



Morphology and molecular evidence reveal hidden diversity among snapping shrimp of the *Alpheus obesomanus* group (Decapoda: Alpheidae) with the description of a new species from Brazil

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Abstract

The snapping shrimp family Alpheidae Rafinesque, 1815 includes numerous species, most of which present controversial geographical distributions. The disjunct distribution of *Alpheus simus* Guérin-Méneville, 1856 in the western Atlantic, from Florida to the south of the Caribbean Sea and then from Rio Grande do Norte to Bahia in Brazil, suggests that Brazilian material may belong to an undescribed species. The examination of specimens previously identified as *A. simus* revealed the distinct morphology of material from Brazil, resulting in the description of a new species based on morphological and molecular evidence. The specimens were collected from fragments of fire coral at the Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil. *Alpheus coralvivo* sp. nov. belongs to the *A. obesomanus* group and is morphologically similar to *A. simus* (northwestern Atlantic) and *A. saxidomus* Holthuis, 1980 (eastern Pacific), differing mainly in the stylocerite and scaphocerite lengths and in the large gap between the cephalothorax and pleuron of the first pleonal segment. Molecular analysis using the mitochondrial cytochrome oxidase subunit I gene support the existence of the new species.

Key words: Alpheid, coral reefs, new taxon, integrative taxonomy, western Atlantic

Introduction

Species exhibiting a disjunct distribution are common in the marine realm (e.g., Rodrigues *et al.* 2017; Sales *et al.* 2017; Dudoit *et al.* 2018; Mandai *et al.* 2018; Santos *et al.* 2019; Terossi *et al.* 2022). Such distributions can arise due to factors such as poor taxonomic resolution, misinterpretation of distributional ranges, and limited sampling efforts in specific areas. In essence, when this distributional pattern occurs, new taxa may be implicated (Tavares 2011; Almeida *et al.* 2012). Indeed, upon comparing specimens from populations in the southwestern and northwestern Atlantic, new species were repeatedly identified in the former region (Tavares 2011).

Gaps in the distribution of crustacean species have been used to test the reality of their distribution (e.g., Morrone & Lopretto 1994; Santos & D'Incao 2004; Jesse *et al.* 2009; Santos *et al.* 2019). The use of integrative taxonomy in caridean shrimps, for instance, has helped to reveal an unknown biodiversity and elucidated the actual limited distribution of species previously considered widespread, which were in some cases reported from different ocean basins (e.g., Williams *et al.* 2001; Anker & Pachelles 2013; Hurt *et al.* 2013; Salgado-Barragán *et al.* 2014, 2017; França *et al.* 2020; Anker & Baeza 2021; Mantelatto *et al.* 2023). In numerous instances, these studies employ integrative taxonomy including molecular data. The cytochrome oxidase subunit I mitochondrial gene (COI), a rapidly evolving marker, is one of the genes used to assist in the separation of taxa that have not been identified based on morphology only (Tourinho *et al.* 2012; Carvalho-Batista *et al.* 2019; Anker & Baeza 2021).

The family Alpheidae Rafinesque, 1815 comprises more than 600 shrimp species (De Grave & Fransen 2011). With 327 valid species (Poore & Ah Yong 2023), *Alpheus* Fabricius, 1798 is the largest genus of alpheid shrimp. Species of *Alpheus* are important components of the benthic fauna in tropical and subtropical marine habitats and occur from the intertidal zone to great depths (Chace 1988; Anker *et al.* 2006). They can be found under rocks, in dead coral crevices (Santos *et al.* 2012), sponges (Anker *et al.* 2012; Anker & Pachelles 2014), and in burrows in soft substrates such as mangroves swamps and estuaries (Crosnier & Forest 1966).

The western Atlantic *Alpheus simus* Guérin-Méneville, 1856 (type locality Cuba) belongs to the *Alpheus obesomanus* group, which currently comprises 11 species: *A. chamorro* Banner, 1956; *A. idiocheles* Coutière, 1905; *A. malleodigitus* (Spence Bate, 1888); *A. microscaphis* (Banner, 1959); *A. microstylus* (Spence Bate, 1888); *A. nobili* Banner & Banner, 1966; *A. obesomanus* Dana, 1852; *A. perplexus* Banner, 1956; *A. samoa* Banner & Banner, 1966; *A. saxidomus* Holthuis, 1980; and *A. simus*. These species share the following morphological characteristics (Anker 2001): absence of a rostrum and orbital teeth; ocular peduncles devoid of processes; short antennae; major chela inflated, presenting oval or cylindrical cross-section, with hammer-shaped dactylus; minor cheliped never with "balaeniceps" setae; second pereopods often elongated and asymmetrical.

Alpheus simus lives endolithically in cavities of living and dead coral rocks (Grajal & Laughlin 1984; Werding 1990; Santos *et al.* 2012). This species was reported in Florida, Yucatan, Antilles, Central America, northern South America, and Brazil (states of Rio Grande do Norte and Bahia) (Chace 1972; Christoffersen 1979 as *Thunor rathbunae* (Schmitt, 1924)—junior subjective synonym of *A. simus*, see Bezerra & Almeida 2008; De Grave & Fransen 2011; Santos *et al.* 2012). However, the species' distribution has a substantial latitudinal gap that includes the North Brazil Shelf province (*sensu* Spalding *et al.* 2007), from Curaçao to Rio Grande do Norte (Brazil) (approximately 16°S latitude).

The distributional gap of *A. simus* and morphological evidence from previous and new collected specimens led us to test the hypothesis that material from northern and southern portions of its distribution range belong to a single species using morphological and molecular data. This culminated in the discovery of a new species from Brazil, which is herein described and illustrated.

Materials and methods

Sampling and morphological analyses

The material analyzed is deposited in the following collections: Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); Museu de Oceanografia Professor Petrônio Alves Coelho, Pernambuco, Brazil (MOUFPE); Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil (CCDB); Naturalis Biodiversity Centre, Leiden, The Netherlands (RMNH); National Museum of Natural History, Smithsonian Institution, USA (USNM); Muséum National d'Histoire Naturelle, France (MNHN); and Museo de Zoología de la Universidad de Costa Rica, Costa Rica (MZUCR).

Additional material was collected in April 2012 and May 2013 at the Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil from fragments of the fire coral *Millepora alcicornis* Linnaeus, 1758. Collections were performed under MMA/IBAMA/SISBIO authorization N°. 24408-1. Samples were taken from the bottom of a reef bank (depths of 1–12 m) by scuba diving and using a hammer and chisel to remove the fragments attached to the colonies or by collecting fragments of dead coral rubble that were at the bottom. The samples were then individually

wrapped in tissue bags to prevent organisms from escaping. In the laboratory the fragments were carefully broken into small pieces and searched for shrimps with an endolithic habit. The obtained specimens were anesthetized on ice, photographed, and fixed in 70% ethanol.

Drawings were made under a dissecting stereomicroscope equipped with a camera lucida, and the final illustrations were prepared using Adobe Illustrator CS6[®]. Abbreviation: carapace length (CL; measured dorsally, from sinus situated between the ocular hoods to posterior margin).

