

A new *Callichirus* ghost shrimp species from the south-western Atlantic, long confounded with *C. major* (Say, 1818)(Decapoda: Axiidea: Callichiridae)

Patricio Hernandez, Marcel S. Miranda, Juliana P.P. Rio & Marcelo A.A. Pinheiro

To cite this article: Patricio Hernandez, Marcel S. Miranda, Juliana P.P. Rio & Marcelo A.A. Pinheiro (2022) A new *Callichirus* ghost shrimp species from the south-western Atlantic, long confounded with *C. major* (Say, 1818)(Decapoda: Axiidea: Callichiridae), *Journal of Natural History*, 56:9-12, 533-563, DOI: [10.1080/00222933.2022.2067016](https://doi.org/10.1080/00222933.2022.2067016)

To link to this article: <https://doi.org/10.1080/00222933.2022.2067016>



Published online: 14 Jul 2022.



Submit your article to this journal [↗](#)



Article views: 20







View related articles [↗](#)



View Crossmark data [↗](#)



A new *Callichirus* ghost shrimp species from the south-western Atlantic, long confounded with *C. major* (Say, 1818) (Decapoda: Axiidea: Callichiridae)

Patricio Hernández ^a, Marcel S. Miranda ^b, Juliana P.P. Rio ^c and Marcelo A.A. Pinheiro ^c

^aLimnológicos, Facultad de Ciencias, Universidad de Tarapacá (UTA) Centro de Estudios Marinos y, Arica, Chile; ^bGraduação em Biologia Animal, Universidade Estadual de Campinas Programa de Pós-, Campinas, Brazil; ^c– CRUSTA, Instituto de Biociências, Campus do Litoral Paulista, Universidade Estadual Paulista – UNESP Grupo de Pesquisa em Biologia de Crustáceos, São Vicente, Brazil

ABSTRACT

Morphological and molecular evidence suggests that the ghost shrimp population in Brazil that had been assigned to *Callichirus major* (Say, 1818) represents a distinct species. A neotype of *C. major* is designated in the interest of nomenclature, because the holotype is no longer extant. Based on material from Brazil, a new species, *Callichirus corruptus*, is described. Differentiating characters between the new species and *C. major* are discussed and an identification key to species of *Callichirus* is provided.

<http://www.zoobank.org/urn:lsid:zoobank.org:pub:29450E54-130A-4838-B923-F9676609DB3A>

ARTICLE HISTORY

Received 7 April 2021
Accepted 12 April 2022
Published online
14 July 2022

KEYWORDS

burrowing ghost shrimps; coast of Brazil; morphology; neotype; sandy beaches; key to *Callichirus* species


PALABRAS CLAVES

Camarones fantasmas excavadores; Costa de Brasil; morfología; neotipo; playas de arena; clave para las especies de *Callichirus*

Introduction

The description of *Callianassa major* by Say (Say 1818) was based upon a single specimen from the bay shore of the St. John River, east Florida. Stimpson (1866) transferred this ghost shrimp to his new genus *Callichirus* and regarded it as the type species. This species has been recorded from many localities along the western Atlantic coasts where it has a broad distribution ranging from North Carolina (~23°N) to Santa Catarina (~26°S), Brazil, including the Gulf of Mexico, and the Caribbean coast of Colombia. *Callichirus major* has also been reported from the eastern tropical Pacific (Hay and Shore 1918; Felder 1973; Rodrigues 1983; Williams 1984; Melo 1999, 2001; Sakai 2011).

Evidence, however, has been accumulating over many years that *C. major* is a species complex (Staton and Felder 1995; Rodrigues and Shimizu 1997; Strasser and Felder 1998, 1999a, 1999b, 1999c; Felder and Robles 2009; Peiró 2012). The taxonomic dilemma was discussed in part by Felder and Dworschak (2015), who recommended the name *Callichirus*

CONTACT Patricio Hernández  pahernaез@gmail.com

This article was originally published with an error, which has now been corrected in the online version. Please see Correction (<http://dx.doi.org/10.1080/00222933.2022.2111818>)

© 2022 Informa UK Limited, trading as Taylor & Francis Group

santarosaensis Sakai and Türkay, 2012 be applied to northern Gulf of Mexico populations formerly assigned to *C. major*. Also, two unpublished theses have recognised that the Brazilian *Callichirus* population represents an undescribed species, although the names proposed by Peiró (2012) and Rio (2018) are not available. The name *C. major* continues to be widely and frequently used in ecological, distributional and morphological checklists and taxonomic studies undertaken along its implied geographic distribution, specifically for those populations in the south-western Atlantic (Rodrigues 1966, 1971, 1983; Souza and Borzone 1996; Blanco Rambla 1997; Souza et al. 1998; Botter-Carvalho et al. 2007; Coelho et al. 2007, 2012; Rio et al. 2019, 2020). The current lack of clarity in the use of the name *C. major* has hence resulted in nomenclatural instability, unreliability and miscommunication of the available ecological and distributional information.

On the basis of a detailed morphological and molecular comparison between specimens of *C. major* from the north-western Atlantic and Caribbean coast, deposited in museum collections, and freshly collected material assigned to *C. major*, collected along the coast of Brazil, we herein recognise that the Brazilian *Callichirus* population represents a distinct species. That new species, named *Callichirus corruptus* sp. nov., is herein described. In addition, a neotype is selected to clarify the identity of *C. major* s. str., and an illustrated key to the species of *Callichirus* is provided.

Material and methods

Most specimens obtained along the Brazilian coast were collected during the low tide using a yabby pump (diameter = 77 mm, length = 100 cm) in the intertidal zone (< 1 m depth) (Figure 1). The studied material is deposited in the reference collections of the following institutions: Museo del Mar, Universidad Arturo Prat (MUAP), Museo de Zoología, Universidad de Concepción (MZUC), Museo de Zoología, Universidad de Costa Rica (MZUCR), Museu de Zoologia, Universidade de São Paulo (MZUSP) and National Museum of Natural History, Smithsonian Institution (USNM).

Measurements (mm) were made under a stereomicroscope (Zeiss® Stemi® SV-6) equipped with a digital analysis image system (Zeiss® AxioCam® MRc5). Each image was digitised using an electronic tablet for graphic design (Wacom®). Size is expressed as postorbital carapace length (cl) measured along the mid-dorsal line of the carapace from the anterior margin of the rostrum to the posterior margin of the carapace.

Abbreviations include: coll. (collector or collected by); cl (carapace length); EA (eastern Atlantic); EP (eastern Pacific); tl (total length); WA (western Atlantic); WP (western Pacific).

Molecular data analysis

The partial sequences of the mitochondrial loci 16S rDNA were retrieved from GenBank (Table 1). All *Callichirus* species with suitable 16S rDNA sequences available were included. Other Callichiridae and Axiidea species were included to test the monophyletic status of *Callichirus* (Table 1). Sampling locality information, GenBank accession numbers, museum voucher numbers and references for taxa included in the molecular analyses are provided in Table 1.

The phylogenetic analysis was inferred using the maximum likelihood method and the general time reversible model (Nei and Kumar 2000). The tree with the highest log likelihood (-2817.72) is presented. Initial tree(s) for the heuristic search were obtained

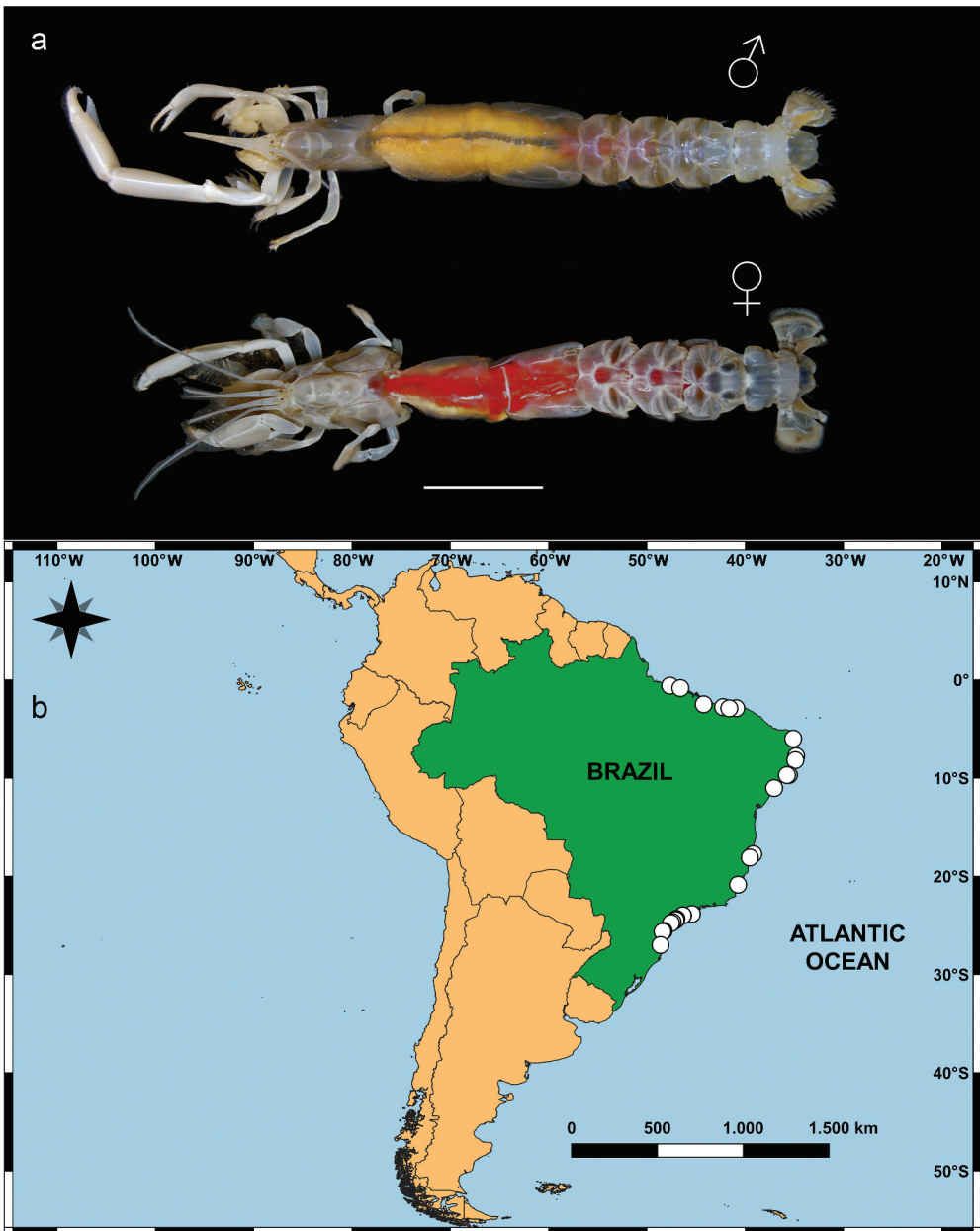


Figure 1. a, male and female specimen of *Callichirus corruptus* sp. nov. from the Brazilian coast (MZUSP 39027); b, collection sites (empty circles) for *Callichirus corruptus* sp. nov. along the Brazilian coast. Scale bar: A = 1 cm.

automatically by applying Neighbour-Join and BioNJ algorithms to the matrix of pairwise distances estimated using the maximum composite likelihood (MCL) approach, and then selecting the topology with the highest log likelihood value. A discrete gamma distribution was used to model evolutionary rate differences among sites [five categories (+G, parameter = 0.4201)]. The rate variation model allowed for some sites to be evolutionarily



Table 1. Taxa included in the molecular phylogenetic analyses to place *Callichirus corruptus* sp. nov. within the context of the genus *Callichirus* Stimpson, 1866.

GenBank taxon name	Taxon name	Sampling locality	Country	Ocean	Catalogue no.	GenBank accession no.	Reference
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Praia do Perequê-açu, São Paulo	Brazil	WA	CCDB 2938-3	JX878478.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Praia do Perequê-açu, São Paulo	Brazil	WA	CCDB 2938-2	JX878477.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Ilha comprida, São Paulo	Brazil	WA	CCDB 3184	JX878476.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Ilhéus, Bahia	Brazil	WA	CCDB 3102	JX878475.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Maxaranguape, Rio Grande do Norte	Brazil	WA	CCDB 429	JX878474.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Maxaranguape, Rio Grande do Norte	Brazil	WA	CCDB 429	JX878473.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Barra do Sai, Sao Paulo	Brazil	WA	MZUSP 14557	JX878470.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Jaboatão dos Guararapes, Pernambuco	Brazil	WA	MZUESC n.n.	JX878469.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Acaú, Paraíba	Brazil	WA	MOUFPE 8391	JX878468.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Itapoá, Santa Catarina	Brazil	WA	CCDB 2184	JX878467.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Itapoá, Santa Catarina	Brazil	WA	CCDB 2184	JX878466.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Luis Correia, Piauí	Brazil	WA	CCDB 2973	JX878465.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Luis Correia, Piauí	Brazil	WA	CCDB 2973	JX878464.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Balneário Camboriú, Santa Catarina	Brazil	WA	CCDB 2868	JX878463.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Balneário Camboriú, Santa Catarina	Brazil	WA	CCDB 2868	JX878462.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Bragança, Pará	Brazil	WA	CCDB 2864	JX878461.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Bragança, Pará	Brazil	WA	CCDB 2864	JX878460.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Passo do Camaragibe, Alagoas	Brazil	WA	CCDB 2678	JX878454.1	Peiró (2012)

(Continued)

Table 1. (Continued).

