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PATRICIA SOUZA DOS SANTOS

# TAXONOMIA INTEGRATIVA DE QUATRO ESPÉCIES DE CAMARÕES ALPHEIDAE (CRUSTACEA: DECAPODA) COM PADRÃO DE DISTRIBUIÇÃO DISJUNTA

Recife
2019

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Doutora em Biologia Animal.

**Área de Concentração:** Biologia Animal

**Orientador:** Prof. Dr. Alexandre Oliveira de Almeida
**Coorientador:** Prof. Dr. Fernando Luis Medina Mantelatto

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Aprovada em: 27/02/2019.

## COMISSÃO EXAMINADORA

Prof. Dr. Alexandre Oliveira de Almeida/Universidade Federal de Pernambuco
(Orientador)

Prof. Dr. Felipe Bezerra Ribeiro /Universidade Federal do Rio Grande do Sul
(Membro externo)

Prof. Dr. Jesser Fidelis de Souza Filho/Universidade Federal de Pernambuco
(Membro externo)

Dr$^{a}$. Débora Lucatelli de Albuquerque/Universidade Federal de Pernambuco
(Membro externo)

Prof. Dr. Pedro Murilo Sales Nunes/Universidade Federal de Pernambuco
(Membro interno)

Prof. Dr. André Morgado Esteves /Universidade Federal de Pernambuco
(Membro interno)

Dr$^{a}$. Catarina de Lourdes Araújo Silva /Universidade Federal de Pernambuco
(Membro suplente externo)

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“Deus quer, o homem sonha, a obra nasce.”
(PESSOA, 1934, p. 57).

# RESUMO

Estudos envolvendo a problemática de espécies crípticas em camarões Alpheidae, possibilitam o esclarecimento sobre a distribuição de espécies que primariamente apresentavam distribuição geográfica controversa. O presente estudo teve como objetivo utilizar a taxonomia integrativa para detectar possíveis complexos de espécies crípticas em *Alpheus peasei*, *Alpheus simus*, *Synalpheus dardeaui* e *Synalpheus ul* com distribuição disjunta no Atlântico Ocidental. Foram analisados espécimes ao longo da distribuição conhecida incluindo a localidade-tipo. Alguns exemplares foram submetidos a análises genéticas utilizando os genes mitocondriais Citocromo Oxidase I e/ou 16S. *Alpheus peasei,* foi redescrita da espécie, e a hipótese da existência de um complexo de espécies foi refutada. Além disso, confirmou-se que há conectividade entre suas populações do Atlântico Norte e Sul e ampliando-se o limite de distribuição no noroeste do Atlântico (Barbados, Belize e Costa Rica) e registrando uma nova ocorrência para a costa brasileira (Pernambuco). Ao examinar os espécimes atribuídos à *A. simus*, verificou-se que o material proveniente da Bahia, previamente identificado como *A. simus* se tratava de um novo táxon, *Alpheus* sp.n. com distribuição restrita no Atlântico Sul Ocidental (Rio Grande do Norte e Bahia). Desta forma, foi fornecida a descrição da espécie e, constatou-se a existência do complexo de espécies envolvendo *Alpheus* sp.n., *A. simus* sensu stricto e *A. saxidomus*. Em *S. ul* e *S. dardeaui* não foram encontradas variações morfológicas e moleculares consistentes. Por isso, a hipótese da existência de um complexo de espécies foi refutada. Mas, confirma-se que há conectividade entre a população caribenha e do Atlântico Sul Ocidental. Além disso, nossos resultados trazem a expansão da distribuição de *S. dardeaui* e *S. ul* no Atlântico Sul Ocidental para o Rio de Janeiro e Pernambuco, respectivamente.

Palavras-chave: Caridea. Oceano Atlântico. COI. 16S.

# ABSTRACT

Studies involving the problematic of cryptic species in Alpheidae shrimps, make it possible to elucidate the distribution of species that primarily presented controversial geographical distribution. The present study aimed to use integrative taxonomy to detect possible complexes of cryptic species in *Alpheus peasei*, *Alpheus simus*, *Synalpheus dardeaui* and *Synalpheus ul* with disjoint distribution in the Western Atlantic. Specimens were analyzed along the known distribution including the type locality. Some specimens were submitted to genetic analysis using the mitochondrial Cytochrome Oxidase I and / or 16S genes. *Alpheus peasei*, was redescribed, and the hypothesis of the existence of a species complex was refuted. In addition, it was confirmed that there is connectivity between the populations of the North and South Atlantic and increasing the distribution limit in the northwestern Atlantic (Barbados, Belize and Costa Rica) and provide a new record for the Brazilian coast (Pernambuco). Examining the specimens designate to *A. simus*, it was found that material from Bahia, previously identified as *A. simus*, was *Alpheus* sp. n. with restricted distribution in the southwestern Atlantic (Rio Grande do Norte and Bahia). Thus, the description of the species was provided and, the existence of the species complex involving *Alpheus* sp.n., *A. simus* sensu stricto and *A. saxidomus* was confirmed. In *S. ul* and *S. dardeaui* no solid morphological and molecular variations were found. Therefore, the hypothesis of the existence of a species complex was refuted. But, it is confirmed that there is connectivity between the Caribbean population and the southwestern Atlantic. In addition, our results extend the distribution of *S. dardeaui* and *S. ul* in the southwestern Atlantic to Rio de Janeiro and Pernambuco, respectively.

Keywords: Caridea. Atlantic Ocean. COI. 16S.

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## SUMÁRIO

# 1 INTRODUÇÃO

Classificar os organismos em grupos é a premissa da taxonomia, enquanto a sistemática visa além de ordenar, compreender as relações filogenéticas e os processos evolutivos entre os organismos (RUGGIERO et al., 2015; WIENS, 2007). Os maiores impedimentos que os taxomomistas e sistematas tradicionais enfrentam é conseguir diferenciar a plesiomorfia da apomorfia, homologia da homoplasia (AVISE et al., 1987; STEBBINS; AYALA, 1981) e a ação de processos microevolutivos como mutação, migração, deriva genética e seleção natural baseado apenas em caracteres morfológicos.

Para tentar solucionar essa problemática, abordagens multidisciplinares como o uso da taxonomia integrativa vêm sendo amplamente utilizadas (e.g. DAYRAT, 2005; HUPALO et al., 2018; NOVIKOV; SHEVCHENKO, 2001; WANG; SHA, 2015). Em crustáceos, os genes Citocromo Oxidase subunidade 1 (COI) e genes mitocondriais que codificam o rRNA das subunidades ribossômicas (12S e 16S), têm sido os mais utilizados para a resolução de indecisões taxonômicas em diferentes níveis hierárquicos (e.g. AHYONG; O'MEALLY, 2004; BRACKEN; DE GRAVE; FELDER, 2009; BRACKEN-GRISSOM; FELDER, 2014; KOU et al., 2013; LAI et al., 2013;).

Entre todos os animais e plantas do planeta, não há grupo que expresse a alta diversidade morfológica observada entre os crustáceos (MARTIN; DAVIS, 2001), compreendendo desde micro até grandes organismos como o caranguejo aranha. Essa pluralidade morfológica é observada na infraordem Caridea Dana, 1852, segundo táxon com maior riqueza de espécies entre os crustáceos da ordem Decapoda Latreille, 1802, com pelo menos 389 gêneros e 3438 espécies (DE GRAVE; FRANSEN, 2011). Dentro dessa infraordem, a família Alpheidae Rafinesque, 1815 se destaca por ser uma das mais numerosas em nível específico e possuírem *Alpheus* Fabricius, 1798 e *Synalpheus* Spence Bate, 1888 como os principais representantes.

