Morphology and DNA analyses reveal a new cryptic snapping shrimp of the *Alpheus heterochaelis* Say, 1818 (Decapoda: Alpheidae) species complex from the western Atlantic

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ABSTRACT
Previous evidence regarding morphology led us to examine an exhaustive set of specimens assigned to *Alpheus heterochaelis* Say, 1818 and closely allied species, in order to test for the existence of possible cryptic taxa. The analysis of material assignable to this species from the states of Pará, Bahia and São Paulo in Brazil, and from Venezuela and Colombia revealed minor morphological differences between these specimens and others that could be confidently identified as *A. heterochaelis* from the eastern USA coast and the Gulf of Mexico, such as the absence of spiniform setae on the ischium of the fifth pereiopods (vs present in *A. heterochaelis* s.s.). Additionally, genetic analysis using the ribosomal 16S subunit also indicated levels of genetic difference supporting the existence of a cryptic species and revealing that *A. heterochaelis* is, in fact, a species complex. Thus, a new species, *A. petronioi* n. sp. is described and illustrated for the material from northern South America and Brazil. The new species is also compared with other, similar species of *Alpheus* Fabricius, 1798 in terms of morphology and DNA sequences in a phylogenetic context.

KEY WORDS
Crustacea,
Caridea,
cryptic taxa,
molecular analysis,
South America,
new species.

RÉSUMÉ
L'analyse de la morphologie et de l'ADN révèle une nouvelle espèce cryptique de crevette pistolet du complexe d'espèces Alpheus heterochaelis *Say, 1818 (Decapoda: Alpheidae) de l'Atlantique occidental.*
Des données antérieures concernant la morphologie nous ont conduit à examiner un ensemble exhaustif de spécimens attribués à *Alpheus heterochaelis* Say, 1818 et à des espèces voisines, afin de tester l'existence d'éventuels taxons cryptiques. L'analyse du matériel assignable à cette espèce, provenant des États de Pará, Bahia et du São Paulo au Brésil, du Venezuela et de la Colombie, a révélé des différences morphologiques mineures, comme l'absence de soies spiniformes sur l'ischium du cinquième péréiopode (présente dans *A. heterochaelis* s.s.) entre ces échantillons et d'autres originaires de la côte est des États-Unis et du golfe du Mexique qui pouvait être, en toute confiance, identifiés *A. heterochaelis* Say, 1818. En outre, l'analyse de la sous-unité ribosomale 16S montre des niveaux de différences génétiques étayant l'existence d'espèces cryptiques, et révélant que *A. heterochaelis* est, en fait, un complexe d'espèces. Ainsi, une nouvelle espèce, *A. petronioi* n. sp. est décrite et illustrée pour le matériel originaire du nord de l'Amérique du Sud et du Brésil. La nouvelle espèce est comparée avec d'autres espèces similaires de *Alpheus* Fabricius, 1798 pour la morphologie et en termes de séquences d'ADN dans un contexte phylogénétique.

MOTS CLÉS
Crustacea,
Caridea,
taxons cryptiques,
analyse moléculaire,
Amérique du Sud,
espèce nouvelle.

INTRODUCTION

The snapping shrimp genus *Alpheus* Fabricius, 1798 includes 296 valid species worldwide (De Grave & Fransen 2011; Anker 2012; Anker & De Grave 2012; Almeida *et al.* 2013; Anker & Pachelle 2013). However, this number represents an underestimate of the actual diversity within the genus, and the number of species described is expected to increase, mainly because of the existence of various complexes of cryptic species (e.g., Anker 2001, 2012; Anker *et al.* 2008a-c, 2009; Mathews & Anker 2009; Almeida & Anker 2011; Almeida *et al.* 2013). Several species that were formerly believed to have a wide geographic range, sometimes including two or more ocean basins, have been split into two or more cryptic taxa by means of multidisciplinary approaches (e.g., Anker *et al.* 2008a-c, 2009; Anker & Pachelle 2013).

Alpheus heterochaelis Say, 1818 belongs to the heterogeneous *A. edwardsii* (Audouin, 1826) group, characterized mainly by unarmed orbital hoods and the presence of dorsal and ventral notches on the palm of the major chelae (Banner & Banner 1982). The species was described by Say (1818) from Fort Saint George Inlet, Duval County, Florida, USA. As the holotype of *A. heterochaelis* is not extant, McClure (1995) redescribed the species and established a neotype based on material from this same locality. *Alpheus heterochaelis* is currently understood to occur in estuaries along the western Atlantic coast, from Delaware, USA to Bahia, Brazil (Christoffersen 1984; Silliman *et al.* 2003; Soledade & Almeida 2013).

Alpheus heterochaelis is, undoubtedly, the most-studied alpheid shrimp. Studies have targeted biological aspects of this species such as the larval development (Knowlton 1973), claw regeneration (e.g., Pearce & Govind 1987; Govind & Read 1994; Read & Govind 1997), snapping mechanism (e.g., Versluis *et al.* 2000; Herberholz & Schmitz 2001; Lohse *et al.* 2001), behavior (e.g., Nolan & Salmon 1970; Schein 1977; Schmitz & Herberholz 1998), ecology (e.g., Beal 1983; Schultz *et al.* 1998; Silliman *et al.* 2003; Rodrigues *et al.* 2009) and sexual system (Rahman *et al.* 2003). Almost

all these studies were published based on material of *A. heterochaelis* from the northern part of its distribution.

In fact, many previous records of *A. heterochaelis* throughout its distribution were based on misidentifications and confusion with various congeners (Chace 1972; Christoffersen 1984), and its occurrence south of Surinam has been questioned (Chace 1972; Christoffersen 1980a; Rodrigues *et al.* 2009). However, Christoffersen (1984) confirmed the occurrence of *A. heterochaelis* in Brazil, providing illustrations of Brazilian material, reporting misidentifications and furnishing a key to distinguish it from similar species occurring in the western Atlantic. In Brazil, for example, the frequent misidentifications have obscured the fact that *A. heterochaelis* is an estuarine species. More recently, Rodrigues *et al.* (2009) pointed out that their material treated under *A.* cf. *heterochaelis* did not agree fully with the description of *A. heterochaelis* from the northern hemisphere. Thus, an important question regarding the taxonomic status of this western Atlantic taxon remains unanswered: is there only one species occurring from Delaware to Brazil, or are more than one species involved?

As part of a long-term investigation on the taxonomy and biology of the genus *Alpheus*, and based on this questionable taxonomic situation, we examined a considerable set of specimens assigned to *A. heterochaelis* and closely allied species in order to test for the existence of possible cryptic taxa. The analysis of material assignable to this species from the states of Bahia (recorded by Almeida *et al.* 2006, 2012), Pará and São Paulo, Brazil, and from Venezuela and Colombia, has revealed some minor morphological differences between these specimens and others that could be confidently identified as *A. heterochaelis* from the eastern USA coast and the Gulf of Mexico. Molecular analysis also indicated levels of genetic difference, supporting the existence of cryptic species and revealing that *A. heterochaelis* is, in fact, a species complex. Therefore, herein a new species is described and illustrated for the material from northern South America and Brazil. The new species is also compared with closely allied species of *Alpheus*.

MATERIAL AND METHODS

The type material of the new species is deposited in the collections of the MZUSP, CCDB, UESC and MNHN. Additional material of the new species is deposited in the former three collections and also in those of the NMNH, OUMNH and SMF. Comparative material of *A. heterochaelis* and *A. pontederiae* de Rochebrune, 1883 is deposited in the carcinological collections of UESC, NMNH, OUMNH, RMNH, FLMNH, MFN and MNHN. The comparison with *A. firmus* Kim & Abele, 1988 and *A. distinctus* Kim & Abele, 1988 was based on the illustrations and description provided by Kim & Abele (1988).

Drawings were made under a dissecting microscope equipped with a camera lucida. Carapace length (CL) was measured from the tip of the rostrum to the posterior margin of the carapace. The term "spiniform seta" is used for the robust articulated cuticular extensions that are usually referred to as a "spine" or "movable spine" in the literature.