GenBank taxon name	Taxon name	Sampling locality	Country	Ocean	Catalogue no.	GenBank accession no.	Reference
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Passo do Camaragibe, Alagoas	Brazil	WA	CCDB 2678	JX878453.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	São Sebastião, São Paulo	Brazil	WA	CCDB 2677	JX878452.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	São Sebastião, São Paulo	Brazil	WA	CCDB 2677	JX878451.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Praia do Lázaro, São Paulo	Brazil	WA	CCDB 2661	JX878450.1	Peiró (2012)
<i>Callichirus</i> sp. 3	<i>Callichirus corruptus</i> sp. nov.	Praia do Lázaro, São Paulo	Brazil	WA	CCDB 2661	JX878449.1	Peiró (2012)
<i>Callichirus major</i>	<i>Callichirus corruptus</i> sp. nov.	São Paulo	Brazil	WA	UILLZ 6056	EU882918.1	Robles et al. (2020)
<i>Callichirus major</i>	<i>Callichirus corruptus</i> sp. nov.	São Paulo	Brazil	WA	UILLZ 6056	EU882917.1	Robles et al. (2020)
<i>Callichirus aff. major</i>	<i>Callichirus corruptus</i> sp. nov.	São Paulo	Brazil	WA	UILLZ 6056	MN238261.1	Robles et al. (2020)
<i>Callichirus aff. major</i>	<i>Callichirus corruptus</i> sp. nov.	São Paulo	Brazil	WA	UILLZ 6055	MN238260.1	Robles et al. (2020)
<i>Callichirus</i> sp. 2	<i>Callichirus</i> sp. 2	Cartagena	Colombia	WA	CCDB 3426	JX878472.1	Peiró (2012)
<i>Callichirus</i> sp. 2	<i>Callichirus</i> sp. 2	Cartagena	Colombia	WA	CCDB 3425	JX878471.1	Peiró (2012)
<i>Callichirus</i> sp. 1	<i>Callichirus</i> sp. 1	Playa Curu, Puntarenas	Costa Rica	EP	CCDB 2869	JX878459.1	Peiró (2012)
<i>Callichirus</i> sp. 1	<i>Callichirus</i> sp. 1	Playa Curu, Puntarenas	Costa Rica	EP	CCDB 2869	JX878458.1	Peiró (2012)
<i>Callichirus</i> sp. 1	<i>Callichirus</i> sp. 1	Playa Curu, Puntarenas	Costa Rica	EP	CCDB 2869	JX878457.1	Peiró (2012)
<i>Callichirus</i> sp. 1	<i>Callichirus</i> sp. 1	Playa Curu, Puntarenas	Costa Rica	EP	CCDB 2869	JX878456.1	Peiró (2012)
<i>Callichirus</i> sp.	<i>Callichirus</i> sp. 1	Baja California	Mexico	EP	UILLZ 4163	EU882922.1	Felder and Robles (2009)
<i>Callichirus seilacheri</i>	<i>Callichirus garthi</i>	E Tongoy, Coquimbo	Chile	EP	UILLZ 9002	KR003900.1	Robles and Felder (2015)
<i>Callichirus</i> sp.	<i>Callichirus islagrande</i>	Gulf of Mexico, Tabasco	Mexico	WA	UILLZ 5773	KR003899.1	Robles and Felder (2015)
<i>Callichirus</i> sp.	<i>Callichirus islagrande</i>	Gulf of Mexico, Tabasco	Mexico	WA	UILLZ 5773	KR003898.1	Robles and Felder (2015)
<i>Callichirus islagrande</i>	<i>Callichirus islagrande</i>	Gulf of Mexico, Mississippi	USA	WA	UILLZ 6052	EU882916.1	Robles et al. (2020)
<i>Callichirus major</i>	<i>Callichirus major</i>	Isles Dernieres, Louisiana	USA	WA	unknown	AF436041.1	Morrison et al. (2002)
<i>Callichirus major</i>	<i>Callichirus major</i>	Unknown	Unknown	WA	KCT1864	DO079707.1	Porter et al. (2005)
<i>Callichirus seilacheri</i>	<i>Callichirus seilacheri</i>	Playa Curu, Puntarenas	Costa Rica	EP	CCDB 561	JX878455.1	Peiró (2012)
<i>Callichirus seilacheri</i>	<i>Callichirus seilacheri</i>	Unknown	Nicaragua	EP	UILLZ 6053	EU882921.1	Robles et al. (2020)
<i>Callichirus seilacheri</i>	<i>Callichirus seilacheri</i>	Baja California	Mexico	EP	UILLZ 6054	EU882920.1	Robles et al. (2020)
<i>Callianassa aqabaensis</i>	<i>Aqaballianassa aqabaensis</i>	Unknown	Jordan	Red Sea	UILLZ 7924	EU874925.1	Robles et al. (2020)
<i>Sergio miririm</i>	<i>Audacallichirus miririm</i>	São Paulo	Brazil	WA	CCDB 2975	MF490166.1	Mantelatto et al. (2018)

(Continued)



Table 1. (Continued).

GenBank taxon name	Taxon name	Sampling locality	Country	Ocean	Catalogue no.	GenBank accession no.	Reference
<i>Biffarius delicatulus</i>	<i>Biffarius biformis</i>	Indian River, Florida	USA	WA	USNM 309754	EU874953.1	Robles et al. (2020)
<i>Callianassa ceramica</i>	<i>Filholianassa ceramica</i>	South of Port Authority Pier, Queenscliff	Australia	WP	NMV J40715	KU350630.1	Tan et al. (2017)
<i>Callianassa ceramica</i>	<i>Filholianassa ceramica</i>	Anglesea beach, Victoria	Australia	WP	unknown	KU362925.1	Gan et al. (2016)
<i>Callianassa filholi</i>	<i>Filholianassa filholi</i>	Unknown	New Zealand	WP	NMV J44818	EU874949.1	Robles et al. (2020)
<i>Lepidophthalmus siriboia</i>	<i>Lepidophthalmus siriboia</i>	Estuario do Roteiro	Brazil	WA	ULLZ 5611	KR003930.1	Robles and Felder (2015)
<i>Lepidophthalmus siriboia</i>	<i>Lepidophthalmus siriboia</i>	Estuario do Roteiro	Brazil	WA	ULLZ 5611	KR003929.1	Robles and Felder (2015)
<i>Sergio guassutunga</i>	<i>Neocallichirus guassutunga</i>	Bocas Del Toro, Bocas del Toro	Panamá	WA	BOC-035b	MK971568.1	Venera-Pontón et al. (2020)
<i>Sergio guassutunga</i>	<i>Neocallichirus guassutunga</i>	Isla Colón, Bocas Del Toro	Panamá	WA	ULLZ13324	MK971507.1	Venera-Pontón et al. (2020)
<i>Sergio guassutunga</i>	<i>Neocallichirus guassutunga</i>	Isla Colón, Bocas Del Toro	Panamá	WA	ULLZ13323	MK971363.1	Venera-Pontón et al. (2020)
<i>Sergio guassutunga</i>	<i>Neocallichirus guassutunga</i>	Isla Colón, Bocas Del Toro	Panamá	WA	ULLZ13322	MK971307.1	Venera-Pontón et al. (2020)
<i>Callianassa</i> sp.	<i>Pugnatorypaea</i> sp.	Gulf of Mexico, Louisiana	USA	WA	ULLZ 6058	EU882915.1	Robles et al. (2020)
<i>Callianassa</i> sp.	<i>Pugnatorypaea</i> sp.	Gulf of Mexico, Louisiana	USA	WA	ULLZ 8279	EU882903.1	Robles et al. (2020)

Catalogue number abbreviations: CCDB, Crustacean Collection of the Department of Biology; FFCLRP, University of São Paulo; MOUPPE, Museu de Oceanografia Prof. Petrónio Alves Coelho; MZUESC, Museu de Zoologia da Universidade Estadual de Santa Cruz; MZUSP, Museum of Zoology of University of São Paulo; NHMW, Naturhistorisches Museum Wien; NMV, Museums Victoria, Melbourne, Australia; ULLZ, University of Louisiana at Lafayette Zoological Collection; USNM, United States National Museum, Smithsonian Institution. n.n., not numbered; EP, eastern Pacific; WP, western Pacific; EA, eastern Atlantic; WA, western Atlantic.

invariable [(+), 33.03% sites]. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis used 54 nucleotide sequences with a total of 455 positions in the final data set. Phylogenetic analyses were conducted in MEGA X (Kumar et al. 2018). Branch support values were calculated using bootstrap analyses with 1000 replicates (Felsenstein 1985). Bootstrap support values are shown on nodes of the phylogenetic tree, when support is greater than 50. Nucleotide divergence estimated from pairwise distance was calculated in MEGA X with the same best-fit model (Table 2).

Results

Taxonomy

Infraorder AXIIDEA de Saint Laurent, 1979

Family CALLICHIRIDAE Manning and Felder, 1991

Genus *Callichirus* Stimpson, 1866

Type species

Callichirus major (Say, 1818), by original designation.

Included species

Callichirus adamas (Kensley, 1974) (EA); *C. corruptus* sp. nov. (WA); *C. garthi* (Retamal, 1975) (EP); *C. islagrande* (Schmitt, 1935) (WA); *C. major* (Say, 1818) (WA); *C. santarosaensis* Sakai and Türkay, 2012 (WA); and *C. seilacheri* (Bott, 1955) (EP).

Callichirus corruptus **sp. nov.**

(Figures 1a, 2, 3, 4, 5, 8a, 9b, 10b, c)

Callianassa (*Callichirus*) *major* – Rodrigues 1971: 192, Figure 1–20 [not *Callichirus major* (Say, 1818)].

Callichirus major – Rodrigues 1976: 85, figs 1–35, 1985: 195, Figure 1–30; Rodrigues and Höld 1990: 48; Borzone and Souza 1996: 67; Souza and Borzone 1996: 553; Rodrigues and Shimizu 1997: 155, Figure 1; Souza et al. 1998: 151; Coelho and Rodrigues 2001: 1447, figs 13–21; Botter-Carvalho et al. 2002: 97; Souza and Borzone 2003: 625; Botter-Carvalho et al. 2007: 508; Peiró and Mantelatto 2011: 5; Peiró et al. 2011: 261; Botter-Carvalho et al. 2012: 89; Dworschak et al. 2012: 151, fig. 69.29a,b, 69.31t; Alves-Junior et al. 2014a: 109; Alves-Junior et al. 2014b: 13; Peiró et al. 2014: 294; Pachellet et al. 2016: 20; Peiró and Mantelatto 2016: 103, pl. 1; Alves-Junior et al. 2018: 166; Hernáez et al. 2018: 97; Rosa et al. 2018: 1; Souza et al. 2018: 1; Hernáez et al. 2019: 1, Figure 1; Rio et al. 2019: 1, Figure 2; Hernáez et al. 2020: 1, fig. 4c; Laurino et al. 2020: 1 [not *Callichirus major* (Say, 1818)]; Moschetto et al. 2020: 1.



Table 2. Estimation of evolutionary divergence over sequence pairs from the portion of the mitochondrial 16S rDNA with ~510 bp.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	<i>Callichirus corruptus</i> sp. nov.														
2	<i>Callichirus</i> sp. 2	0.03													
3	<i>Callichirus</i> sp. 1	0.05	0.05												
4	<i>Callichirus major</i>	0.05	0.06	0.06											
5	<i>Callichirus seilacheri</i> ?	0.08	0.09	0.09	0.09										
6	<i>Callichirus garthi</i>	0.09	0.10	0.10	0.10	0.06									
7	<i>Callichirus islagrande</i>	0.09	0.08	0.09	0.09	0.05	0.05								
8	<i>Callichirus seilacheri</i>	0.12	0.11	0.12	0.11	0.07	0.06	0.06							
9	<i>Audacallichirus mirim</i>	0.19	0.17	0.19	0.19	0.20	0.19	0.19	0.21						
10	<i>Filholianassa ceramica</i>	0.19	0.19	0.18	0.20	0.21	0.19	0.19	0.22	0.22					
11	<i>Filholianassa filholi</i>	0.20	0.18	0.18	0.20	0.21	0.19	0.19	0.22	0.22	0.05				
12	<i>Lepidophthalmus siriboia</i>	0.21	0.19	0.20	0.20	0.21	0.20	0.21	0.23	0.16	0.22	0.22			
13	<i>Biffarius biformis</i>	0.23	0.21	0.22	0.23	0.23	0.22	0.22	0.24	0.22	0.18	0.24	0.19		
14	<i>Pugnatrypaea</i> sp.	0.24	0.23	0.22	0.23	0.22	0.25	0.23	0.25	0.20	0.22	0.26	0.19	0.31	0.32
15	<i>Neocallichirus guassutunga</i>	0.25	0.24	0.23	0.27	0.26	0.26	0.28	0.25	0.27	0.28	0.29	0.31	0.23	0.23
16	<i>Aqaballianassa aqbaensis</i>	0.26	0.25	0.26	0.27	0.29	0.25	0.26	0.28	0.24	0.22	0.29	0.23	0.23	0.37

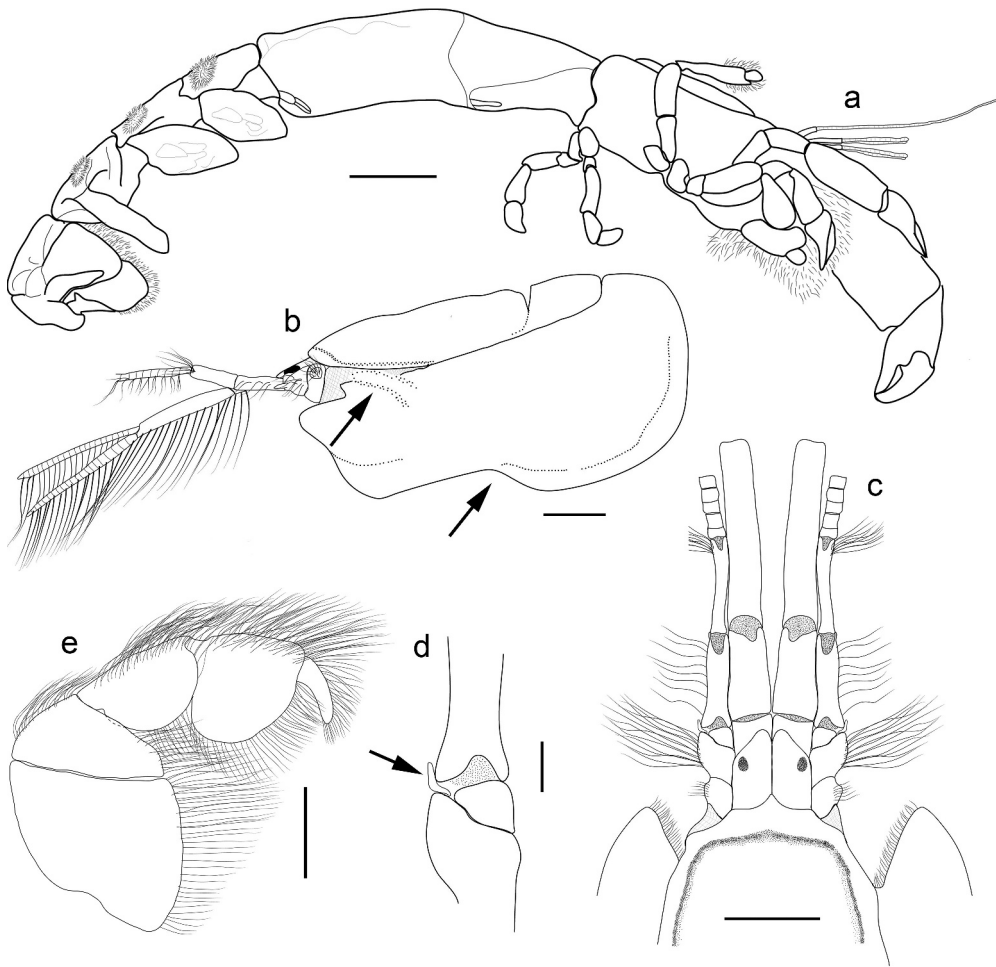


Figure 2. *Callichirus corruptus* sp. nov. a–d, holotype, male (cl: 18.8 mm), MZUSP 41251; e, paratype, male (cl: 18.6 mm), MZUSP 41253. a, body, lateral view; b, carapace and cephalic appendages, lateral view (arrows indicate branchiostegal lobe and emargination on central part of carapace); c, anterior part of carapace and cephalic appendages, dorsal view; d, basal part of antennal peduncle, dorsal view (setae omitted; arrow indicates scaphocerite); e, right third maxilliped, external surface. Scale bars: a = 1 cm; b, c = 2 mm; d = 1 mm; e = 4 mm.

