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Research article

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A new western Atlantic snapping shrimp of the *Alpheus macrocheles* group (Caridea, Alpheidae) revealed by morphological, molecular and color data

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Abstract. *Alpheus macrocheles* (Hailstone, 1835), a species originally described from the northeastern Atlantic, has been reported from Brazil based on material from the north and northeast coasts and Espírito Santo. However, a thorough morphological comparison between Brazilian material reported as *A. macrocheles* and eastern Atlantic material of *A. macrocheles* revealed consistent differences, suggesting that the Brazilian specimens belong to an undescribed species. *Alpheus ramosportoae* sp. nov. is therefore now described based on material from Amapá to Pernambuco, Brazil. Morphological differences between the new species and *A. macrocheles* s. str. were supported by the clear divergence of 16S rRNA gene sequences (18% of genetic distance), separating the species in two distinct clades. Differences in the color pattern also were observed and illustrated.

Keywords. Alpheid, new species, South-West Atlantic, Brazil, 16S.

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Introduction

The highly diverse genus *Alpheus* Fabricius, 1798, currently with 313 valid species throughout the world (e.g., De Grave & Fransen 2011; Anker 2012; Komai & Ohtomi 2018; Dehghani *et al.* 2019), was subdivided into seven informal morphological groups by Coutière (1897, 1905). This infrageneric division was continued in several subsequent major taxonomic works (Banner 1953; Crosnier & Forest 1966; Kim & Abele 1988). However, preliminary molecular data suggested that some of these morphological groups may not be monophyletic (Williams *et al.* 2001). In addition, molecular evidence has demonstrated that many species of *Alpheus* are in fact species complexes (e.g., Williams *et al.* 2001; Anker *et al.* 2006; Mathews & Anker 2009), many of which have been resolved by integrative taxonomy (e.g., Anker *et al.* 2009; Almeida *et al.* 2014; Bracken-Grissom *et al.* 2014). Despite these numerous revisions, many unresolved taxonomic issues still persist in *Alpheus*, good examples being the large pantropical *A. paracrinitus* Miers, 1881 species complex, or the speciose American *A. packardii* Kingsley, 1880 species complex (Williams *et al.* 2001).

The species of the *Alpheus macrocheles* (Hailstone, 1835) species group (*sensu* Coutière 1905) are characterized by a diagnostic major cheliped morphology, with the chela strongly twisted and compressed, and the plane of dactylar articulation deviating from the plane perpendicular to the dorsal margin, often resulting in a pair of distinct grooves on the lateral face of the chela. Based on this typical morphology, the group currently includes 33 valid species distributed worldwide. Within the *A. macrocheles* group, several species appear to be morphologically more or less close to *A. macrocheles* s. str. and have been tentatively grouped together as *A. macrocheles* complex (Anker & De Grave 2012). Whether this morphologically vaguely defined complex also forms a monophyletic group remains to be shown in the broader analysis of the entire *A. macrocheles* group. Nevertheless, the *A. macrocheles* complex *sensu* Anker & De Grave (2012) includes 10 species: *A. amblyonyx* Chace, 1972, *A. lentiginosus* Anker & Nizinski, 2011, *A. pouang* Christoffersen, 1979 and *A. puapeba* Christoffersen, 1979 in the western Atlantic; *A. cedrici* Anker & De Grave, 2012 in the central Atlantic; *A. macrocheles* in the eastern and central Atlantic (with questionable records from the western Atlantic, see below); *A. platydactylus* Coutière, 1897 in the eastern Atlantic; *A. bellimanus* Lockington, 1877 and *A. rectus* Kim & Abele, 1988 in the eastern Pacific; and finally, *A. albatrossae* Banner, 1953 in the Indo-West Pacific (Anker & De Grave 2012).

The type locality of *A. macrocheles* is off Hastings, England, in the English Channel (Hailstone 1835). Subsequently, this species has been recorded throughout the Mediterranean Sea and on both sides of the Atlantic Ocean, as well as from Ascension Island in the Central Atlantic (Holthuis 1951; Crosnier & Forest 1966; d'Udekem d'Acoz 1999; De Grave *et al.* 2017). In Brazil, the species has been recorded from several localities, ranging from Amapá to Espírito Santo (see Soledade & Almeida 2013 for records). However, the true identity of records of *A. macrocheles* on the Brazilian coast is uncertain for the following main reasons: many records of *A. macrocheles* from Brazil lack detailed morphological information or illustrations and, unfortunately, specimens associated with these records were not always deposited in zoological collections, making confirmation of their identity impossible (Anker & De Grave 2012; Soledade & Almeida 2013). Exceptionally, Ramos-Porto (1979) provided a detailed morphological account and good illustrations of the Brazilian material of *A. macrocheles*, showing that specimens examined by her were in fact not *A. amblyonyx*. The material used by Ramos-Porto (1979) was deposited in the carcinological collection of the Universidade Federal de Pernambuco in Recife (UFPE), which is currently integrated in the collections of the Museu de Oceanografia Professor Petrônio Alves

Coelho, Universidade Federal de Pernambuco (MOUFPE). Additional fresh specimens of the Brazilian *A. macrocheles* were collected during two expeditions carried out off Recife, Pernambuco, northeastern Brazil, in 2018. This material was collected by dredges between 50 and 65 m, on mud, sand, calcareous algae and fragmented coral rubble.

While examining a series of specimens identified as *A. macrocheles* from northeastern Brazil deposited in the MOUFPE collection, including the Ramos-Porto (1979) specimens, we observed subtle morphological differences between them and the eastern Atlantic material of *A. macrocheles*. These differences were corroborated by DNA sequencing of the freshly collected material and also by slight differences in the color patterns between the two forms. In the present study, we describe a new species of *Alpheus* from the Brazilian coast, putatively closely related to *A. macrocheles* based on the combined morphological and molecular datasets.

Material and methods

Specimens examined in this study remain deposited in the following institutions:

CCDB	=	Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Ribeirão Preto, Brazil
MNHN	=	Muséum national d'histoire naturelle, Paris, France
MNRJ	=	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
MOUFPE	=	Museu de Oceanografia Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco, Recife, Brazil
MZUSP	=	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
RMNH	=	Naturalis Biodiversity Center, Leiden, The Netherlands
UNAM-CNCR	=	Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

We carried out a detailed morphological analysis of 48 specimens (*A. macrocheles* Brazil vs East Atlantic) compared to three specimens of *A. amblyonyx* (Caribbean Sea) using 42 characters photographed through a stereo microscope with an image capture system. Illustrations were generated from these images through vectorization in the Adobe Illustrator® program (Coleman 2003, 2009). This analysis yielded a set of characters useful for species distinction that were used in the morphological comparisons carried out in the Discussion section.