Genetic analyses

Protocols proposed by Mantelatto *et al.* (2006, 2007) were used with appropriate modifications (adjustments in the concentration of DNA sample and temperature of annealing) for the specific materials. For DNA extraction, the pleonal tissue was placed in a 1.5 ml tube and incubated for 24 h in 600 µl lysis buffer and 10 µl Proteinase K (20 mg/ml) at 55°C in a dry bath. Then, the samples were removed from the dry bath and placed on ice for 10 min. The proteins were then separated by adding 200 µl of ammonium acetate (7.5 M) followed by centrifugation. DNA was precipitated by adding 600 µl cold isopropanol (-20°C) followed by centrifugation; after 48 h of resting at -20°C, the resulting pellet was washed with 15 µl of 70% ethanol, dried, and resuspended in 20 µl TE buffer. The DNA concentrations in the samples were then quantified using a Nanodrop 2000[®] Spectrophotometer.

Polymerase chain reaction (PCR) targeting the mitochondrial cytochrome oxidase subunit I (COI) gene (Sambrook *et al.* 1989) was performed using the primers COL6B2 (5'-ACAAATCATAAAGATATYGG-3') and COH6 (5'-TADACTTCDGGRTGDCCAAARAAYCA-3') (Mantelatto *et al.* 2016; Schubart & Huber 2006, respectively) in a 25 µl volume reaction containing distilled and deionized H₂O, PCR Buffer (10X), MgCl₂ (25 mM), betaine (5 M), DNTPs, primers, *Thermus aquaticus* polymerase, and the DNA previously extracted (50 ng) in a Veriti Thermal Cycler[®] (Applied Biosystems) with specific thermal cycles for the primer set. The PCR results were observed in 1.5% agarose gel electrophoresis stained with Gel Red[™] and in a UVP Transilluminator M20 UV. The PCR products were purified using a SureClean[®] Purification Kit, and a Big Dye[®] Terminator Cycle Sequencing (Applied Biosystems) kit was used in the sequencing reaction. Sequencing was carried out in an ABI 3100 Genetic Analyzer[®] automatic sequencer of the Departamento de Tecnologia da Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal, Universidade Estadual Paulista (UNESP).

All sequences were confirmed by sequencing both strands. Sequences were edited by eye and the consensus sequences were obtained using BioEdit v7.0.9.0 (Hall 1999). All consensus sequences were confirmed using BLASTn from the NCBI database (<http://blast.ncbi.nlm.nih.gov/blast.cgi>). Some sequences of *A. simus* and other congeneric species of the *obesomanus* group were obtained from GenBank and Barcode of Life Data System v4 (BOLD) for comparison (Table 1). Sequences of *Synalpheus* Spence Bate, 1888 retrieved from GenBank were used as the outgroup (Table 1).

TABLE 1. List of specimens of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888 used in the genetic analyses with cytochrome oxidase subunit I gene. Abbreviations: Atl, Atlantic Ocean; BA, Bahia; Pac, Pacific Ocean; SP, São Paulo.

Species	Locality	Gene Bank or Bold number	Reference
<i>Alpheus armatus</i> Rathbun, 1901	Caribbean Sea	KF131481	Hurt <i>et al.</i> (2013)
<i>Alpheus coralvivo</i> sp. nov.	Brazil (BA)	MT483210–MT483212	Present study
<i>Alpheus formosus</i> Gibbes, 1850	USA	KP254069	Leray & Knowlton (2015)

.....continued on the next page

TABLE 1. (Continued)

Species	Locality	Gene Bank or Bold number	Reference
<i>Alpheus idiocheles</i> Coutière, 1905	French Polynesia	MBMIA293-06 MBMIA294-06	No reference
<i>Alpheus immaculatus</i> Knowlton & Keller, 1983	Caribbean Sea	KF131503	Hurt <i>et al.</i> (2013)
<i>Alpheus lottini</i> Guérin-Méneville, 1838	New Caledonia	KY746843 KY746844	Rouzé <i>et al.</i> (2017)
<i>Alpheus malleator</i> Dana, 1852	Panama (Atl)	FJ013923	Hurt <i>et al.</i> (2009)
<i>Alpheus malleodigitus</i> (Spence Bate, 1888)	French Polynesia	MBMIA627-06 MBMIA628-06	No reference
<i>Alpheus obesomanus</i> Dana, 1852	French Polynesia	MBMIA360-06 MBMIA361-06 MBMIA402-06	No reference
<i>Alpheus polystictus</i> Knowlton & Keller, 1985	Caribbean Sea	KF131508	Hurt <i>et al.</i> (2013)
<i>Alpheus roquensis</i> Knowlton & Keller, 1985	Venezuela	KF131529 KF131530	Hurt <i>et al.</i> (2013)
<i>Alpheus saxidomus</i> Holthuis, 1980	Panama (Pac)	FJ013929–FJ013933	Hurt <i>et al.</i> (2009)
<i>Alpheus simus</i> Guérin-Méneville, 1855	Panama (Atl)	FJ013945 FJ013946 FJ013948	Hurt <i>et al.</i> (2009)
<i>Synalpheus fritzmuelleri</i> Coutière, 1909	Jamaica	KJ595081	Hultgren <i>et al.</i> (2014)
<i>Synalpheus townsendi</i> Coutière, 1909	Brazil (SP)	KU313018	Almeida <i>et al.</i> (2018)

Sequence alignment was performed using the Multiple Sequence Comparison by Log-Expectation (MUSCLE) (Edgar 2004), available on the platform Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller *et al.* 2010). The substitution model best fitted to the obtained data was calculated using jModelTest (Darriba *et al.* 2012) implemented in the CIPRES platform, using the Bayesian information criterion (BIC). MrBayes v3.2.6 (Ronquist *et al.* 2012) implemented in CIPRES was used in the Bayesian Inference analysis with the parameters obtained using jModelTest. In the analysis, one tree was sampled for every 1,000 generations of 20,000,000 generations, starting with a random tree. Four independent chains were performed, and their convergences were analyzed using Tracer 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 1.8.4 (implemented in the BEAST package, Drummond *et al.* 2012). Posterior probability values greater than 80% were reported. A matrix of genetic divergence was obtained using the Kimura 2-parameter model (K2P) (Kimura 1980) in MEGA v6 (Tamura *et al.* 2013). All sequences obtained in this study were deposited in GenBank.

Results

SYSTEMATICS

Family Alpheidae Rafinesque, 1815

Genus *Alpheus* Fabricius, 1798

Alpheus coralvivo sp. nov.