Callichirus sp. – Strasser and Felder 1999a: 865.

Callichirus macrotelsonis – Peiró 2012: 58, figs 3–7 [*nomen nudum*].

Callichirus brasiliensis Rio 2018: 20, figs 1a, 2a, 3a, 3b, 4a [*nomen nudum*].

Type material

Brazil. São Paulo: holotype, male, cl: 18.8 mm (MZUSP 41251), Praia do Gonzaga, 23.970° S, 46.334°W, lower intertidal, Santos, P. Hernáez coll., 1 September 2016. Paratypes: 1 female, cl: 20.4 mm (MZUSP 41252), 4 males (one dissected), cl: 15.4–19.4 mm, and 4 females, cl: 16.4–22.2 mm (2 ovigerous females) (MZUSP 41253), same data as holotype.

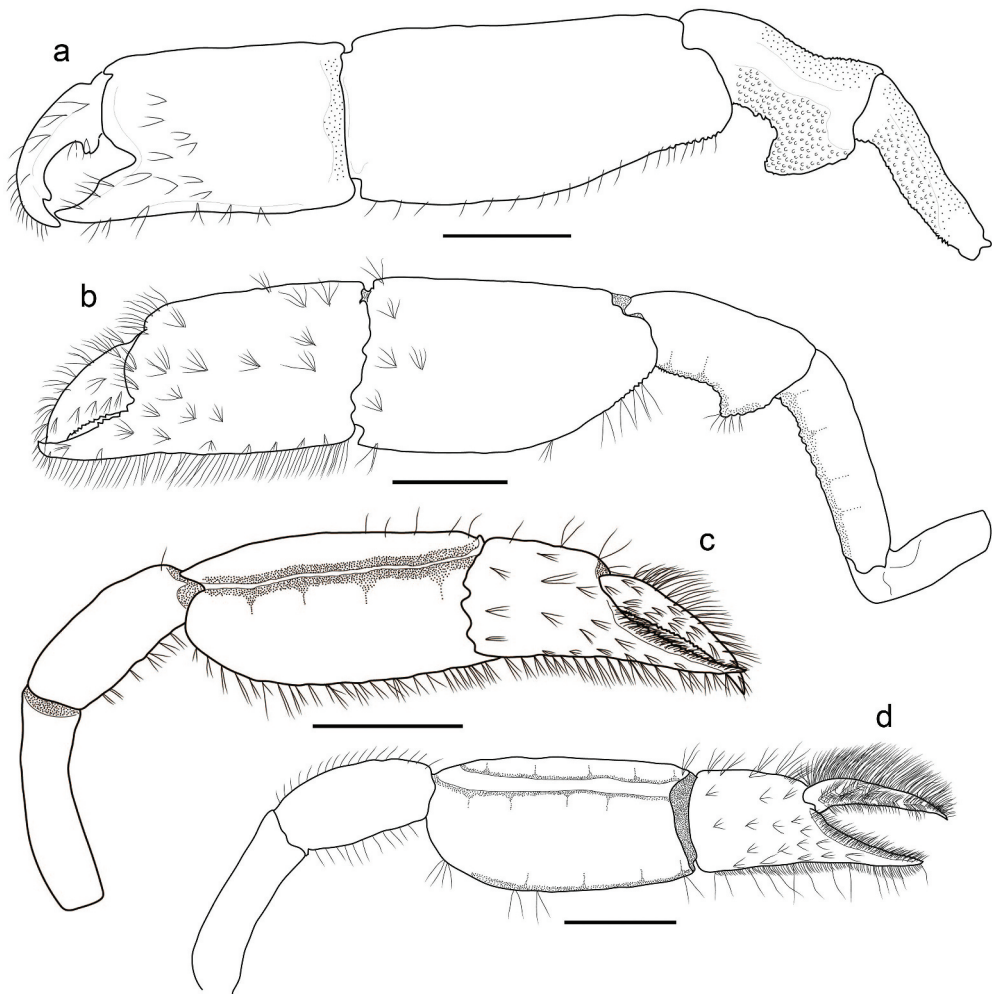


Figure 3. *Callichirus corruptus* sp. nov. a, c, holotype, male (cl: 18.8 mm), MZUSP 41251; b, d, paratype, female (cl: 20.4 mm), MZUSP 41252. a, c, male major and minor chelipeds, respectively, lateral view; b, d, female major and minor chelipeds, respectively, lateral view. Scale bars: 1 cm.

Non-type material

Brazil. Pará: 8 males, cl: 10.1–18.3 mm, and 15 females, cl: 10.4–19.2 mm, Praia do Crispim, 0.583°S, 47.651°W, lower intertidal, Marapanim, coll. P. Hernáez, 9 July 2017 (MZUSP 38995); 8 males, cl: 13.7–19.6 mm, and 11 females, cl: 10.5–21.2 mm, Praia de Ajuruteua, 0.828°S, 46.606°W, lower intertidal, Bragança, P. Hernáez coll., 7 July 2017 (MZUSP 38993). Maranhão: 10 males, cl: 10.8–17.6 mm, and 15 females, cl: 12.5–19.8 mm, Praia Olho d’água, 2.479°S, 44.231°W, lower intertidal, São Luis, P. Hernáez coll., 6 July 2017 (MZUSP 38994); 1 male, cl 12.4 mm, and 2 females, cl: 15.6–18.7 mm, Praia de Tutoia, 2.761°S, 42.263°W, lower intertidal, Tutóia, P. Hernáez coll., 5 July 2017 (MZUSP 39001). Piauí: 9 males, cl: 9.6–15.6 mm, and 14 females, cl: 10.2–17.7 mm, Praia da Atalaia, 2.889°S, 41.628°W, lower intertidal, Luis Correia, P. Hernáez coll., 3 July 2017

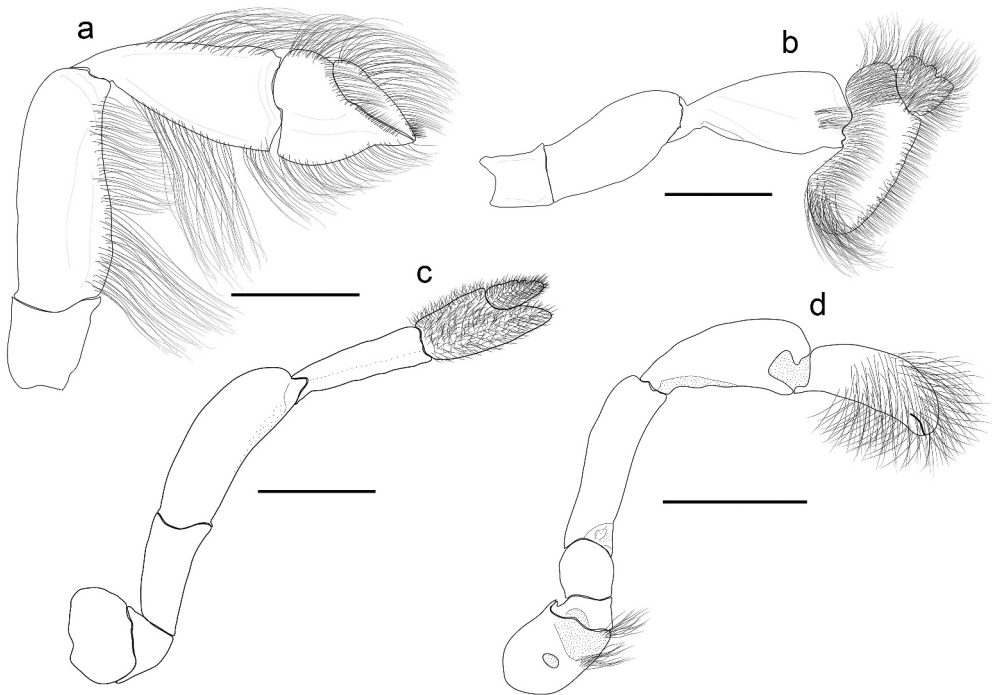


Figure 4. *Callichirus corruptus* sp. nov.; holotype, male (cl: 18.8 mm), MZUSP 41251. a–d, second, third, fourth and fifth pereopods, respectively, lateral view. Scale bars: 2 mm.

(MZUSP 38998). Ceará: 2 females, cl: 5.8–10.4 mm, close to the marine lighthouse, 2.876°S, 40.923°W, lower intertidal, Camocim, P. Hernáez coll., 3 July 2017 (MZUSP 39006). Rio Grande do Norte: 22 males, cl: 5.6–12.8 mm, and 19 females, cl: 7.6–13.3 mm, Praia do Pirangi, 5.974°S, 35.124°W, lower intertidal, Pirangi, P. Hernáez coll., 11 June 2016 (MZUSP 39011). Pernambuco: 1 male, cl: 10.5 mm, and 4 females, cl: 13.9–16.1 mm, Praia de Baixa Verde, 7.755°S, 34.824°W, lower intertidal, Ilha de Itamaracá, P. Hernáez coll., 17 June 2016 (MZUSP 39012); 6 males, cl: 7.9–15.9 mm, and 5 females, cl: 7.8–15.3 mm, Praia Piedade, 8.167°S, 34.913°W, lower intertidal, Recife, P. Hernáez coll., 10 June 2016 (MZUSP 39013). Alagoas: 15 males, cl: 9.0–16.0 mm, and 14 females, cl: 12.9–17.7 mm, Praia do Sobral, 9.673°S, 35.562°W, lower intertidal, Maceió, P. Hernáez coll., 9 June 2016 (MZUSP 39014). Sergipe: 9 males, cl: 11.5–15.8 mm, and 18 females, cl: 10.3–18.0 mm, Praia Aruana, 11.014°S, 37.064°W, lower intertidal, Aracajú, P. Hernáez coll., 8 June 2016 (MZUSP 39016). Bahia: 16 males, cl: 12.6–15.7 mm, and 16 females, cl: 11.8–14.7 mm, Praia Malvinas, 18.080°S, 39.543°W, lower intertidal, Mucuri, P. Hernáez coll., 20 June 2016 (MZUSP 39022). Espírito Santo: 15 males, cl: 7.8–12.5 mm, and 11 females, cl: 6.8–12.2 mm, Praia de Piúma, 20.844°S, 40.734°W, lower intertidal, Piúma, P. Hernáez coll., 3 June 2016 (MZUSP 39023). São Paulo: 14 males, cl: 5.7–11.9 mm, and 8 females, cl: 7.4–11.5 mm, Praia de Barequeçaba, 23.828°S, 45.434°W, lower intertidal, Barequeçaba, São Paulo, P. Hernáez coll., 2 June 2016 (MZUSP 39028); 28 males, cl: 10.1–19.1 mm, and 64 females, cl: 8.0–23.2 mm, Praia do Gonzaga, 23.970°S, 46.334°W, lower intertidal, Santos, P. Hernáez coll., 1 September 2016 (MZUSP 39027); 3 males, cl: 8.6–15.5 mm, and 3

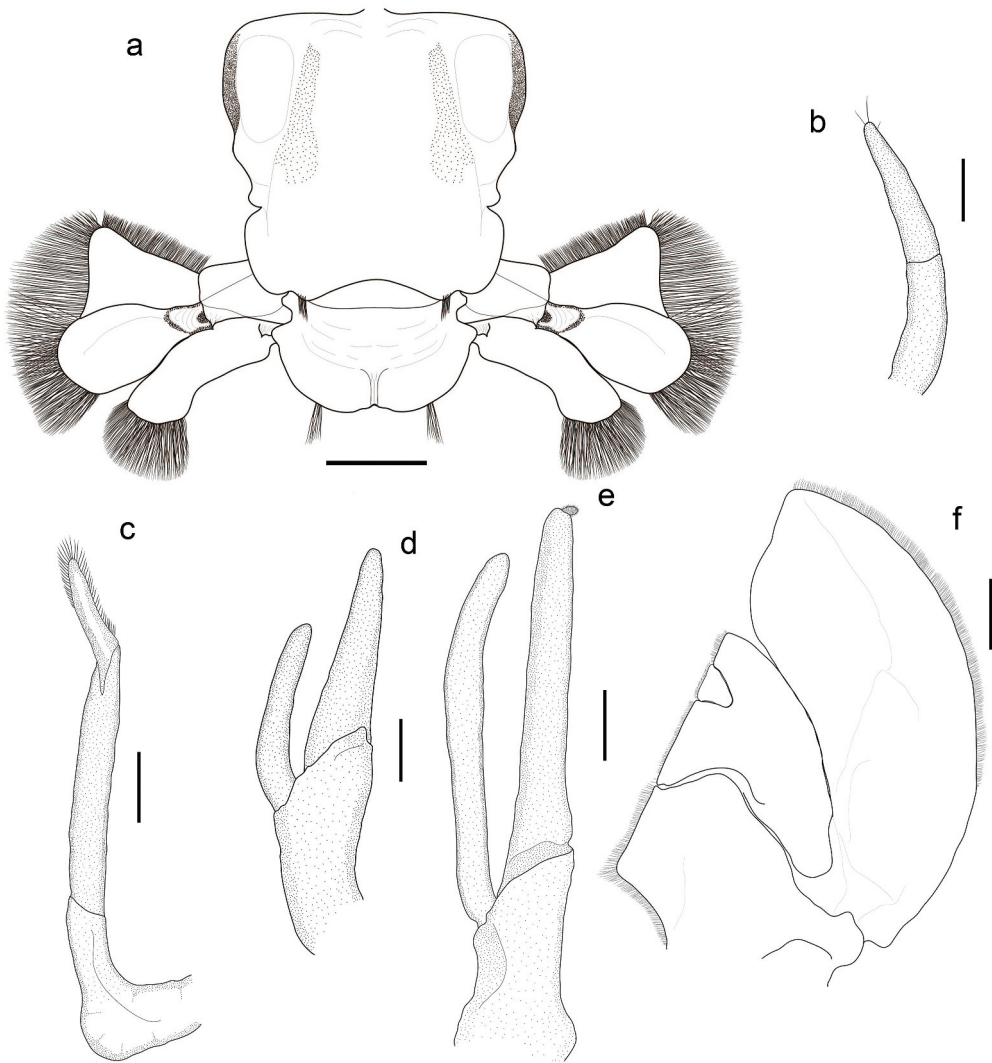


Figure 5. *Callichirus corruptus* sp. nov. a, b, d, f, holotype, male (cl: 18.8 mm), MZUSP 41251; c, e, paratype, female (cl: 20.4 mm), MZUSP 41252. a, sixth pleomere, uropods and telson, dorsal view; b, c, male and female first pleopods, respectively, external surface; d, e, male and female second pleopods, respectively, external surface; f, third to fifth pleopods, external surface. Scale bars: a, c, e, f = 2 mm; b, d = 1 mm.