For the genetic analyses, almost all sequences used in this study were generated from our own extractions. Specimens of the new species from three localities in Colombia, Venezuela and Brazil were used to assess the genetic information and considered as genetic vouchers (Table 1). We also used 13 specimens from other species of *Alpheus* (Table 1) to compare the genetic divergence among the new species and the other congeners. Two sequences from species of *Synalpheus* Spence Bate, 1888, were obtained in order to make the analysis more consistent (Table 1); one of these was retrieved from GenBank. Tissue extraction, PCR amplification with specific primers, product cleanup, and sequencing were conducted following our laboratory protocols as described in Almeida *et al.* (2013). All sequences were confirmed by sequencing both strands. A consensus sequence for the two strands was obtained using the computational program Bioedit 7.0.5 (Hall 2005). All new sequences were submitted to GenBank (Table 1). The sequences were aligned using Clustal W in Bioedit. The maximum likelihood (ML) analysis was conducted with RAxML 7.2.8 (Stamatakis 2006) using the online version at the Cyberinfrastructure for Phylogenetic

TABLE 1. — Specimens used in genetic analyses and respective accession numbers. Abbreviations: See Material and methods.

Species	Locality	Catalogue number	GenBank	Reference
Alpheus buckupi Almeida, Terossi, Araújo-Silva & Mantelatto, 2013	Timbó River, Paulista, Pernambuco, Brazil	UESC 1366	JX286603	Almeida *et al.* 2013
Alpheus carlae Anker, 2012	Maramata Beach, Cachoeira River, Ilhéus, Bahia, Brazil	UESC 1528	JX286602	Almeida *et al.* 2013
Alpheus chacei Carvacho, 1979	Cachoeira River, Ilhéus, Bahia, Brazil	UESC 1527	JX286606	Almeida *et al.* 2013
Alpheus estuariensis Christoffersen, 1984	Paripe River, Itamaracá, Pernambuco, Brazil	UESC 1526	JX286607	Almeida *et al.* 2013
Alpheus estuariensis	Cananéia, São Paulo, Brazil	CCDB 3809	JX286608	Almeida *et al.* 2013
Alpheus heterochaelis Say, 1818	Whitney Marine Laboratory, Florida, USA	FLMNH UF 23208"	JX286610	Almeida *et al.* 2013
Alpheus petronioi n. sp.	Orinoco Delta, Venezuela	OUMNH.ZC. 2011-06.001	KF667543	Present study
Alpheus petronioi n. sp.	Cano Atascosa, Barranquilla, Colombia (Caribbean coast)	SMF 9901	KF667544	Present study
Alpheus petronioi n. sp.	Estuary of the Mojuim River, São Caetano de Odivelas, Pará, Brazil	CCDB 4509	KF667545	Present study
Alpheus pontederiae de Rochebrune, 1883	Orinoco Delta, Venezuela	OUMNH.ZC. 2011-06.004	KC525923	Almeida *et al.* 2013
Alpheus pontederiae	Estuary of the Mojuim River, São Caetano de Odivelas, Pará, Brazil	CCDB 4510	KF667547	Present study
Alpheus pontederiae	São Vicente, São Paulo, Brazil	CCDB 4462	KF667546	Present study
Synalpheus cf. *brevicarpus* (Herrick, 1891)	Itaguá Beach, Ubatuba, São Paulo, Brazil	CCDB 3419	KF667548	Present study
Synalpheus fritzmuelleri Coutière, 1909	Southern Gulf of Mexico, Mexico	ULLZ 7136	EU868642	Bracken *et al.* 2009

Research (CIPRES) website (Stamatakis *et al.* 2008). Maximum likelihood analysis was conducted with the default parameters for RAxML for the GTR model of evolution, using the option to automatically determine the number of bootstraps to be run in RAxML. Thus, 1000 bootstrap pseudo-replicates were run, and only confidence values > 50% were reported. A matrix of genetic distances was calculated under the Kimura 2-parameter (K2P) model (Kimura 1980) in MEGA v5 (Tamura *et al.* 2011).

ABBREVIATIONS

Institutions

CCDB Crustacean Collection of the Department of Biology of FFCLRP, University of São Paulo, Ribeirão Preto;
FLMNH Florida Natural History Museum, Gainesville;
MFN Museum für Naturkunde, Berlin;
MNHN Muséum national d'Histoire naturelle, Paris;
MZUSP Museu de Zoologia, Universidade de São Paulo, São Paulo;
NMHN Smithsonian Institution, Washington, DC;
OUMNH Oxford University Museum of Natural History, Oxford;
RMNH Netherlands Centre for Biodiversity Naturalis, Leiden;
SMF Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main;
UESC Universidade Estadual de Santa Cruz, Ilhéus;
UF University of Florida;
ULLZ University of Louisiana, Lafayette Zoological; Collections, Lafayette;
USNM National Museum of Natural History;
ZC Zoological collection.

Other abbreviations

CIPRES Cyberinfrastructure for Phylogenetic Research;
CL carapace length;
GTR generalised time-reversible;

ft	fathom;
K2P	Kimura 2-parameter;
ML	maximum likelihood;
ovf	ovigerous female;
PCR	Polymerase Chain Reaction;
ni	sex not identified;
RAxML	randomized axelerated maximum likelihood;
St.	station.

SYSTEMATICS

Family ALPHEIDAE Rafinesque, 1815
Genus *Alpheus* Fabricius, 1798

Alpheus petronioi n. sp.
(Figs 1-3; 4C, D)

Alpheus sp. nov. 1 – Christoffersen 1980a: 236.

Alpheus heterochaelis – Christoffersen 1984: 200, figs 5-7; 1998: 358; Barros & Pimentel 2001: 21; Coelho *et al.* 2006: 51 (in part); Almeida *et al.* 2006: 9, fig. 6; 2012: 11; Soledade & Almeida 2013: 100 (not *A. heterochaelis* Say, 1818: 243).

Alpheus andronyx Christoffersen, 1998: 358 (*nomen nudum*).

Alpheus cf. *heterochaelis* – Rodrigues *et al.* 2009: 336 (identity to be confirmed).

TYPE MATERIAL. — Holotype male (CL 11.1 mm): Brazil, Pará, São Caetano de Odivelas, estuary of the Mojuim River, coll. A. O. Almeida, G. O. Soledade & P. S. Santos, 16.XI.2012, under rocks, mud-sand bottom, salinity 31 (MZUSP 28314). Paratypes: 1 ovf (CL 10.6 mm, forming a pair with the holotype), same data as the holotype (MZUSP 28315); 1 ♂, 1 ♀, same data as the holotype (CCDB 4509); 13 ♂♂, 15 ♀♀(8 ovf), same data as the holotype (UESC 1533); 1 ♂, 1 ♀, same data as the holotype (MNHN-IU-2013-8627).

ETYMOLOGY. — It is our great pleasure to name this new species in honor of the late Brazilian carcinologist, Prof. Dr Petrônio Alves Coelho (Universidade Federal de Pernambuco, Recife, Brazil) in recognition of his dedication and contributions to the knowledge of South American crustaceans.

MATERIAL EXAMINED. — **Colombia.** 1 ♂, Caribbean coast of Colombia, Golfo de Morrosquillo, Bahía Cispata, Punta Calixto, mangroves just outside entrance to canal of Ciénaga de Soledad, St. #6, trap, coll. R. Lemaitre, 04.III.1997 (USNM 1171071); 1 ♂, 1 ovf, Department of Magdalena, Magdalena Delta, Los Cocos, Cano Atascosa, northeastern Barranquilla, colls H. Türkay & M. Türkay, 27.X.1978 (SMF 9901).
Venezuela. 2 ♂♂, 2 ♀♀, Orinoco Delta, XI-5226, coll. G. Pereira, 2003, AA fcn 03-031 (OUMNH.ZC. 2011-06.001); 1 ovf, manglar la Rosita, colls J. Delgado & A. Godoy, 14.VI.1995 (OUMNH.ZC. 2011-06.014).
Brazil. Pará, same data as the holotype, 10 ♂♂, 10 ♀♀(2 ovf) (UESC 1534); 2 ♀♀, Pará, Salinópolis, estuary near Maçarico Beach (00°35'49.24"S; 47°20'35.36"W), coll. F. L. Carvalho, L. Pileggi, R. Robles & E. Souza-Carvalho, 15.XI.2012 (CCDB 4426); 4 ♂♂, Pará, São João de Pirabas, city harbor (00°46'01.21"S; 47°10'12.4"W), coll. F. L. Carvalho, L. Pileggi, R. Robles & E. Souza-Carvalho, 16.XI.2012 (CCDB 4443); 1 ♂, 1 ♀, Bahia, Ilhéus, Santana River, trawl, St. 3 (14°50' 35.8"S; 39°02'45.1"W), colls A. O. Almeida, J. T. A. Santos, N. R. Ferraz & C. S. Soares, 19.IX.2004 (CCDB 4279); 1 ♂, 1 ♀, Bahia, Ilhéus, Santana River, trawl, St. 3 (14°50' 35.8"S; 39°02'45.1"W), colls A. O. Almeida, J. T. A. Santos, N. R. Ferraz & C. S. Soares, 19.IX.2004 (UESC 580); 1 ♂, 3 ♀♀, Bahia, Ilhéus, Cachoeira River, trawl, St. 4 (14°48'15.6"S; 39°04'22.3"W), colls A. O. Almeida, J. T. A. Santos & J. R. Luz, 24.IX.2004 (UESC 592); 2 ♂♂, 5 ♀♀(4 ovf), Bahia, Una, Comandatuba Island, Project Diversitas Neotropica, 26.V.1994 (MZUSP 25486); 1 ♂, Bahia, Canavieiras, Patipe River, near bridge to Atalaia Island (15°40'34.8.15"S; 38°56'19.3"W), colls G. O. Soledade & A. C. C. Souza, 22.VI.2012, under rocks, salinity 15 (UESC 1535); 1 ♀, São Paulo, Cananéia, near raft to Ilha Comprida (25°01'14.88"S; 47°55'25.01"W), colls T. Davanso & R. Pescinelli, 26.IX.2013 (CCDB 4728).