(Figs. 1–3)

Thunor rathbunae—Christoffersen 1979: 355 (? possibly *A. coralvivo*; see discussion)

Alpheus simus—Bezerra & Almeida 2008: 1; Santos *et al.* 2012: 154, fig. 4B; Soledade & Almeida 2013: 105, fig. 6F; Almeida *et al.* 2016: 66 (not *A. simus* Guérin-Méneville, 1855)

Type material. Holotype: female (CL 7.3 mm), Brazil, Bahia, Porto Seguro, Parque Municipal Marinho Recife de Fora, on dead portions of *Millepora alcicornis* colony, 13.IV.2012, colls. G.M. Reuss Strenzel, G.O. Soledade, P.S. Santos, L.M. Fernandes, I. Matos, MZUSP 36753 (genetic data MT483210). **Paratypes:** *Rio Grande do Norte*—1 male (CL 2.8 mm, obs. carapace partially damaged), Maxaranguape, Parrachos de Maracajaú, 3–4 m, on *M. alcicornis* colony, 12.II.2004, coll. T.M. Garcia, MOUFPE 20048 (previously UESC 995). *Bahia*—1 female (CL 6.1 mm), same data as holotype, MZUSP 36754; 1 female (CL 6.5 mm), same data as holotype, MOUFPE 18747 (genetic data MT483211); 1 female (CL 6.9 mm), Porto Seguro, Parque Municipal Marinho Recife de Fora, on living portions of *M. alcicornis* colony, 06.V.2013, colls. G.M. Reuss Strenzel, G.O. Soledade, P.S. Santos, L.M. Fernandes, J.C. Viaggi, MOUFPE 18748; 1 male (CL 4.2 mm), Porto Seguro, Parque Municipal Marinho Recife de Fora, on coral rubble, 06.V.2013, colls. G.M. Reuss Strenzel, G.O. Soledade, P.S. Santos, L.M. Fernandes, J.C. Viaggi, MOUFPE 18749 (genetic data MT483212); 1 male (CL 3.9 mm), 1 female (CL 6.6 mm), Santa Cruz Cabralia, Praia de Coroa Vermelha, salinity 36, on dead portions of *M. alcicornis* colony, 22.III.2011, colls. P.S. Santos, G.O. Soledade, A.O. Almeida, CCDB 7080 (previously UESC 1411); 1 female (CL 5.6 mm), Porto Seguro, Praia do Mutá, salinity 40, on dead portions of *M. alcicornis* colony, 25.IX.2011, colls. P.S. Santos, G.O. Soledade, A.G.L.M. Pedra, MOUFPE 20047 (previously UESC 1503); 1 male (CL 4.4 mm), 1 ovigerous female (CL not provided, carapace damaged), Abrolhos Archipelago, Parcel de Paredes, 1982, MNRJ 15400 (See Appendix 1 for a list of comparative material).

Diagnosis. Rostrum and orbital teeth absent. Antennular stylocerite shorter than half length of visible part of first article of antennular peduncle. Antenna unarmed. Scaphocerite, in females, short, rounded distally, reaching distal margin of carapocerite; in males, distally acute, overreaching distal margin of carapocerite. Large gap between cephalothorax and pleuron of first pleonal segment.

Description. Based on female holotype (MZUSP 36753) and male paratype (MOUFPE 18749). Carapace smooth, dorsally convex, unarmed; rostrum absent; ocular hoods dorsally inflated, unarmed, margin between two orbital hoods slightly deep. Eyes well pigmented, completely covered by ocular hoods in dorsal and lateral views (Fig. 1A–C).

Pleonal segments smooth; posteroventral margin of pleura 1–5 rounded, sixth pleuron semi-triangular, without articulated plate; large gap between cephalothorax and pleura of first pleonal segment; cardiac notch well-developed (Fig. 1D). Telson (Fig. 1E–F) tapering distally, proximal region about 4.2 times wider than distal; dorsal spiniform setae absent; dorsal surface of telson bearing one pair of exceedingly spiniform setae, placed slightly closer to lateral margin of telson than to its midline; distal margin of telson narrow and straight, posterolateral angle each with three pairs of spiniform setae; anal tubercles well-developed. Uropods (Fig. 1E) with bifid protopods, each lobe ending in rounded tip; exopod slightly longer than endopod; lateral margin of exopod slightly convex proximally and straight distally; diaeresis absent; distolateral margin of exopod with one lateral tooth and one dark-colored spiniform seta overreaching distal margin of exopod, noticeably longer than lateral tooth.

Second antennular article approx. 4 times longer than first and third articles; stylocerite short and rounded distally, not reaching half-length of visible part of first article of antennular peduncle. Antenna unarmed; carapocerite shorter than half length of second article of antennular peduncle; scaphocerite in female short, rounded distally, reaching proximal margin of carapocerite; scaphocerite, in male, elongate, distally acute, overreaching proximal margin of carapocerite; blade absent in both sexes (Fig. 1A–C).