females, cl: 7.9–8.3 mm, Cibratel, 24.201°S, 46.813°W, lower intertidal, Itanhaém, P. Hernáez coll., 12 August 2016 (MZUSP 39026); 3 males, cl: 7.3–10.8 mm, and 3 females, cl: 7.4–14.4 mm, Rio Peruíbe, 24.330°S, 47.000°W, estuary, Peruíbe, P. Hernáez coll., 1 September 2016 (MZUSP 39025); 8 males, cl: 6.4–18.7 mm, and 4 females, cl: 12.6–15.9 mm, Praia Ilha Comprida, 24.756°S, 47.559°W, lower intertidal, Ilha Comprida, P. Hernáez and J. Rio coll., 1 July 2016 (MZUSP 39029). Paraná: 15 males, cl: 7.9–16.7 mm, and 22 females, cl: 10.0–16.4 mm, Praia de Leste, 25.631°S, 48.421°W, lower intertidal, Pontal de Paraná, P. Hernáez and J. Rio coll., 2 July 2016 (MZUSP 39037). Santa

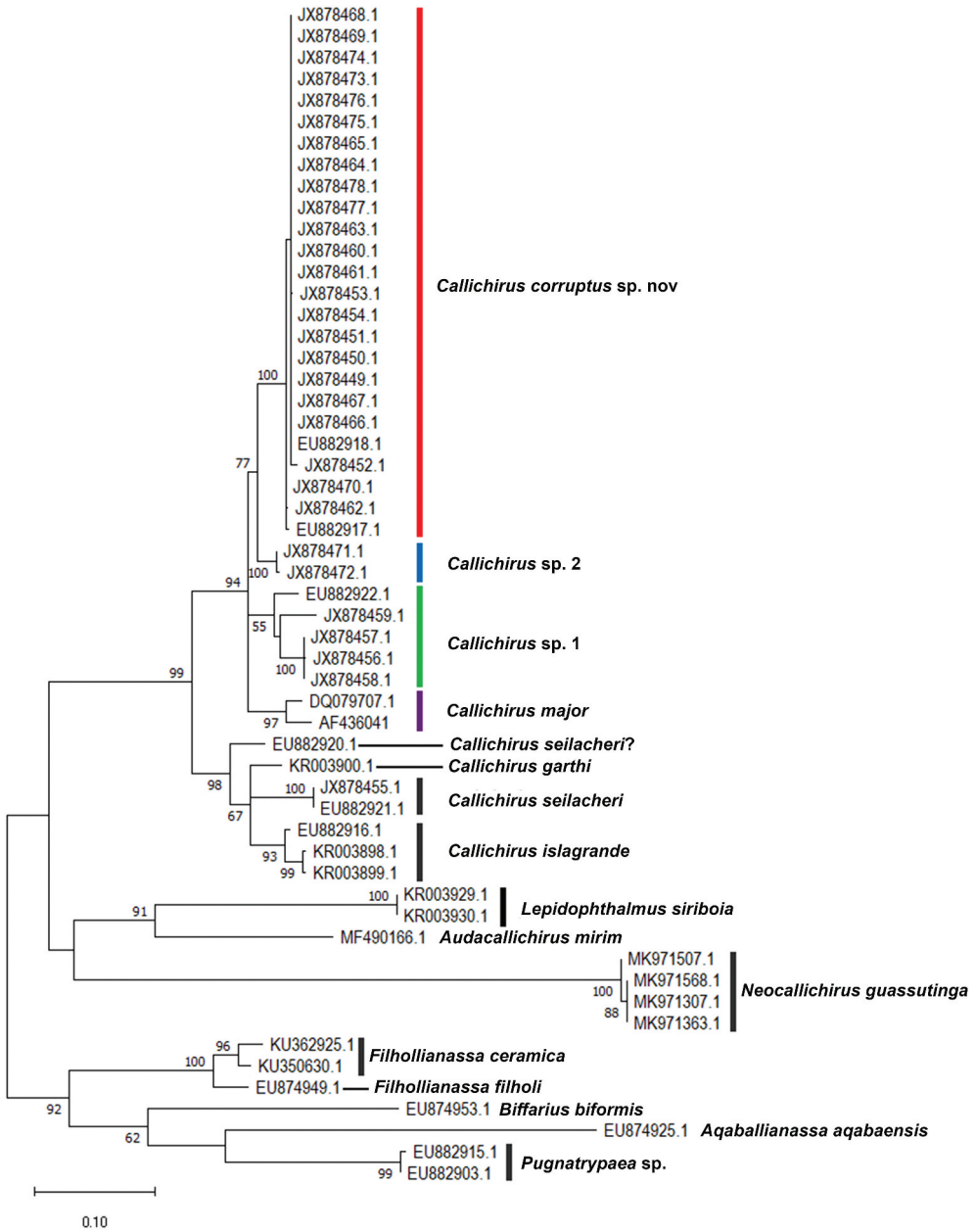


Figure 6. Molecular phylogenetic tree represented as maximum likelihood topology of the partial mitochondrial DNA sequence of the 16S rDNA gene to place *Callichirus corruptus* sp. nov. Nodal support values represent the frequencies observed using 1000 bootstrap pseudo-replicates. Values below 50% are not represented.

Catarina: 10 males, cl: 11.0–16.7 mm, and 27 females, cl: 8.9–22.3 mm, Balneário Camboriú, 26.989°S, 48.629°W, lower intertidal, Camboriú, P. Hernáez and J. Rio coll., 3 July 2016 (MZUSP 39039).

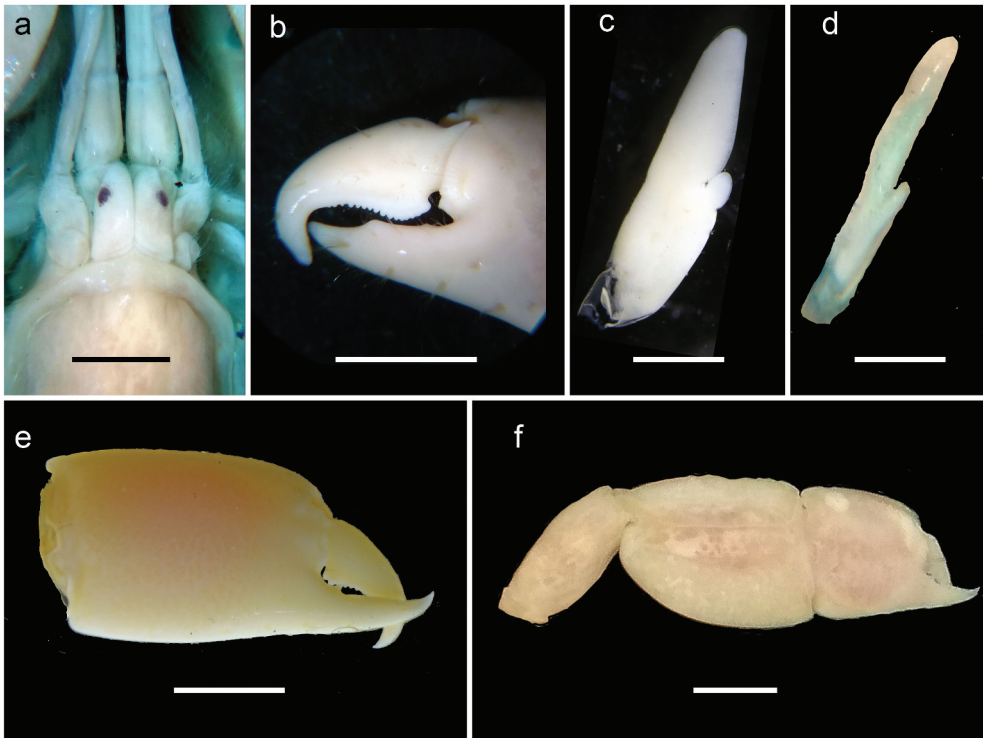


Figure 7. *Callichirus major*. a, b, neotype, male (cl 13.2 mm), Indian River, Florida, USA, USNM 228086. c, e, male (cl: 20.6 mm), New River, North Carolina, USA, USNM 266227. d, male (cl: 24.4 mm), Louisiana, Gulf Of Mexico, USA, USNM 79171. f, female (cl: 16.3 mm), Indian River, Florida, USA, USNM 228087. a, carapace front, eyestalks, and antennular and antennal peduncles, dorsal view; b, male major cheliped claw, lateral view; c, d, male second pleopod, external surface; e, male major cheliped claw, lateral view; f, female major cheliped, lateral view. Scale bars: a = 2 mm; b, e, f = 1 cm; c, d = 1 mm.

Comparative material examined

***Callichirus garthi* (Retamal, 1975).** Chile: 53 males, cl: 3.8–23.3 mm, and 54 females, cl: 4.3–21.9 mm, Las Machas, 18.437°S, 70.304°W, Arica, P. Hernández coll., 27 August 2011, MUAP-CD 0426/2011; holotype, male, cl: 35 mm, Lenga, 36.75°S, 73.17°W, Concepción, M. A. Retamal coll., May 1975 (MZUC-UCCC 7311); paratype, male, cl: 30 mm, same site as holotype, March 1974, coll. M.A. Retamal (MZUC-UCCC 7313); 66 males, cl: 7.6–21.3 mm, and 68 females, cl: 8.6–20.0 mm, Lenga, 36.77°S, 73.172°W, Concepción, P. Hernández coll., 9 March 2011 (MUAPCD 0432/2011). *Callichirus islagrande* (Schmitt, 1935): USA: Gulf of Mexico: holotype, male, cl: 19 mm, Grand Isle, Louisiana, W.W. Anderson coll., summer of 1930 (USNM 69362). *Callichirus major* (Say, 1818): USA: North Carolina: 1 male, cl: 20.6 mm, Onslow Bay, 34.606°N, 77.210°W, New River, R.B. Manning and D.B. Bixler coll., 30 July 1989 (USNM 266227); 1 female, cl: 11.9 mm, Onslow Bay, 34.606°N, 77.210°W, New River, R.B. Manning and D.B. Bixler coll., 7 August 1990 (USNM 266232). Georgia: 1 male, cl: 21.2 mm, Tybee Island, 31.999°N, 80.841°W, G.A. Bishop coll., 1 April 1988 (USNM 266247). Louisiana: 2 males, cl: 15.0–24.4 mm, Grand Island, 30.133°N, 89.417°W, Gulf of Mexico, E.R. Willis

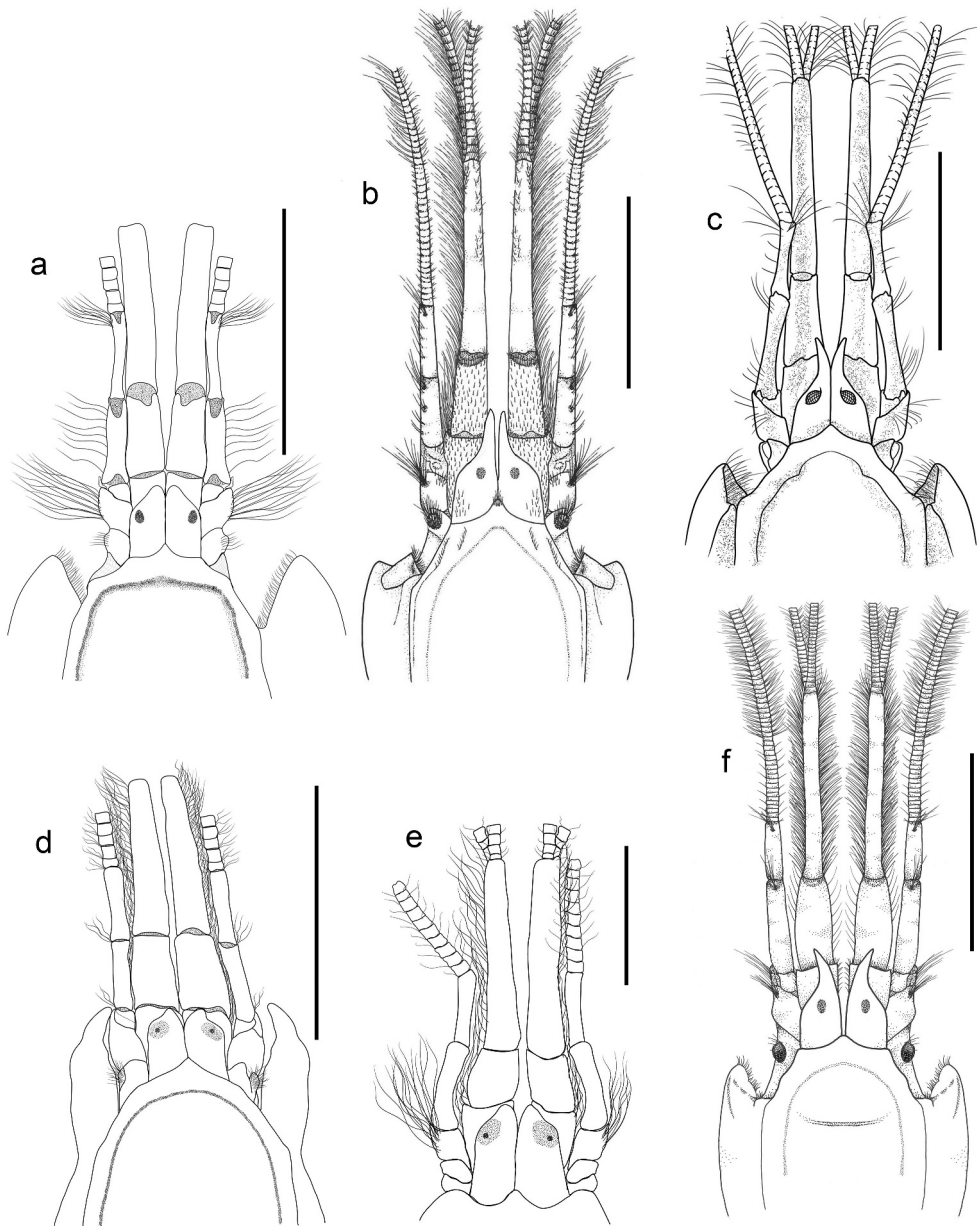


Figure 8. Carapace and cephalic appendages, dorsal view. a, *Callichirus corruptus* sp. nov., MZUSP 41251; b, *Callichirus garthi*, MUAP-CD 0426/2011; c, *Callichirus islagrande* (courtesy of Nuno Simões); d, *Callichirus major*, USNM 228086; e, *Callichirus santarosaensis* (modified from Sakai and Türkay 2012); f, *Callichirus seilacheri*, MZUCR 3335-01. Scale bars: 10 mm.