For the phylogenetic analysis of *A. macrocheles* Brazil vs East Atlantic, we used a combination of original molecular sequence data (e.g., for the new species) and sequence data retrieved from GenBank (Table 1). Whole genomic DNA was extracted from pleon tissue using the Qiagen DNeasy® Blood and Tissue Kit (Cat. No. 69504) following the manufacturer's instructions. A ~550 base pair region of the 16S small ribosomal subunit gene was amplified from the extracted DNA through PCR (Polymerase Chain Reaction) (Sambrook *et al.* 1989) using the primers: 1472 (5'-AGATAGAAACCAACCTGG-3') and 16SL2 (5'-TGCCTGTTTATCAAAAACAT-3') (Crandall & Fitzpatrick 1996; Schubart *et al.* 2002). PCR reactions were done according to the protocol of Mantelatto *et al.* (2009, 2018), in 25 µl volumes containing 5 M betaine, 10X PCR buffer, primers, 25 mM MgCl₂, 200 µM dNTPs, deionized water, 1 unit *Taq* polymerase and 2 µl of extracted genomic DNA, and reactions were performed in a Veriti 96-Well Thermal Cycler® (Applied Biosystems) with specific thermal cycles for the utilized set of primers (melting temperature of 48°C). PCR products were visualized using gel electrophoresis with 1% agarose gel on a Transilluminator. PCR products were purified using the Exo-sap® Purification Kit following the manufacturer's instructions. Cycle sequencing reactions were performed in 20 µl volumes using Big Dye® Terminator ver. 3.1 Cycle Sequencing Kit (Applied Biosystems) following the manufacturer's instructions. Sequencing was performed on an ABI 3100 Genetic Analyzers® at the ACTGENE - Análises

Table 1. List of specimens used in genetic analysis. Abbreviations: CCDB = Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Ribeirão Preto, Brazil; MNHN = Muséum national d’histoire naturelle, Paris, France; MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MOUFPE = Museu de Oceanografia Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco, Recife, Brazil; MZUSP = Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; OUMNH = Oxford University Museum of Natural History, United Kingdom; RMNH = Naturalis Biodiversity Center, Leiden, The Netherlands; UF = Florida Museum of Natural History, USA; ULLZ = University of Louisiana, Lafayette Zoological Collection, USA; UNAM-CNCR = Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México, Ciudad de México, Mexico.

Taxon	Locality	Catalogue number	GenBank	Reference
<i>Alpheus amblyonyx</i> Chace, 1972	Mexico (Gulf of Mexico)	ULLZ 6615	MK714200	Soledade <i>et al.</i> (2019)
<i>Alpheus amblyonyx</i>	Quintana Roo, Mexico	UNAM-CNCR 21271	MK714201	Soledade <i>et al.</i> (2019)
<i>Alpheus amblyonyx</i>	Belize	ULLZ 16584	MK714202	Soledade <i>et al.</i> (2019)
<i>Alpheus amblyonyx</i>	Guadeloupe	MNHN 12026	MK714203	Soledade <i>et al.</i> (2019)
<i>Alpheus amblyonyx</i>	French Antilles	UF 32400	MK714204	Soledade <i>et al.</i> (2019)
<i>Alpheus crockeri</i> (Armstrong, 1941)	Cape Verde	OUMNH 2014-01-00330	MK714205	Soledade <i>et al.</i> (2019)
<i>Alpheus macrocheles</i> (Hailstone, 1835)	Azores, Portugal	RMNH 51342	MK714206	Soledade <i>et al.</i> (2019)
<i>Alpheus macrocheles</i>	Azores, Portugal	OUMNH 2002-09-0003	MK714208	Soledade <i>et al.</i> (2019)
<i>Alpheus macrocheles</i>	Canary Islands, Spain	RMNH 51363	MK714207	Soledade <i>et al.</i> (2019)
<i>Alpheus puapeba</i> Christoffersen, 1979	Rio de Janeiro, Brazil	MNRJ 21836	MK714209	Soledade <i>et al.</i> (2019)
<i>Alpheus ramosportoae</i> sp. nov.	off Ceará, Brazil	MOUFPE 13703	MK918615	Present study
<i>Alpheus ramosportoae</i> sp. nov.	off Recife, Brazil	MOUFPE 19470	MK918616	Present study
<i>Alpheus ramosportoae</i> sp. nov.	off Recife, Brazil	MZUSP 39146	MK918617	Present study
<i>Alpheus ramosportoae</i> sp. nov.	off Recife, Brazil	CCDB 6120	MK918618	Present study
<i>Synalpheus</i> cf. <i>brevicarpus</i> Herrick, 1891	Ubatuba, São Paulo, Brazil	CCDB 3419	KF667548	Almeida <i>et al.</i> (2014)
<i>Synalpheus fritzmulleri</i> Coutière, 1909	Gulf of Mexico	ULLZ 7136	EU868642	Bracken <i>et al.</i> (2009)

Moleculares Ltda – ME, Porto Alegre, Brazil. Sequences were confirmed by sequencing both forward and reverse strands. Sequence assembly was performed using the program Bioedit ver. 7.0.9.0 (Hall 2005). Sequences were aligned using MUSCLE (Edgar 2004), with default parameters, on the platform Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller *et al.* 2010).

Initially, an analysis was performed using jModelTest (Darriba *et al.* 2012), implemented on CIPRES, to find out which substitution model best fits the data, using the Bayesian Information Criterion (BIC). Bayesian inference analysis was carried out using the software MrBayes ver. 3.2.6 (Ronquist *et al.* 2012), implemented on CIPRES, using the optimal parameters obtained from jModelTest. In the analysis, one tree was sampled for every 1000 generations of 20 000 000 generations, starting with a randomly generated tree. Four independent runs were performed and the convergence of runs was analyzed using Tracer ver. 1.6 (Rambaut *et al.* 2014). The first 15% of trees and parameters were discarded as burn-in and a final tree was generated in Tree Annotator ver. 1.8.4 (implemented in BEAST, Drummond *et al.* 2012). Posterior probability values greater than 95% were reported. A genetic distance matrix was constructed in MEGA ver. 5 (Tamura *et al.* 2011) based on the optimal substitution model selected by jModelTest.

Abbreviations

exped.	=	expedition
NE	=	northeast
NI	=	sex not identified
ov	=	ovigerous female
PE	=	Pernambuco
REC	=	dredging campaign off Recife conducted by Laboratory of Crustacean Biology, Department of Zoology, Biosciences Center, Federal University of Pernambuco
REVIZEE	=	Recursos Vivos da Zona Econômica Exclusiva Program
RV	=	research vessel
stn	=	station

Results

Class Malacostraca Latreille, 1802
 Order Decapoda Latreille, 1802
 Infraorder Caridea Dana, 1852
 Family Alpheidae Rafinesque, 1815
 Genus *Alpheus* Fabricius, 1798

Alpheus ramosportoae sp. nov.

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Figs 1–4

Alpheus macrocheles – Ramos-Porto 1979: 118, figs. 1–6 [not *Alpheus macrocheles* (Hailstone, 1835)].
 (?) *Alpheus macrocheles* – Coelho & Ramos-Porto 1980: 135; 1995: 116 — Coelho *et al.* 1980: 55; 1986: 84 — Fausto Filho 1980: 113 — Ramos-Porto *et al.* 1996: 219 — Christoffersen 1998: 359 — Barros & Pimentel 2001: 21 — Guterres *et al.* 2005: 231, fig. 1 — Coelho *et al.* 2006: 51 — Coelho Filho 2006: 8 — Alves *et al.* 2008: 49 — Souza *et al.* 2011: 47 — Almeida *et al.* 2012: 27 — Soledade & Almeida 2013: 101 [not *Alpheus macrocheles* (Hailstone, 1835)].

Diagnosis

Rostrum without setae, reaching well beyond half length of first segment of antennular peduncle; scaphocerite with lateral margin slightly concave, lateral tooth strong, surpassing distal margin of blade; blade reaching middle of third article of antennular peduncle; distal tooth distinctly exceeding distal

margin of peduncle. Major cheliped with ischium armed with four spiniform setae; ventromesial margin of merus with five spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; dactylus flattened, laterally twisted, dorsally convex and slightly bulbous distally; plunger developed, with anterior surface distinctly angular. Minor cheliped with ischium armed with four spiniform setae; ventromesial margin of merus with seven spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; dactylus with strong crest on extensor margin. Second pereopod elongated, slender; ischium slightly longer than merus; carpus with five articles with ratio approximately equal to 4:2:1:1.5:2; distolateral margin of uropodal exopod with one mesial tooth and one lateral tooth adjacent to spiniform seta.