COMPARATIVE MATERIAL. — ***Alpheus heterochaelis*: USA.** 1 ♂, Georgia, Sapelo Island Sound, coll. M. Gray, 26.I.1962, 58-86 ft (USNM 181864); 1 ♀, Georgia, Sapelo Island, Doboy Sound, coll. M. Gray, 16.III.1961 (USNM 181865); 1 ♀, Georgia, Sapelo Island, High Point, coll. M. Gray, 16.III.1961 (USNM 181866); 1 ♂, Georgia, Sapelo Island, Doboy Sound, coll. M. Gray, 17.II.1966, 15-20 ft (USNM 181867); 1 ovf, Florida, Whitney Marine Lab, coll. I. Marin, 13.II.2010, saltwater pool, sand, under rocks, 0.2 m (FLMNH UF Arthropoda 23208); 1 ♂, 2 ♀♀(1 ovf), Florida, western side of Biscayne Bay at Cutler, south of Miami, coll. L. B. Holthuis, 15.IX.1960, in mangrove (RMNH.Crus.D.13039); 1 ♂, 1 ♀, Florida, Florida Keys, Key West, coll. A. L. Packard Jr. (USNM 57635); 2 ♂♂, Florida, Marco Beach, south of Marco, coll. L. B. Holthuis, 12.IX.1960 (RMNH.Crus.D.17038); 1 ♂, 1 ♀, Mississippi, Dier Island (USNM 64243); 2 ♂♂, Texas, Galveston Island, Offat's Bayou, St. 8, coll. W. G. Hewatt, 24.III.1940 (USNM 82116); 1 ♂, Texas, Ransom Island, coll. H. B. Paske, VII.1936 (USNM 72186).
***Alpheus pontederiae*: Venezuela.** 1 ♂, north of Ma-

racaibo, El Nazareth, coll. A. Godoy, collection year unknown (OUMNH.ZC. 2011-06.010); 1 ♂, Orinoco delta, XI-5037, coll. G. Pereira, 2003, AA fcn 03-029 (OUMNH.ZC. 2011-06.002); 1 ♀, Orinoco Delta, XI-5224, coll. G. Pereira, AA fcn 03-028 (OUMNH. ZC. 2011-06.004); 2 ♂♂, 1 ♀, manglar la Rosita, colls J. Delgado & A. Godoy, 14.VI.1995 (OUMNH.ZC. 2011-06.013).

Surinam. 1 ♂, 1 ovf, Surinam River mouth, eastern shore, Braamspunt, on soft intertidal mud, coll. L. B. Holthuis, 05.IV.1957 (RMNH.Crus.D.11461).

Brazil. Pará: 2 ♂♂, Baía do Sol, coll. C. Pantoja, I.1998 (MZUSP 9680); 1 ♂, 4 ♀♀(2 ovf), Marajó Island, Soure River, coll. Ehrhardt, 21.II.1923 (SMF 8122); 3 ♂♂, 7 ♀♀, Marajó Island, Soure River, coll. Ehrhardt, XII.1923 (SMF 8123); 4 ovf, Marajó Island, Soure River, coll. Ehrhardt, 1924 (SMF 8130); 4 ovf, Marajó Island, Soure River, coll. Ehrhardt, 21.XI.1923 (SMF 8136); 1 ♂, 1 ♀, Marajó Island, Soure River (MFN 23280); 6 ♂♂, 11 ♀♀(7 ovf), same data as the holotype of *A. petronioi* n. sp. (UESC 1566); 2 ♂♂, 1 ♀, Pará, Salinópolis, estuary near Maçarico Beach (00°35' 49.24"S; 47°20'35.36"W), coll. F. L. Carvalho, L. Pileggi, R. Robles & E. Souza-Carvalho, 15.XI.2012 (CCDB 4438); Rio Grande do Norte: 1 ovf, Porto do Mangue, Conchas River estuary, St. 26, mangrove (05°04.039'S, 36°45.702'W), colls M. Tavares *et al.*, 25.XI.2009 (MZUSP 22634); Bahia: see material reported by Almeida *et al.* (2006; 2012); São Paulo: 4 ni, Cananéia, near raft to Ilha Comprida, coll. M. L. Christoffersen, 08.II.1976, under rocks (MZUSP 22295).

Guinea. 2 ♂♂, 4 ♀♀, Conakry, coll. M. Dellais, 14.III.1953 (MNHN-Na-3301).

Sierra Leone. 4 ♂♂, 2 ovf, Sierra Leone River, coll. A. R. Longhurst, 25.XI.1954 (RMNH. Crus.D.20179).

Benin. 1 ♀, Lac Nokoué, Awansouri, north of Cotonou, coll. H. Hoestlandt, 17.VII.1963 (RMNH. Crus.D.20176).

Nigeria. 13 ♂♂, 13 ♀♀(8 ovf), Niger Delta, between Brass and Port Harcourt, coll. H. J. G. Beets, V-VIII.1960 (RMNH.Crus.D.15531).

Congo Brazaville. 5 ♂♂, 3 ♀♀, Pointe Noire, Lagune de Djeno, coll. M. Rossignol (MNHN-Na-3299); 1 ♂, Pointe Noire, Lagune de Djeno, coll. A. Stauch, V.1964 (MNHN-Na-3300); 1 ♂, 2 ♀♀, Pointe Noire, Lagune de Djeno, coll. A. Crosnier (MNHN-Na-3302).

São Tomé. 1 ♂, São Tomé, St. 7, mangrove lagoon near Porto Alegre, coll. A. Anker, 05.II.2006, low tide, in mud among mangrove roots, debris (coconuts) and rocks (in burrows), AA fcn 06-154 (OUMNH.ZC. 2011-06.008).

DISTRIBUTION. — Western Atlantic: Colombia, Venezuela and Brazil (Pará, Bahia and São Paulo).

DESCRIPTION. — Carapace smooth, with some dorsal pubescence (Fig. 1A), laterally not compressed; rostrum triangular, with acute tip almost reaching midlength of first segment of antennular peduncle; rostral carina sharply delimited between orbital hoods, slightly overreaching posterior margin of orbital hoods, not broadening posteriorly (Fig. 1B); adrostral furrows moderately deep, not abruptly delimited posteriorly (Fig. 1B); orbital hoods inflated dorsally, distally rounded, unarmed (Fig. 1B); pterygostomial angle rounded (Fig. 1A, C); cardiac notch well developed (Fig. 1A).

Abdominal somites smooth, with some dorsal pubescence on proximal somites (Fig. 1A); ventral and posterior margins of pleurae 1-4 broadly rounded and pleura 5 forming angle of approximately 90° with tip rounded; sixth pleura without articulated plate (Fig. 1A); protopod pleopods without spines; male pleopod 2 with appendix masculina slightly shorter than appendix interna; abdominal sternites without median processes; preanal plate with rounded tip. Telson broad, tapering distally, approximately 1.3 times as long as wide at base; lateral margins slightly sinuous; dorsal surface slightly convex, without median groove, with two pairs of spiniform setae, inserted at some distance from lateral margins, first pair slightly anterior to midlength, second pair well posterior to telson midlength (Fig. 1I); posterior margin broadly rounded, fringed with spinules (short spiniform setae) and long setae, posterolateral angle each with two pairs of spiniform setae, lateral spiniform seta approximately 1/2 length of mesial spiniform seta (Fig. 1I); anal tubercles well developed.