coll., 26 June 1939 (USNM 79171). Texas: 1 ovigerous female, cl: 16.4 mm, Heald Bank, 29.727°N, 93.708°W, Sabine, W.G. Hewatt coll., 1967 (USNM 97653). Florida: 2 ovigerous females, cl: 9.7–20.2 mm, Indian River, 27.88°N, 80.457°W, R.B. Manning, W. Lee, M. Schotte and C. King coll., 20 April 1988 (USNM 266125); 1 female, cl: 21.0 mm, Indian River, 27.636°

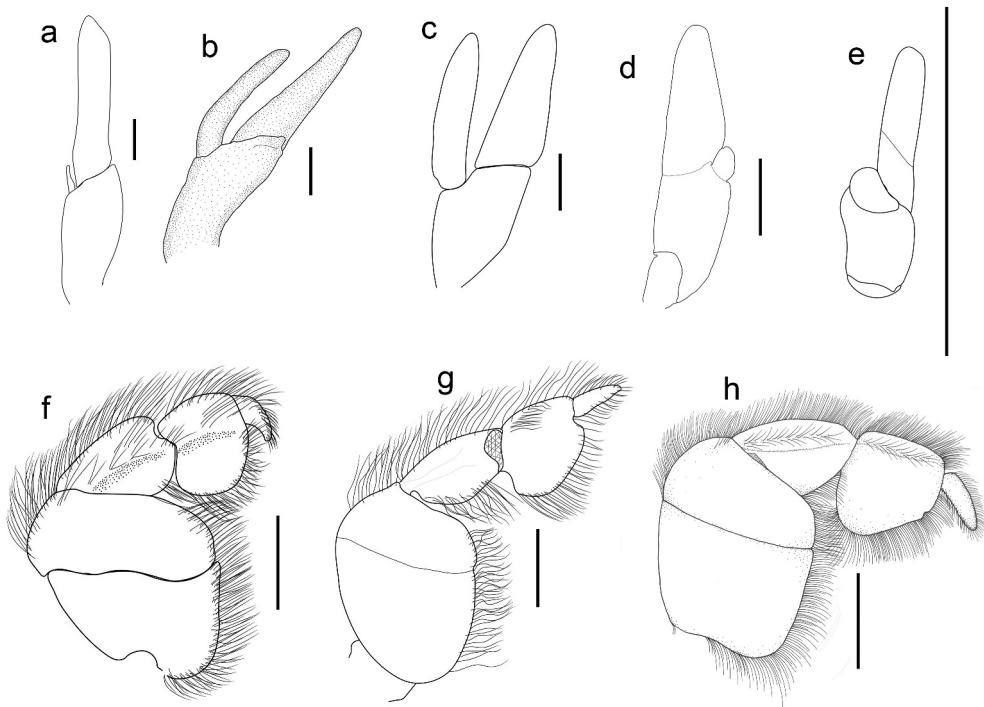


Figure 9. Male pleopod 2 and third maxilliped, external surface. a, *Callichirus adamas* (modified from Kensley 1974); b, *Callichirus corruptus* sp. nov., MZUSP 41251; c, *Callichirus islagrande*, USNM 69362; d, *Callichirus major*, USNM 228086; e, *Callichirus santarosaensis* (modified from Sakai and Türkay 2012); f, *Callichirus adamas* (modified from Kensley 1974); g, *Callichirus garthi*, MZUC-UCCC 7311; h, *Callichirus seilacheri*, MZUCR 3335-01. Scale bars: a–d = 1 mm; e–h = 5 mm.

N, 80.364°W, North Hutchinson Island, Fort Pierce, D.L. Felder and W. Lee coll., 14 August 1987, USNM 266118; 1 male, cl: 11.1 mm, Fort Pierce area, 27.472°N, 80.297°W, R.B. Manning coll., 2 March 1987 (USNM 266127); 1 female, cl: 15.4 mm, Indian River, 27.472°N, 87.297°W, North Hutchinson Island, Fort Pierce, R.B. Manning and W. Lee coll., 2 March 1987 (USNM 266126); 1 female, cl 16.3 mm, Indian River, 27.183°N, 80.158°W, Seminole Shores, R.B. Manning and L.K. Manning coll., 7 July 1984 (USNM 266111); 1 female, cl 16.3 mm, Indian River, 27.175°N, 80.173°W, Flat Just Inside Saint Lucie Inlet, R.B. Manning coll., 11 February 1983 (USNM 228087); topotype, male, cl 13.2 mm, Indian River, 27.171°N, 80.173°W, R.B. Manning coll., 9 February 1983 (USNM 228086); 1 male, cl 18.6 mm, Lake Worth Inlet, 26.771°N, 80.037°W, Peanut Island, R.B. Manning and D.L. Felder coll., 11 August 1987 (USNM 266114). *Callichirus* aff. *major*: Colombia: Caribbean coast: 1 male, cl 22.2 mm, La Boquilla, 10.472°N, 75.500°W, Cartagena, R. Lemaitre coll., 10 August 1980 (USNM 266208); 1 male, cl 13.9 mm, and 1 ovigerous female, cl 13.7 mm, La Boquilla, 10.472°N, 75.500°W, Cartagena, R. Lemaitre coll., 10 August 1988 (USNM 266225); 1 female, cl 23.6 mm, Castillo Grande, 10.395°N, 75.551°W, Cartagena Bay, Cartagena, R. Lemaitre coll., 7 July 1988 (USNM 266211). *Callichirus seilacheri* (Bott, 1955): El Salvador: 1 male, cl 16.3 mm, and 1 female, cl 24.1 mm, Los Blancos, topotype, 13.327°N, 88.969°W, P. Hernández and A. Gamboa-González coll., 22 July 2013

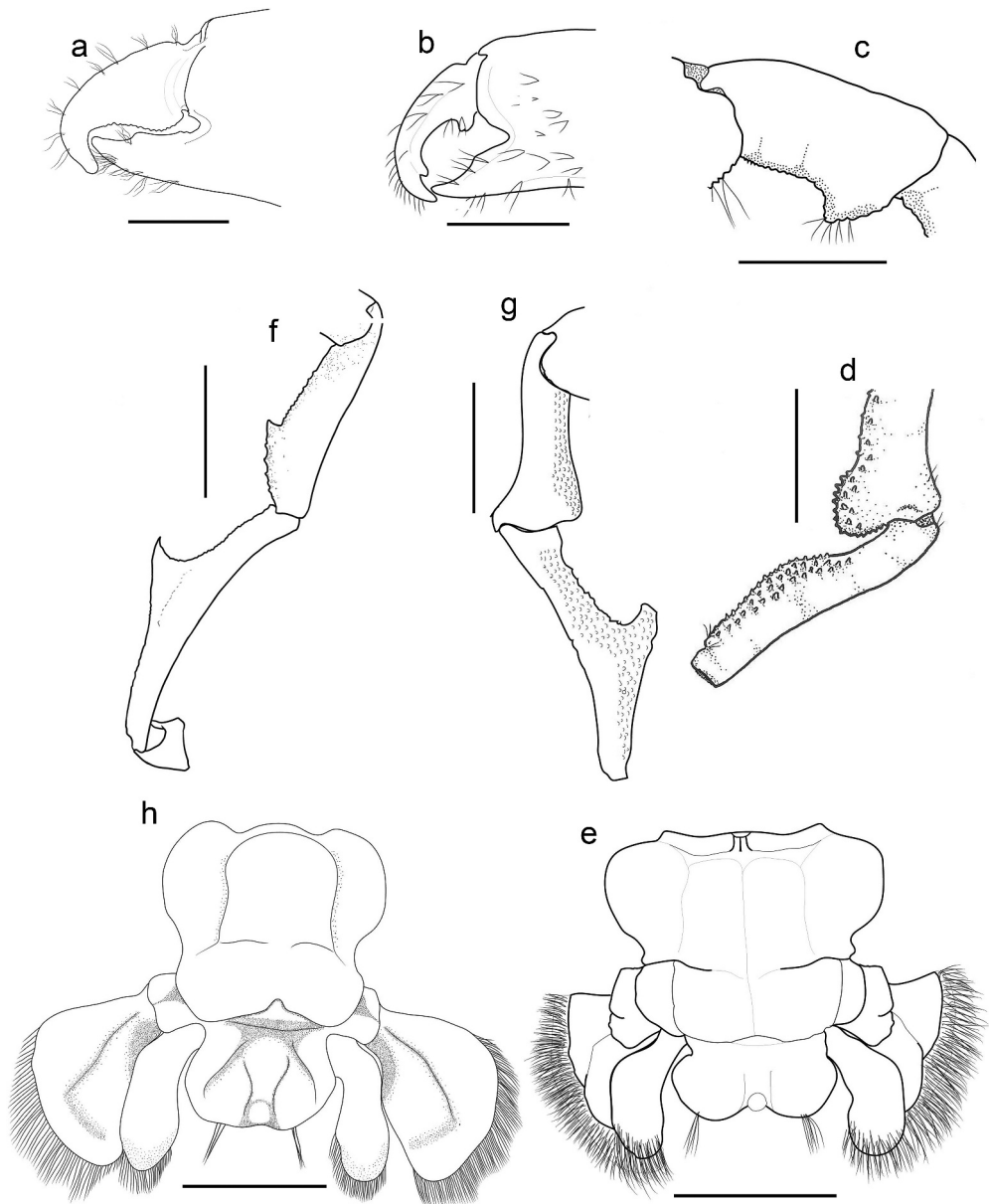


Figure 10. a, *Callichirus* aff. *major* Colombia, male major cheliped dactylus and fixed finger, lateral view, USNM 266225; b, *Callichirus corruptus* sp. nov., male major cheliped dactylus and fixed finger, lateral view, MZUSP 41251; c, *Callichirus corruptus* sp. nov., female major cheliped merus, lateral view, MZUSP 41252; d, *Callichirus garthi*, male major cheliped ischium, lateral view, MUAP-CD 0432–2011; e, *Callichirus garthi*, sixth pleomere, uropods and telson, dorsal view, MUAP-CD 0432–2011; f, *Callichirus islagrande*, male major cheliped merus and ischium (courtesy of Nuno Simões), lateral view; g, *Callichirus adamas*, male major cheliped merus and ischium (modified from Kensley 1974), lateral view; h, *Callichirus islagrande*, sixth pleomere, uropods and telson, dorsal view, USNM 69362. Scale bars: 10 mm.

Antennal peduncle (Figure 2b) reaching mid length of antennular peduncle third article; basal article short, excretory pore protruded, densely setose; second article with setose laterally; third article shorter than second; fourth and fifth articles subequal in length, fourth article with sparse setae laterally, fifth article with tuft of short setae distolaterally; scaphocerite small, blade-shape (Figure 2d).

Mouthparts typical for genus according to external observation, not illustrated. Maxilliped 3 (Figure 2e) without exopod; ischium-merus operculiform, length about 1.2 times its width, setose marginally; ischium without crista dentata on mesial surface, 1.4 times length of merus; distal and proximal margin of merus not parallel, strongly oblique distally, not projecting beyond carpo-meral articulation; carpus and propodus expanded ventrally; dactylus digitiform, shorter than propodus.

Chelipeds (pereopods 1) unequal and dissimilar in males and females (Figures 1a, 2a, 3a–d). Male major cheliped (Figure 3a) extremely elongated and strongly calcified; ischium ventral margin with row of well-spaced blunt teeth, dorsal margin nearly straight; merus with prominent hook on lower margin, hook margin strongly serrate, remainder of hook lower margin with irregular rounded denticles, hook dorsal margin slightly denticulate and concave; carpus length about 1.5 times as long as palm, about twice longer than wide, dorsal margin straight, unarmed, ventral margin slightly expanded medially, with rounded denticles at proximal third, sparse setae; palm rectangular, longer than width, dorsal and ventral margins smooth, with sparse setae on ventral margin; fixed finger with triangular tooth at mid length of cutting edge; dactylus strongly arcuate with tip curved downward, bifid, longer than fixed finger, cutting edge with large bifid tooth proximally, otherwise unarmed. Male minor cheliped (Figure 3c) slender; ischium longer than merus, dorsal and ventral margin smooth; merus narrower than carpus, dorsal margin smooth, slightly convex, ventral margin with spaced tufts of short setae; carpus longest article, lateral sulcus, dorsal margin of carpus slightly curved, ventral margin of carpus slightly expanded, with row of tufts of short setae; palm about half length of carpus, dorsal margin unarmed, ventral margin with row of tufts of short setae, fixed finger approximately as long as dactylus, occlusal margin armed by serration of small acute denticles; dactylus slightly arcuate, occlusal margin armed by serration of small acute denticles, with tuft of setae dorsally.