Com 313 espécies descritas, (ANKER; DE GRAVE, 2012; DE GRAVE; FRANSEN, 2011; DEHGHANI; SARI; NADERLOO, 2018; KOMAI; OHTOMI, 2018; RAMOS-TAFUR, 2018; SALGADO-BARRÁGAN; AYON-PARENTE; ZAMORA-TAVARES, 2017) a maioria dos representantes em *Alpheus* são marinhos com apenas um registro confirmado para água doce, *A. cyanoteles* Yeo & Ng, 1996 (YEO; NG, 1996), podendo ser encontrados do infralitoral raso até grandes profundidades, habitando recifes de coral, estuários e manguezais nas regiões tropicais e subtropicais (ANKER et al., 2006; CHACE, 1988). Além disso, muitas espécies podem desenvolver associação obrigatóriacom outros organismos como, peixes gobiídeos

(ANKER, 2000), corais mortos (CORTES, 1985; WERDING, 1990), poliquetos (ANKER; KOMAI; MARIN, 2015) e até outros crustáceos (DWORSCHAK; ANKER; ABED-NAVANDI, 2000).

*Synalpheus*, segundo gênero com maior riqueza dentro de Alpheidae, apresenta 169 espécies válidas (ANKER; HULTGREN; DE GRAVE, 2017; ANKER; TAVARES; MENDONÇA, 2016; DE GRAVE; FRANSEN, 2011; RÍOS; DUFFY, 2007) São encontrados associados a esponjas e substratos consolidados de águas marinhas tropicais (ANKER; DE GRAVE, 2012; RÍOS; DUFFY, 2007). Muitas espécies habitam canais de esponjas e algumas são simbiontes obrigatórios destes organismos, podendo viver em grupos eusociais como *Synalpheus chacei* Duffy, 1998 (DUFFY, 1998).

Tendo em vista a capacidade de dispersão de fases larvais planctônicas que ocorrem na maioria dos crustáceos (ANGER, 2006) e a aparente falta de barreiras à dispersão oceânica, muitos táxons marinhos parecem apresentar distribuições globais (BURTON, 2009). Contudo, essas distribuições muitas vezes devem ser analisadas com cautela por causa da existência das espécies crípticas, visto que, não são fáceis de distinguir usando apenas a sistemática tradicional (KNOWLTON, 1986). A problemática envolvendo espécies crípticas inclui principalmente incertezas, equívocos taxonômicos e/ou distribucionais (e.g. COLBORN et al., 2001; SALES et al., 2017) e registros de substituição de espécie nativa por espécie invasora, como o caso do mexilhão *Mytilus galloprovincialis* Lamarck, 1819 no Sul da Califórnia (GELLER, 1999).

Dificuldades intrínsecas à identificação de espécies crípticas baseadas apenas em caracteres morfológicos podem resultar em baixa resolução taxonômica ou em complexos de espécies, o que pode ocasiornar subestimativas no número de espécies. Em *Alpheus* e *Synalpheus*, as indefinições e confusões envolvendo a distribuição e o status taxonômico vêm sendo resolvidas com uso da taxonomia tradicional associada à inclusão de informações moleculares (e.g. ALMEIDA et al., 2013; ANKER; TÓTH, 2008; HULTGREN; HURT; ANKER, 2014; MATHEWS; ANKER, 2009; MORRISON; RÍOS, 2004).

## 1.1 HIPÓTESES

$H_0$: *Alpheus simus, A. peasei, S. dardeaui* e *S. ul* constituem espécies com distribuição disjunta, sem evidências de complexos de espécies crípticas;
$H_1$: *Alpheus simus, A. peasei, S. dardeaui* e *S. ul* constituem complexos de espécies crípticas.

## 1.2 JUSTIFICATIVA

A existência de espécies crípticas e lacunas de distribuição podem refletir diretamente em subestimativas de riqueza. Com isso, nossos resultados poderão contribuir para o esclarecimento sobre a verdadeira distribuição das espécies e para o aumento da diversidade em Alpheidae com a descrição de novos táxons. Cabe ressaltar que, em diversas ocasiões em que houve comparações entre sudoeste e noroeste do Atlântico, novas espécies foram descritas (TAVARES, 2011).

## 1.3 OBJETIVOS

### 1.3.1 Objetivo geral

- Verificar o status taxonômico e distribucional de *Alpheus simus, A. peasei, S. dardeaui* e *S. ul* no Atlântico ocidental.

### 1.3.2 Objetivos específicos

- Comparar morfologicamente e com técnicas de biologia molecular exemplares de *A. simus, A. peasei, S. dardeaui* e *S. ul*;
- Estudar a variabilidade morfológica das espécies;
- Contribuir para o conhecimento da distribuição geográfica das espécies.

## 1.4 ESTRUTURAÇÃO DA TESE

A tese está dividida em três capítulos. Em ambos é empregado o uso da taxonomia integrativa para avaliar o verdadeiro status de distribuição dos camarões Alpheidae e verificar a existência de complexos. Capítulo 1, que versa sobre *Alpheus peasei*, foi submetido e está formatado de acordo com as normas da Revista Zootaxa. O capítulo 2, sobre *Alpheus simus*, foi formatado com as normas do Zoological Journal of the Linnean Society e o 3, sobre *Synalpheus dardeaui* e *S. ul*, foi formatado nas normas do Journal of the Marine Biological Association of the United Kingdom.

Os sites abaixo podem ser acessados para visualização das normas dos periódicos.

Revista Zootaxa:
https://www.mapress.com/j/zt/pages/view/forauthors

Zoological Journal of the Linnean Society:
https://academic.oup.com/zoolinnean/pages/General_Instructions

Journal of the Marine Biological Association of the United Kingdom:
https://www.cambridge.org/core/journals/journal-of-the-marine-biological-association-of-the-united-kingdom/information/instructions-contributors

ARTIGO I

## 2 USING INTEGRATIVE TAXONOMY TO ESTABLISH THE STATUS OF A*lpheus peasei* (ARMSTRONG, 1940) (DECAPODA: ALPHEIDAE) AS A SINGLE SPECIES THROUGHOUT ITS DISTRIBUTION

### ABSTRACT

*Alpheus peasei* (Armstrong, 1940), a Western Atlantic snapping shrimp species, has a disjunct distribution. There is a large gap in its distribution (approx. 12° of latitude) between Tobago and the northeast of Brazil (State of Ceará). Here we analyzed specimens of *A. peasei* from its entire distribution range and type-locality (Bermuda), to test the hypothesis that they belong to a single species. The morphological analysis included the usual taxonomic characters as well as additional ones (such as mouthparts). The molecular analysis was based on the mitochondrial genes Cytochrome Oxidase I and 16S. The results of both analyses were congruent and indicated that *A. peasei* is a single species throughout its known distribution. As such, they indicated a connectivity between Northwestern and Southwestern Atlantic populations of *A. peasei*. The gap in distribution may be explained by scarce samplings in the North Brazil Shelf province and/or by passive larvae dispersal. Our results also extend the known distribution of *A. peasei* in the Northwestern Atlantic (Barbados, Belize and Costa Rica), and add a new record from the Brazilian coast (Pernambuco).

Key-words: Caridea, Snapping shrimp, COI, 16S, Western Atlantic.