Eyes totally concealed in lateral, dorsal, and frontal views; cornea well developed, rounded (Fig. 1A-C). Ocellar beak protruding dorsally between eyes, apically rounded (Fig. 1D).

Antennular peduncle moderately slender (Fig. 1B). Stylocerite distally acute, reaching distal margin of first segment of antennular peduncle (Fig. 1B); ventromesial carina of first segment with tooth ending rounded, anterior margin straight, forming obtuse angle with posterior margin (Fig. 1F); visible part of first segment as long as wide; second segment longest, 1.9 times as long as wide and 1.3 times as long as visible part of first segment; third segment as long as wide, 0.5 times length of second segment (Fig. 1B); lateral antennular flagellum with row of aesthetascs starting at 16th segment (Fig. 1E). Antenna with basicerite bearing acute distolateral tooth (Fig. 1C); carpocerite moderately slender, reaching slightly beyond end of antennular peduncle (Fig. 1C); scaphocerite with lateral margin slightly concave; blade broad, reaching tip of antennular peduncle, separated from distolateral tooth by deep cleft running about 1/3 length of blade (Fig. 1B); distolateral tooth well developed, approximately 1/2 blade width at tip of scaphocerite, distinctly overreaching distal margin of blade, and slightly overreaching end of antennular peduncle and carpocerite (Fig. 1B).

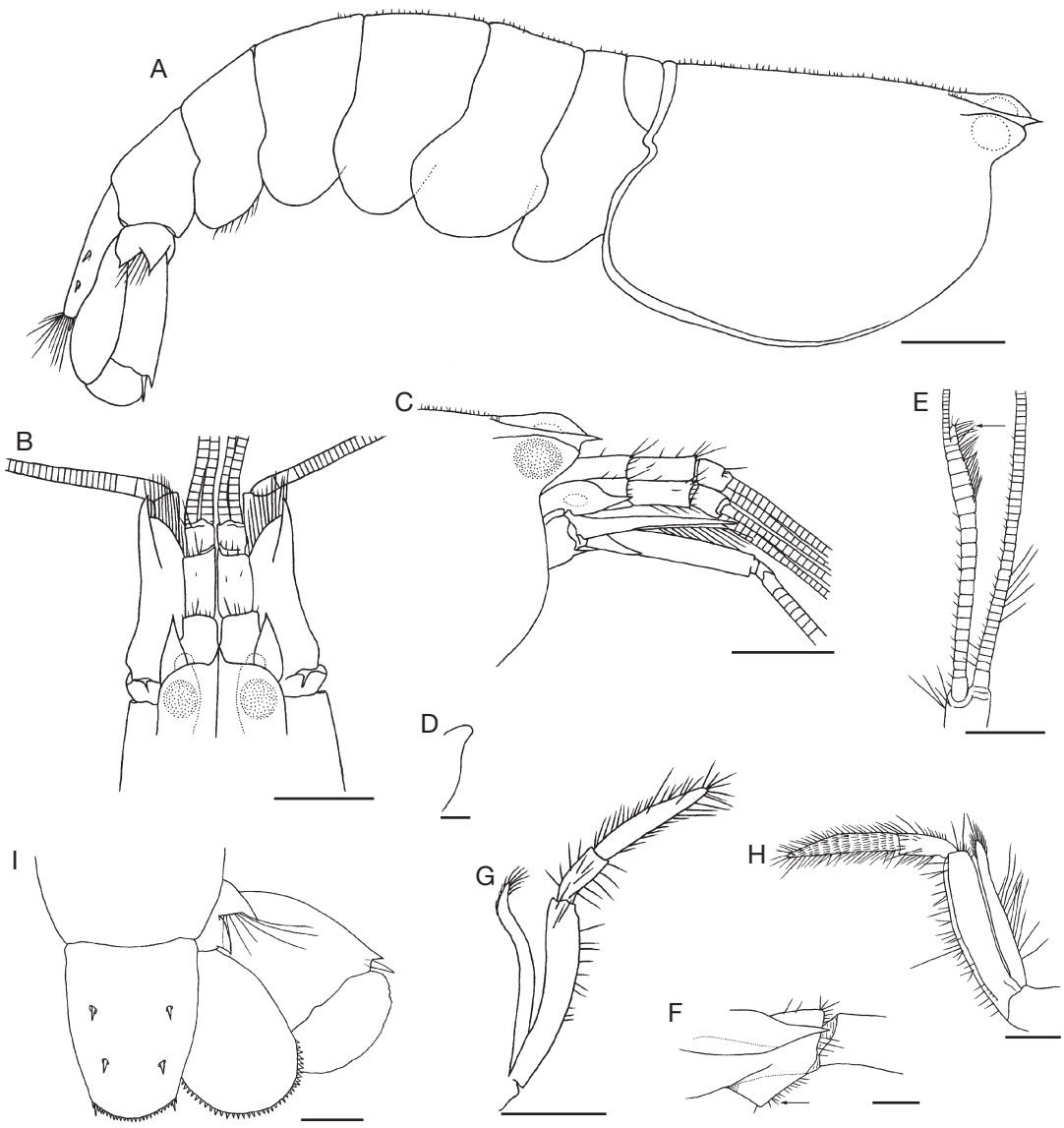

Fig. 1. — *Alpheus petronioi* n. sp.: **A**-**C**, **G**, **I**, holotype, male (MZUSP 28314); **D**-**F**, **H**, paratype, male (UESC 1533): **A**, body, lateral view (appendages excluded, except uropods); **B**, frontal region and cephalic appendages, dorsal view; **C**, frontal region and cephalic appendages, lateral view; **D**, ocellar beak, lateral view; **E**, antennular flagella, proximal part with aesthetascs (arrow), ventral view; **F**, tooth (arrow) on ventromesial carina of first segment of antennular peduncle, lateral view; **G**, third maxilliped, lateral view; **H**, third maxilliped, mesial view; **I**, telson and right uropods, dorsal view (setae partially omitted). Scale bars: A, D, 2.5 mm; B, C, H, 2 mm; E, G, I, 1 mm; F, 0.5 mm.

Mouthparts not dissected, appearing typical for *Alpheus* in external view. Third maxilliped relatively slender, conspicuously longer than antennular peduncle and slightly overreaching carpocerite when extended; lateral plate ending distally on acute curved tooth and laterally rounded; antepenultimate segment not flattened or expanded, mesial margin distinct and thick, distodorsal portion not protruding (Fig. 1G, H); penultimate segment