Etymology

The name of this new species is our tribute to the Brazilian carcinologist Dr Marilena Ramos-Porto, retired professor of the Universidade Federal Rural de Pernambuco, Recife. Dr Marilena contributed substantially to the knowledge of the caridean shrimps of the northern and northeastern Brazil.

Material examined

Holotype

BRAZIL • ♂; Pernambuco, off Recife, approximately 20 nautical miles from the coast, REC I, dredge 4; 8°08'51.5" S, 34°34'08.0" W; 65 m depth; 7 Feb. 2018; agglomerations of sponges, rhodoliths and calcareous algae; GenBank 16S gene MK918616; MOUFPE 19470.

Paratypes

BRAZIL – **Ceará** • 1 ♂; Ceará, seamounts of the North Chain, REVIZEE NE III, stn 75A; 54 m depth; 7 Apr. 1998; calcareous algae; GenBank 16S gene MK918615; MOUFPE 13703. – **Pernambuco** • 1 ♂; exact locality unknown; 31–33 m depth; 7 Mar. 1969; calcareous algae; MOUFPE 8826 • 2 ♂♂; exped. Pesquisador IV, stn 5; 54 m depth; 12 Apr. 1971; MOUFPE 8856 • 1 ♀; off Recife, REC I, dredge 6; 8°09'06.8" S, 34°34'28.4" W; 53 m depth; 7 Feb. 2018; rhodolite crevice; GenBank 16S gene MK918618; CCDB 6120 • 1 ♀ ov; off Recife, REC I, dredge 3; 8°08'44.2" S, 34°34'23.2" W; 55 m depth; 7 Feb. 2018; rhodolith crevice; GenBank 16S gene MK918617; MZUSP 39146.

Additional material

BRAZIL – **Amapá** • 3 ♂♂; exped. GEOMAR II, stn 116; 81.5 m depth; 13 Sep. 1970; calcareous algae; MOUFPE 8848 – **Pará** • 1 ♂, 1 ♀ ov; exped. GEOMAR II, stn 2441; 1970; MOUFPE 8855 • 1 ♂, 1 ♀ ov; exped. GEOMAR II, stn 2528; 60 m depth; 1971; MOUFPE 8836 – **Maranhão** • 1 ♀; Tutóia, RV *Almirante Saldanha*, stn 1732A; 69 m depth; 30 Oct. 1967; calcareous algae; MOUFPE 8829 • 9 NI; RV *Almirante Saldanha*, stn 1750; 52 m depth; 6 Nov. 1967; calcareous algae; MOUFPE 8830 • 1 ♂, 1 ♀; São Luis, RV *Almirante Saldanha*, stn 1875; 49 m depth; 23 Apr. 1968; calcareous algae; MOUFPE 8831 • 1 NI; Tutóia, RV *Almirante Saldanha*, stn 1813; 83 m depth; 28 Nov. 1967; calcareous algae; MOUFPE 8837 • 1 ♀; RV *Almirante Saldanha*, stn 1751; 44 m depth; 6 Nov. 1967; calcareous algae; MOUFPE 8845 • 1 ♂; RV *Almirante Saldanha*, stn 1750; 52 m depth; 6 Nov. 1967; calcareous algae; MOUFPE 8847 – **Ceará** • 1 ♂; REVIZEE NE III, stn 72A; 2°4'48" S, 38°12'0" W; 8 Jun. 1998; MOUFPE 13647.

Comparative material analyzed

Alpheus amblyonyx Chace, 1972

FRANCE – **Guadeloupe** • 1 ♂; KARUBENTHOS, stn GB20; 16 m depth; 18 May 2012; MNHN-IU-12112 • 1 ♀ ov; KARUBENTHOS, stn GB24; 16 m depth; 18 May 2012; GenBank 16S gene MK714203; MNHN-IU-12026.

MEXICO • 1 NI; Quintana Roo, southeast of Arrecife Chinchorro; 28 Aug. 1990; GenBank 16S gene MK714201; UNAM-CNCR 21271.

Alpheus macrocheles (Hailstone, 1835)

ANGOLA • 3 ♀♀ (2 ov), 1 ♂; Cuanza River; 31 Jan. 1949; RMNH.Crus.D.7821.

CAPE VERDE • 1 ♀ ov, 3 NI; “Tydeman” Cancap–VI, Cape Verde Islands exped., stn 6.109, off Santa Luzia; 16°44' N, 24°46' W; 55–80 m depth; 16 Jun. 1982; calcareous algae; RMNH.Crus.D.51345 • 1 ♂; Tarrafal Bay; 1959; MNHN 3163.

FRANCE • 1 ♀; Roscoff; RMNH.Crus.D.34508 • 1 ♂; Roscoff; RMNH.Crus.D.29789 • 1 ♂; Guéthary; 27 Oct. 1947; RMNH.Crus.D.1869.

MOROCCO • 1 ♀; 33°50' N, 07°07' W; 25 Jan. 1956; RMNH.Crus.D.34495 • 1 ♂; Témara; 1952; RMNH.Crus.D.34496 • 1 ♂; Témara; 1954; RMNH.Crus.D.34497.

PORTUGAL – **Azores** • 1 ♂, 1 NI; stn 5.142; 108–118 m depth; 7 Jun. 1981; GenBank 16S gene MK714206; RMNH.Crus.D.51342. – **Madeira** • 1 ♂; Cais de Porto Novo; 18 Aug. 1993; under rocks; RMNH.Crus.D.42706.

SPAIN – **Canary Islands** • 1 ♂; southeast of Lanzarote, stn 4.070; 41–50 m depth; 20 May 1980; sand and calcareous algae; GenBank 16S gene MK714207; RMNH.Crus.D.51363.

Description

CARAPACE. Smooth, frontal margin with well-developed sharp rostrum; orbital hoods with well-developed acute teeth originating from anterior margin of orbital hoods (Fig. 1A); rostrum slightly flattened dorsally, distinctly longer than wide, distally tapering and ending in acute point, without setae, reaching well beyond half-length of first article of antennular peduncle (Fig. 1A–B); margin between orbital teeth and rostrum V-shaped with slightly rounded angle (Fig. 1A); orbital process weak. Pterygostomial angle rounded, not anteriorly protruding (Fig. 1B); cardiac notch deep.

HEAD. Eyes with well-developed corneas; ocellar beak projecting, acute, visible in lateral view. Antennular peduncle moderately slender; stylocerite with acute tip reaching distal margin of first article of antennular peduncle; ventromesial carina with very large, triangular tooth bearing small acute point (Fig. 1C); second article of antennular peduncle much longer than visible part of first article, approx. three times longer than wide, twice as long as third article (Fig. 1A–B); lateral flagellum with several groups of aesthetascs extending to article 10. Antenna with basicerite ending in sharp ventrolateral tooth, extending just beyond orbital tooth; carpocerite slightly overreaching scaphocerite and antennular peduncle; scaphocerite with lateral margin slightly concave, ending in strong distolateral tooth distinctly overreaching antennal peduncle and surpassing distal margin of blade (Fig. 1A), latter reaching to middle of third article. Mouthparts typical for *Alpheus*, as illustrated (Fig. 1D–I). Third maxilliped slender; coxa with lateral plate slightly truncate distally; exopod overreaching antepenultimate article when extended; antepenultimate article somewhat flattened, approximately four times longer than wide, ventral surface sparsely setose; penultimate article about three times longer than wide, slightly broadened distally and densely setose; ultimate article unarmed, distally tapering, with dense transverse rows of long setae (Fig. 1I).