## INTRODUCTION

Species with a disjunct distribution pattern in space (Carvalho 2011) are common in the marine environment (e.g., Sales *et al*. 2017; Rodrigues *et al*. 2017; Dudoit *et al.* 2018; Mandai *et al.* 2018). A disjunct distribution may be caused by a complex combination of ocean currents, benthic topologies, and dispersion capacities of organisms at different developmental stages. These combinations may also lead to different gene flow patterns and influence the evolutionary history of marine species (Hauser & Carvalho 2008; Weersing & Toonen 2009; Villamor *et al*. 2014).

The family Alpheidae Rafinesque, 1815 stand out among decapods due to its high species richness (more than 600 species), extreme ecological diversification, and wide variety of microhabitats (Anker *et al*. 2006; De Grave & Fransen 2011). Alpheid shrimps are found in shallow tropical and subtropical waters of coastal regions, often associated with other crustaceans and marine invertebrates, and with fishes of the family Gobiidae Cuvier, 1816 (Boltaña & Thiel 2001; Bauer 2004; Anker *et al*. 2006). The recent description of several new Alpheidae taxa indicates that the worldwide diversity of this family is far from being completely known (e.g. Soledade *et al*. 2014; Ďuriš & Horká 2016; Anker *et al*. 2017; Salgado-Barragán *et al*. 2017; Dehghani *et al*. 2018).

To date, the genus *Alpheus* Fabricius, 1798 is the most diverse of the family, with 313 known species (De Grave & Fransen 2011; Komai & Ohtomi 2018; Dehghani *et al*. 2018). However, the real diversity has been estimated in more than 400 species (Anker *et al*. 2006). Many cryptic lineages exist in the Alpheidae family and in the genus *Alpheus* (e.g., Anker 2001; Williams *et al*. 2001; Mathews & Anker 2009; Heuring *et al*. 2017). These lineages include numerous species previously regarded as single species of wide geographic distribution and high morphological variability (e.g. Anker *et al.* 2008a; 2008b; 2008c; Bracken-Grissom & Felder 2014; Almeida *et al*. 2014).

Information on body coloration patterns has been useful to recognize species within complexes where morphological differences are insignificant (e.g., Knowlton & Keller, 1985; Knowlton & Mills, 1992; Anker 2001; Mathews & Anker, 2009; Anker & De Grave 2012). Also, integrative approaches combining classic taxonomy and molecular biology to study the cryptic biodiversity of alpheids has contributed to the taxonomical knowledge of the family (e.g., Anker *et al.* 2008a; 2008b; Bracken-Grissom *et al.* 2009; Bracken-Grissom & Felder 2014; Almeida *et al.* 2013, 2014). In this context, the mitochondrial markers 16S and Cytochrome Oxidase I (COI) have been widely used as very informative tools in taxonomic and phylogenetic studies of different decapod groups (e.g., Pileggi & Mantelatto 2010; Terossi & Mantelatto 2012; Hurt *et al*. 2013; Hultgren *et al*. 2014; Timm & Bracken-Grissom 2015; Terossi *et al.* 2017; Ribeiro *et al*. 2017; Miranda *et al*. 2018).

Recent reviews of alpheid cryptic species complexes recognized and described new species (e.g., Mathews & Anker 2009; Anker 2012; Almeida *et al.* 2013, 2014; Bracken-Grissom & Felder 2014). However, there are still many understudied species complexes, and the occurrence of cryptic species among species of wide and/or disjunct distribution has not been investigated (see Soledade & Almeida 2013). Disjunct distributions may result from introductions of exotic species that might have been missed, and from poor taxonomic resolution, i.e., more than one species may be involved (Tavares 2011; Almeida *et al*. 2012). Indeed, when comparisons of specimens from the southwestern and northwestern Atlantic populations were carried out, new species were recognized in the former several times (Tavares 2011).

Some Western Atlantic alpheids have a disjunct distribution where the latitudinal gap corresponds to the North Brazil Shelf province, which includes the Guianan and Amazonia ecoregions (Spalding *et al*. 2007). This particular gap may be explained by two non-exclusive hypotheses. One is that the gap may be an artifact since the crustacean fauna of the North Brazil

Shelf province is still understudied. Samplings along the gap may reveal that species occur where the substrate is suitable. The other hypothesis is that species might lack adaptations to oceanographic features of the North Brazil Shelf province, such as muddy bottoms and low salinity (Coelho 1969; Coelho & Ramos 1972; Collette & Rützler 1977). Some of the alpheids with disjunct distributions live in consolidated substrates of intertidal and shallow subtidal regions, including coral reefs (Soledade & Almeida 2013), or associated with other organisms (e.g., sponges) (Anker 2008b). Thus, the North Brazil Shelf province may act as an ecological barrier for these species, restricting the gene flow and perhaps leading to speciation.

*Alpheus peasei* (Armstrong, 1940) is an example of a species with disjunct distribution. These shrimps are commonly found in crevices of consolidated substrates such as rocks and dead corals (Chace 1972; Santos *et al*. 2012; Anker *et al*. 2016) in the intertidal region and up to 25 m of depth (Martínez-Iglesias *et al.* 1996). *Alpheus peasei* has been reported in Florida Keys (USA), Yucatan Peninsula, and Tobago Providencia Island (Armstrong 1940, as *Crangon peasei*; Chace 1972; Rodriguez 1980) and its type-locality is Bermudas. In Brazil, it occurs from Ceará to Rio de Janeiro, and in Trindade and Martin Vaz Archipelago (Santos *et al.* 2012; Cunha *et al*. 2015; Anker *et al*. 2016; Pachelle *et al*. 2016). Therefore, there is a substantial gap (approx. 12 degrees of latitude) between Tobago and Ceará (Brazil), which includes the North Brazil Shelf province.

Motivated by the distribution gap explained above, and by a known variation in the coloration pattern (see Anker *et al.* 2016), we combined morphological and molecular data to test the hypothesis that *A. peasei* is a single species throughout its known distribution. Since the original species description is very simple, we also provide a detailed redescription.

## MATERIAL AND METHODS

We obtained specimens identified as *A. peasei* from almost all localities where it has been recorded to date. These specimens are deposited in the crustacean collections of the following institutions: Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil (MNRJ); Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil (CCDB); National Museum of Natural History, Smithsonian Institution, United States of America (USNM); American Museum of Natural History (AMNH); Muséum National d'Histoire Naturelle, France (MNHN); Naturalis Biodiversity Centre, Leiden, the Netherlands (RMNH); Museo de Zoología de la Universidad de Costa Rica, Costa Rica (MZUCR); Colección Nacional de Crustaceos, Universidad Nacional Autonoma de Mexico, Mexico (CNCR). We alsocollected fresh specimens for morphological and molecular analyses by dredging in the continental shelf off Recife (Brazil), at depths of 50−68 m.

The identification and morphological analyses were based on the original description and on its diagnostic characters (Armstrong 1940; Chace 1972; Soledade & Almeida 2013). We examined 57 morphological characters of 124 specimens of *A. peasei*, including traditional and additional characters such as mouthparts. To avoid damaging the paratypes from Bermuda, the redescription and illustrations were based on a specimen from Pernambuco, northeastern Brazil. Drawings were made under a dissecting stereomicroscope equipped with a camera lucida, and the final illustrations were prepared using Adobe Illustrator CS6®.

Most of the sequences used in the genetic analyses were generated from our own DNA extractions. DNA extraction, amplification, and sequencing of target regions were performed using the protocols proposed by Mantelatto *et al.* (2006; 2007; 2018) with occasional adjustments. In addition, sequences from the GenBank were used (Table 1).