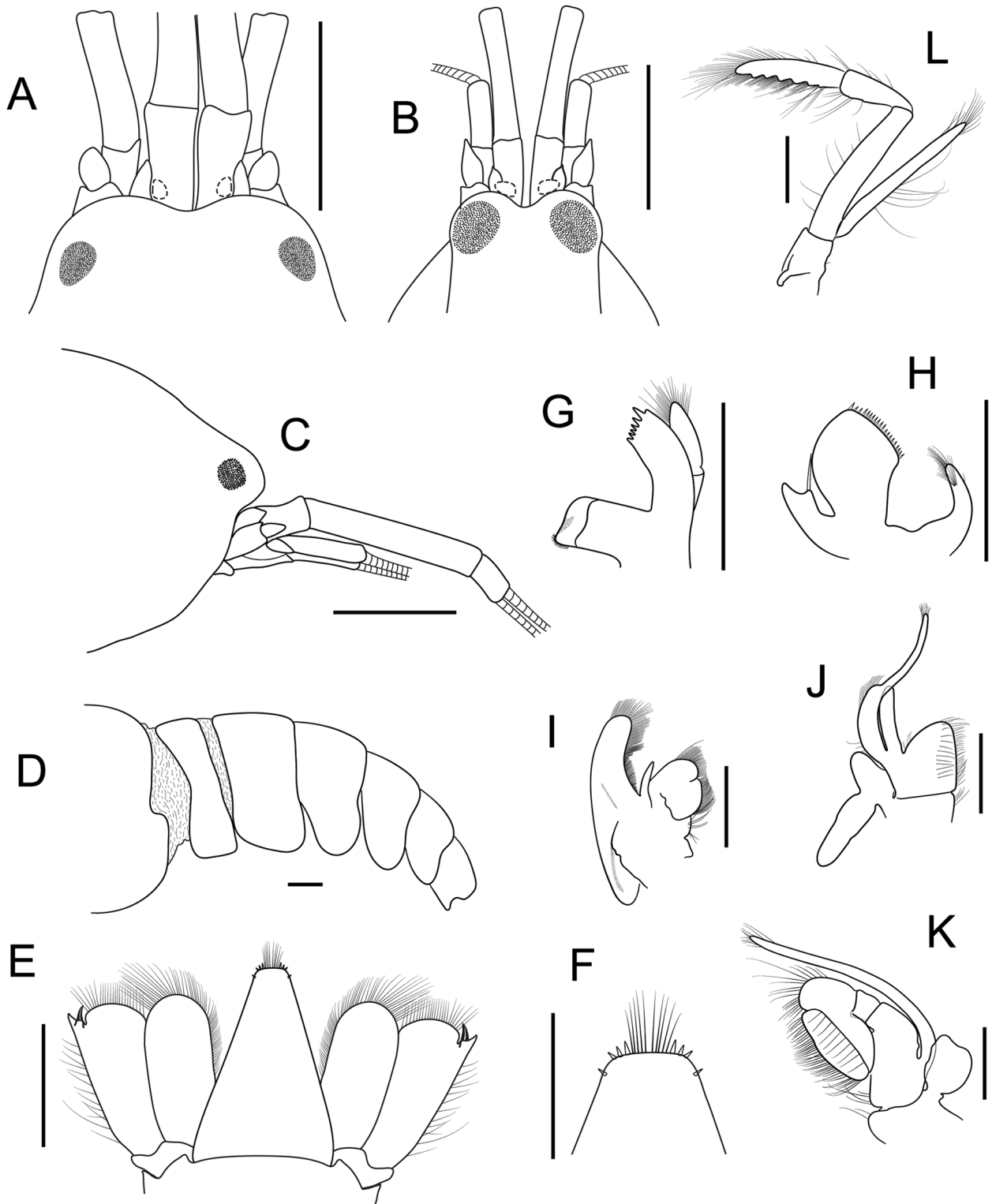


FIGURE 1. *Alpheus coralvivo* sp. nov., Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil: A, C–F, female holotype (MZUSP 36753); B, male paratype (MOUFPE 18749); G–L, female paratype (MZUSP 36754, dissected); (A) frontal region and cephalic appendages, dorsal view; (B) same, male dorsal view; (C) frontal region and cephalic appendages, lateral view; (D) posterior region of carapace and pleon, lateral view, appendages omitted; (E) telson and uropods, dorsal view; (F) telson, detail of distal margin; (G) mandible, lateral view; (H) first maxilla, mesial view; (I) second maxilla, mesial view; (J) first maxilliped, mesial view; (K) second maxilliped, lateral view; (L) third maxilliped, lateral view. Scale bars = 1 mm.

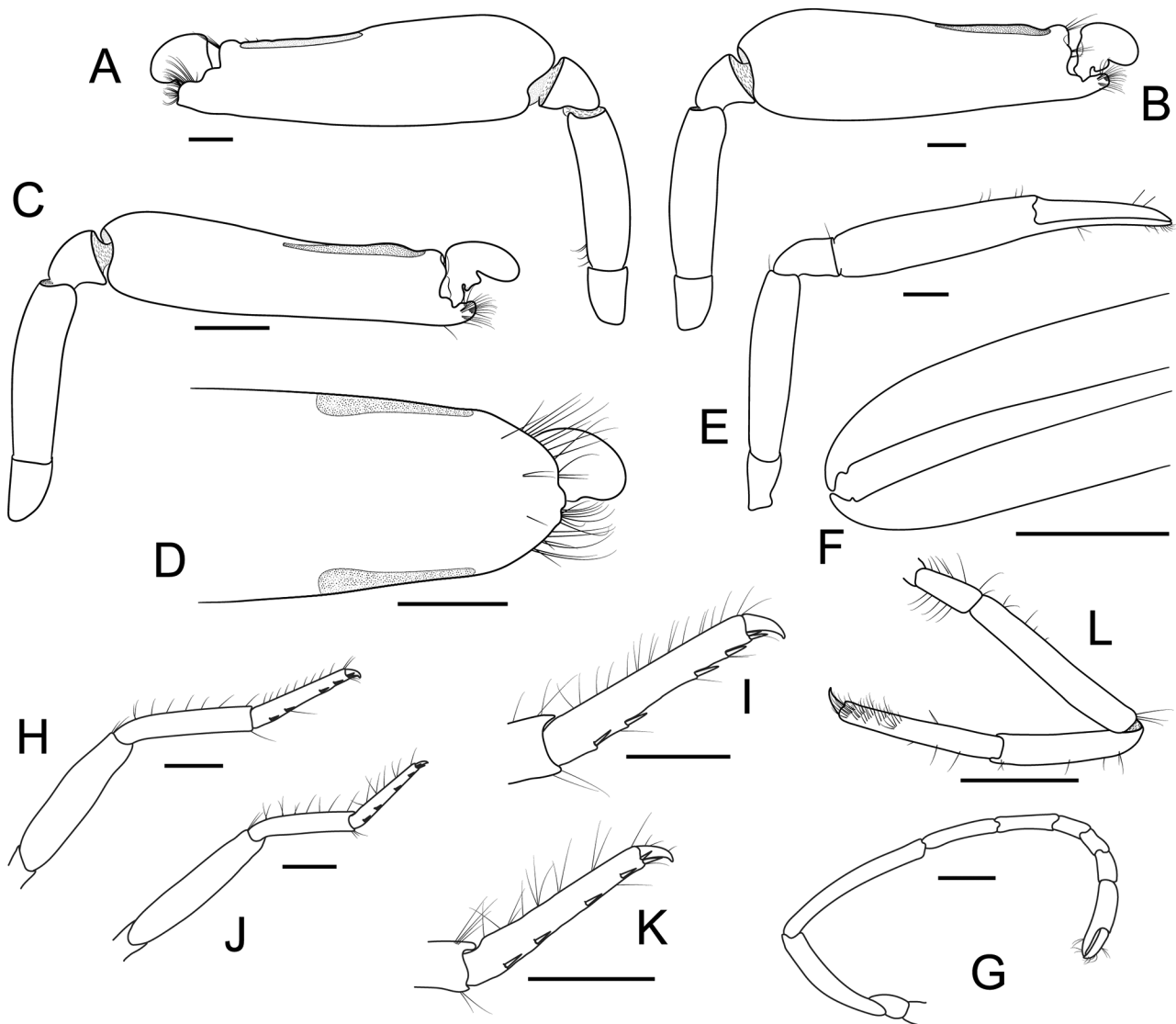


FIGURE 2. *Alpheus coralvivo* sp. nov., Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil: A, B, D–J, female holotype (MZUSP 36753); C, male paratype (MOUFPE 18749). (A) major chela, mesial view; (B) same, lateral view (C) male major chela, lateral view; (D) detail of major chela, ventral view; (E) minor chela, lateral view; (F) minor chela, detail of tip of fingers, ventral view; (G) second pereopod, lateral view; (H) third pereopod, lateral view; (I) same, detail of dactylus and propodus; (J) fourth pereopod, lateral view; (K) same, detail of dactylus and propodus; (L) fifth pereopod, lateral view. Scale bars = 1 mm.