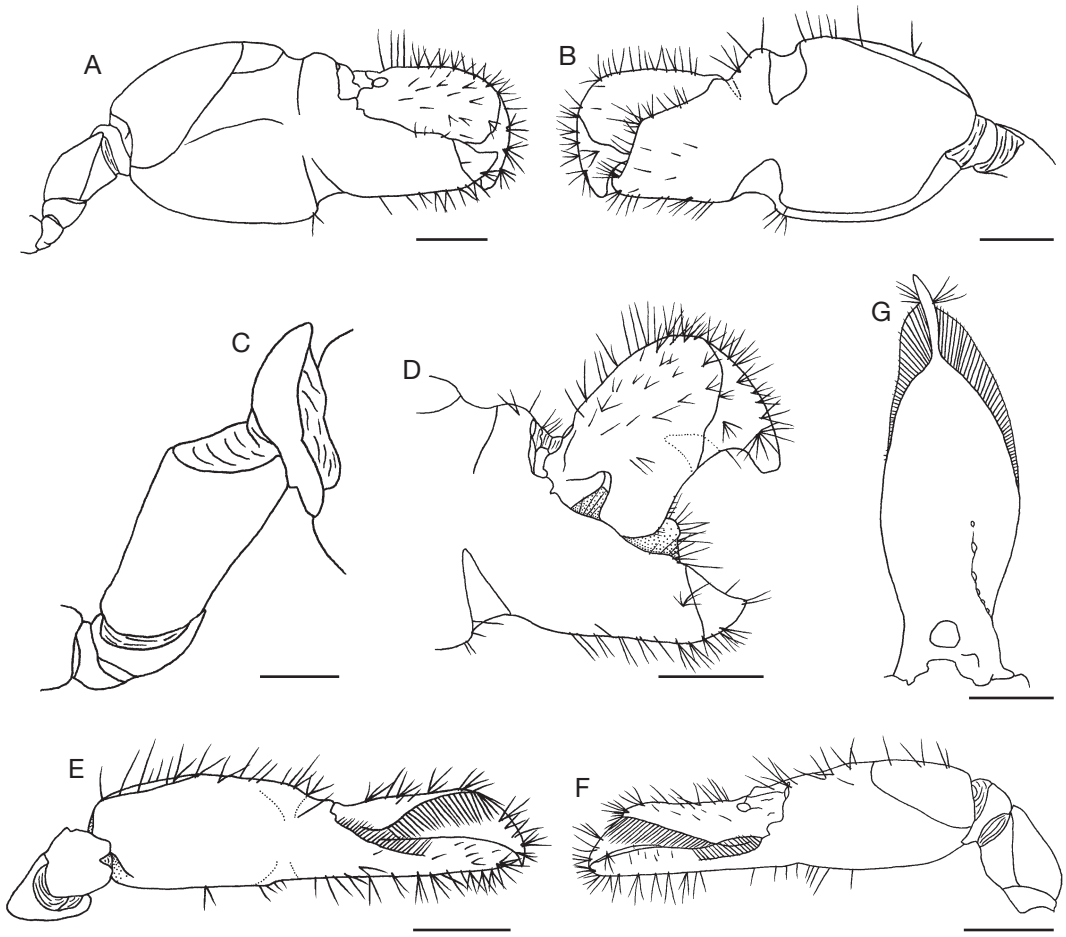

Fig. 2. — *Alpheus petronioi* n. sp., holotype, male (MZUSP 28314): **A**, major cheliped, lateral view; **B**, same, mesial view; **C**, same, detail of ischium, merus and carpus, lateral view; **D**, detail of major chela, lateral view; **E**, minor cheliped, mesial view; **F**, same, lateral view; **G**, dactylus of minor cheliped, dorsal view. Scale bars: A, B, D-F, 2.5 mm; C, G, 1 mm.

about three times as long as wide, lateral margin smooth, with tufts of setae; last segment tapering distally, smooth, with several bands of setae; exopod reaching slightly beyond distal margin of antepenultimate segment (Fig. 1G, H). Major male cheliped with short, stout ischium (Fig. 2A, C); merus slightly excavated ventrally; ventrolateral and ventromesial margins straight, ending bluntly, unarmed (Fig. 2A); carpus short, cup-shaped (Fig. 2C); chela somewhat compressed; fingers closing in same plane as palm; palm with dorsal and ventral margins convex, with broad transverse grooves (Fig. 2A, B); dorsal grooves extending to mesial and lateral surfaces as deep depressions, latter extending posteriorly (Fig. 2A, B); dorsal shoulder rounded, not overhanging groove; ventral groove broad, oblique, deep, also extending mesially and laterally as well-delimited deep depressions, latter not extending posteriorly (Fig. 2A, B); ventral shoulder rounded, not protruding anteriorly (Fig. 2A, B); lateral and mesial surfaces mostly smooth; dorsal surface and shoulders with sparse long setae; linea impressa well marked on lateral surface (Fig. 2A); mesial surface ending bluntly distally (Fig. 2B); fingers compressed, longer than half palm length (Fig. 2A, B); pollex with tip curved upward, with shallow obtuse notch on cutting edge anterior to deep fossa (Fig. 2D); mesial surface surrounding fossa forming obtuse angle, fringed with rows of setae; lateral surface surrounding fossa slightly convex, with sparse long setae; dactylus reaching slightly beyond pollex, with

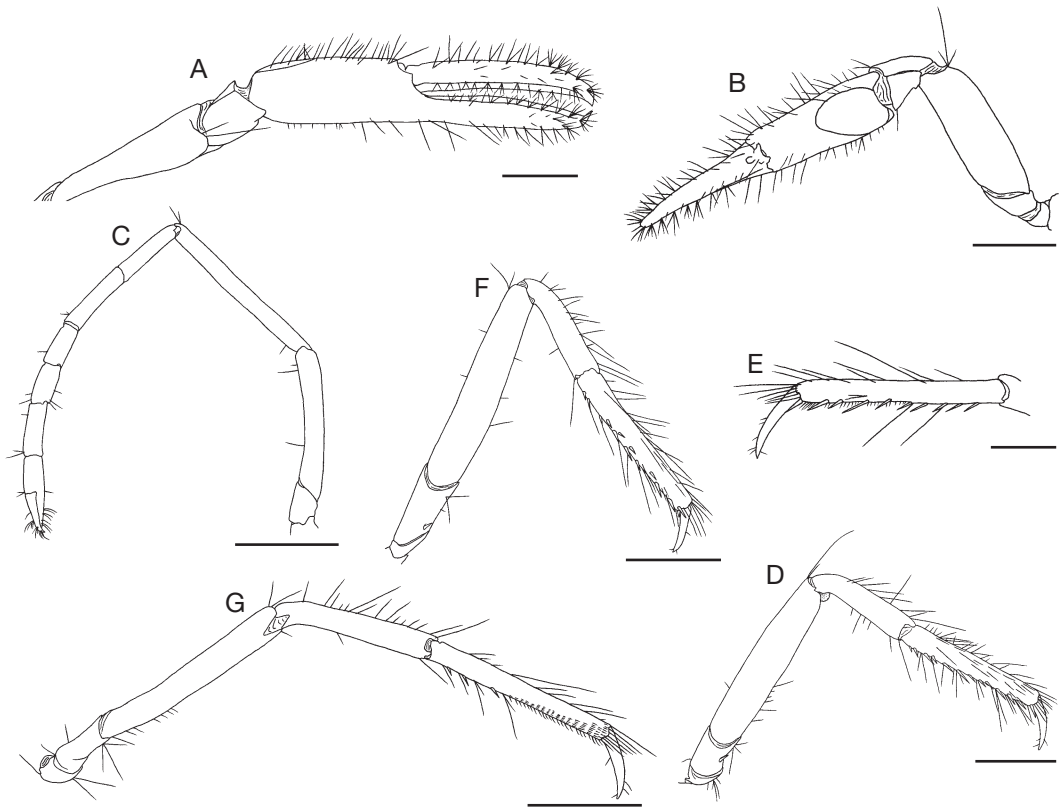

FIG. 3. — *Alpheus petronioi* n. sp.: **A**, **B**, paratype, female (UESC 1533); **C**-**F**, holotype, male (MZUSP 28314): **A**, minor cheliped, mesial view; **B**, same, chela in dorsal view, merus and ischium in lateral view; **C**, second pereiopod, lateral view; **D**, third pereiopod, lateral view; **E**, same, dactylus and propodus, lateral view; **F**, fourth pereiopod, lateral view; **G**, fifth pereiopod, lateral view. Scale bars: A, C, F, G, 2 mm; B, 2.5 mm; D, E, 1 mm.

rounded tip, cutting edge with long plunger, proximal height around. 0.7 times length of distolateral margin (Fig. 2D); adhesive disks conspicuous (Fig. 2A, D). Female major cheliped similar in shape, but proportionally smaller than that of male.

Minor male cheliped with ischium short and stout; merus proportionally longer and broader than that of major cheliped, slightly excavated ventrally; ventrolateral and ventromesial margins as in major cheliped (Fig. 2F); carpus short, cup-shaped (Fig. 2F); chela somewhat compressed laterally; palm with dorsal and ventral margins slightly convex, slightly sculptured, with very shallow dorsal depression extending to mesial and lateral surfaces, and with very shallow ventral groove, not markedly extending laterally or mesially (Fig. 2E, F); lateral and mesial surfaces mostly smooth; linea impressa well marked on lateral surface (Fig. 2F); dorsomesial angle of palm with blunt tooth (Fig. 2E); fingers as long as palm or slightly shorter, with conspicuous rows of balaeniceps setae, cutting edges sharp, tip curved (Fig. 2E, F); dactylus expanded laterally, with dorsal disk similar to adhesive disk of dactylus of major cheliped, and conspicuous carina on proximal region, ending at half dactylus length (Fig. 2G). Female minor cheliped more slender than that of males. Palm with lateral and mesial surfaces mostly smooth; linea impressa well marked on lateral surface (Fig. 3A, B); dorsal and ventral margins slightly convex; dorsal and ventral grooves absent; fingers as long as palm, without balaeniceps setae, cutting edges blade-like, tip curved (Fig. 3A, B); dactylus not expanded laterally, without proximal carina on dorsal margin, but with inconspicuously marked disk similar to that of male minor chela (Fig. 3B).