CHELIPEDS. Major cheliped with ischium short, robust, ventromesial surface with four small spiniform setae (Fig. 2F); merus robust, about twice as long as wide, subtriangular in cross-section; ventrolateral margin unarmed; ventromesial margin straight, bearing five small spiniform setae, ending in robust sharp tooth; carpus short, cup-shaped, slightly compressed (Fig. 2F); lateral surface of palm with low crest (inferior crest) starting at approximately 0.6 of palm length, ending in sharp distolateral tooth, latter slightly directed laterally (Fig. 2A); mesial surface convex, smooth, without grooves (Fig. 2B); ventral surface with rounded smooth shoulder slightly projecting into adjacent deep notch, latter extending

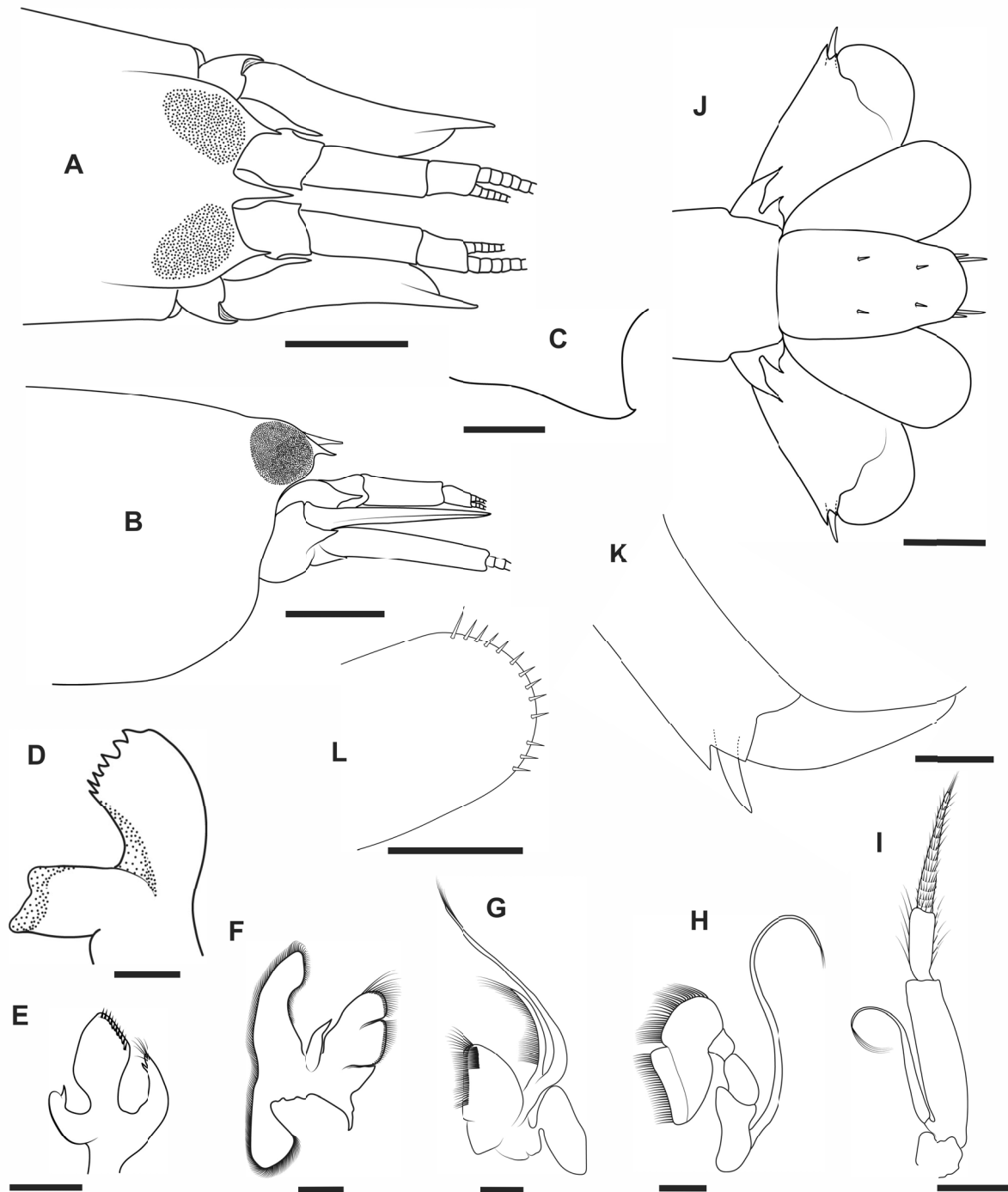


Fig. 1. *Alpheus ramosportoae* sp. nov. **A–D.** Holotype, ♂, from off Recife, state of Pernambuco, northeastern Brazil (MOUFPE 19470). **A.** Carapace and cephalic appendages, dorsal view (setae omitted). **B.** Same, lateral view. **C.** Tooth on ventromesial carina of antennular peduncle. **D.** Left mandible, mesial view. **E–L.** Paratype, ♂, from seamounts of the North Chain, Ceará, northeastern Brazil (MOUFPE 13703). **E.** First maxilla, lateral view. **F.** Second maxilla, lateral view. **G.** First maxilliped, lateral view. **H.** Second maxilliped, lateral view. **I.** Third maxilliped, lateral view. **J.** Telson and uropods, dorsal view (setae omitted). **K.** Uropod, detail of the distolateral angle of the exopod. **L.** Uropod, detail of the posterior margin of endopod. Scale bars: A–B, J = 1 mm; C–I, K–L = 0.5 mm.

transversely to groove on mesial surface (inferior groove); dorsal margin with subcylindrical elevation (plaque crest) ending distally in large adhesive disk; distomesial surface with deep transversally notched crest (superior crest) ending in sharp tooth; distal third of ventral margin with long, robust setae extending to distomesial margin; pollex shorter than dactylus, strongly curved laterally, cutting edge slightly excavate, bearing one small rounded tooth proximally (Fig. 2A); dactylus flattened, laterally twisted, dorsally convex, slightly bulbous distally (Fig. 2A); plunger moderately developed, its proximal margin with sharp angle (Fig. 2E); adhesive disks of dactylus well-developed (Fig. 2A). Minor cheliped not sexually dimorphic; ischium, short, stout, its distomesial margin armed with four spiniform setae; merus broad, subtriangular in cross-section; ventrolateral surface unarmed; ventromesial margin slightly convex, ending in small acute tooth, with seven spiniform setae similar in size and shape, spaced almost equidistantly along entire length of mesial margin; carpus cup-shaped (Fig. 2G); chela strongly compressed; palm with grooves and notches on distal half of lateral surface (Fig. 2C–D); lateral surface with low crest (inferior crest) starting at about middle of palm and ending in acute distolateral tooth (Fig. 2C); mesial surface convex and devoid of depressions or grooves (Fig. 2D); ventral surface smooth, ending in well-defined notch; dorsal margin also smooth, with sub-cylindrical elevation (plaque crest) ending distally in small adhesive disk; distomesial surface with high ridge ending in strong sharp tooth (superior crest); fingers as long as palm (Fig. 2C–D); pollex lightly excavate on cutting edge; dactylus slightly flattened and twisted laterally, with broad crest on extensor margin, bearing small adhesive disk proximally (Fig. 2C–D).