Mandible (Fig. 1G) with 2-jointed palp; incisor process robust, with 7 distinct teeth, second anterior tooth conspicuously wider and longer than others; molar process flat, with semicircular rows of short setae. First maxilla (Fig. 1H) with palp deeply bilobed, inferior lobe bearing 1 slender seta, superior lobe not setose. Second maxilla (Fig. 1I) palp well-developed, slender; with upper lacinia cleft, lower lacinia with single lobe; scaphognathite well-developed, with setae around distal and internal edge, tips rounded and lateral margin convex. First maxilliped (Fig. 1J) palp approx. 3.5 times longer than wide, tip truncated; two laciniae separated by distinct cleft, exopod well-developed with long flagellum, exopodal lobe poorly developed; epipod about 3 times as long as wide. Second maxilliped (Fig. 1K) exopod well-developed, flagellum 3.3 times longer than epipod; epipod about 1.6 times as long as wide. Third maxilliped (Fig. 1L) slender, overreaching half-length of second antennal article; ultimate article 1.6 times longer than penultimate, with many transverse rows of stiff setae; antepenultimate article 2.2 times longer than penultimate; exopod overreaching distal end of penultimate article, ending in with long setae; epipod present. Pleurobranch and epipod present from pereopods 1–4.

First pereopods very unequal. Major female cheliped (Fig. 2A, B) ischium short, stout and unarmed; carpus unarmed, cup-shaped, short, as long as ischium, 5.8 and 6.4 times palm length in female and male, respectively, 2.4 times merus length; cheliped long, approx. 5.7 times as long as dactylus and 3.2 times as long as maximum height; palm gradually narrowing anteriorly; shallow furrow on dorsal surface, mesial and lateral view smooth, with deep furrow on distal third of ventrolateral margins, with distoventral lobe, sometimes denticle (Fig. 2D); dactylus strongly bent and hammer-shaped, ending in blunt rounded apex directed down over tip of pollex; pollex half dactylus length, with numerous long and stiff setae on distal margin; cheliped articles free of spines and teeth (Fig. 2A, B). Major male cheliped (Fig. 2C) similar in shape, but slenderer than female; palm approx. 4.8 times as long as dactylus and 3.7 times as long as maximum height.

Minor cheliped (Fig. 2E) ischium short, approx. 1.2 times carpus length; carpus unarmed, cup-shaped, approx. 3 times merus and approx 3.4 times palm length; palm cylindrical, without teeth or grooves, approx. 4 times as long as maximum height; cheliped with slender fingers, approx. 1.5 times palm length; fingertips curved, obscurely biunguiculate (Fig. 2F); "balaeniceps" setae absent. Articles free of teeth or spines. Second pereopod slender (Fig. 2G), left conspicuously longer than right; ischium short, approx. 3 times merus length; carpus five-segmented, approx. 4 times longer than chela; segment ratio (proximal to distal): right 2.8: 2.1: 1.2: 1: 1.1 and left 2.3: 2.3: 1.1: 1: 1; fingers approx. 1.3 times palm length.

Third (Fig. 2H) and fourth (Fig. 2J) pereopods long, similar in shape and length; ischium, merus and carpus unarmed; merus approx. 1.5 times propodus length, ventrodiscal tooth absent; carpus approx. 1.3 times propodus length; propodus approx. 5 times dactylus length, with 4 strong spiniform setae along ventral margin and one pair of spiniform setae at propodo-dactylar articulation; dactylus slender and simple (Fig. 2I, K). Fifth pereopod (Fig. 2L) shorter than third and fourth pereopods; merus 1.1 times propodus length; ischium, merus and carpus unarmed; propodus about 6 times longer than dactylus; with one ventral spiniform setae; distolateral surface with cleaning brush consisting of transverse rows of setae; dactylus similar in shape to that of third and fourth pereopods; carpus approx. 1.2 times propodus length.

Pleopods with sparse setae on lateral margin of protopod; endopod and exopod with setose edges; male first pleopod reduced. Second pleopod of male with *appendix masculina* overreaching distal margin of *appendix interna*.

Morphological variation. Scaphocerite in females presenting two forms: (1) rounded distally, reaching about half length of first article of antennular peduncle, with very reduced blade; (2) rounded distally, shorter than half length of first article of antennular peduncle (Fig. 1A). Scaphocerite elongate in males, distally acute, slightly overreaching distal margin of first article of antennular peduncle (Fig. 1B) with blade little developed. Number of ventral spiniform setae on propodus of third and fourth pereopods ranging from 4 to 6 (usually 4). Number of distolateral spiniform setae on uropodal exopod ranging from 1 to 2 (usually 1). Female with smaller and more widely set eyes than male.

Color pattern. Body semi-transparent; some specimens with reddish chromatophores, mainly on cephalothorax (Fig. 3A); palm, distal margin of chelipeds and second pereopod pale yellowish; second pereopod also showing dark yellow coloration on joints (Fig. 3B). Distolateral spiniform setae of the uropodal exopod dark-brown, black or not pigmented.

Type locality. Brazil, Bahia, Porto Seguro, Parque Municipal Marinho do Recife de Fora, 16°24'07.0"S 38°58'55.2"W.

Distribution. Brazil: Rio Grande do Norte and Bahia.

Ecology. In shallow subtidal reef pools; in crevices on living and dead portions of fire coral (*Millepora alcicornis*) colonies and coral rubble (Fig. 3A, B); depth range 1–12 m.

Etymology. The name refers to the 'Projeto Coral Vivo', a project which aims at the conservation and social and environmental sustainability of coral reefs; used as a noun in apposition.

Genetic analyses. The best-fit substitution model selected using the BIC was GTR+I+G, assuming the nucleotide frequencies A = 0.3622, C = 0.2670, G = 0.0996, and T = 0.2712; and the replacement rates AC = 0.0899, AG = 6.8412, AT = 0.2764, CG = 0.3997, CT = 3.6794, and GT = 1. The substitution model variable sites followed a gamma distribution with shape parameter = 0.5590 and invariable sites = 0.4880.

The analysis included species of the *A. obesomanus* group that are morphologically similar to the new species: *A. idiocheles*, *A. malleodigitus*, *A. obesomanus*, *A. saxidomus*, and *A. simus*. The topology obtained in the Bayesian Inference analysis (Fig. 4) clearly separates *A. coralvivo* **sp. nov.** specimens from the other analyzed species and

indicate a close relation of the new species with *A. simus* and *A. saxidomus*. The genetic distance among specimens of the new species was null. The species of *Alpheus* with the lowest genetic distance values compared to *A. coralvivo* sp. nov. were *A. saxidomus* (11.4–12.4%) and *A. simus* (12.9–14.6%), whereas the species with the highest genetic distance values was *A. obesomanus* (21.7–23.6%).