Female major cheliped (Figure 3b) less elongate than in males, differing from male larger cheliped as follows: dorsal and ventral margin of ischium straight; merus with less prominent hook on lower margin, margin of hook weakly granulate, dorsal margin hook smooth, curved; carpus as long as palm; cutting edge of fixed finger with two acute teeth at proximal third, as long as dactylus; dactylus slightly curved, occlusal margin with small acute denticles. Female minor cheliped (Figure 3d) as in males, differing only in having dorsal and ventral margins of merus convex, cutting edges of fixed finger, dactylus unarmed and setation pattern.

Pereopod 2 (Figure 4a) chelate, densely setose ventrally; ischium about 1.4 times as long as wide; merus slightly longer than carpus, lower margin sinuous, with row of long setae, dorsal margin slightly convex; carpus subtriangular, widening distally, dorsal and ventral margin with sparse long setae; palm less than 0.5 times as long as carpus, fixed finger subtriangular, cutting edge smooth; dactylus lanceolate, cutting edge smooth, densely setose dorsally. Pereopod 3 (Figure 4b) pediform; ischium subsquare, unarmed; merus about two times longer than ischium, ventral and dorsal margins slightly convex and non-setose; carpus subtriangular, widening distally, distal margin with tuft of setae

dorsally; propodus expanded proximally, produced into rounded posterior lobe, heavily setose; dactylus broad, with two small notches distally, heavily setose. Pereopod 4 (Figure 4c) subchelate; ischium more than half of merus, unarmed, margins non-setose; merus slightly wider than ischium, arcuate ventrally; carpus widening distally, almost equal in length to propodus, margins non-setose; propodus wider than carpus, with lower-distal projection, surface densely covered with short setae; dactylus digitiform, two small notches on the upper border, surface densely covered with short setae. Pereopod 5 (Figure 4d) chelate, fingers not gaping; ischium rectangular, unarmed; merus longest, about 2.7 times longer than ischium, unarmed; carpus subtriangular, widening distally, unarmed; inner and outer surface of propodus densely setose in distal half; surface of dactylus covered with dense setae.

Pleon (Figure 2a) glabrous dorsally, except for subcircular patches of setae adjacent to lateral margins of somites 3 to 5 representing integumental glands; pleon about 5.7 times as long as carapace; length ratio of first to sixth pleomeres and telson measured along midline 3.3:4.3:1.7:1.6:2.0:1.9:1.0, first and second pleomeres combined longer than third to fifth pleomeres combined (1.3:1.0). First and second pleomeres translucent (Figure 1a); first pleomere narrowing anteriorly in dorsal view, shorter than second one, connection between the dorsal and ventral sclerites perceptible as a fine suture running obliquely in the anteposterior sense; second pleomere longest, widening posteriorly in dorsal view, tergite rounded posterolateral lobe below suture sclerotised at least as heavily as remainder of tergite. Pleomeres 3–5 (Figure 1a) similar in length, third to fifth tergites each laterally encompassing finely pubescent, membranous subcircular area below posterolateral suture, membranous areas of third and fourth tergite more posteriorly positioned than on fifth, that of fifth tergite slightly smaller, less circular. Sixth pleomere (Figure 5a) saddle-like, 1.2 times as wide as long; pleurites globose dorsally, tergite with a transverse groove on each side and a longitudinal groove at posterior half; posterior margin bilobed by short median notch, with 2 pairs of tufts of short setae posteriorly. Telson (Figure 5a) slightly broader than long, tapering distally, emarginate posteriorly; lateral margin with small lobe proximally, followed by deep notch and another large lobe at mid length to lateral margin; dorsal surface separated into three lobes, one large anterior and two smaller posterolateral separated by deep central notch.

Pleopod 1 (Figure 5b, c) uniramous and slender in both sexes, composed of two articles in males, three articles in females. Male first pleopod (Figure 5b) with two equally long articles, distal article narrowing distally, sparse setae on the tip. Female first pleopod (Figure 5c) longer than male one, basal article L-shaped, second article about twice as long as terminal article, terminal article forming narrow flattened blade, terminal article margin fringed by short setae. Pleopod 2 (Figure 5d, e) biramous in both sexes; in males and females endopod and exopod well developed, exopod slightly shorter than endopod; second pleopod of male non-setose, male endopod without appendices interna and masculina; in females endopod with well-developed and terminal appendix interna, surface of appendix interna covered with patch of short hooked setae. Pleopods 3 to 5 (Figure 5f) biramous, leaf-like, endopod broadened, with subtriangular appendix interna embedded into mesial margin of endopod in both sexes. Uropod (Figure 5a) with protopod dorsally divided into four irregular lobes, posterolateral lobe ending in spinous process projected distally; endopod strap-shaped,

much longer than wide, exceeding posterior margin of telson, base with rounded lobe ending in a spine protruded distally; exopod triangular with anterodorsal plate shorter than posterodorsal plate, both with distal margin densely setose.

Colour

In life (Figure 1a) most individuals appear white to hyaline on all sclerotised parts, including chelipeds, sixth pleomere, telson and uropods. The branchiostegites and part of the dorsal oval of the carapace are poorly sclerotised, whereas most of the pleon is translucent in dorsal view. In males, the liver gland is visible in deep yellow through the cuticle of the first and second abdominal somites in dorsal view. Interestingly, the male gonad has an ovarian section that runs between the posterior region of the second pleomere and the anterior region of the fourth pleomere, which is dorsally visible due to its orange colouration. In females, this gland is partially covered by the ovaries, which in mature females are reddish orange. Pattern of dorsal abdominal grooves more whitish in adult males and females.

Distribution

Known from Praia do Crispim, Pará to Balneário Camboriú, Santa Catarina, Brazil (Figure 1b).

Habitat

Callichirus corruptus sp. nov. forms simple burrows with one opening, normally inhabited by only one individual, in the intertidal zone of fine-grained sandy beaches. This ghost shrimp is often the only axiidean species present in the intertidal zone of many beaches. The pinnotherid crabs *Austinixa aida* (Righi, 1967) and *A. patagoniensis* (Rathbun, 1918) are normally found living within the galleries of *C. corruptus* sp. nov. (Hernández 2018).

Etymology

From the Latin, *corruptus* referring to the name that local harvesters give to the species of *Callichirus* along the Brazilian coast.

Taxonomic background of *Callichirus major* (Say, 1818)

Larval and molecular evidence have been accumulating to suggest that *Callichirus major* (Say, 1818) is in fact a species complex (e.g. Staton and Felder 1995; Strasser and Felder 1998, 1999a; Felder and Robles 2009; Peiró 2012; Rio 2018). Long before molecular data was available, comparative morphological studies by Rodrigues (1971, 1985) showed that Southern (Santos, Brazil) and Northern (North Carolina, USA) specimens differ. The differences concerned the presence of a subterminal tooth on the cutting edge of the dactylus of the male major cheliped (absent in northern specimens) and the absence of an acute tooth at the proximal third of the propodus of the female cheliped (present in northern specimens). Rodrigues (1985) suggested that the Brazilian *Callichirus* population would ultimately prove to be a different species from *C. major*. Rodrigues felt that more specimens from both Northern and Southern localities were required for further examination before a new species could be established. Many years later, Strasser and

Felder (1999a) commented on several morphological differences between larvae from Northern and Southern (Brazilian) localities and referred to the Brazilian material as *Callichirus* sp.

Ortmann (1893, p. 87) described *Anomalocaris macrotelsonis* from northern Brazil based on a fourth-stage larva and commented on the resemblance of *A. macrotelsonis* to the mysis (= zoeal stage) of *Callianassa*. The taxon of Ortmann, however, has a distinctly projecting dorsal carina on the first pleomere (Ortmann 1893, p. 87, pl. VI, Figure 5), a characteristic not seen in larvae of callichirid or other callianassoid taxa (see also Pohle et al. 2011; Pohle and Santana 2014 for a compilation of available larval information).

The molecular data (16S) analysed by Peiró (2012, Figure 1) showed a distinct clade for Brazilian *Callichirus* populations. Unfortunately, Peiró (2012) mistakenly assigned his Brazilian clade to the taxon of Ortmann. Surprisingly, he designated [sic] several males and females from Santos (Brazil) as syntypes [sic] for what he considered to be '*Callichirus macrotelsonis* Ortmann, 1893'. There is no doubt that the larval material of Ortmann's (1893) taxon does not represent any callichirid or even callianassid species.

In her master's dissertation, Rio (2018) clarified the morphological differentiation of the Brazilian population from *C. major*, but her name, *Callichirus brasiliensis*, has not been published, and is not available because it does not comply with the International Code of Zoological Nomenclature (ICZN 1999: Articles 8 and 9).

Neotype designation for *Callichirus major* (Say, 1818)

Callichirus major was originally described from a single specimen from Florida, deposited in the Academy of Natural Sciences of Philadelphia, USA. The holotype, however, is no longer extant (Spamer and Bogan 1992, p. 162; P. Callomon, pers. comm. 2020). White (1847, p. 70) listed 2 'arms' of '*Callianassa major*' presented by Th. Say to the Natural History Museum in London (see Spamer and Bogan 1992, p. 162). It is unlikely that these chelae represent the holotype of *C. major*. Consequently, the designation of a neotype for *C. major* is here proposed, i.e. male, cl: 13.2 mm, Indian River, flat just inside Saint Lucie Inlet, Florida, USNM 228086. Therefore, the distribution of *C. major* is restricted to populations between Florida and North Carolina, and *C. santarosaensis* is limited to northern Gulf of Mexico, as suggested by Felder and Dworschak (2015).

Molecular analysis

The rate of divergence between *C. major* s. str. (northern localities) and *C. corruptus* sp. nov. (Southern localities) is 5%, the same value as for the well established *C. islagrande* and *C. garthi* and *Filholianassa filholi* (A. Milne-Edwards 1879) and *F. ceramica* (Fulton and Grant, 1906) (Table 2). Thus, morphology (see below) and molecular data support *C. major* and *C. corruptus* sp. nov. as distinct species.

Callichirus sp. 1 and *Callichirus* sp. 2 (Figure 6), from the eastern Pacific and Caribbean Colombia, respectively, have a divergence rate of 3% from *C. corruptus* sp. nov., and 5% from *C. major* (Table 2). These divergence rates also suggest that *Callichirus* sp. 1 and *Callichirus* sp. 2 are both undescribed species. Additional material, however, is required to clarify this assumption.

Callichirus taxa were found to be nested within a well-supported clade (Figure 6). The terminals previously assigned to *C. major* s. l. were recovered into a well-supported clade and the sister-group relationship between *C. corruptus* sp. nov. and *Callichirus* sp. 2 is also well supported (bootstrap values of 94 and 77, respectively). *Callichirus* sp. 1 representatives grouped together (bootstrap value 55) but their relationship with *C. major* s. str. and the clade (*C. corruptus* sp. nov. + *Callichirus* sp. 2) is still unresolved. A morphological resolution of this polytomy will require the establishment of additional characters.

Species differentiation

Morphologically, *C. corruptus* sp. nov. differs from *C. major* s. str. by a combination of characters including: (1) the ocular peduncle reaches the distal one-third of the first article of the antennular peduncle (vs reaches to or slightly beyond the distal end of the first article of the antennular peduncle in *C. major*; Manning and Felder 1986: Figure 1; Figures 2c, 7a, 8a, d); (2) the third article of the antennular peduncle is about 2.0 times as long as the second article (vs 2.4 times as long as the second article; Manning and Felder 1986: Figure 1; Figures 2c, 8a, d); (3) the dactylus of the male major cheliped is bifid distally (vs simple in *C. major*; Manning and Felder 1986: Figure 1; Figures 3a, 7b, 10b); (4) the occlusal propodal margin of the male major chela is armed with one tooth (vs two teeth in *C. major*; Figures 3a, 7b, 10b); (5) the propodus of the male major chela is blunt at the tip and slightly curved upward (vs acute at the tip and strongly curved upward in *C. major*; Figures 3a, 7e); (6) the male pleopod 2 exopod well developed (vs reduced in *C. major*; Figures 5d, 7c, d, 9b, d); (7) the female chelae are unequal in size and dissimilar in shape (vs subequal and similar in *C. major*; Figure 3b, d) and (8) the female major chela with a large meral hook on flexor margin (vs without meral hook in *C. major*; Figures 3b, 7f).

Callichirus corruptus sp. nov. can be distinguished from its four American congeners by the following combination of characters: (1) eyestalks with obtuse tip (distomesial projection absent), not exceeding the second article of the antennular peduncle in the new species (Figure 2c), whereas it is elongate with distomesial projections exceeding the second article of the antennular peduncle in *C. garthi*, *C. islagrande* and *C. seilacheri* (Figure 8b, c, f, respectively); (2) second article of antennular peduncle slightly exceeding the fourth article of antennal peduncle in *C. corruptus* sp. nov. (Figure 2c), whereas it is distinctly exceeding the fourth article of antennal peduncle in *C. garthi* and *C. islagrande* (Figure 8b, c, respectively); (3) maxilliped 3 merus with distal margin strongly oblique in the new species (Figure 2e), but slightly oblique in *C. garthi*, *C. islagrande* and *C. seilacheri* (Figure 9g, h); (4) male major cheliped having the ventral margin of ischium with a row of well-spaced blunt teeth in *C. corruptus* sp. nov. (Figure 2a), but armed with a hook in *C. islagrande* (Figure 10f) and *C. seilacheri* and a lobe in *C. garthi* (Figure 10d); and (5) male pleopod 2 with the endopod well developed and exopod unarticulated in the new species (Figures 5d, 9b), but with endopod reduced and exopod bisegmented in *C. santarosaensis* (Figure 9e) (cf. Manning and Felder 1986, Figure 2; Hernandez et al. 2015, Figures 2a, b, 3a, b; Sakai and Turkay 2012, Figure 10h; Hernandez et al. 2018, Figure 2b, c).

Staton and Felder (1995) molecular analysis recovered a distinct clade representing an undescribed species from the Gulf of Mexico. Sakai and Türkay (2012) described *C. santarosaensis* based on small, damaged specimens from Santa Rosa Island, Pensacola, Florida, Gulf of Mexico. Later, Felder and Dworschak (2015) re-examined the type material of *C. santarosaensis*, and the species for the populations in the Gulf of Mexico. Sakai and Türkay (2012) distinguished *C. santarosaensis* from *C. major* by the following characters: (1) the antennular peduncle is about as long as the antennal peduncle; and (2) the telson is bisected, slightly converging towards the truncate end. Felder and Dworschak (2015), however, showed that misinterpretations of the morphology of the antennule, antenna and telson led Sakai and Türkay (2012) astray, such that no morphological characters remain that justify *C. santarosaensis*. Yet Felder and Dworschak (2015) argued that the name *C. santarosaensis* can still be applied 'on the basis of geographical origins of materials, underpinned by genetic analyses (*sensu* Staton and Felder 1995) when possible' (p. 270). Sakai and Türkay (2012), and Felder and Dworschak (2015) however, overlooked that the male second pleopod endopod is greatly reduced in *C. santarosaensis* (Sakai and Türkay 2012, p. 746, Figure 10h; see also Figure 9e) while it is well developed in *C. major s. str.* (Figures 7c, d, 9c). This character can be used with confidence to separate *C. santarosaensis* from *C. major s. str.* – unless Sakai and Türkay (2012) confused the endopod with the exopod in their description of *C. santarosaensis*.