PEREIOPODS. Second pereopod elongate, slender; ischium slightly longer than merus; carpus with five subdivisions with ratio approximately equal to 4 : 2 : 1 : 1.5 : 2; chela fingers as long as palm, with small tufts of setae on distal region (Fig. 3A). Third pereopod with ischium armed with one strong spiniform seta on ventrolateral surface (Fig. 3B); merus five times longer than broad, unarmed distoventrally; carpus slender, about half-length of merus (Fig. 3B); propodus approximately 1.2 times as long as carpus, with about nine robust spiniform setae along ventral margin and one pair of spiniform setae at propodo-dactylar articulation (Fig. 3E); dactylus slightly shorter than half-length of propodus, conical, slightly curved, acute, extensor margin with one subdistal denticle (Fig. 3E, H). Fourth pereopod similar to third in shape and proportion of articles, slightly less robust (Fig. 3C); ischium armed with one strong spiniform seta on ventrolateral surface (Fig. 3C); propodus with about eight robust spiniform setae along ventral margin and one pair of spiniform setae at propodo-dactylar articulation, extensor margin with one subdistal denticle (Fig. 3F, I). Fifth pereopod more slender than third and fourth (Fig. 3D); merus slightly longer than carpus; ischium with one spiniform seta; propodus with about eight spiniform setae along ventral margin and nine well-developed rows of setae distolaterally (omitted) (Fig. 3G).

PLEON. Pleonites 1–4 with posteroventral margins broadly rounded, fifth pleonite slightly angular. Telson subrectangular, tapering to posterior margin; proximal margin twice as wide as distal margin; lateral margin slightly convex; dorsal surface with two pairs of spiniform setae, first pair located at telson half-length, second pair at approximately 0.7 of telson length; posterior margin broadly convex, with two pairs of spiniform setae, mesial pair about three times as long as lateral pair (Fig. 1J); anal tubercles well-developed.

PLEOPODS. With sparse setae on lateral margin of protopod. First pleopod reduced; distal margin of endopod with setae. Second pleopod of male with appendix masculina subequal in length to appendix interna, not reaching distal margin of endopod, with numerous rigid setae distally. Uropod with lateral lobe of protopod ending in strong sharp tooth (Fig. 1J); diaeresis sinuous; distolateral margin of exopod with one mesial tooth and one lateral tooth flanking spiniform seta (Fig. 1K); endopod with row of spiniform setae along distal margin, mesial ones stronger than lateral ones (Fig. 1L).

Color in life

Body predominantly reddish; carapace uniformly reddish; pleon reddish with whitish transverse bands and whitish spots on lateral surface; major cheliped palm reddish, with three transverse white patches on both lateral and mesial surfaces, more defined on mesial surface; fingers of both chelae reddish; telson and uropods intensely reddish; protopods of uropods whitish; pereopods (2–5) pale reddish (Fig. 4A–C). This color pattern was homogeneous in all specimens collected.

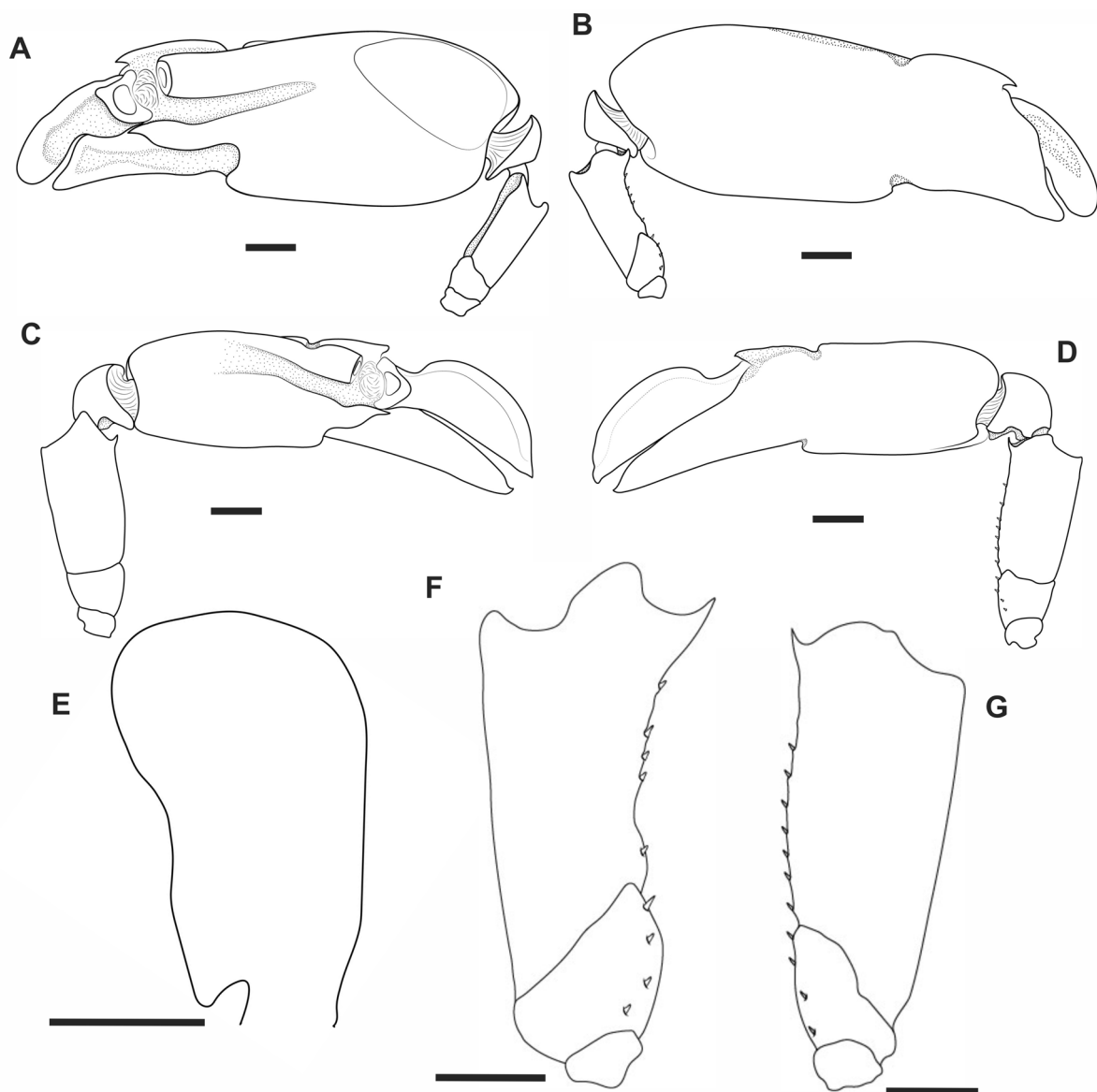


Fig. 2. *Alpheus ramosportoae* sp. nov., paratype, ♂, from seamounts of the North Chain, Ceará, northeastern Brazil (MOUFPE 13703). **A.** Major cheliped, lateral view. **B.** Same, mesial view. **C.** Minor cheliped, lateral view. **D.** Same, mesial view. **E.** Major chela dactylus, mesial view, detail of plunger. **F–G.** Detail of spiniform setae on ischium and propodus of major and minor chelae, respectively. Scale bars: A–E = 1 mm; F–G = 0.5 mm.