Second pereiopod slender, ischium and merus subequal in length; carpus five-segmented, first segment longest; segment ratio (proximal to distal) subequal to 2.4: 1.8: 1: 1: 1.3; chela simple, fingers as long as palm and bearing tufts of curved setae distally (Fig. 3C). Third pereiopod

with ischium armed with spiniform seta on ventrolateral surface; merus longer than propodus, about five times as long as wide, distoventral margin unarmed; carpus unarmed, about 0.5 times merus length and 0.7 times propodus length (Fig. 3D); propodus with about 12 irregularly spaced strong spiniform setae of variable size along ventral margin, plus one distal pair of spiniform setae near dactylus; dactylus around 0.3 times propodus length, simple, slightly flattened and curved, acute distally (Fig. 3E). Fourth pereiopod similar in shape and length to third pereiopods, dactylus conical (Fig. 3F). Fifth pereiopod with ischium and merus unarmed; merus slender, about eight times as long as wide; carpus about 0.7 times merus length (Fig. 3G); propodus 1.3 times as long as carpus, with 6-8 spiniform setae along ventral margin plus one distal pair of spiniform setae near dactylus; distolateral surface with cleaning brush consisting of about 17 transverse rows of short setae; dactylus similar in shape to third and fourth pereiopods, proportionally slightly longer, corresponding to almost 0.3 times propodus length (Fig. 3G).

Uropods with bifid protopods, each lobe ending in acute tooth (Fig. 1I); endopod suboval, with posterior margin fringed with spinules (short spiniform setae) and long setae; exopod slightly longer than endopod (Fig. 1I); distolateral spiniform setae slender, distinctly shorter than posterior margin of exopods, not pigmented; exopodal diaeresis with two small lobes separated by median notch; distolateral tooth acute, approximately 1/2 length of or slightly shorter than distolateral spiniform seta (Fig. 1I). Gill formula typical for genus: pleurobranchs above first to fifth pereiopods; podobranch absent; one arthrobranch on third maxilliped; exopods on first to third maxillipeds; mastigobranchs (epipods) on coxae of third to fourth pereiopods; setobranchs on coxae of first to fifth pereiopods.

Morphological variation. — Sexual dimorphism between male and female major and minor chelae as described above. The notch on the cutting edge anterior to the fossa on the pollex of the major chela is in general shallow and obtuse, but the width and depth of this notch may vary (deeper and more acute). The sculpturing of the palm of the minor chela in males may vary from weak to moderate, and it is generally stronger in larger shrimp. The relative length of segments 1 (proximal) and 2 of the carpus of pereiopod 2 to the subequal segments 3 and 4 varies from 2.3-2.6: 1 and 1.6-1.9: 1, respectively. The number of spiniform setae on the propodus of pereiopods 3-5 may vary, especially on P5, as may also the number of transverse rows of short setae on the distolateral surface of the propodus of P5.

Color pattern (based on analysis of color photograph of fresh specimens, Fig. 4C, D). — Body of a small individual (CL 6.2 mm), from Canavieiras, Bahia (UESC 1535) semitransparent, with brownish chromatophores on palm of minor chela, carapace, abdomen, and uropods; major chela green, fingers darker than palm; depressions extending from transverse dorsal and ventral grooves whitish (Fig. 4D). Overall color pattern of a male-female pair photographed in the field shows the presence of dark-green to brownish dots on the chelae, carapace, abdomen and uropods (Fig. 4C).

Ecology. — Pair-bonding species living in upper parts of estuaries. The material from the type locality was collected in the intertidal, under rocks, on mud and fine sand bottoms, at a salinity of 31. Also occurring under rocks at the type locality were the alpheids *A. pontederiae* and *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013. The material from Canavieiras, Bahia, was also collected under rocks on mud in the intertidal zone, at a salinity of 15. *Alpheus pontederiae* was also recorded syntopically with the new species in that locality. No habitat information is available for the other collection sites.

DISCUSSION

The present description raises the total number of recognized species of the genus *Alpheus* in the western Atlantic to 53. In this region, *A. petronioi* n. sp. has morphological similarities with other species of the *A. edwardsii* group, such as *A. heterochaelis* (western Atlantic) and *A. pontederiae* (also occurring in the eastern Atlantic) such as the presence of balaeniceps setae on the fingers of the minor chela and the rounded ventral margin of the pollex of the major chela, among other characters (see Christoffersen 1984). These latter taxa also occur in the same habitats where the new species is found. *Alpheus pontederiae* has been collected syntopically with *A. petronioi* n. sp. in Pará and Bahia, Brazil.

Alpheus petronioi n. sp. is morphologically very similar to *A. heterochaelis*. In fact, in the keys of Chace (1972) and Christoffersen (1984), the new species matches with *A. heterochaelis*. However, based on the description of the neotype provided by McClure (1995) and on the analysis of several specimens of *A. heterochaelis* s.s., it is possible to distinguish the two species morphologically, based on the presence (*A. heterochaelis*) and absence (*A. petronioi* n. sp.) of a spiniform seta on the ischium of the fifth pair of pereiopods. This difference was observed in all specimens analyzed from both species. Other, minor

FIG. 4. — *Alpheus petronioi* n. sp.: **A**, **B**, views of the type locality, Mojuim River, São Caetano de Odivelas, Pará, Brazil, where the type material was obtained under rocks in the intertidal on a mud and fine sand bottom; **C**, male-female pair under rocks in the type locality (female on the left, male on the right); **D**, young male from Patipe River, Canavieiras, Bahia, Brazil (UESC 1535), dorsal view. Carapace lenght: D, 6.2 mm. Photographs: Alexandre O. Almeida.

differences between these two species, in more-variable characters, have been observed (Table 2).

Alpheus petronioi n. sp. differs from *A. pontederiae* by the absence of two small prominences on the mesial side of the major chela pollex (present in *A. pontederiae*), and by having the distolateral spiniform seta of the uropodal exopod flanked by one small, acute outer tooth (vs flanked by two acute teeth, inner and outer) (see Fig. 1A, I and Christoffersen 1984: 198, fig. 3d for comparison).

Alpheus buckupi was recorded syntopically with *A. petronioi* n. sp. in the type locality of the latter. *Alpheus buckupi* also has well-developed balaeniceps setae on the male minor chela, as does *A. petronioi* n. sp. However, it can be easily distinguished from the new species by the presence of a tooth on the distal portion of the ventromesial margin of the merus of the major and minor chelipeds (absent in *A. petronioi* n. sp.).

Alpheus petronioi n. sp. is also similar to the eastern Pacific *A. firmus* and *A. distinctus*. *Alpheus petronioi* n. sp. differs from *A. firmus* mainly by the relative length of the penultimate segment of the third maxilliped (less elongated, slightly shorter than half the length of the last segment in *A. petronioi* n. sp. vs more elongated, slightly shorter than the last segment in *A. firmus*) (see Fig. 1G, H and Kim & Abele 1988: 94, fig. 39d for comparison). *Alpheus*

TABLE 2. — Selected characters useful for separation of *Alpheus petronioi* n. sp. and morphologically similar species of *Alpheus* Fabricius, 1798.

Species Characters	*A. petronioi* n. sp.	*A. heterochaelis* Say, 1818 (mostly based on comparative material cited above)	*A. firmus* Kim & Abele, 1988 (based on illustrations and description provided by Kim & Abele 1988)	*Alpheus distinctus* Kim & Abele, 1988 (based on illustrations and description provided by Kim & Abele 1988)	*A. pontederiae* de Rochebrune, 1883 (based on comparative material cited above)
Rostrum length relative to first segment of antennular peduncle	Almost reaching midlength of first segment of antennular peduncle	Reaching to or slightly longer than midlength of visible part of first segment	Conspicuously shorter than midlength of first segment of antennular peduncle	Slightly overreaching midlength of visible part of first segment	Reaching to or slightly shorter than midlength of visible part of first segment
Rostral carina	Not broadening posteriorly, slightly overreaching posterior margin of orbital hoods	Not broadening posteriorly, slightly overreaching posterior margin of orbital hoods	Not broadening posteriorly, reaching posterior margin of orbital hoods	Slightly broadening posteriorly, reaching far beyond posterior margin of orbital hoods	Not broadening posteriorly, slightly overreaching posterior margin of orbital hoods
Adrostral furrows	Moderately deep	Moderately deep	Shallow	Moderately deep	Shallow
Stylocerite length	Reaching distal margin of first segment of antennular peduncle	Slightly shorter than distal end of first segment of antennular peduncle	Slightly shorter than distal end of first segment of antennular peduncle	Reaching distal margin of first segment of antennular peduncle	Slightly overreaching distal end of first segment of antennular peduncle
Relative length of the second segment of antennular peduncle	Around 1.3 times as long as visible part of first segment	Around 1.3 times as long as visible part of first segment	Around 2 times as long as visible part of first segment	Around 1.6 times as long as visible part of first segment	Around 1.5 times as long as visible part of first segment
Distolateral tooth on basicerite	Present, acute	Present, acute	Very small or absent	Present, acute	Present, sub-triangular
Distolateral tooth of scaphocerite	Distinctly overreaching distal margin of blade	Distinctly overreaching distal margin of blade	Distinctly overreaching distal margin of blade	Distinctly overreaching distal margin of blade	Reaching or slightly overreaching distal margin of blade
Relative length of penultimate segment of third maxilliped	Slightly shorter than half length of last segment	Slightly shorter than half length of last segment	Slightly shorter than last segment	Slightly longer than half length of last segment	Longer than half length of last segment
Length of exopod of third maxilliped	Reaching slightly beyond distal margin of penultimate segment	Reaching or overreaching midlength of penultimate segment	Reaching slightly beyond distal margin of penultimate segment	Reaching slightly beyond distal margin of penultimate segment	Reaching midlength of antepenultimate segment
Dorsal transverse groove of palm of major chela	Narrow and moderately deep; proximal dorsal shoulder not overhanging groove	Narrow and moderately deep; proximal dorsal shoulder not overhanging groove	Broad and moderately deep; proximal shoulder not overhanging groove	Narrow and moderately deep; proximal shoulder not overhanging groove	Broad and shallow; proximal shoulder not overhanging groove
Ventral transverse groove of palm of major chela	Moderately deep; proximal shoulder not produced anteriorly	Moderately deep; proximal shoulder slightly produced anteriorly	Moderately deep; proximal shoulder not produced anteriorly	Moderately deep; proximal shoulder slightly produced anteriorly	Broad and shallow; proximal shoulder not produced anteriorly