Callichirus corruptus sp. nov. is distinguished from the only non-American species in the genus, namely *C. adamas*, by the absence of a distomesial projection on the ocular peduncle (vs ocular peduncles with elongated distomesial projections in *C. adamas*; Kensley 1974, Figure 1a; Figures 2c, 8d) and the male second pleopod with well-developed exopod (vs vestigial or strongly reduced in *C. adamas*; Kensley 1974, Figure 2h; Figures 5d, 9a, d).

Callichirus now consists of seven species, namely *C. adamas* (Senegal to Orange River mouth, South Africa), *C. corruptus* sp. nov. (Pará to Santa Catarina, Brazil), *C. garthi* (Huanchaco, Peru, to Tubul, Chile), *C. islagrande* (Gulf of Mexico), *C. major* (North Carolina, USA, to the Caribbean coast of Colombia), *C. santarosaensis* (northern coast of the Gulf of Mexico, Florida, USA) and *C. seilacheri* (Jalisco, Mexico, to Puntarenas, Costa Rica).

During this study, specimens from Caribbean Colombia, currently referred to *C. major*, were examined. They are similar to *C. corruptus* sp. nov. in characters of the ocular peduncles and the male second pleopods, but differ in the simple tip of the major male cheliped dactylus and the absence of a meral hook on the female major cheliped. There is no doubt that the Colombian specimens represent an undescribed species of the *C. major* species complex. The following key facilitates the identification of the species of *Callichirus*.

Key to the species of the genus *Callichirus* Stimpson, 1866 (Figures 8, 9, 10)

1. Ocular peduncle with obtuse tip, not exceeding or slightly exceeding junction between first and second articles of the antennular peduncle (Figure 8a, d, e) 2
 - Ocular peduncle with prominent distomesial projection distinctly exceeding junction between first and second articles of antennular peduncle (Figure 8b, c, f) 5
2. Ocular peduncle reaching to about 2/3 of the length of the first article of the antennular peduncle (Figure 8a). Male pleopod 2 with endopod and exopod well developed (Figure 9b) 3
 - Ocular peduncle reaching the limit between the first and second articles of antennular peduncle, or a little beyond (Figure 8d, e). Male pleopod 2 with endopod or exopod reduced (Figure 9d, e) 4
3. Male major cheliped dactylus with bifid tip (Figure 10b). Female major cheliped merus armed with ventral hook (Figure 10c) *C. corruptus* sp. nov.
 - Male major cheliped dactylus simple (Figure 10a). Female major cheliped merus unarmed *Callichirus* sp. (Caribbean Colombia)
4. Male pleopod 2 with endopod underdeveloped (Figure 9e) *C. santarosaensis*
 - Male pleopod 2 with exopod reduced (Figure 9d) *C. major* s. str.
5. Antennular peduncle article 2 reaching as far as antennal peduncle article 4 (Figure 8f). Maxilliped 3 with tiny notch at the flexor distal angle of propodus (Figure 9h) *C. seilacheri*
 - Antennular peduncle article 2 exceeding antennal peduncle article 4 (Figure 8b, c). Maxilliped 3 without notch on flexor distal margin of propodus (Figure 9f, g) 6
6. Male major cheliped ischium unarmed ventrally (Figure 10d). Telson with small convexity within median emargination (Figure 10e) *C. garthi*
 - Male major cheliped ischium armed with a ventral hook (Figure 10f). Telson without convexity within median emargination (Figure 10h) 7
7. Male pleopod 2 with exopod reduced (Figure 9a). Male major cheliped merus unarmed ventrally (Figure 10g) *C. adamas*
 - Male pleopod 2 with exopod well developed (Figure 9c). Male major cheliped merus armed with ventral hook (Figure 10f) *C. islagrande*

Acknowledgements

Firstly, we thank our colleagues Marcos Tavares and William Santana for their help in the construction, organisation, analysis and conclusions of an early version of this work. Without their help and work we would not have been able to bring this work to fruition. Also, we are grateful to Rafael Lemaitre and Karen Reed, who kindly provided access to material of *Callichirus* and provided working space at the USNM; Paul Callomon (Academy of Natural Sciences of Philadelphia) and Paul F. Clark and Miranda Lowe (Natural History Museum, London), who kindly searched for the holotype of *Callichirus major* in the collections of the ANSP and NHM, respectively; and Joana D'Arc de Jesus Pinto and Maria José de Souza Coelho (MZUSP) for the help with the MZUSP collections. We thank in particular Mr Andrew Polaszek, Editor in Chief, for the vital work he has done during the laborious revision process of our article. Without his fair and professional intervention, this work

would never have seen the light of day. Finally, we thank the four anonymous referees, who helped to improve the content and format of this article.

Disclosure statement

No potential conflict of interest has been declared by the author(s).

Funding

PH and MSM thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for financial aid through a post-doctoral grant [process 2015/09020-0] and a PhD sandwich grant [process 2018/17718-5], respectively. PH also thanks Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) for financial aid through a Researcher Fixation Scholarship [process BFP-0196-1.08/20]. JPPR thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial aid through an MSc grant [process 1688290]. MAAP thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial aid through research grants [305714/2015-5].

ORCID

Patricio Hernández  <http://orcid.org/0000-0002-3785-2050>
Marcel S. Miranda  <http://orcid.org/0000-0002-9594-6426>
Juliana P.P. Rio  <http://orcid.org/0000-0002-8195-3596>
Marcelo A.A. Pinheiro  <http://orcid.org/0000-0003-0758-5526>

Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed by the authors.

Data availability

All data generated or analysed during this study are included in this published article.

Sampling and field studies

All necessary permits for sampling and observational field studies were obtained by the authors from the competent authorities. Licences to collect zoological material issued to PH (#51,578-1, #58,845-1) were provided by the Brazilian Institute of the Environment and Renewable Natural Resources (SISBIO/IBAMA-MMA).

References

- Alves-Júnior FDAA, de Araújo MDSL, Coelho PA. 2014a. Population biology of *Callichirus major* (Say, 1818) (Crustacea: Callianassidae) at Piedade Beach, Brazil. *J Integr Coast Zone Manag.* 14 (1):109–118. doi:10.5894/rgci435.
- Alves-Júnior FDAA, de Araújo MDSL, Feitosa FADN. 2014b. Crescimento alométrico de *Callichirus major* (Say, 1818) (Crustacea: Callianassidae) em uma Praia arenosa do nordeste brasileiro. *Trop Oceanogr, Recife.* 42(special number):13–21. doi:10.5914/1679-3013.2013.0088.

- Alves-Júnior FDAA, Santana JDL, Figueiredo AMF, de Araújo MDSLC. 2018. Population and reproductive biology of *Callinectes major* (Say, 1818) (Decapoda: Axiidae: Callianassidae) in an urban beach, Northeastern Brazil. *Pan-Am J Aquat Sci.* 13(2):166–178.
- Blanco Rambla JP. 1997. Primer reporte de *Callinectes major* (Say) (Decapoda: thalassinidea para aguas venezolanas. *Boletín del Instituto Oceanográfico, Venezuela.* 36(1&2):7–13.
- Borzzone CA, Souza JRB. 1996. A extração de corrupto, *Callinectes major* (Decapoda: Callianassidae) para uso como isca em praias do litoral do Paraná: características da pesca. *Nerítica.* 10:69–79.
- Bott R. 1955. Dekapoden (Crustacea) aus El Salvador. 2. Litorale Dekapoden, außer *Uca*. *Senckenb Biol.* 36:45–70.
- Botter-Carvalho ML, Carvalho PVVC, Santos PJP. 2012. New records confirming the occurrence of the ghost shrimps *Biffarius biformis* (Biffar, 1970) and *B. fragilis* (Biffar, 1971) (Decapoda, Callianassidae) in Brazil and the southwestern Atlantic. *Biota Netrop.* 12(3):88–93. doi:10.1590/S1676-06032012000300009.
- Botter-Carvalho ML, Santos PJP, Carvalho PVVC. 2002. Spatial distribution of *Callinectes major* (Say 1818) (Decapoda, Callianassidae) on a sandy beach, Piedade, Pernambuco, Brazil. *Nauplius.* 10:97–109.
- Botter-Carvalho ML, Santos PJP, Carvalho PVVC. 2007. Population dynamics of *Callinectes major* (Say, 1818) (Crustacea, Thalassinidea) on a beach in northeastern Brazil. *Estuar Coast Shelf Sci.* 71:508–516. doi:10.1016/j.ecss.2006.09.001.
- Coelho PA, de Almeida AO, Bezerra LEA, de Souza-filho JF. 2007. An updated checklist of decapod crustaceans (infraorders Astacidea, Thalassinidea, Polychelida, Palinura, and Anomura) from the northern and northeastern Brazilian coast. *Zootaxa.* 1519:1–16. doi:10.11646/zootaxa.1519.1.1.
- Coelho VR, Rodrigues SDA. 2001. Setal diversity, trophic modes and functional morphology of feeding appendages of two callianassid shrimps, *Callinectes major* and *Sergio mirim* (Decapoda: Thalassinidea: Callianassidae). *J Nat Hist.* 35(10):1447–1483. doi:10.1080/002229301317067638.
- de Saint Laurent M. 1979. Vers une nouvelle classification des Crustacés Décapodes Reptantia. *Bulletin de l'Office National Des Pêches République Tunisienne.* 3:15–31.
- Dworschak PC, Felder DL, Tudge CC. 2012. Infraorders Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979 (formerly known collectively as Thalassinidea). In: Schram FR, von Vaupel Klein JC, Forest J, Charmantier-Daures M, editors. *Treatise on zoology – anatomy, taxonomy, biology. The Crustacea. Complementary to the volumes translated from the French of the Traité de Zoologie [founded by P.P. Grassé], volume 9 part B. The Crustacea. Complementary to the volumes translated from the French of the Traité de Zoologie [founded by P.P. Grassé], volume 9 part B. Eucarida: Decapoda: Astacidea p.p. (Enoplometopoidea, Nephropoidea), Glypheidea, Axiidea, Gebiidea, and Anomura.* Leiden: Brill; p. 109–219.
- Felder DL. 1973. An annotated key to crabs and lobsters (Decapoda: Reptantia) from coastal waters of the northwestern Gulf Of Mexico. Baton Rouge: Center for Land Resources, Louisiana State University; p. 103.
- Felder DL. 2001. Diversity and ecological significance of deep-burrowing macrocrustaceans in coastal tropical waters of Americas (Decapoda: Thalassinidea). *Interciencia.* 26:440–449.
- Felder DL, Dworschak PC. 2015. Comments on two questionably new axiidean taxa from the Gulf Of Mexico (Crustacea: Decapoda). *Zootaxa.* 4057(2):265–272. doi:10.11646/zootaxa.4057.2.7.
- Felder DL, Robles R. 2009. Molecular phylogeny of the family Callianassidae based on preliminary analyses of two mitochondrial genes. In: Martin JW, Crandall KA, Felder DL, editors. *Decapod crustacean phylogenetics. Crustacean Issues. Vol. 18.* Boca Raton (FL; London; New York): CRC Press; p. 327–342.
- Felder DL, Robles R. 2015. Two new species of the genus *Lepidophthalmus* (Decapoda, Axiidea, Callianassidae) from coastal Pacific waters of Central America. *Zootaxa.* 4020(3):431–452.
- Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution.* 39(4):783–791. doi:10.1111/j.1558-5646.1985.tb00420.x.
- Fulton SW, Grant FE. 1906. Some little known Victorian decapod Crustacea, with descriptions of new species. No. III. *Proc R Soc Vic.* 19(1):5–15, pls. 3–5.