Habitat

On sand mixed with calcareous algae, rhodoliths and sponges (Fig. 4D–F), at depths ranging from 33 to 90 m (Ramos-Porto 1979, as *A. macrocheles*; present study).

Distribution

Brazil: Amapá, Pará, Maranhão, Ceará and Pernambuco (Ramos-Porto 1979, as *A. macrocheles*; present study).

Molecular analysis

The best-fit substitution model selected with a corrected Bayesian information criterion was TPM3uf+I, assuming the nucleotide frequencies A = 0.2847, C = 0.1194, G = 0.2561, T = 0.3398, replacement rates AC = 0.0010, AG = 4.5910, AT = 1, CG = 0.0010, CT = 4.5910, GT = 1, proportion of invariable sites = 0.5410. The Bayesian Inference analysis (Fig. 5) retrieved two clades, one being formed by

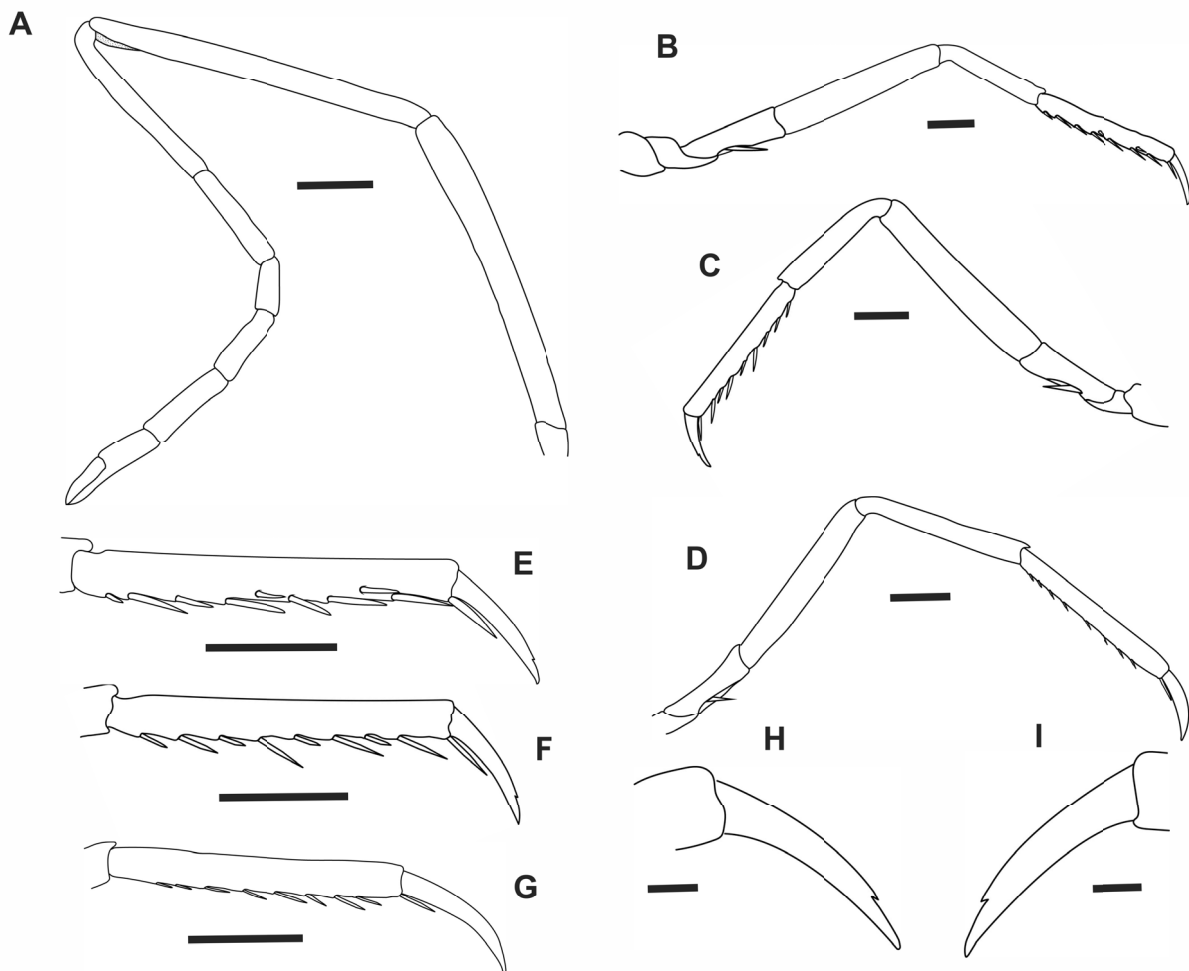


Fig. 3. *Alpheus ramosportoae* sp. nov., paratype, ♂, from seamounts of the North Chain, Ceará, northeastern Brazil (MOUFPE 13703). **A.** Second pereiopod, lateral view. **B.** Third pereiopod, lateral view. **C.** Fourth pereiopod, lateral view. **D.** Fifth pereiopod, lateral view. **E–G.** Third to fifth pereiopods, detail of propodus, lateral view. **H–I.** Third and fourth pereiopods, detail of dactylus. Scale bars: A–G = 0.5 mm; H–I = 0.25 mm.

A. amblyonyx and another including *A. ramosportoae* sp. nov. as sister to a clade formed by *A. crockeri* (Armstrong, 1941), *A. puapeba* and *A. macrocheles*. Genetic distance estimates (Table 2) support these results. The range of the genetic distance values between *A. ramosportoae* sp. nov. and other species was 15.9–22.9% according to the TPM3 model. *Alpheus ramosportoae* sp. nov., as well as *A. amblyonyx* and *A. macrocheles*, show no significant intraspecific divergence in 16S sequences.

Discussion

Alpheus ramosportoae sp. nov. can be separated from other Atlantic representatives of the *A. macrocheles* complex (sensu Anker & De Grave 2012, see above) by morphology, DNA and coloration. *Alpheus ramosportoae* sp. nov. may be distinguished from most of them by the presence of a small subdistal