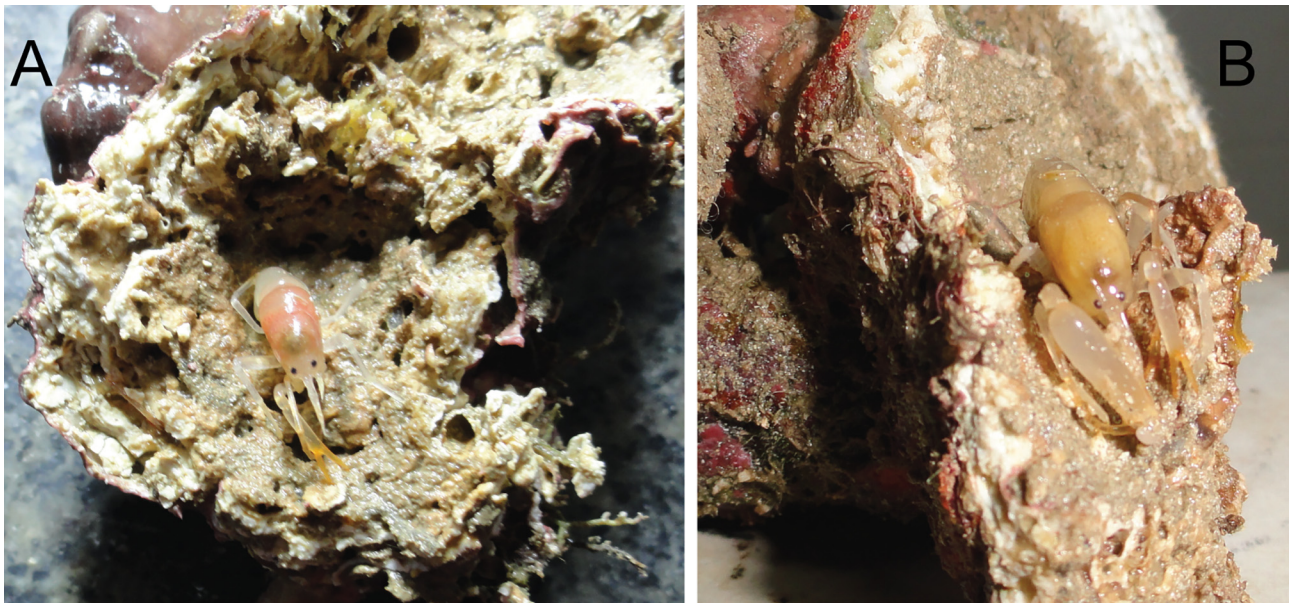


FIGURE 3. *Alpheus coralvivo* sp. nov., Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil: (A, B) specimens retrieved from a dead fragment of a *Millepora alcicornis* colony evidencing color pattern. Photographs: P.S. Santos.

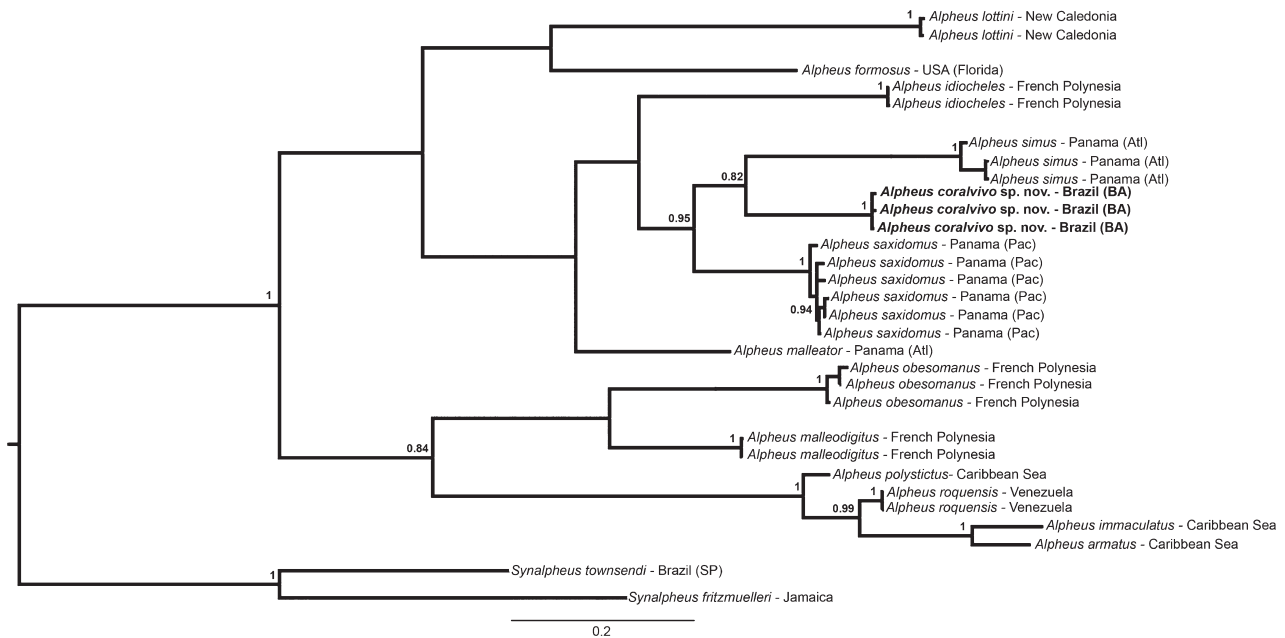


FIGURE 4. Phylogenetic tree of species of the *obesomanus* group including *Alpheus coralvivo* sp. nov., obtained using Bayesian Inference analysis and cytochrome oxidase subunit I. Numbers indicate the support values for posterior probabilities; values < 0.80 are not showed. Abbreviations: Atl, Atlantic Ocean; BA, Bahia; Pac, Pacific Ocean; SP, São Paulo.

Discussion

The molecular analysis based on the COI gene supported the establishment of the new species (Fig. 4). *Alpheus coralvivo* **sp. nov.** formed a well-supported clade in the phylogenetic tree, distinctly separated from its congeners belonging to the *A. obesomanus* group (*A. idiocheles*, *A. malleodigitus*, *A. obesomanus*, *A. saxidomus*, and *A. simus*). Previous studies have shown that the transisthmian *A. simus* from the Caribbean Sea and *A. saxidomus* from the Pacific coast are sister species (Knowlton *et al.* 1993; Knowlton & Weigt 1998; Williams *et al.* 2001). However, in our analysis, *A. saxidomus* was recovered as sister species to the clade formed by *A. coralvivo* **sp. nov.** and *A. simus*. Our results emphasize how COI gene is very valuable as one of the molecular markers of useful evidence to support discovering of new species (e.g., Anker *et al.* 2008; Hurt *et al.* 2009; Silva *et al.* 2011; Hultgren *et al.* 2014; Jamaluddin *et al.* 2019).

Although *A. coralvivo* **sp. nov.** (from northeastern Brazil), *A. simus* (south Florida to Caribbean Sea), and *A. saxidomus* (eastern Pacific), are superficially similar, the analysis of 54 morphological characters confirmed these three species are different from each other (Table 2). *Alpheus coralvivo* **sp. nov.** differs from *A. simus* and *A. saxidomus* by the narrow and elongated anterior part of the epipod of the first maxilliped, which is approximately three times as long as broad (vs. approximately twice as long as broad in *A. simus* and approximately 2.5 times in *A. saxidomus*); the scaphocerite reaches or is slightly shorter than half the length of the visible part of the first article of antennular peduncle and the blade, if present, is reduced (vs. scaphocerite elongate, reaching half the length of the second article of the antennular peduncle and a present blade in *A. simus* and *A. saxidomus*); and a large gap between the posterolateral margin of the carapace and the pleuron of the first pleonal segment (vs. absence of gap in *A. simus* and absence or presence of a narrow gap in *A. saxidomus*). Additionally, *A. coralvivo* **sp. nov.** differs from *A. saxidomus* by having three pairs of posterolateral spiniform setae on the telson (vs. two pairs in *A. saxidomus*) and by the absence of spiniform setae on the dorsal surface of the telson (vs. two pairs in *A. saxidomus*). The new species shares spiniform setae on the propodus of the fifth pereopod with *A. saxidomus* and the absence of diaeresis on the exopod of the uropod with *A. simus*. No sexual dimorphism was found in spiniform setae on the uropodal exopod as observed in *A. saxidomus* (males with shorter and broader setae than females) (see Holthuis 1980).

