revealed that *Macrocoeloma* is a Pisidae member. The monophyly of *Macrocoeloma* was demonstrated here, after exclusion of New genus *septemspinosa* gen. nov., comb. nov. and New genus *heptacantha* gen. nov., comb. nov. The monotypic genus *Thersandrus* Rathbun, 1897 is sister to *Macrocoeloma* followed by the New genus *septemspinosa* gen. nov., comb. nov. and New genus *heptacantha* gen. nov., comb. nov.

Macrocoeloma is an exclusively amphi-American genus comprising 12 species. Lectotypes have been designated for *M. concavum*, *M. euthecum* and *M. subparallelum*; and neotypes for *M. camptocerum*, *M. nodipes*, and *M. trispinosum*. Although needed, the neotypes of *M. diplacanthum*, *M. laevigatum*, and *M. trigonum* will be designated in the future when more suitable specimens become available.

Pericera diacantha is here considered a junior synonym of *M. camptocerum*.

The Brazilian specimens previously identified as *M. trispinosum* revealed to be a distinct and valid species, *M. trigonum*, with molecular support. The type locality of this species was also corrected to the Rio de Janeiro.

Macrocoeloma concavum, *M. euthecum* and *M. laevigatum* had the range of occurrence expanded to the southeast coast of Brazil.

Despite of the lack of molecular support to separate *Macrocoeloma trispinosum* and *M. nodipes*, they are treated as two valid species considering their distinct morphology.

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