TABLE 2. — Continuation.

Species Characters	*A. petronioi* n. sp.	*A. heterochaelis* Say, 1818 (mostly based on comparative material cited above)	*A. firmus* Kim & Abele, 1988 (based on illustrations and description provided by Kim & Abele 1988)	*Alpheus distinctus* Kim & Abele, 1988 (based on illustrations and description provided by Kim & Abele 1988)	*A. pontederiae* de Rochebrune, 1883 (based on comparative material cited above)
Small prominences on mesial side of the major chela pollex	Absent	Absent	Absent	Absent	Present
Rectangular ridge on lateral side of major chela	Absent	Absent	Absent	Absent	Present
Sculpturing of palm of male minor chela	Weak to moderate	Weak to moderate	Weak to moderate	Strong (similar to that of major chela)	Moderate
Transverse notches of male minor chela	Generally both inconspicuous	Generally both inconspicuous	Generally both inconspicuous	Dorsal and ventral conspicuous and narrow	Dorsal broad and shallow; ventral inconspicuous
Length of fingers of male minor chela	As long as or slightly shorter than palm length	Slightly shorter than palm length	Slightly shorter than palm length	Slightly longer than palm length	As long as or slightly shorter than palm length
Development of balaeniceps setae on fingers of male minor chelae	Well-developed, not remarkably massive as in *A. firmus* Kim & Abele, 1988	Well-developed, not remarkably massive as in *A. firmus* Kim & Abele, 1988	Well-developed, remarkably massive	Well-developed, not remarkably massive as in *A. firmus* Kim & Abele, 1988	Well-developed, not remarkably massive as in *A. firmus* Kim & Abele, 1988
Ratio of carpal segments of pereiopod 2 (proximal to distal)	Subequal to 2.4: 1.8: 1: 1: 1.3	Subequal to 3.5: 2.5: 1: 1: 1.5	Subequal to 2.5: 2: 1: 1: 1.1	Subequal to 3.1: 2.3: 1: 1: 1.4	Subequal to 4: 2.5: 1: 1: 1.5
Form of dactylus of pereiopods 3 and 4	P3 very slightly flattened; P4 conical	P3 slightly flattened; P4 conical	Form not mentioned	P3 and P4 conical	P3 and P4 subspatulate
Spiniform setae on the ischium of pereiopods 3-5	Present on P3 and P4, absent on P5	Present on P3-P5	Present on P3 and P4, absent on P5	Present on P3 and P4, absent on P5	Present on P3 and P4, absent on P5
Distolateral spiniform seta of uropodal exopod	Flanked by one acute outer tooth and rounded inner lobe	Flanked by one acute outer tooth and rounded inner lobe	Flanked by one acute outer tooth and rounded inner lobe	Flanked by two acute teeth, inner and outer	Flanked by two acute teeth, inner and outer
Overall color pattern	Olive-green to brown	Olive-green to brown (McClure 1995)	Pinkish (A. Anker, pers. com.)	Olive-green (A. Anker, pers. com.)	Olive-green to brown

petronioi n. sp. differs from *A. distinctus* by the rostral carina not broadening posteriorly, slightly overreaching the posterior margin of the orbital hoods (vs slightly broadening posteriorly, reaching far beyond the posterior margin of the orbital hoods in *A. distinctus*) (see Fig. 1B and Kim & Abele 1988: 96, fig. 40l for comparison). Additional characters that may be useful to separate *A. petronioi* n. sp. from similar species are listed in Table 2.

The material identified as *A. heterochaelis* from Pará, illustrated by Christoffersen (1984), agrees very well with *A. petronioi* n. sp. *Alpheus andronyx* Christoffersen, 1998 is a *nomen nudum*, representing the same species identified above as *A. heterochaelis* (Christoffersen 1998; De Grave & Fransen 2011), and herein considered to belong to *A. petronioi* n. sp. The material of *A. andronyx* was described and illustrated by Christoffersen (1980b, unpublished thesis) and cited by the same author as "*Alpheus* sp. nov. 1" (Christoffersen 1980a) from Pará. This material corresponds to the species identified as *A. heterochaelis* in his article from 1984 (herein included in *A. petronioi* n. sp.). The synonymy provided above includes only these records and the material previously reported by the first author (Almeida *et al.* 2006, 2012), and other references from Brazil based on these reports (Barros & Pimentel 2001; Coelho *et al.* 2006). The strongest previous evidence for the occurrence of *A. heterochaelis* in the southern hemisphere is herein shown to be based on material belonging to the new species *A. petronioi* n. sp.

The taxon recorded as *A.* cf. *heterochaelis* from Cabo Branco Beach, Paraíba, by Rodrigues *et al.* (2009) may not belong to *A. petronioi* n. sp. The habitat described for their specimens in Paraíba, i.e. the upper intertidal zone, under rocks, does not match the locations where we collected *A. petronioi* n. sp. (upper part of estuaries), but does match the situations where *A. buckupi*, which resembles *A. petronioi* n. sp. in certain morphological aspects, has been recorded.

The material from Cananéia, São Paulo, recorded by Holthuis (1956) as *A. heterochaelis* belongs to *A. estuariensis* Christoffersen, 1984 and not to *A. petronioi* n. sp. (1 ♂, 3 ovf, 1 juvenile, det. A. O. Almeida, RMNH.Crus.D.10979). However, the occurrence of *A. petronioi* n. sp. in Cananéia was confirmed by us (1 ♀, CCDB 4728), and this locality is the southern known limit of distribution of this species in the western Atlantic. All other Brazilian records (for a compilation, see Soledade & Almeida 2013) must be treated with much caution because they potentially include misidentified material, i.e. they may correspond to *A. petronioi* n. sp. or any other similar species of *Alpheus*. Records from northern South America must also be treated with care. We have not found any specimen assignable to *A. heterochaelis* s.s. in the material examined by us, from Colombia to southern Brazil. At least part of the material reported by Holthuis (1959) from Surinam belongs to *A. pontederiae* (p. 102, lot RMNH.Crus.D.11461, pl. III, fig. 1). However, the possibility that *A. heterochaelis* occurs in northern South America, including northern Brazil, cannot be discarded because the estuaries from those regions are still far from being sufficiently studied with respect to the composition of the alpheid fauna. Finally, it is clear that the occurrence of *A. petronioi* n. sp. in only three Brazilian states is most probably due to the lack of recent sampling efforts in other regions.

Furthermore, *A. petronioi* n. sp. can be distinguished genetically from the species that are morphologically close (Figs 5, 6), in which our DNA data from the ribosomal mt16S gene support the establishment of the new species. The multiple sequence alignment obtained for the 16S gene had 540 positions. The sequences of *A. petronioi* n. sp. from three localities (Colombia, Venezuela and Brazil-Pará) had low values of genetic distance (0.004), and a similar result occurred with well-defined, morphologically close species (Fig. 5): two specimens of *A. estuariensis* (Brazil: Pernambuco and São Paulo; value 0) and three specimens of *A. pontederiae* (Venezuela and Brazil: Pará and São Paulo; value 0). Therefore, in this analysis the intraspecific variation among specimens of the genus *Alpheus* ranged from 0 to 0.004 and the interspecific variation ranged from 0.049 to 0.170 (Fig. 5). In turn, the gap between intraspecific and interspecific variations was from 0.004 to 0.049. These results are in accordance with the genetic variation within the genus, and support the establishment of the new species.