**TABLE 1.** Specimens of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888 used in genetic analyses. COI: Cytochrome Oxidase I.

| **Species** | **Locality** | **Catalogue number** | **GenBank COI** | **Genbank 16S** | **Reference** |
|---|---|---|---|---|---|
| *Alpheus peasei* (Armstrong, 1940) | Brazil, Trindade Island | MZUSP 33336 | pendent | pendent | This study |
| *Alpheus peasei* | Brazil, Bahia | MOUFPE 19433 | pendent | - | This study |
| *Alpheus peasei* | Mexico, Quintana Roo | CNCR 10872 | pendent | pendent | This study |
| *Alpheus peasei* | Mexico, Quintana Roo | CNCR 5733 | - | pendent | This study |
| *Alpheus peasei* | Guadaloupe | MNHN-IU-2013-12050 | pendent | - | This study |
| *Alpheus peasei* | Panama, Bocas del Toro | CCDB 3493 | pendent | - | This study |
| *Alpheus peasei* | Brazil, Pernambuco | MOUFPE 19427 | - | pendent | This study |
| *Alpheus peasei* | Brazil, Pernambuco | MOUFPE 19429 | - | pendent | This study |
| *Alpheus peasei* | Brazil, Pernambuco | MOUFPE 19430 | - | pendent | This study |
| *Alpheus peasei* | Brazil, Pernambuco | MOUFPE 19431 | - | pendent | This study |
| *Alpheus amblyonyx* Chace, 1972 | Guadaloupe | MNHN 12112 | pendent | pendent | Soledade *et al.* (in prep.) |
| *Alpheus amblyonyx* | Guadaloupe | MNHN-Na-12026 | pendent | pendent | Soledade *et al.* (in prep.) |
| *Alpheus macrocheles* (Hailstone, 1835) | Portugal, Azores | RMNH.Crus.D 51342 | - | pendent | Soledade *et al.* (in prep.) |
| *Alpheus macrocheles* | Spain, Canary Islands | RMNH.Crus.D 51363 | - | pendent | Soledade *et al.* (in prep.) |
| *Alpheus puapeba* Christoffersen, 1979 | Brazil, Rio de Janeiro | MNRJ 21836 | pendent | pendent | Soledade *et al.* (in prep.) |

| | | | | | |
|---|---|---|---|---|---|
| *Synalpheus scaphoceris* Coutière, 1910 | Brazil, São Paulo | CCDB 4859 | KU313017 | KU312989 | Mantelatto *et al.* (2018) |
| *Synalpheus townsendi* Coutière, 1909 | Brazil, São Paulo | CCDB 5630 | KU313018 | KU312993 | Mantelatto *et al.* (2018) |

Total genomic DNA was extracted from the abdominal muscle tissue. The tissue was stored in 1.5 ml tubes and incubated in a dry bath for 24 h at 55 °C, in 600 µl of lysis buffer with 10 µl Proteinase K (20 mg ml$^{-1}$). After incubation, the samples were placed on dry ice for 10 min to inactivate the Proteinase K. Proteins were separated by the addition of 200 µl ammonium acetate (7.5 M) before centrifugation. The DNA was precipitated by the addition of 600 µl cold absolute isopropanol (-20 °C) followed by centrifugation. The resulting pellet (after 48 h at -20 ºC) was washed with 15 µl 70% ethanol, dried, and resuspended in 20 µl TE buffer. The DNA was quantified using Nanodrop 2000c.

Two mitochondrial genes, Cytochrome Oxidase I (COI mtDNA) and 16S, were studied. The target regions were amplified by the Polymerase Chain Reaction – PCR (Sambrook *et al.* 1989) using the primer pairs: COL6B2 (5'-ACAAATCATAAAGATATYGG-3') and COH6 (5'-TADACTTCDGGRTGDCCAAARAAYCA-3') (Schubart & Huber 2006; Mantelatto *et al.* 2016), and 1472 (5'-AGATAGAAACCAACCTGG-3') and 16L2 5'-TGCCTGTTTATCAAAAACAT-3') (Crandall & Fitzpatrick 1996; Schubart *et al.* 2002). PCR products were obtained in a total reaction volume of 25 µl containing distilled and deionized $H_2O$, PCR Buffer (10 X), $MgCl_2$ (25 mM), betaine (5 M), DNTPs, primers, *Thermus aquaticus* polymerase, and 1 µl of DNA (50 ng).

The DNA amplification by PCR was conducted in a Veriti 96-Well Thermal Cycler® (Applied Biosystems) using primer-specific thermal cycles. Amplicons were checked in a 1.5% agarose gel stained with GelRed ™ in a UVP® M20 transilluminator. PCR products were purified with the SureClean® Purification kit and sequenced with the Big Dye® Terminator sequencing reaction Cycle Sequencing (Applied Biosystems). The sequencing was conducted in an ABI 3100 Genetic Analyzer® from the Departamento de Tecnologia da Faculdade de Ciências Agrárias e Veterinárias da Universidade Estadual Paulista de Jaboticabal. Both forward and reverse strands were sequenced and the consensus sequence was obtained using Bioedit 7.0.9.0 (Hall 1999). The sequences were blasted against the NCBI database (http://blast.ncbi.ncbi.nlm.nih.gov/blast.cgi) to confirm the identity.

The phylogenetic tree and the genetic divergence were obtained for each gene. Sequences were aligned using MUSCLE (Multiple Sequence Comparison by Log-Expectation) (Edgar 2004). The jModelTest (Darriba *et al.* 2012) was used to find the best substitution model based on the Bayesian Information Criterion (BIC). A Bayesian Inference Analysis was done with MrBayes 3.2.6 (Ronquist *et al*. 2012) using the parameters obtained with the jModelTest. During the analysis, one tree was sampled for every 1,000 generations of 20,000,000 generations, starting with a random tree. These analyses were made using the Cyberinfrastructure for Phylogenetic Research platform (CIPRES) (Miller *et al.* 2010). Four independent races were performed and the convergence among races was analyzed using Tracer 1.6 (Rambaut *et al.* 2014). The first trees and parameters (20 %) were discarded (burn-in) and a final tree was generated using Tree Annotator 1.8.4 (conducted in BEAST; Drummond *et al*. 2012). Posterior probabilities above 60% were recorded. A genetic divergence matrix was created with the Kimura 2 parameter model (K2P) (Kimura 1980) using MEGA 6 (Tamura *et al.* 2013). Genbank sequences were used for comparison (Table I). Abbreviations used: (ovig.) ovigerous, (ni) unidentified, (juv) juveniles, (m) meters, (P) pereiopod.

## RESULTS

### Taxonomy

### Family Alpheidae Rafinesque, 1815

### Genus *Alpheus* Fabricius, 1798

### *Alpheus peasei* (Armstrong, 1940)

(Figs 1, 2)

*Crangon peasei* Armstrong, 1940: 1. [Castle Harbor Reefs, Bermuda A.M.N.H. 8184 from Castle Harbor Reefs. Not examined]

*Alpheus peasei*–Chace 1956: 146; 1972: 69; Hazlett 1962: 82; Hazlett & Winn 1962: 26; Knowlton & Moulton 1963: 313, Fig. 3; Hendrix 1971: 128, 19; Pequegnat & Ray 1974: 247; Ray 1974: 120, Figs. 100–104; Abele 1976: 273, Table 9; Carvacho 1979: 454; Abele & Kim 1986: 197, 210–211, Figs. A–C; Sterrer, 1986: 325, text-pl. 105; Rodriguez 1986: 152; Martinez-Iglesias *et al*. 1993: 11; 1996: 34; 1997: 424, Fig. 15; Santos *et al*. 2012: 152, Fig. 3J; Soledade & Almeida 2013: 104, Fig. 6C; Cunha *et al*. 2015: 48, Fig. 1; Anker *et al*. 2016: 25, Figs. 7A–B, 8A–B; Pachelle *et al*. 2016: 9.