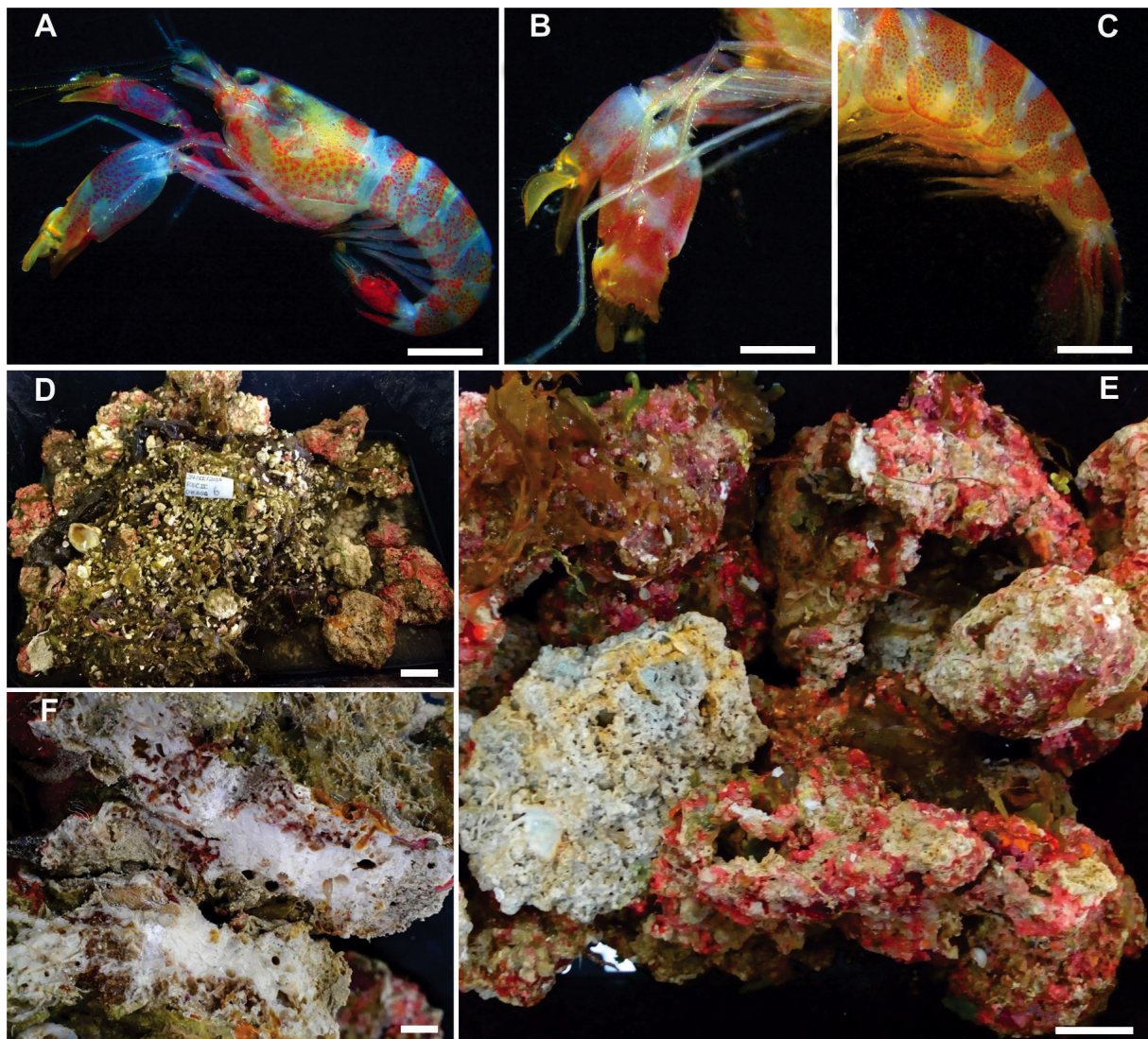


Fig. 4. *Alpheus ramosportoae* sp. nov. from off Recife, state of Pernambuco, northeastern Brazil. **A–C.** Color pattern in life of the species. **A.** Body color pattern, lateral view. **B.** Coloration of major (mesial view) and minor (lateral view) chelipeds. **C.** Coloration of pleon, lateral view. **D–F.** Substrates where the specimens were obtained. **D.** Calcareous algae, sponges and sandy sediment clusters. **E.** External appearance of rhodolith fragments. **F.** Detail of a fragment of rhodolith broken in half, showing crevices from which specimens were retrieved. Scale bars: A–C = 1 mm; D–F = 2 cm.

denticle on the extensor margin of the dactylus of pereiopods 3–4, a character shared only with *A. macrocheles* and *A. amblyonyx* (Fig. 3H–I). Furthermore, *A. ramosportoae* sp. nov. can be separated from *A. cedrici* and *A. puapeba* by the presence of a strong crest on the extensor surface of the minor cheliped dactylus (absent in *A. cedrici* and *A. puapeba*) and two teeth on the distolateral margin of the uropodal exopod (vs only one tooth in *A. cedrici* and *A. puapeba*) (cf. Fig. 2C–D and Christoffersen 1979: fig. 16F–H; Anker & De Grave 2012: fig. 2A–C). The new species can be distinguished from *A. platydactylus* by the presence of a well-developed plunger on the major cheliped dactylus (absent in *A. platydactylus*) (cf. Fig. 2E and Crosnier & Forest 1966: fig. 2F) and by the absence of tubercles on the ventral surface of the major chela palm (present in *A. platydactylus*). *Alpheus ramosportoae* sp. nov. differs from *A. pouang* by the presence of a well-defined ventral notch on the major cheliped palm (obsolete in *A. pouang*) (cf. Fig. 2A–B and Christoffersen 1979: fig. 15J). Finally, the new species can be distinguished from *A. lentiginosus* by the presence of a well-defined plunger on the major cheliped dactylus (rudimentary in *A. lentiginosus*) (cf. Fig. 2E and Anker & Nizinski 2011: fig. 1G) and the absence of a minute subdistal denticle on the flexor surface of the pereiopods 3–5 dactyli (present in *A. lentiginosus*) (cf. Fig. 3H–I and Anker & Nizinski 2011: fig. 2C, E).

Alpheus ramosportoae sp. nov. differs from *A. amblyonyx* and *A. macrocheles* by several morphological characters listed in Table 3. The most conspicuous difference between the new species and *A. amblyonyx* is the presence of a strong crest on the extensor surface of the minor cheliped dactylus in the former vs its absence in the latter (cf. Fig. 2C–D and Chace 1972: fig. 16L–M, Y, V and Soledade *et al.* 2019: fig. 5C–D). Other differences between *A. ramosportoae* sp. nov. and *A. amblyonyx* include the second article of the antennular peduncle twice as long as the third (vs second article less than 1.5 times the length of the third in *A. amblyonyx*) and the distolateral tooth of the scaphocerite overreaching the

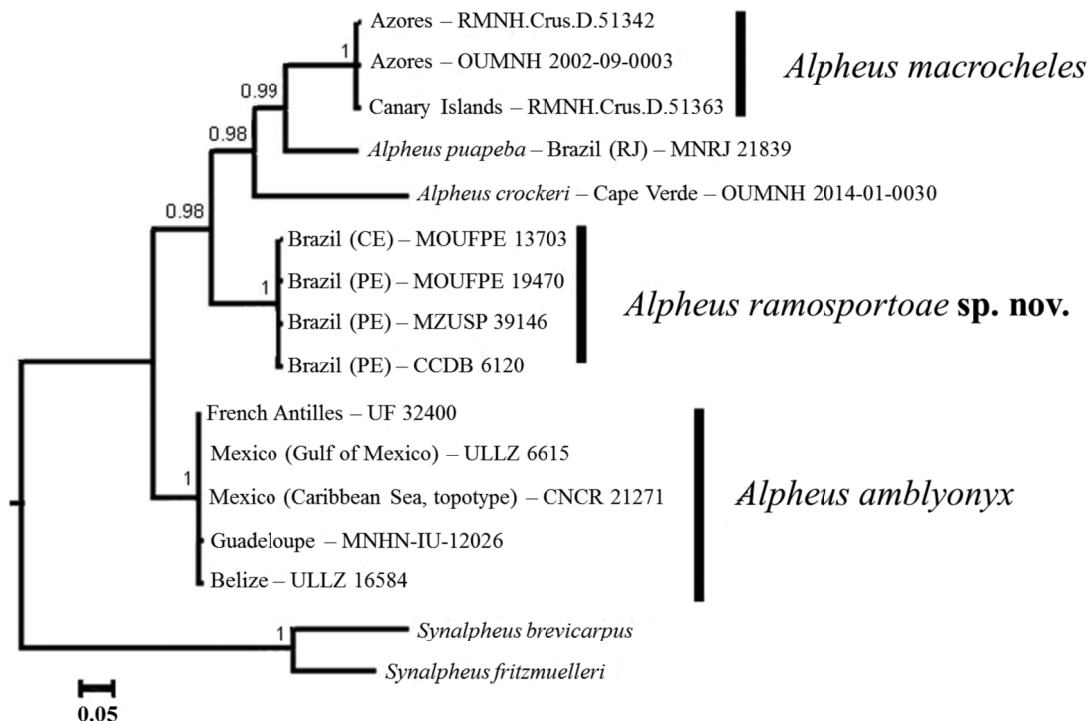


Fig. 5. Bayesian Inference Tree of the 16S gene including specimens of *Alpheus ramosportoae* sp. nov., selected species of the *A. macrocheles* complex, and *Synalpheus* C.S. Bate, 1888. Numbers close to nodes represent posterior probabilities. Abbreviations: CE = state of Ceará; PE = state of Pernambuco.

