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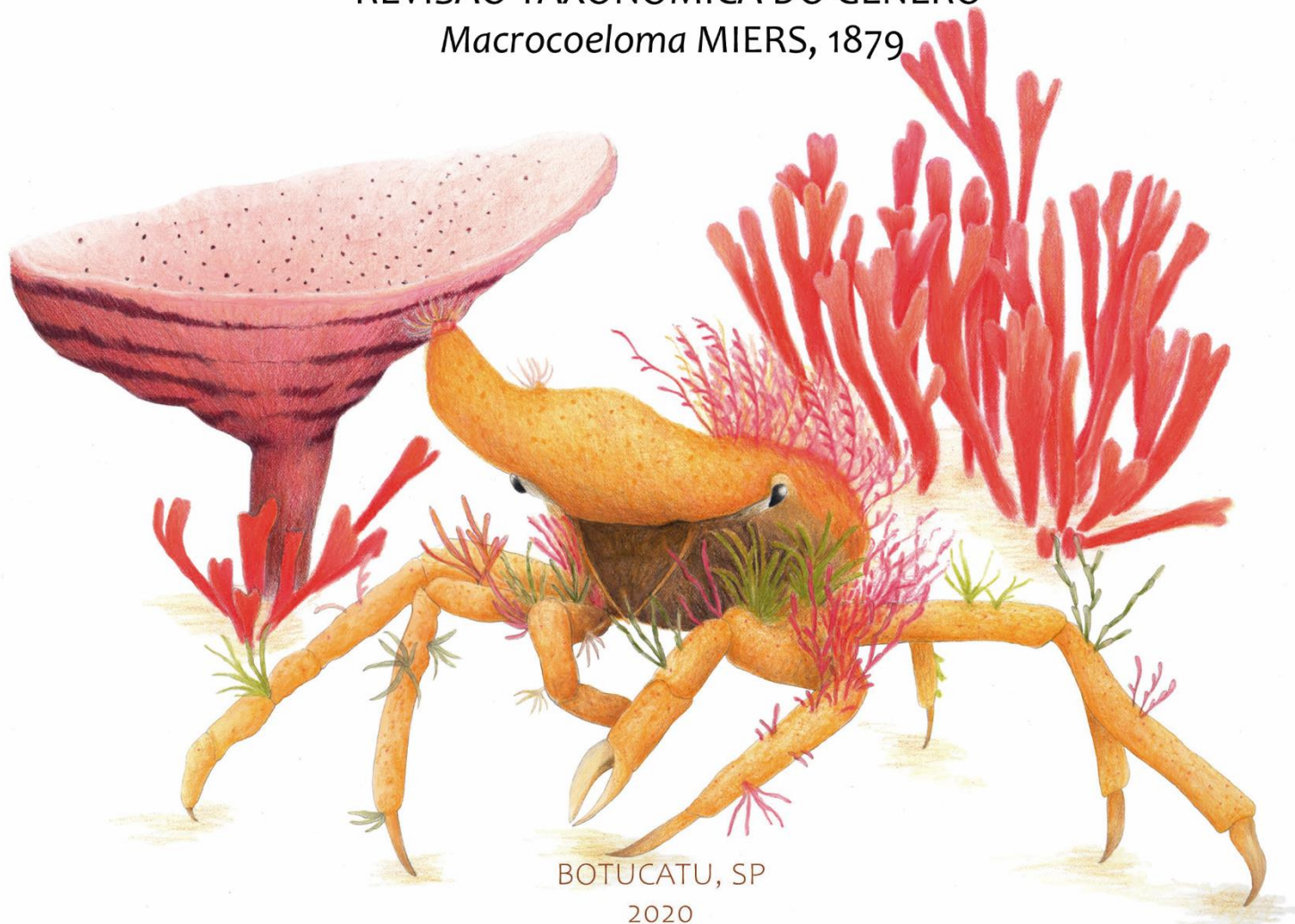
Tese de Doutorado

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)**

Tese apresentada ao Instituto de Biociências
da Universidade do Estado de São Paulo–
IBB UNESP, como pré-requisito para
obtenção do título de Doutor em Ciências
Biológicas, Zoologia.