**Material examinado: Bermuda. Paratypes**: 2 males, 2 ovig. females, Castle Harbor, VIII.1938, lot 123, AMNH 8186; 9 males, 4 (3 ovig.) females, Grazbury's id, VIII.1938, lot 127, AMNH 8186; 5 males, 4 (2 ovig.) females, Castle Harbor, on reef, VIII.1938, lot 133, AMNH 8186; 2 males, St. Davids, on reef, VIII.1938, lot 138, AMNH 8186; 4 males, 4 (2 ovig.) females, Ferry Beach, on rocks, coll. B.A. Hazlett, 02.VIII.1960, USNM 107080; 2 ovig. females, South Shore, on rocks, coll. B.A. Hazlett, 10.VIII.1960, USNM 107079; 2 males, Castle Harbor, in calcareous rocks, coll. B.A. Hazlett, 21.VII.1960, USNM 107081; 2 males, 1 ovig. female, Castle Harbor, off Charles Island, in calcareous rocks, coll. J.M. Moulton, 25.VII.1958, USNM 102370. **United States of America.** 1 male, Florida, St. Lucie County, in limestone reef and *Phragmatopoma* sp., 6 m, USNM 170085. **Mexico.** 1 male, 1 ovig. female, 1 juv, Quintana Roo, Ascension Bay, Center of Nicchehabin Reef, coll. E.L. Bousfield, 1–2 m, 14.IV.1960, USNM 136040; 1 male, Quintana Roo, Puerto Morelos, María Irene Beach, CNCR 9631; 1 male, Quintana Roo, Isla Cozumel, Playa Aventura, CNCR 20292; 1 ovig. female, Quintana Roo, Arrecife Cacarracas, Frente Puerto Morelos, CNCR 5733; 1 ni, Quintana Roo, Punta El Placer, Campaña Edwin Link, CNCR-10872; 1 ni, Quintana Roo, Punta Pulticub, CNCR 20306. **Belize.** 1 male, Carrie Bow Cay, coll. K. Sandved, 1 m, IV.1974, USNM 184488. **Costa Rica.** 2 males, 1 ovig. female, Parque Nacional Cahuita, Limón, Puerto Vargas, colls. R. Heard, L. Rodriguez & R. Vargas, 19.XI.1999, UCR 2312-33. **Panama.** 1 male, Isla Grande, off W point, on coral rocks, colls. A. Anker & C. Hurt, 1–2 m, 06.X.2005, MZUSP 33123; 1 male, Bocas del Toro, Bocas del Drago, colls. F.L. Mantelatto, A. Baeza, I. Miranda & M. Terossi, 17.II.2009, CCDB 3493; **Colombia.** 4 males, 3 ovig. females, old Providence, in reef, coll. W.L. Schmitt, 06.VIII.1938, USNM 77890. **Netherlands Antilles:** 1 male, Curaçao, Psicaderabaai, coll. J.G den Hartog, 26.I.1972, RMNH.CRUS.D.30635; 1 ovig. female, Bonaire, Kralendijk, 09.VIII.1994, RMNH.CRUS.D.46177; 1 ovig. female, coll. R.V. Harrison, 2–3 m, II.1975, USNM 155674. **Saint Kitts and Nevis.** 1 male, 3 (2 ovig.) females, St. Kitts, Windward Beach, on coral reef, colls. W.L. Schmitt & D.V. Nicholson, 12.VI.1956, USNM 136030. **Antigua and Barbuda.** 2 males, 3 ovig. females, Antigua Island, English Harbor, Charlotte point, 02.VI.1956, USNM 136029. **Guadeloupe.** 1 male, 1 ovig. female, Guadeloupe, Karubenthos, GB 09, MNHN-IU-2013-12050. **Dominica.** 1 male, 2 ovig. females, 5 juv, West of Portsmouth, between rocks and dead coral *Acropora* sp., 1 m, 19.VI.1959, USNM 136035. **Saint Lucia.** 1 male, 1 ovig. female, the outside Pigeon Island Reef, in coral, 16.VI.1959, USNM 136034. **Barbados.** 1 male, off the Castle E, side Barbados, coll. C.C. Nutting, 1–4 m, USNM 68724. **Trinidad and Tobago.** 5 (3 ovig.) females, Tobago

Island, Buccoo Reef, coll. W.L. Schmitt, 05.VI.1959, USNM 136033. **Brazil.** 1 male, 1 ovig. female, Pernambuco, Recife, 8°13'52.1"S 34°37'41.2"W, REC II, dredge 8, coral rubble, colls. A.M.S. Cunha, C.A.L. Santos Júnior, G.O. Soledade, F.D. Silva, R. Guéron & P.S. Santos, 51.8 m, 27.II.2018, MOUFPE 19427; 1 ovig. female, 8°13'33.0"S 34°37'40.3"W, dredge 5, 50.6 m, same collection data, MOUFPE 19428; 1 ovig. female, 8°13'52.1"S 34°37'42.7"W dredge 10, 50 m, same collection data, MOUFPE 19429; 1 male, 8°13'52.1"S 34°37'42.7"W, dredge 10, in dead coral, 50 m, same collection data, MOUFPE 19430; 1 male, 8°13'52.1"S 34°37'41.2"W, dredge 8, 51.8 m, same collection data, MOUFPE 19431; 1 male, 1 ovig. female, Bahia, Maraú, Taipús de Fora Beach, colls. P.S. Santos, G.O. Soledade & A.O. Almeida, in dead coral, salinity 38, 30.VII.2011, MOUFPE 19432; 2 males, 3 (2 ovig.) females, Bahia, Maraú, Algodões Beach, colls. P.S. Santos, G.O. Soledade & A.O. Almeida, salinity 38, 01.VIII.2011, MOUFPE 19433; 2 males, 4 (3 ovig.) females, Rio de Janeiro, Campos Basin, Petrobrás, Station, Biofouling on Platform P-55 (Old SS-06), coll. J.B. Mendonça, 16 m, 30.III.2010, MZUSP 25346; 1 male, 1 ovig. female, Rio de Janeiro, Búzios, Tartaruga Beach, MNRJ 3478; 1 male, Trindade Island, between Crista do Galo and Ponta Norte, 20°29'14.8"S 29°20'13.9" W, scuba diving, coll. J.B. Mendonça, 15 m, 21.V.2014, MZUSP 33263; 1 male, Trindade Island, Enseada dos Portugueses, Ponta da Calheta, 20°30'18.7"S 29°18'31.6"W, scuba diving, coll. J.B. Mendonça, 16.3 m, 21.V.2014, MZUSP 33295; 1 male, Trindade Island, Enseada dos Portugueses, SECON / ECIT, 20°30'20.9.3 "S–29°18'43.7"W, scuba diving, 9 m, 21.V.2014, MZUSP 33246; 3 males, 2 ovig. females, Trindade Island, Enseada da Cachoeira, Farrilhões, 20°31'22.4"S 29°19'52.0"W, scuba diving, 14.4 m, 5.V.2014, MZUSP 33336.

**Diagnosis.** Rostrum dorsally carinate. Orbital hoods toothed. Ventrolateral tooth on basicerite overreaching stylocerite. Third and fourth pereiopods with spiniform setae on ventrolateral surface of ischium and one tooth on ventrodistal margin of merus.