The material identified and illustrated as *A. simus* from Parrachos de Maracajaú, Rio Grande do Norte, by Bezerra & Almeida (2008) and the material from southern Bahia (Santa Cruz Cabrália and Porto Seguro) by Santos *et al.* (2012) were herein analyzed and defined as belonging to *A. coralvivo* **sp. nov.**

Alpheus simus was previously assigned to *Thunor* Armstrong, 1949 (as *T. rathbunae*—formerly described as *Crangon rathbunae* by Schmitt 1924, a junior subjective synonym of *A. simus*—or *T. simus*). Holthuis (1980) revised the synonymy of *A. simus* and compared it to *A. saxidomus*. The validity of *Thunor* was questioned by Holthuis (1980) and Williams *et al.* (2001). The latter authors recovered *Thunor* (represented by *A. simus* and *A. saxidomus*) nested within *Alpheus*, making *Alpheus* paraphyletic. Therefore, *Thunor* is not currently supported as a distinct group of alpheid shrimps. Based on this taxonomic history and on the collection site (Brazil, Bahia, Abrolhos Archipelago, R/V "Calypso", 1961, St. 85, between Santa Barbara Island and Siriba, 2–5 m, on sand and calcareous algae bottoms), the material reported as *Thunor rathbunae* by Christoffersen (1979) very likely belongs to *A. coralvivo* **sp. nov.**

Zoogeography

The Caribbean Sea is a remarkable ecoregion in terms of endemism of marine fauna and is one of the main biodiversity hotspots under threat (Roberts *et al.* 2002). The vicariant phenomenon resulting from the GAARlandia land-bridge, which putatively closed the communication between the Caribbean Sea and the North Brazil Shelf province, is the most well-supported hypothesis explaining the diversification of the marine species of the Caribbean Sea (Iturralde-Vinent & MacPhee 1999; Ali & Hedges 2021). The isolation of *A. simus* in the Caribbean Sea may have resulted from this vicariance event, as is indicated by the particular oceanographic conditions in the North Brazil Shelf province (Spalding *et al.* 2007) such as the soft substrate and low water salinity (Coelho & Ramos 1972) influenced by the Orinoco, Tocantins, and Amazonas Rivers Basins. These features have been suggested as barriers to the dispersion of different groups of decapods (Mandai *et al.* 2018; Buranelli & Mantelatto 2019; Peres & Mantelatto 2023). The freshwater effluent of the rivers in the Guyana region cover an area of approximately 2700 km and have a high

TABLE 2. Characters used to differentiate *Alpheus coralvivo* **sp. nov.** from the morphologically similar *Alpheus* Fabricius, 1798 species. *Mostly based on the comparative material cited in Appendix 1 and **based on the comparative material, illustrations, and description provided by Holthuis (1980).

Characters/Species	<i>Alpheus coralvivo</i> sp. nov.	<i>Alpheus simus</i> *	<i>Alpheus saxidomus</i> **
Rostrum	Absent	Absent	Absent or vestigial
Relative length of the second article of antennular peduncle	Approx. 4 times as long as visible part of first article	Around 3 times as long as visible part of first article	Approx. 2.5 times as long as visible part of first article
Propodus spines (excluding distal pair)	4–6	3–4	5–6
Shape of distolateral spiniform seta of uropodal exopod	Slender	Slender	Stout
Colour of distolateral spiniform seta uropodal exopod	Dark brown, black or not pigmented	Not pigmented	Dark brown or black
Diaeresis	Absent	Absent	Present
Depth	1–12 m	2–146 m	2–12 m
Distribution	Northwestern Brazil (Rio Grande do Norte and Bahia)	South Florida to Caribbean Sea	Eastern Pacific (Costa Rica, Panama south to Colombia and Galapagos)