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

BOTUCATU

2020

FICHA CATALOGRÁFICA ELABORADA PELA SEÇÃO TÉC. AQUIS. TRATAMENTO DA INFORM.
DIVISÃO TÉCNICA DE BIBLIOTECA E DOCUMENTAÇÃO - CÂMPUS DE BOTUCATU - UNESP
BIBLIOTECÁRIA RESPONSÁVEL: ROSEMEIRE APARECIDA VICENTE-CRB 8/5651

Colavite, Jessica.

Phylogenetic relationships and taxonomic revision of the genus *Macrocoeloma* Miers, 1879 (Crustacea: Decapoda: Brachyura) / Jessica Colavite. - Botucatu, 2020

Tese (doutorado) - Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Biociências de Botucatu

Orientador: William Santana
Coorientador: Amanda Windsor
Capes: 20405006

1. Caranguejo - Distribuição geográfica. 2. Biologia - Classificação. 3. Filogenia.

Palavras-chave: Caranguejos decoradores;
Caranguejos-aranha; Epialtidae; Majoidea; Pisidae.

“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!

AGRADECIMENTOS/ ACKNOWLEDGMENTS

Primeiramente, eu gostaria de agradecer ao Programa de Pós-graduação em Ciências Biológicas (Zoologia) do Instituto de Biociências da Unesp, *campus* Botucatu e à coordenação, por oferecer excelência e infraestrutura para realização desse trabalho e para a ciência de forma geral.

Meus sinceros agradecimentos ao meu orientador, Prof. Dr. William Santana, que acreditou no meu potencial desde a graduação, quando eu não tinha a mínima noção do que estava fazendo, e que continua acreditando até hoje. Agradeço pela sua generosidade em compartilhar seus conhecimentos e por ter me apresentados o fantástico mundo dos caranguejos aranha.

Agradeço à Fapesp por financiar meus estudos durante o meu doutorado, bem como meu estágio no exterior, essencial para a realização desse projeto (FAPESP 2016/02775-8 e BEPE 2017/08969-1).

I express my sincere appreciation to my co-advisor, Dra. Amanda M. Windsor (NMNH, Smithsonian Institution), for her cordiality, support, guidance and patience to teaches me molecular biology, and for always remember me that we are all in constant learning.

Meus agradecimentos ao Prof. Dr. Marcos Tavares (MZUSP, Universidade de São Paulo) por seus comentários e conselhos úteis no curso de meu doutorado e pelo acesso a coleção de carcinologia e uso das instalações necessárias no MZUSP.

Many thanks to Dr. Rafael Lemaitre, for accepting to supervise me during my internship, to give me access to the collection and for all help during my visit at the National Museum of Natural History, Smithsonian Institution.

Esse trabalho foi realizado graças a quatro instituições, agradeço as em ordem cronológica pelo espaço cedido e por facilitar o acesso as instalações necessárias e apoio contínuo a esse projeto. Primeiramente, a USC (hoje Centro Universitário do Sagrado Coração - Unisagrado, Bauru) que me cedeu espaço para trabalhar durante o início do projeto.

Second, I thank the National Museum of Natural History, Smithsonian Institution, that hosts me for 10 months, during my internship (BEPE). Thank to all the technicians for all the assistance during my visit, in special to Karen Reed that included me in all lab events, for shown me the flowers during the spring and the American culture.

Agradeço a Unesp de Botucatu, Departamento de Zoologia, Instituição sede desta pesquisa nos dois últimos anos, pelo suporte e espaço físico cedido para nosso laboratório.

Agradeço em especial ao Prof. Dr. Ricardo Benine por ter me acolhido em seu laboratório por quase um ano.

Por último, agradeço ao MZUSP- Museu de Zoologia da Universidade de São Paulo (MZUSP) por ceder espaço para a realização das análises moleculares. Às técnicas Jaqueline, Joana e Maria José por me acolherem e auxiliarem. À Luciane pelas fotos dos gonópodos e Luciana e Maria pelo auxílio durante a molecular, compra de materiais e amizade.