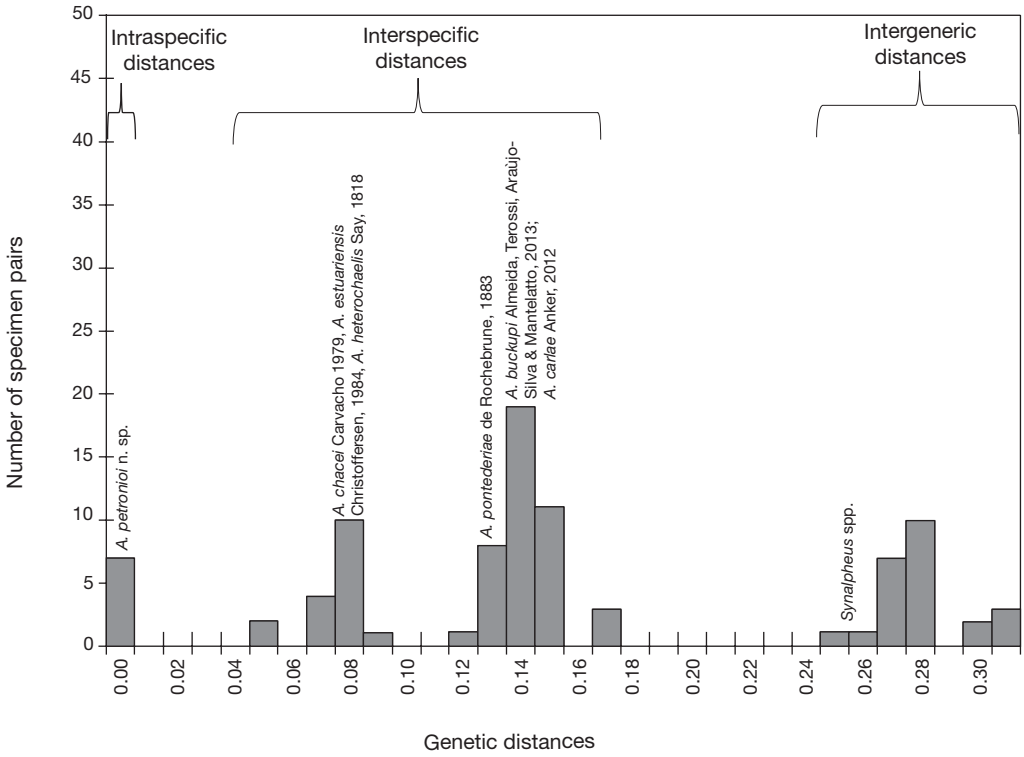

Fig. 5. — Histogram of Kimura two-parameter genetic distances for the 16S gene sequences. The distances were calculated between all pairs of specimens (detailed in Table 1) in order to see how is the genetic variation of the present data, and here the data were put together (91 values to 91 pairs of specimens). The name of the species above the bars indicate just the position of the genetic distances between specimens of *A. petronioi* n. sp. and other specimens. The bars without names indicate genetic distances among other specimens, excluding those of *A. petronioi* n. sp.

The phylogenetic tree generated by ML analysis showed a clear separation of the specimens of *A. petronioi* n. sp. from the other analyzed species (Fig. 6). The genetic distances estimated among the specimens of *A. petronioi* n. sp. and other species of *Alpheus* ranged from 0.070 to 0.145 (Fig. 5). Although *A. petronioi* n. sp. is morphologically very similar to *A. heterochaelis*, the new species is also genetically similar to *A. chacei* Carvacho, 1979 and *A. estuariensis* (Fig. 5). The genetic divergence between *A. petronioi* n. sp. and *A. heterochaelis* (0.076 – 0.081) was slightly larger than the divergence between the former and *A. chacei* (0.070 – 0.075) and *A. estuariensis* (0.073 – 0.077). However, these small differences among the values of divergence are not enough to be considered significant.

This pattern was also confirmed by the ML analysis (Fig. 6). Analyzing the clade that includes these species, three minor clades were supported by high bootstrap values (*A. petronioi* n. sp. – 97%, *A. estuariensis* – 99% and *A. chacei* + *A. estuariensis* – 63%). Nevertheless the group including *A. petronioi* n. sp., *A. heterochaelis* and *A. chacei* + *A. estuariensis* had low bootstrap values, indicating that the relationships among these three groups are still uncertain on the basis of genetic distances.

Morphologically, *Alpheus petronioi* n. sp. can be easily distinguished from *A. chacei* and *A. estuariensis* by the presence of well-developed balaeniceps setae on the male minor chela (absent in males of *A. chacei* and *A. estuariensis*) (see Christoffersen 1984). Also, there seems to be an ecological

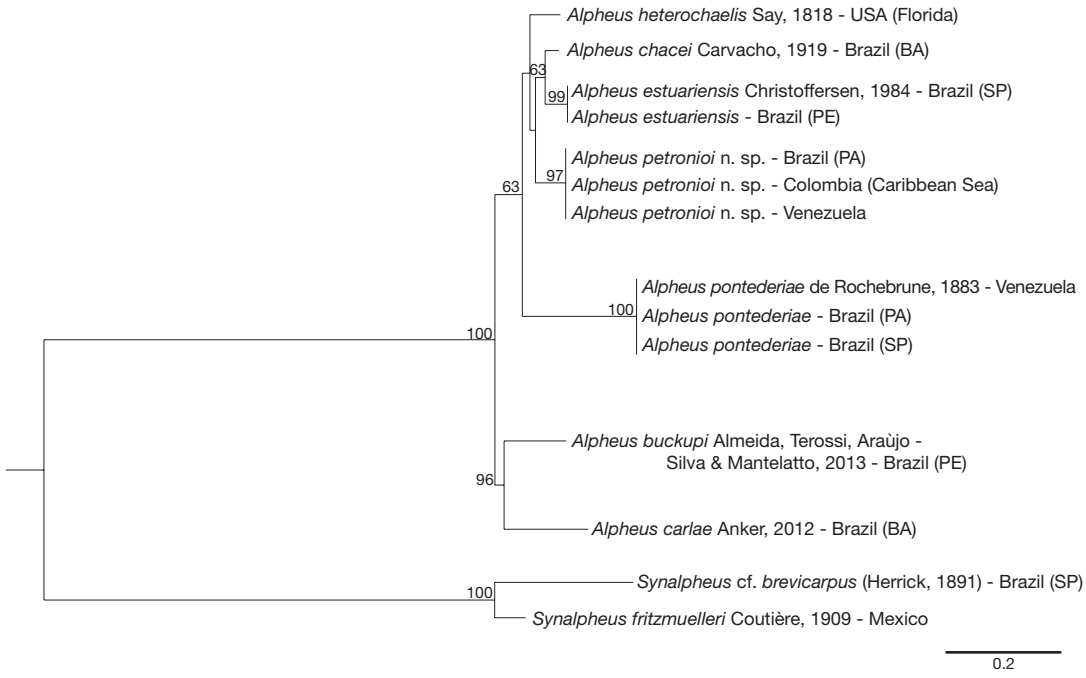

Fig. 6. — Phylogenetic tree of *Alpheus petronioi* n. sp. and other species of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888, using Maximum Likelihood analysis of 16S gene sequences. Numbers are support values for 1000 bootstraps; values < 50% are not shown. Abbreviations: **BA**, Bahia; **PA**, Pará; **PE**, Pernambuco; **SP**, São Paulo.

separation between *A. chacei* + *A. estuariensis* and *A. petronioi* n. sp. + *A. pontederiae* in the areas where they occur in sympatry: the former pair of species can be found in the lower (more saline) portions of estuaries, while the latter pair seems to occur in upper (less saline) parts of estuaries (A. O. Almeida, pers. obs.).

Thus, considering that *A. heterochaelis* is not the sister group of *A. petronioi* n. sp., we can conjecture that these species are cryptic species but not sibling species as was expected. According to Knowlton (1986), all morphologically similar species are cryptic species, and they can also be considered sibling species when biochemical data exist to indicate that they are in fact close. Future studies are necessary, including other species such as *A. firmus* and *A. distinctus*, in order to determine which species is in fact the sister taxon of *A. petronioi* n. sp.

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