Table 2. Genetic distance matrix of the 16S gene between *Alpheus ramosportoae* sp. nov. and some selected species assigned to the *A. macrocheles* species complex, as well as *Synalpheus* C.S. Bate, 1888, built with the TPM3 model. The number of specimens used in the analysis for each taxon is presented along with the collection localities.

	1	2	3	4	5	6
1. <i>Alpheus amblyonyx</i> Chace, 1972 (5 specs, Belize, French Antilles, Guadeloupe and Mexico)	0					
2. <i>Alpheus crockeri</i> (Armstrong, 1941) (1 spec., Cape Verde)	25.1	–				
3. <i>Alpheus macrocheles</i> (Hailstone, 1835) (3 specs, Azores, Canary Islands)	21.0	21.9	0			
4. <i>Alpheus puapeba</i> Christoffersen, 1979 (1 spec., Rio de Janeiro – Brazil)	19.3	21.9	14.5	0		
5. <i>Alpheus ramosportoae</i> sp. nov. (4 specs, Recife – Brazil)	15.9	22.9	18.3	22.2	0	
6. <i>Synalpheus</i> spp. (2 specs, Gulf of Mexico and Brazil)	33.3–34.7	38.4–40.4	39.4–41.9	34.9–38.2	39.9–41.2	15.4

distal margin of the antennular peduncle (vs reaching to the distal margin of the antennular peduncle in *A. amblyonyx*) (see Table 3).

The presence of a strong crest on the extensor surface of the minor cheliped dactylus is a feature shared by *A. ramosportoae* sp. nov. and *A. macrocheles* (cf. Crosnier & Forest 1966: fig. 2C). However, *A. ramosportoae* sp. nov. differs from *A. macrocheles* by the longer rostrum, reaching well beyond mid-length of the first article of the antennular peduncle (vs only reaching it in *A. macrocheles*; cf. Soledade *et al.* 2019: fig. 1A–B); a well-developed plunger on the major cheliped dactylus (vs rudimentary and flat, with a small tooth on the proximal surface, in *A. macrocheles*; cf. Soledade *et al.* 2019: fig. 2I–J); and the presence of two well-defined teeth on the distolateral margin of the uropodal exopod (vs one acute lateral tooth and one blunt mesial lobe in *A. macrocheles*; cf. Soledade *et al.* 2019: fig. 1J) (Table 3).

The genetic analysis corroborated the separation of *A. ramosportoae* sp. nov. from both *A. amblyonyx* and *A. macrocheles*. The four specimens of *A. ramosportoae* sp. nov. included in the Bayesian analysis formed a single clade, very distinct from all the other species included. Pairwise genetic distances obtained in this analysis (15.9% between *A. ramosportoae* sp. nov. and *A. amblyonyx*; 18.3% between *A. ramosportoae* sp. nov. and *A. macrocheles*) are consistent with the values used for the separation of cryptic and pseudocryptic lineages within *Alpheus* (Mathews *et al.* 2002; Mathews 2006; Almeida *et al.* 2013, 2014).

The new species also shows marked differences in the color pattern, e.g., compared to specimens of *A. amblyonyx* from Guadeloupe and Panama, as well as specimens of *A. macrocheles* from the Mediterranean coast of Spain and Madeira (cf. Anker & De Grave 2012: fig. 4), especially in the

Table 3. Characters useful for separation between *Alpheus ramosportuae* sp. nov., *A. amblyonyx* Chace, 1972 and *A. macrocheles* (Hailstone, 1835).

Characters	<i>Alpheus amblyonyx</i> Chace, 1972	<i>Alpheus macrocheles</i> (Hailstone, 1835)	<i>Alpheus ramosportuae</i> sp. nov.
Relative length of rostrum to first article of antennular peduncle	Nearly reaching distal margin	Reaching mid-length	Reaching well beyond mid-length
Length ratio of second and third articles of antennular peduncle	Approx. 1.5	Approx. 2.0	Approx. 2.0
Size of stylocerite relative to first article of antennular peduncle	Reaching distal end	Reaching beyond distal end	Reaching distal end
Scaphocerite relative to third article of antennular peduncle	Reaching mid-length	Reaching distal end	Reaching mid-length
Distal tooth of scaphocerite relative to antennular peduncle	Reaching distal end	Distinctly exceeding	Distinctly exceeding
Distolateral margin of uropodal exopod	With one mesial tooth and one lateral tooth flanking spiniform seta	With one acute lateral tooth and one mesial lobe flanking spiniform seta	With one mesial tooth and one lateral tooth flanking spiniform seta
Strong crest on extensor margin of dactylus of the minor chela	Absent	Present	Present
Dactylus of the major chela	Tip strongly bulbous	Tip slightly bulbous, with distal extremity slightly acute in some specimens	Tip strongly bulbous
Plunger	Developed, with anterior surface distinctly angular	Rudimentary and flat, with small tooth on anterior surface	Developed, with anterior surface distinctly angular

banding pattern of the pleon. In *A. amblyonyx* and *A. macrocheles*, the pleon is uniformly reddish, not banded (cf. Anker & De Grave 2012: fig. 4A–D). In contrast, in *A. ramosportoae* sp. nov., the pleon is conspicuously banded and also has whitish blotches laterally (Fig. 4A), almost as in *A. cedrici* (cf. Anker & De Grave 2012: fig. 3). The color pattern of the major and minor chelae of *A. ramosportoae* sp. nov. somewhat resembles that of a specimen of *A. amblyonyx* from Guadeloupe in Anker & De Grave (2012). Both have conspicuous white patches and spots on the mesial surface of the palm; however, in *A. amblyonyx*, the patches / spots are sharper (better defined) and thus more conspicuous.

Most of the material previously reported as *A. macrocheles* from Brazil (e.g., Coelho & Ramos 1972; Ramos-Porto 1979; Fausto Filho 1980; Coelho *et al.* 1986; Ramos-Porto *et al.* 1996; Guterres *et al.* 2005) was not deposited in reference collections and could not be located. As mentioned above, these records lack detailed morphological accounts with illustrations and thus cannot be verified. A large part of Ramos-Porto's material (e.g., material from the Expeditions GEOMAR II-III and NORTE\ NORDESTE I-II) was located in the Museu de Oceanografia Professor Petrônio Alves Coelho and most of this material corresponds to *A. ramosportoae* sp. nov. From a total of 15 lots analyzed by Ramos-Porto (1979), only one female from Amapá (GEOMAR II 114, 12.IX.1970) was not located. The specimens of the other lots, with a few exceptions, are in good condition for analysis, including the three specimens illustrated by Ramos-Porto (1979), and matched the characteristics of the new species. Based on the absence of *A. macrocheles* in the MOUFPE collection and in other large national collections visited (MNRJ and MZUSP) and the results of our previous contribution (Soledade *et al.* 2019), it appears that *A. macrocheles* is restricted to the eastern Atlantic, including Mediterranean Sea.

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