I am indebted to many institutions and colleagues which/who facilitated the access to specimens or helped in use of the collections. Among those my special thanks go to Lily Berniker and Dra. Estefania Rodriguez of the American Museum of Natural History, New York (AMNH) (USA); Adam Wall and Dr. Jody Martins of the Natural History Museum of Los Angeles County (NHMLA) (USA). Thanks to Adam Baldinger of Museum of Comparative Zoology (MCZ)(USA), this visit received support from the “Ernst Mayr Travel Grant”, which is financed by the Harvard University.

Thanks for specimens’ loan and photographs: Dra. Laure Corbari of Muséum national d’Histoire naturelle, Paris (MNHN)(France). Obrigada ao Museu Nacional do Rio de Janeiro (MNRJ); Flávio de Almeida Alves Junior do Museu Oceanográfico da Universidade Federal de Pernambuco, Brazil (MOUFPE); Fabrício Carvalho da Coleção de Invertebrados Aquáticos do Sul da Bahia, Universidade Estadual de Santa Cruz, Brazil (CIASB/ UESC). Agradeço também ao Prof. Alexandre Almeida e ao Woody do Laboratório de Biologia de Crustáceos, (DZ-UFPE, Recife) pelo empréstimo de espécimes e fornecimento de tecido para as análises moleculares.

Thanks for collection information and specimen photographs: Roger W. Portell, Florida Museum of Natural History (FLMNH-UFL) (USA). Moritz Sonnewald and Bianca Trautwein from the Senckenberg Museum Frankfurt (SMF) (Germany); Natural History Museum United Kingdom, Londres (NHMUK); and Oxford University Museum of Natural History (OUM). Gracias à Edgardo Londoño Cruz, Colección de Referencia de Biología Marina de la Universidad del Valle; Bibian Martínez Museum of Marine Natural History of Colombia (Invermar) (Colombia). Thanks to Darryl Felder, University of Louisiana at Lafayette Zoological Collection (ULLZ) (USA) for allow me to use the DNA sequences, specimens’ information and photographs. Mi agradecimiento especial a el Grupo de Invetigaciones Carcinologicas, Universidad de Oriente (GIC) (Venezuela), en las personas de Prof. Dr. Juan Bolaños (*in memorian*), Prof. Me. Enrique Hernández, siempre solicito y Prof. Dr. Carlos Lira, por la recepción en 2014 que aún está generando resultados científicos.

Ao Laboratório de Sistemática Zoológica, que me ensinou o significado de trabalho em equipe e minha segunda casa durante esses sete anos. À toda a galera que passou pelo lab nesses

anos, Marina, Rafa, Gabriel, Alan, Daniel Lima e a atual e nova geração Tassia, Janaína, Fran e aos agregados Nadeshinie e Igor. Agradeço em especial a Laira e Michele que leram esse trabalho.

Aos amigos da USC que durante anos dividimos a vida, muito obrigada pela boa convivência e amizade Prof. Dra. Carla Gheler-Costa, Lari, Tamy, Ciça. Às meninas da graduação: Ana Pri, Daia, Even, Patih e Mariana. Em especial a Leticia Gilli, minha roommate e amiga, obrigada por estar ao meu lado durante esse período, pelos conselhos e discussões científicas.

Aos amigos brasileiros que fiz nos USA e que levarei para a vida toda, sem vocês tudo seria muito difícil: à Claudia e família, a toda galera do Poets e amigos de DC, à Glenda, Lia, João e Bruna, Jonathan, Vinicius, em especial à Fernanda Conforto, minha roommate, por dividir os perrengues, por me auxiliar no inglês inúmeras vezes e pela amizade. I express my gratitude to Paul Ross to host me in his house during my stay in US.

Agradeço também à Andressa e Paty, Laboratório de Biologia de Crustáceo, (DZ-UFPE, Recife), pelas fotos de caranguejos frescos e por me auxiliar na busca de exemplares na coleção.

À Tia Vanda e toda família pelas inúmeras vezes que me hospedaram em São Paulo, muito obrigada.