**Redescription.** (based on an ovigerous female, Recife, Pernambuco, MOUFPE 19428 and compared with the examined type material). Carapace smooth; rostrum triangular, carinate, tip acute, reaching half-length of first article of antennular peduncle (Fig. 1A). Ocular hoods dorsally inflated, with a strong acute tooth arising from dorsomesial margin, margin between rostrum and orbital hoods sinuous. Eyes well pigmented, completely covered by ocular hoods in dorsal and lateral views (Fig. 1A, B). Cardiac notch well-developed.

Pleonal somites smooth; ventral and posterior margins of pleurae 1–4 broadly rounded and pleura of fifth segment subtriangular; sixth pleura without articulated plate. Telson (Fig. 1C) tapering distally, proximal region wider than distal; dorsal surface with two pairs of strong spiniform setae inserted at some distance from the lateral margin, first pair anterior and second pair posterior to telson mid-length; distal margin of telson slightly convex, with two pairs of posterolateral spiniform setae, lateral about 2.5 times as long as mesial; anal tubercles well-developed. Uropods (Fig. 1C) with bifid protopods, each lobe ending in acute tooth; exopod longer than endopod; lateral margin of exopod almost straight; diaeresis sinuous, with one adjacent and internal tooth, separated by stout distolateral spiniform setae, overreaching distal margin of exopod; three very small spiniform setae before the distal margin; endopod with a row of small spiniform setae along distolateral margin.

Antennular peduncle moderately slender. Stylocerite distally acute, not reaching the distal margin of first segment; ventromesial carina subtriangular, large, with a small tooth in ventrodistal margin (Fig. 1D); second segment about 1.2 times longer than the dorsally visible portion of first segment, about 2.2 times the length of third segment; third segment about 1.5

times longer than wide (Fig. 1A). Anntena with basicerite broad, distolateral tooth directed forward; carpocerite slightly exceeding both scaphocerite and distal portion of third segment of antennular segment; scaphocerite with shallowly concave lateral margin and large, acute distolateral tooth reaching far beyond the distal margin of narrow blade (Fig. 1A).

Mandible (Fig. 1E) with 2-jointed palp; incisor process robust, with 10 distinct teeth, mesial tooth conspicuously wider and longer than others. Molar process stout, with semicircular rows of short setae. First maxilla (Fig. 1F) with palp bilobed, inferior lobe bearing 1 slender seta, superior lobe not setose. Second maxilla (Fig. 1G) palp well-developed, slender; with upper lacinia cleft, lower lacinia with single lobe; scaphognathite largest than both laciniae, extremities rounded and lateral margin sinuous. First maxilliped (Fig. 1H) palp approximately 2.2 times larger than narrow; two laciniae separated by distinct cleft, exopod well-developed with long flagellum and distinct exopodal lobe; epipod about 8.1 times longer than wide. Second maxilliped (Fig. 1I) exopod well-developed, flagellum 2.6 times longer than epipod; epipod about 2.1 times as long as wide. Third maxilliped (Fig. 1J) slender, when extended forward, slightly overreaching distal margin of third antenular segment; antepenultimate segment not flattened or expanded, 1.6 times longer than the last segment; penultimate segment shorter of all, about 2.2 times as long as wide, lateral margin smooth, with tufts of setae, distomesial margin with two thick setae; last segment tapering distally, smooth, with several bands of setae, 1.4 times longer than the penultimate segment, very setose; exopod overreaching distal margin of the antepenultimate segment, ending in a long flagellum; artrobranch well-developed. Epipod present on third maxilliped and from pereiopods first to fourth.

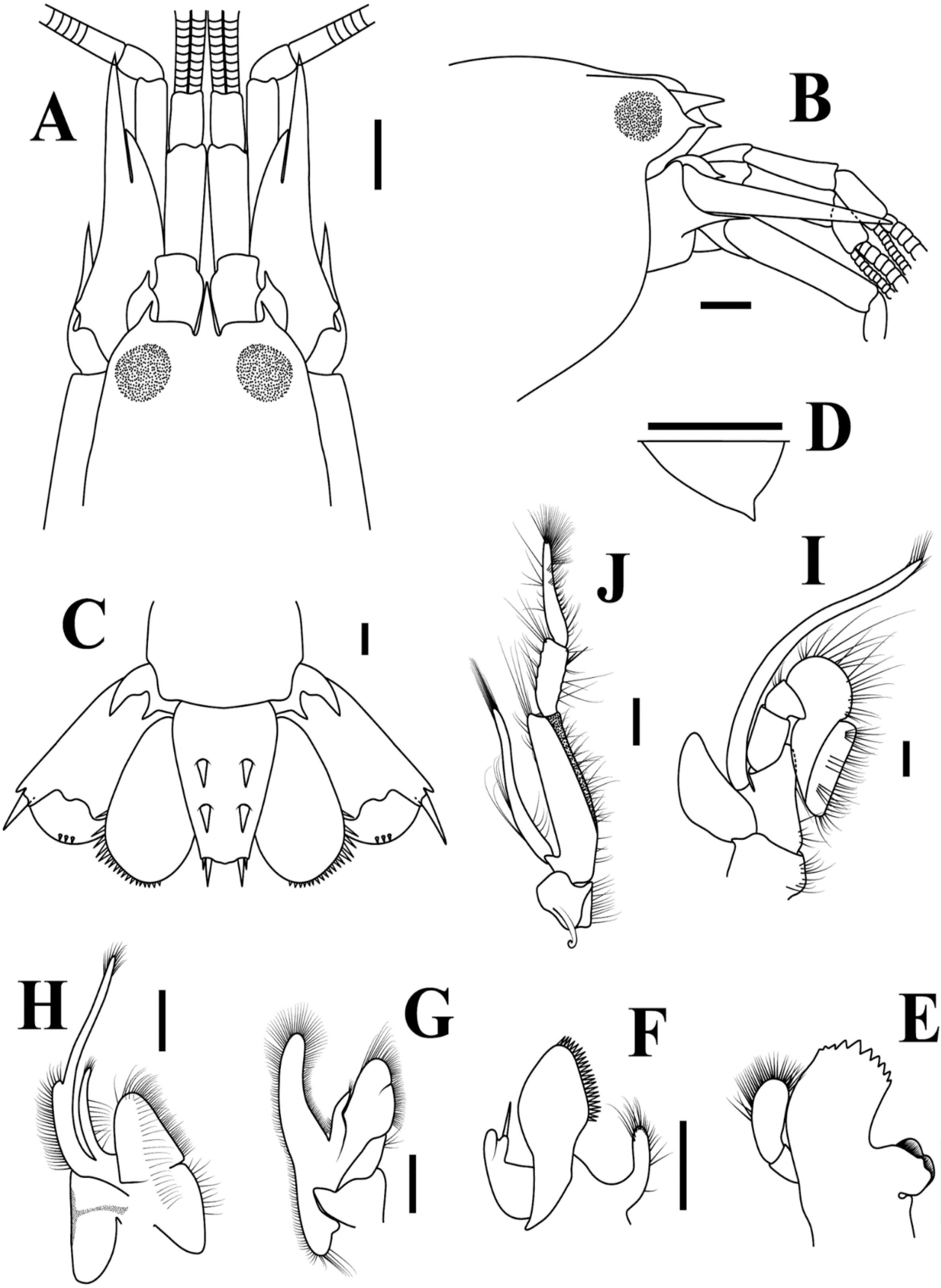

**FIGURE 1.** *Alpheus peasei* (Armstrong, 1940), ovigerous female, Recife, Pernambuco, Brazil, MOUFPE 19428: (A) frontal region and cephalic appendages, dorsal view; (B) the same, lateral view; (C) telson and uropods, dorsal view; (D) tooth on mesioventral carina of

first segment of antennular peduncle, lateral view; (E) mandible, mesial view; (F) first maxilla, lateral view; (G) second maxilla, lateral view; (H) first maxilliped, lateral view; (I) second maxilliped, lateral view; (J) third maxilliped, lateral view. In the figures A–C setae omitted. Scale bars = 0.5 mm.