- Gan HY, Gan HM, Lee YP, Austin CM. 2016. The complete mitochondrial genome of the bass yabby *Trypaea australiensis* Dana 1852, (Crustacea; Decapoda; Callianassidae) – a new gene order for the Decapoda. Mitochondrial DNA Part A. 27:3985–3986. doi:10.3109/19401736.2014.989516.
- Hay WP, Shore CA. 1918. The decapod crustaceans of Beaufort, N.C., and the surrounding region. Fish. Bull. (Wash. D. C.). 35:369–475.
- Hernández P. 2018. Diversidade e distribuição geográfica de camarões corruptos (Infraordens Axiidea e Gebiidea), ao longo do litoral brasileiro: uma aproximação ecológica aos padrões biogeográficos de distribuição. Cap. 1. Relatório Final, Projeto de Pós-Doutorado FAPESP proc. No 2015/09020-0. São Paulo, Brazil; p. 19–72. [Online]. [accessed 2022 Mar 28]. Available: <https://bv.fapesp.br/pt/bolsas/160590/diversidade-e-distribuicao-geografica-de-camaroes-corruptos-infraordens-axiidea-e-gebiidea-ao-lon/>.
- Hernández P, Buchmann FS, Santana W. 2020. A new species of *Callichirus* Stimpson, 1866 (Axiidea, Callianassidae) from the Pleistocene bioclastic sediment of southeast Brazil. J S Am Earth Sci. 101:102602. doi:10.1016/j.jsames.2020.102602.
- Hernández P, Gamboa-González A, de Grave S. 2015. *Callichirus garthi* is a valid species, distinct from *C. seilacheri* (Decapoda: Axiidea: Callianassidae). Mar Biol Res. 11:990–997. doi:10.1080/17451000.2015.1044999.
- Hernández P, Granda-Rodríguez H, Rio JPP, Pinheiro MAA. 2018. Morphological remarks in the ghost shrimp *Callichirus seilacheri* (Bott, 1955) (Decapoda, Callianassidae). Boletim Do Instituto de Pesca. 44:91–99. doi:10.20950/1678-2305.2018.287.
- Hernández P, Hereman MJ, Pimenta CER, Rio JPP, João MCA, Pinheiro MAA. 2019. La efectividad de una ley de protección al servicio de la conservación de un recurso marino: el ejemplo del camarón fantasma *Callichirus major* (Decapoda, Callianassidae) de la Costa de Brasil. Iheringia Série Zoologia. 109:e2019001. doi:10.1590/1678-4766e2019001.
- ICZN. 1999. International Code of Zoological Nomenclature. 4th ed. London: The International Trust for Zoological Nomenclature; p. xxix + 306.
- Kensley B. 1974. The genus *Callianassa* (Crustacea Decapoda) from the west coast of South Africa with a key to the South African species. Ann S Afr Mus. 62:265–278. [accessed 2021 May 5]. <http://biodiversitylibrary.org/page/41097139>.
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol. 35:1547–1549. doi:10.1093/molbev/msy096.
- Laurino IRA, Buchmann FS, Hernández P. 2020. Spatial-temporal distribution of the burrowing shrimp *Callichirus major* (Say, 1818) (Decapoda, Callichiridae) in preserved populations of southeastern Brazil. Thalassas: Int J Mar Sci. 36(2):333–342. doi:10.1007/s41208-020-00243-7.
- Manning RM, Felder DL. 1986. The status of the callianassid genus *Callichirus* Stimpson, 1866 (Crustacea: Decapoda: Thalassinidea). Proc Biol Soc Wash. 99:437–443.
- Manning RM, Felder DL. 1991. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). Proc Biol Soc Wash. 104(4):764–792.
- Mantelatto FL, Terossi M, Negri M, Buranelli RC, Robles R, Magalhães T, Tamburus AF, Rossi N, Miyazaki MJ. 2018. DNA sequence database as a tool to identify decapod crustaceans on the São Paulo coastline. Mitochondrial DNA Part A. 29(5):805–815. doi:10.1080/24701394.2017.1365848.
- Melo GAS 1999. Manual de identificação dos Crustacea Decapoda do litoral Brasileiro: anomura, Thalassinidea, Palinuridea, Astacidea. Editora Plêiade/FAPESP, São Paulo, 551pp.
- Milne-Edwards A. 1879. Additions à la famille des Thalassiens. Bulletin de la Société Philomatique de Paris, Série 7. 7:110–115.
- Morrison CL, Harvey AW, Lavery S, Tieu K, Huang Y, Cunningham CW. 2002. Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like form. Proc R Soc B: Biol Sci. 269:345–350. doi:10.1098/rspb.2001.1886.
- Moschetto FA, Duarte LFA, Borges RP. 2020. Population structure of *Callichirus major* (Say 1818) (Crustacea: Callianassidae) and conservation considerations at Southeast coast of São Paulo, Brazil. An Acad Bras Cienc. 92(1):e20180795. doi:10.1590/0001-3765202020180795.
- Nei M, Kumar S. 2000. Molecular evolution and phylogenetics. New York: Oxford University Press.
- Ortmann AE 1893 Nov. Decapoden und Schizopoden. Ergebnisse der Plankton-Expedition der Humboldt-Stiftung im Atlantischen Ozean, 1889. 2:1–120.

- Pachelle PPG, Anker A, Mendes CB, Bezerra LEA. 2016. Decapod crustaceans from the state of Ceará, northeastern Brazil: an updated checklist of marine and estuarine species, with 23 new records. *Zootaxa*. 4131(1):1–63. doi:10.11646/zootaxa.4131.1.1.
- Peiró DF. 2012. Status taxonômico de *Callinectes major* (Say, 1818) *sensu lato* (Crustacea, Decapoda, Axiidea, Callianassidae) da Costa brasileira: taxonomia, sistemática molecular, biologia populacional e reprodutiva. Ph.D. Thesis. Universidade de São Paulo, São Paulo, 158 pp.
- Peiró DF, Mantelatto FL. 2011. Population dynamics of the pea crab *Austinia aida* (Brachyura, Pinnotheridae): a symbiotic of the ghost shrimp *Callinectes major* (Thalassinidea, Callianassidae) from the southwestern Atlantic. *Iheringia Série Zoologia*. 101(1–2):5–14. doi:10.1590/S0073-47212011000100001.
- Peiró DF, Mantelatto FL. 2016. Avaliação do calianassídeo *Callinectes major* (Say, 1818) *sensu lato*. In: Pinheiro M, Boss H, editors. Livro Vermelho dos Crustáceos do Brasil: avaliação 2010–2014, Chapter: 6. Santa Catarina (Brazil): Sociedade Brasileira de Carcinologia; p. 103–112.
- Peiró DF, Pezzuto PR, Mantelatto FL. 2011. Relative growth and sexual dimorphism of *Austinia aida* (Brachyura: Pinnotheridae): a symbiont of the ghost shrimp *Callinectes major* from the southwestern Atlantic. *Lat Am J Aquat Res*. 39(2):261–270. doi:10.3856/vol39-issue2-fulltext-7.
- Peiró DF, Wehrtmann IS, Mantelatto FL. 2014. Reproductive strategy of the ghost shrimp *Callinectes major* (Crustacea: Axiidea: Callianassidae) from the southwestern Atlantic: sexual maturity of females, fecundity, egg features, and reproductive output. *Invertebr Reprod Dev*. 58(4):294–305. doi:10.1080/07924259.2014.944672.
- Pohle G, Santana W. 2014. Gebiidea and Axiidea (= Thalassinidea). In: Martin JW, Olesen J, Høeg JT, editors. Atlas of Crustacean Larvae. Baltimore: Johns Hopkins University Press; p. 263–271.
- Pohle G, Santana W, Jansen G, Greenlaw M. 2011. Plankton-caught zoeal stages and megalopa of the lobster shrimp *Axius serratus* (Decapoda: Axiidae) from the Bay of Fundy, Canada, with a summary of axiidean and gebiidean literature on larval descriptions. *J Crustac Biol*. 31(1):82–99. doi:10.1651/10-3321.1.
- Porter ML, Pérez-Losada M, Crandall KA. 2005. Model-based multi-locus estimation of decapod phylogeny and divergence times. *Mol Phylogenet Evol*. 37(2):355–369. doi:10.1016/j.ympev.2005.06.021.
- Rathbun MJ. 1918. The Grapoid Crabs of America. *Bull US Natl Mus*. 97:1–461, pls. 1–161.
- Retamal MA. 1975. Descripción de una nueva especie del genero *Callianassa* y clave para reconocer las especies chilenas. *Boletín de la Sociedad de Biología de Concepción*. 49:177–183.
- Righi G. 1967. Sobre alguns Decapoda do Brasil (Crustacea, Brachyura: Pinnotheridae e Parthenopidae). *Papeis Avulsos de Zoologia*. 20:99–116.
- Rio JPP. 2018. Taxonomia, morfologia reprodutiva e crescimento relativo no camarão-fantasma *Callinectes major* (Say, 1818) (Decapoda: Callianassidae), no sudeste do Brasil. M.Sc thesis, Instituto de Biociências do Litoral Paulista, Universidade Estadual Paulista, 91 pp. [In Portuguese]
- Rio JPP, Hernández P, Pinheiro MAA. 2019. Relative growth, sexual maturity and handedness in the ghost shrimp *Callinectes major* (Decapoda: Callianassidae) from the southwestern Atlantic. *Sci Mar*. 83(2):167–175. doi:10.3989/scimar.04869.28A.
- Robles R, Dworschak PC, Felder DL, Poore GCB, Mantelatto FL. 2020. A molecular phylogeny of Callianassidae and related families (Crustacea: Decapoda: Axiidea) with morphological support. *Invertebr Syst*. 34:113–132. doi:10.1071/IS19021.
- Robles R, Felder DL. 2015. Molecular phylogeny of the genus *Lepidophthalmus* (Decapoda, Callianassidae), with re-examination of its species composition. *Zootaxa*. 4020(3):453–472. doi:10.11646/zootaxa.4020.3.3.
- Rodrigues SDA. 1966. Estudos sobre *Callianassa*: sistemática, biologia e anatomia. PhD thesis. São Paulo, Universidade de São Paulo. 168 p.
- Rodrigues SDA. 1971. Mud shrimps of the genus *Callianassa* Leach from the Brazilian coast (Crustacea, Decapoda). *Arq Zool*. 20:191–223. doi:10.11606/2176-7793.v20i3p191-223.
- Rodrigues SDA. 1976. Sobre a reprodução, embriologia e desenvolvimento larval de *Callinectes major* Say, 1818 (Crustacea, Decapoda, Thalassinidea). *Boletim de Zoologia da Universidade de São Paulo*. 1:85–104.

- Rodrigues SDA 1983. Aspectos da biologia de Thalassinidea do Atlântico tropical americano. Livre Docência Thesis, Instituto de Biociências da Universidade de São Paulo, São Paulo (Brazil). 194 pp.
- Rodrigues SDA. 1985. Sobre o crescimento relativo de *Callichirus major* (Say, 1818) (Crustacea, Decapoda, Thalassinidea). Boletim de Zoologia Universidade de São Paulo. 9:195–211.
- Rodrigues SDA, Höld W. 1990. Burrowing behaviour of *Callichirus major* and *C. mirim*. Wissenschaftlichen Film. 41:48–58.
- Rodrigues SDA, Shimizu RM. 1997. Autoecologia de *Callichirus major* (Say, 1818). Oecologia Brasiliensis. 3:155–170. doi:10.4257/oeco.1997.0301.10.
- Rosa LC, Freire KMF, Souza MJM. 2018. Spatial distribution and population dynamics of *Callichirus major* (Crustacea, Callianassidae) in a tropical sandy beach, northeastern Brazil. Invertebr Biol. 137:308–318. doi:10.1111/ivb.12228.
- Sakai K. 2011. Axiidea of the world and a reconsideration of the Callianassoidea (Decapoda, Thalassinidea, Callianassida). Crustac Monogr. 13:1–520.
- Sakai K, Türkay M. 2012. A collection of Thalassinidea Latreille, 1831 (Decapoda, Pleocyemata) from the Senckenberg Forschungsinstitut and Natural History Museum, Frankfurt am main. Crustaceana. 85:723–765. doi:10.1163/156854012X643735.
- Say T. 1818. An account of the Crustacea of the United States. Proc Acad Nat Sci Phila. 1:57–441.
- Schmitt W. 1935. Mud shrimps of the Atlantic coast of North America. Smithsonian Misc Collect. 95 (2):1–21, pls. 1–5.
- Souza JRB, Borzone CA. 1996. Distribuição de Calianassídeos (Crustacea: Decapoda: Thalassinidea) em praias do litoral paranaense, com especial referência a *Callichirus major* (Say, 1818). Arquivos de Biologia e Tecnologia, Curitiba. 39(3):553–565. doi:10.1590/S0101-81752003000400011.
- Souza JRB, Borzone CA. 2003. A extração do corrupto, *Callichirus major* (Say) (Crustacea, Thalassinidea), para uso como isca em praias do litoral do Paraná: as populações exploradas. Revista Brasileira de Zoologia. 20:625–630. doi:10.1590/S0101-81752003000400011.
- Souza JRB, Borzone CA, Brey T. 1998. Population dynamics and secondary production of *Callichirus major* (Crustacea: Thalassinidea) on a southern Brazilian sandy beach. Arch Fish Mar Res, Nehren. 46(2):151–164.
- Souza LT, Braga AA, López-Greco LS, Bertini G, Nunes ET. 2020. Morphological study for understanding the sexual pattern in ghost shrimp *Callichirus major* (Crustacea: Axiidea). Acta Zool. 101:78–88. doi:10.1111/azo.12272.
- Souza TL, Braga AA, López-Greco LS, Nunes ET. 2018. Functional morphology of the male reproductive system in *Callichirus major* (Crustacea: Decapoda: Axiidea): evidence of oocytes in the gonad. Acta Zool. 99:32–41. doi:10.1111/azo.12189.
- Spamer EE, Bogan A. 1992. General invertebrate collection of the Academy of Natural Sciences of Philadelphia. Part 1: guide to the general invertebrates collection. Part 2: annotated catalogue of recent type specimens: Protozoa, Porifera, Cnidaria, Platyhelminthes, Rotifera, Nemata, Nematomorpha, Annelida, Arthropoda (Merostomata, Pycnogonida, and Crustacea), Brachiopoda, and Echinodermata. Tyronia. 26:1–305.
- Staton JL, Felder DL. 1995. Genetic variation in populations of the ghost shrimp genus *Callichirus* (Crustacea: Decapoda: Thalassinidea) in the western Atlantic and Gulf Of Mexico. Bull Mar Sci. 56:523–536.
- Stimpson W. 1866. Descriptions of new genera and species of Macrurous Crustacea from the coasts of North America. Proc Chicago Acad Sci. 1:46–48.
- Strasser KM, Felder DL. 1998. Settlement cues in successive developmental stages of the ghost shrimps *Callichirus major* and *C. islagrande* (Crustacea: Decapoda: Thalassinidea). Mar Biol. 132:599–610. doi:10.1007/s002270050425.
- Strasser KM, Felder DL. 1999a. Larval development of two populations of the ghost shrimp *Callichirus major* (Decapoda: Thalassinidea) under laboratory conditions. J Crustac Biol. 19:844–878. doi:10.2307/1549305.
- Strasser KM, Felder DL. 1999b. Sand as a stimulus for settlement in the ghost shrimp *Callichirus major* (Say) and *C. islagrande* (Schmitt) (Crustacea: Decapoda: Thalassinidea). J Exp Mar Bio Ecol. 239:211–222. doi:10.1016/S0022-0981(99)00036-2.

- Strasser KM, Felder DL. 1999c. Settlement cues in an Atlantic coast population of the ghost shrimp *Callichirus major* (Crustacea: Decapoda: Thalassinidea). *Mar Ecol Prog Ser.* 83:217–225. doi:10.3354/meps183217.
- Tan MH, Gan HM, Lee YP, Poore GCB, Austin CM. 2017. Digging deeper: new gene order rearrangements and distinct patterns of codons usage in mitochondrial genomes among shrimps from the Axiidea, Gebiidea and Caridea (Crustacea: Decapoda). *PeerJ.* 5:e2982. doi:10.7717/peerj.2982.
- Venera-Pontón DE, Driskell AC, De Grave S, Felder DL, Scioli JA, Collin R. 2020. Documenting decapod biodiversity in the Caribbean from DNA barcodes generated during field training in taxonomy. *Biodivers Data J.* 8:e47333. doi:10.3897/BDJ.8.e47333.
- White A. 1847. List of species in the collections of the British Museum. London: British Museum; p. viii+1–143.
- Williams AB. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Washington (DC): Smithsonian Institution Press; p. 1–550.