Aos amigos que Botucatu me trouxe e que me auxiliaram em muitas discussões científicas e existenciais durante o curso: Aninha, Mario, Geslaine, Lucas, Dino, Magrela, Valter e Paula. À Isabela que também auxiliou nas buscas por *Macrocoeloma* em campo e à Bel, pelas inúmeras discussões sobre sistemática e pela leitura e contribuições nesse trabalho. Em especial agradeço à Milena, pela amizade, conversas e cervejas compartilhadas durante esses anos. Muito obrigada por auxiliarem com as análises e sugestões para esse trabalho: Lais, Pinky, Nana e em especial agradeço à Fábio Roxo pelas contribuições durante a qualificação.

Outras pessoas fora da academia contribuíram indiretamente com essa tese, através da amizade e companheirismo, atitudes das quais me fortaleceram durante a caminhada. Agradeço a William Matos, meu companheiro durante esses anos, obrigada pela paciência e compreensão. Agradeço a minha família, meus pais Maria Inês e Nilton, muito obrigada pelo suporte durante esses anos e que muitas vezes mesmo sem entenderem me incentivaram sempre, desculpa pela minha ausência, sei o quanto foi difícil para vocês. À minha vó Maria, pelo exemplo de mulher guerreira e a minha irmã Juliana por todo incentivo e amizade e ao Thiago. Vocês são o meu alicerce nessa caminhada e responsáveis pela pessoa que me tornei.

Thanks to the artist Dr. Stephanie Holm for authorizing the use of your art on the cover of this thesis.

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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 1838 and 1842. 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 *Armasas 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).

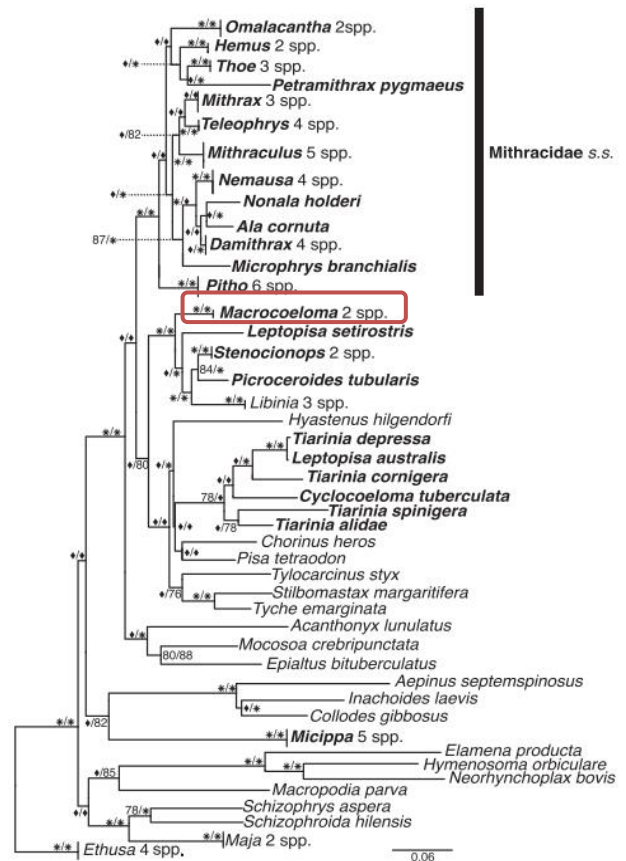
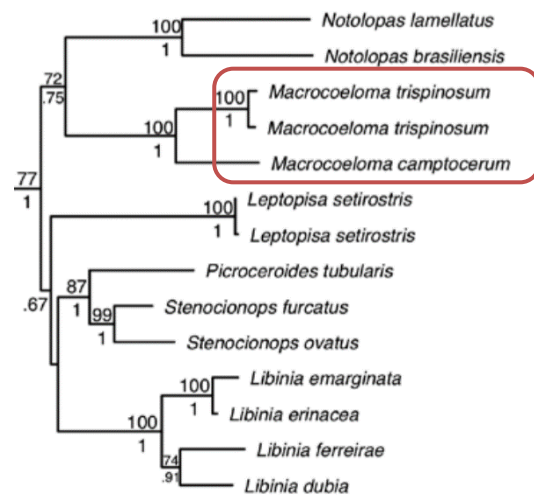


Figure 2. Molecular phylogenetic tree modified from Colavite et al. (2019). Two species of *Macrocoeloma* used in the analyses (marked in dark red).



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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