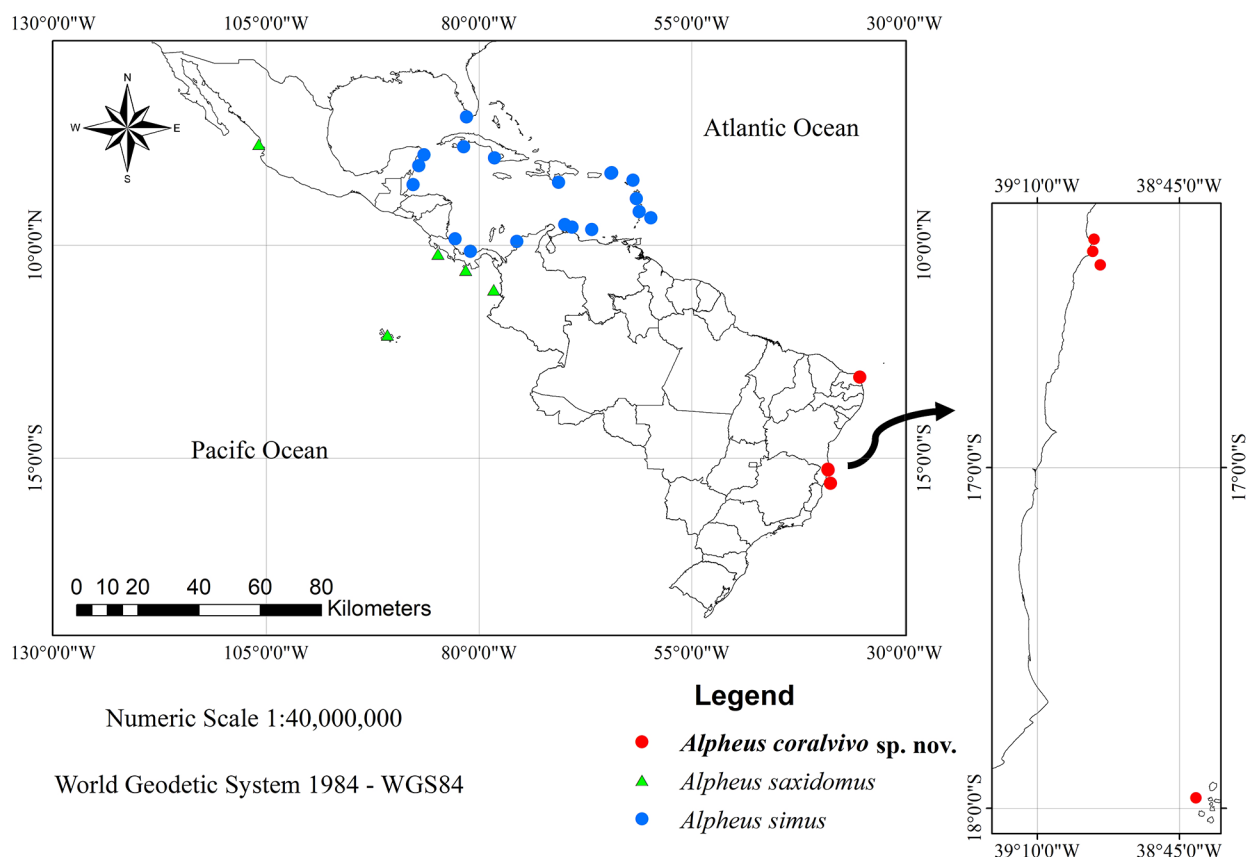


FIGURE 5. Currently known distribution of the shrimp species *Alpheus coralvivo* **sp. nov.**, *A. saxidomus* (Holthuis, 1980), and *A. simus* Guérin-Méneville, 1856 based on the material examined and literature records. Created by L.A. Nascimento.

volume that affects the salinity of the coastal zone (Collette & Rützler 1977). Despite the extensive (~9500 km²) hard-bottom mosaic extending from French Guiana and the *Millepora* cf. *alcicornis* coral and dead corals from the mouth of the Amazon River (Moura *et al.* 2016), abiotic factors such as sediment type, sedimentation rate, intensity of disturbance, and low light and oxygen levels in this region may disfavor the continuous distribution of *A. coralvivo* **sp. nov.** and *A. simus* in the western Atlantic. Furthermore, species that depend on coralline microhabitats cannot use the Amazon reef system as a stepping-stone because of its reef structures and limited availability of habitat and food resources (Moura *et al.* 2016). This results in genetic isolation and absence of gene flow between populations from the Caribbean Sea and Brazil, as reported for some brachyuran species (Peres & Mantelatto 2020).

Except for brachyuran crabs, the crustacean fauna in coral reefs remains largely unknown (Amaral & Jablonski 2005), which emphasizes the importance of fauna surveys in this environment. Even though alpheid shrimps are not currently considered endangered in Brazil (Almeida *et al.* 2016), the vulnerability of coastal areas including coral reefs to anthropic action highlights the need for attention regarding the many animal species that use these environments as refuge and consequently risk extinction (Amaral & Jablonski 2005). Therefore, multidisciplinary approaches should be used to elucidate taxonomic inconsistencies and emphasize areas that contain unique genetic diversity that may be lost in the near future (Burnham & Dawkins 2013). In conclusion, our data allowed the recognition of a new species from Brazil, previously mistaken for *A. simus*, and reports the currently known distribution of the three American species of the *A. obesomanus* group, highlighting the hiatus in the group's distribution in the south Atlantic (Fig. 5).

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APPENDIX 1. List of comparative material.

Alpheus simus, Guérin-Méneville- 1856: WESTERN ATLANTIC—*United States of America*: 1 ovigerous female, Florida, Looe Key Reef, 10.IX.1958, coll. E.L. Pierce, USNM 102355. *Mexico*: 8 males, 12 females (10 ovigerous), Quintana Roo, Espiritu Santo Bay, in coral, 1–3 m, 6.IV.1960, USNM 136350; 3 males, 1 female, Quintana Roo, Ascension Bay, Central Nicchehabin Reef, 1–2 m, 13.IV.1960, USNM 136350. *Belize*: 2 females (1 ovigerous), Carrie Bow Cay, 4.II.2011, colls. R. Lemaitre, C.C. Tudge, D.L. Felder, J.M. Felder, S. Pecnick, USNM 1153629; 1 female, Carrie Bow Cay, in cavities under zoanthid, 23.II.2009, colls. D.L. Felder, J.M. Felder, S. de Grave, B. Thoma, E. Palacios Theil, S. Collier, USNM 1292514. *Costa Rica*: 1 male, 2 ovigerous females, Limón, Parque Nacional Cahuita, Ciesta Interna, in coral reef, 01.VI.1984, coll. J. Cortés, MZUCR 2186–01. *Panama*: 2 females, Caribbean, Isla Grande, Off W. Point, in coral reef, 06.X.2005, colls. A. Anker, C. Hurt, MZUSP 33122. *Colombia*: 1 female, Cartagena, Playa Mohan Baru, MNHN 15651; 10 males, 16 females (15 ovigerous), Islas del Rosario, North of Isla Grande, 14.IV.1991, coll. G.R. Navas, USNM 1150074; 3 males 12 females (11 ovigerous), Cartagena, Bolivar, Baru, Playa Mohan, USNM 310827. *British Virgin Islands*: 1 female, Anegada Island, Pomate Point, Colquhoun Reef at entrance to Gorda Sound, 15.IV.1956, USNM 136353. *Antigua and Barbuda*: 1 female, Antigua Island, English Harbor, Charlotte Point, 2.IV.1956, USNM 136352. *Saint Lucia*: 1 male, 1 female, Outside Pigeon Island Reef, 16.IV.1959, USNM 136354. *Barbados*: 2 males, 3 females (2 ovigerous), Needhams Point, 146

m, 18.V.1918, coll. C.C. Nutting, USNM 68740; 3 males, 6 females (3 ovigerous), Okra Reef, 13.V.1918, coll. C.C. Nutting, USNM 57937. *Netherlands Antilles*: 1 male, 1 female, Curaçao, Psicaderabaai, 24.II.1972, coll. J.C. den Hartog, RMNH.CRUS.D.30377.

***Alpheus saxidomus* Holthuis, 1980**: EASTERN PACIFIC—*Mexico*: 1 female, Nayarit, Isabela Island, 18.III.1933, USNM 237093. *Galapagos Islands*: 8 males, 7 females (4 ovigerous), Santa Maria Island, Onslow Island, Near Post Office Bay, Inside Crater, 23.II.1938, USNM 237074; 1 male, Isabela Island, Albemarle Point, 11.II.1933, coll. W.L. Schmitt, USNM 237094; 2 males, 1 ovigerous female, Isabela Island, Tagus Cove, 14.II.1934, USNM 237089; 2 males, Española Island, in *Pavona* sp., 17.XII.1934, USNM 237095. *Panama*: 3 males, 3 ovigerous females, Secas Islands, 4.II.1935, coll. W.L. Schmitt, USNM 237075; 1 male, Secas Islands, 4.II.1935, coll. W.L. Schmitt, USNM 237077. *Colombia*: 2 females (1 ovigerous), Cauca, Gorgona Island, Off Coconut Beach, in *Pavona* sp., 22.I.1935, USNM 237087; 1 female, Choco, Port Utria, dredging, 37 m, 14.II.1934, USNM 237079; 1 female, Choco, Ensenada de Utria, 28.VIII.1984, coll. G. Ramos, USNM 259390; 1 male, 1 female, Málaga Bay, under rocks, 25.II.1983, coll. G. Ramos, USNM 244242.