Major cheliped (Fig. 2A, B) palm strongly sculptured, twisted. Palm about 2.3 times as long as wide, ventral notch broad and shallow, dorsal notch deep and narrow; linea impressa well-marked; lateral surface with low crest starting at about 0.6 time the length of palm and ending in a sharp distodorsal tooth; ventral margin with rounded, smooth, non-projecting shoulder adjacent to shallow notch, notch continuing transversely to a shallow groove on mesial surface; distomesial margin with subcylindrical elevation ending in a large adhesive disk distally; distomesial surface with transversally deeply notched crest ending in a sharp tooth; dactylus twisted laterally, opening and closing in nearly horizontal plane; strongly arched; compressed proximally; slightly bulbous distally; plunger short (Fig. 2I). Pollex shorter than dactylus; ischium short, stout and unarmed; merus about three times longer than carpus, with distal margin unarmed, ventromesial surface with three small spiniform setae; carpus short and unarmed, cup-shaped.

Minor cheliped (Fig. 2C, D) chela slightly compressed, with palm sculptured distally; lateral surface with short crest starting at distal third of the palm and ending in a sharp distodorsal tooth; ventral margin with blunt, non-protruding shoulder, distomesial margin with subcylindrical elevation ending distally in a small adhesive disk; distomesial surface with crest ending in a short sharp tooth; fingers as long as palm; pollex shallowly excavated on a cutting edge; dactylus somewhat flattened and twisted laterally, slightly convex dorsally, proximally with a small adhesive disk; ischium short, stout and unarmed; merus about 2.5 times longer than carpus, with distal margin unarmed, ventromesial surface unarmed; carpus short and unarmed, cup-shaped.

Second pereiopod slender (Fig. 2E). Merus slightly longer than ischium; carpus five-segmented, segment ratio (proximal to distal) 3: 2.5: 1: 1: 1.5; last carpal article shorter than chela; chela simple; fingers slightly longer than palm.

Third (Fig. 2F) and fourth (Fig. 2G) pereiopods similar in shape and length; both with ischium armed with a spiniform seta on ventrolateral surface; merus with a ventrodistal tooth; carpus with a pair of ventrodistal spiniform setae; propodus with six pairs of strong spiniform setae along ventral margin; dactylus biunguiculate, tooth on flexor margin shorter than extensor margin. Fifth pereiopod (Fig. 2H) shorter than P3 and P4; ischium, merus and carpus unarmed; merus slightly longer than carpus; propodus with five single spiniform setae and one distal pair on ventral margin; dactylus biunguiculate, tooth on flexor margin shorter than extensor margin.

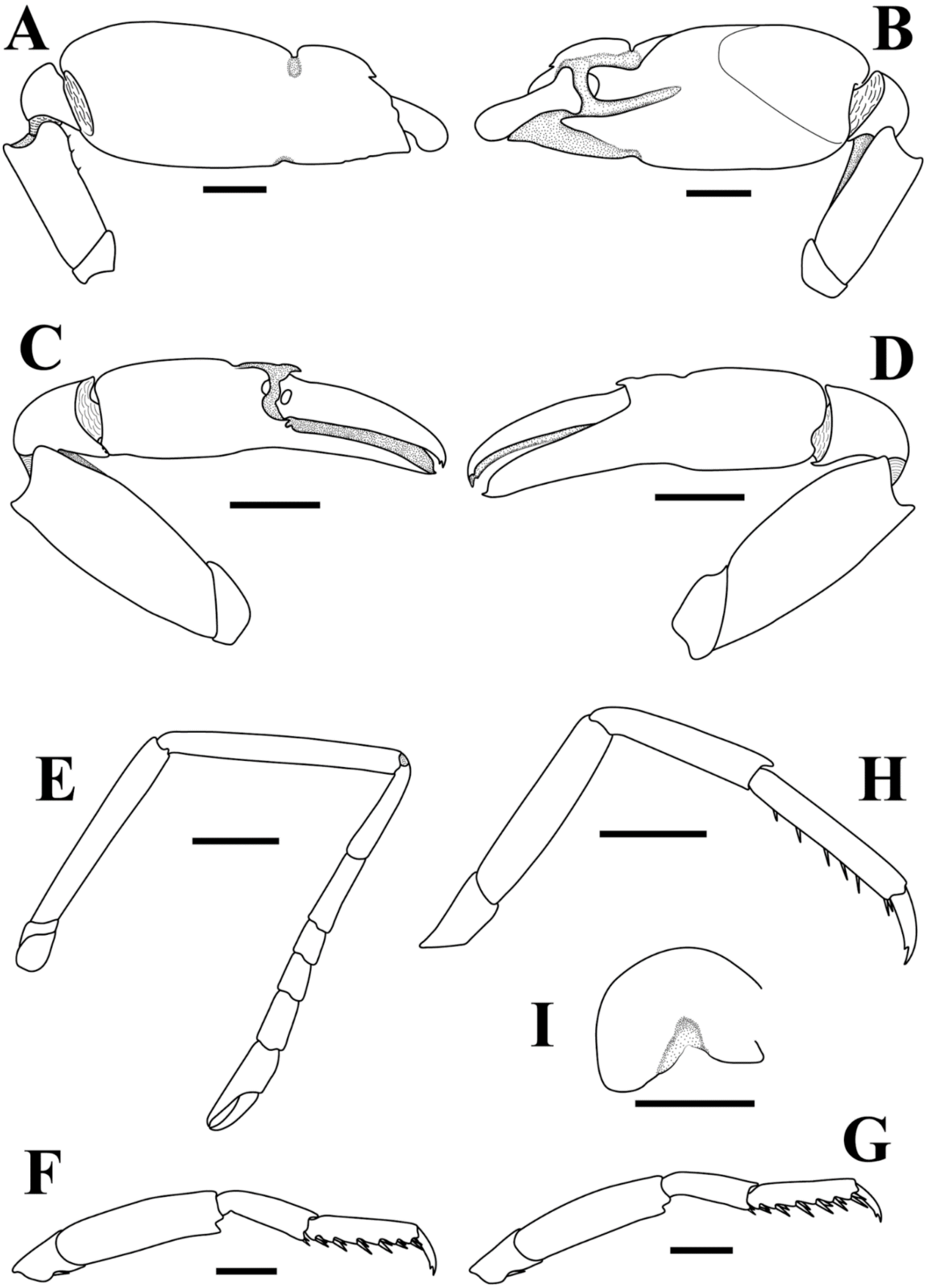

**FIGURE 2.** *Alpheus peasei* (Armstrong, 1940), ovigerous female, Recife, Pernambuco, Brazil, MOUFPE 19428: (A) major cheliped, mesial view; (B) the same, lateral view (C) minor

cheliped, lateral view; (D) the same, mesial view (E) second pereiopod, lateral view; (F) third pereiopod, lateral view; (G) fourth pereiopod, lateral view; (H) fifth pereiopod, lateral view; (I) detail of plunger of the major cheliped. Omitted setae. Scale bars = 1 mm.

**Morphological variation.** There was no consistent morphological variation in the examined characters, considering all specimens and localities. No sexual dimorphism was observed. However, the following variations were detected: ventromesial carina of the first antennular segment was unarmed or armed with a tooth that ranged from small to well-developed. The inner margin of the teeth on ocular hoods ranged from almost straight to slightly convex. The distal scaphocerite tooth may be either shorter, subequal, or slightly overreaching the distal margin of carpocerite and third antennular segment. The number of small spiniform setae near the distal margin of the uropodal exopod varied from one to nine (more frequently five). The number of thickened setae on penultimate segment of third maxilliped varied from one to three (more frequently two). The fingers of the minor chela are slightly longer or shorter than the palm. The number of spiniform setae on the ventromesial margin of merus of major chela varied from none to six (more frequently four); these setae seem to be easily lost. The form of the molar tooth (Fig. 2I) may be either more subtriangular or more subquadrate. The number of pairs of ventral spiniform setae on pereiopods 3 and 4 varied from five to eight (more frequently six pairs in both appendages). The number of single spiniform setae on ventral surface of pereiopod 5 ranged from three to eight (more frequently five).

**Distribution.** Western Atlantic: Bermuda; United States of America: Florida, Texas; Mexico: Yucatan, Isla of Cozumel, Bahía de la Ascension, Bahía del Espíritu Santo; **Belize**; Cuba; **Costa Rica**; Panama; Colombia: Providence Island; Curaçao; Bonaire; Porto Rico; Anguilla; Saint Kitts and Nevis; Barbuda; Antigua; Guadeloupe; Dominica; Saint Lucia Island;

**Barbados**; Tobago Cays; Trinidad and Tobago; Venezuela; Brazil: Ceará, **Pernambuco**, Bahia, Rio de Janeiro, Trindade and Martin Vaz Archipelago (Armstrong 1940; Chace 1972; Rodríguez 1980; Santos *et al*. 2012; Cunha *et al*. 2015; Anker *et al.* 2016; Pachelle *et al.* 2016; **this study**) (Fig. 3).

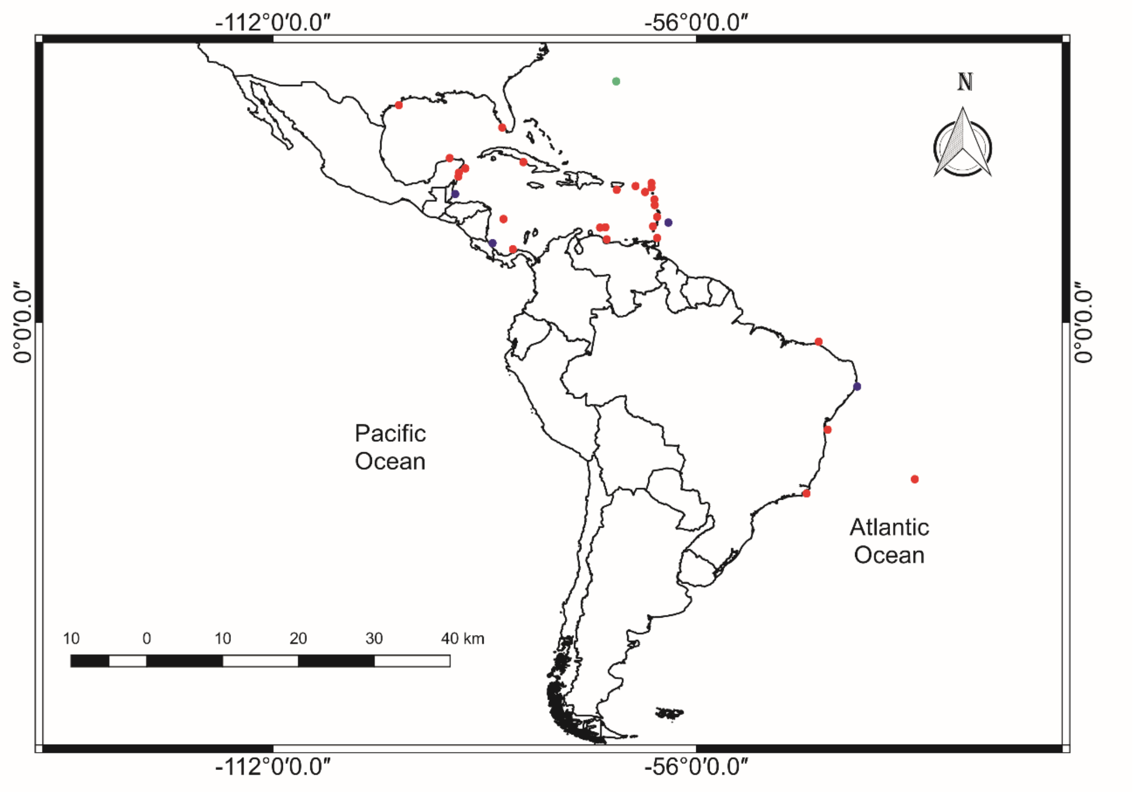

**FIGURE 3.** Current known distribution of the shrimp *Alpheus peasei* (Armstrong, 1940), based on the material examined in this study and on literature records. Green point: type-locality; Red points: occurrence reported previously; Blue points: new records.

**Ecology.** Found in intertidal areas up to **51.8 m** of depth (Hendrix 1971; Martínez-Iglesias *et al*. 1997; Anker *et al.* 2016; this study). Inhabits polychaete tubes, coral rubble, dead corals, and calcareous algae, and it is found under rocks or in rock crevices, among mangrove roots near the coast (Carvacho 1979; Santos *et al*. 2012), and occasionally in sponges of the genus *Callyspongia* (Chace 1956).

**Colour in life.** Body color ranges from greenish-yellow to reddish (Rodriguez 1986; Sterrer 1986; Anker *et al.* 2016). However, according to Anker *et al.* (2016), the large white spots with brown chromatophores on the major chela are an accurate diagnostic character. Fresh specimens examined by us were predominantly greenish-yellow. However, we also observed specimens with body and appendages transparent with reddish chromatophores (see Anker *et al.* 2016: 26, Fig. 8B). Eggs are olive green.

## Phylogenetic analysis and genetic distance

The corrected BIC determined the best-fitted substitution models. For COI the best substitution model was TIM2+G, assuming the nucleotide frequencies of A = 0.2790, C = 0.2387, G = 0.1927, and T = 0.2896 replacement rates of AC = 4.3098, AG = 5.7374, AT = 4.3098, CG = 1, CT = 17.1624, and GT = 1. The substitution model of variable sites was gamma distribution with shape parameter = 0.2850. For 16S the best substitution model was TPM3uf + G assuming the nucleotide frequencies of A = 0.2840, C = 0.1316, G = 0.2495, and T = 0.3349, replacement rates AC = 0.6000, AG = 2.7092, AT = 1, CG = 0.6000, CT = 2.7092, and GT = 1. The substitution model of variable sites followed a gamma distribution with shape parameter = 1.5380. The topologies obtained by the Bayesian Inference Analysis for both COI (Fig. 4A) and 16S markers (Fig. 4B) showed that *A. peasei* forms a well-supported clade with no subdivisions. *A. peasei* is clearly separated from other congeneric species of the *macrocheles* group. In both cases, the groups are well supported by high posterior probabilities.

There was no intraspecific divergence in *A. peasei* COI and 16S genes. The estimated interspecific divergence between *A. peasei* and other *Alpheus* species ranged from 28.4 to 28.8% (COI), and from 16.4 to 18.6% (16S).

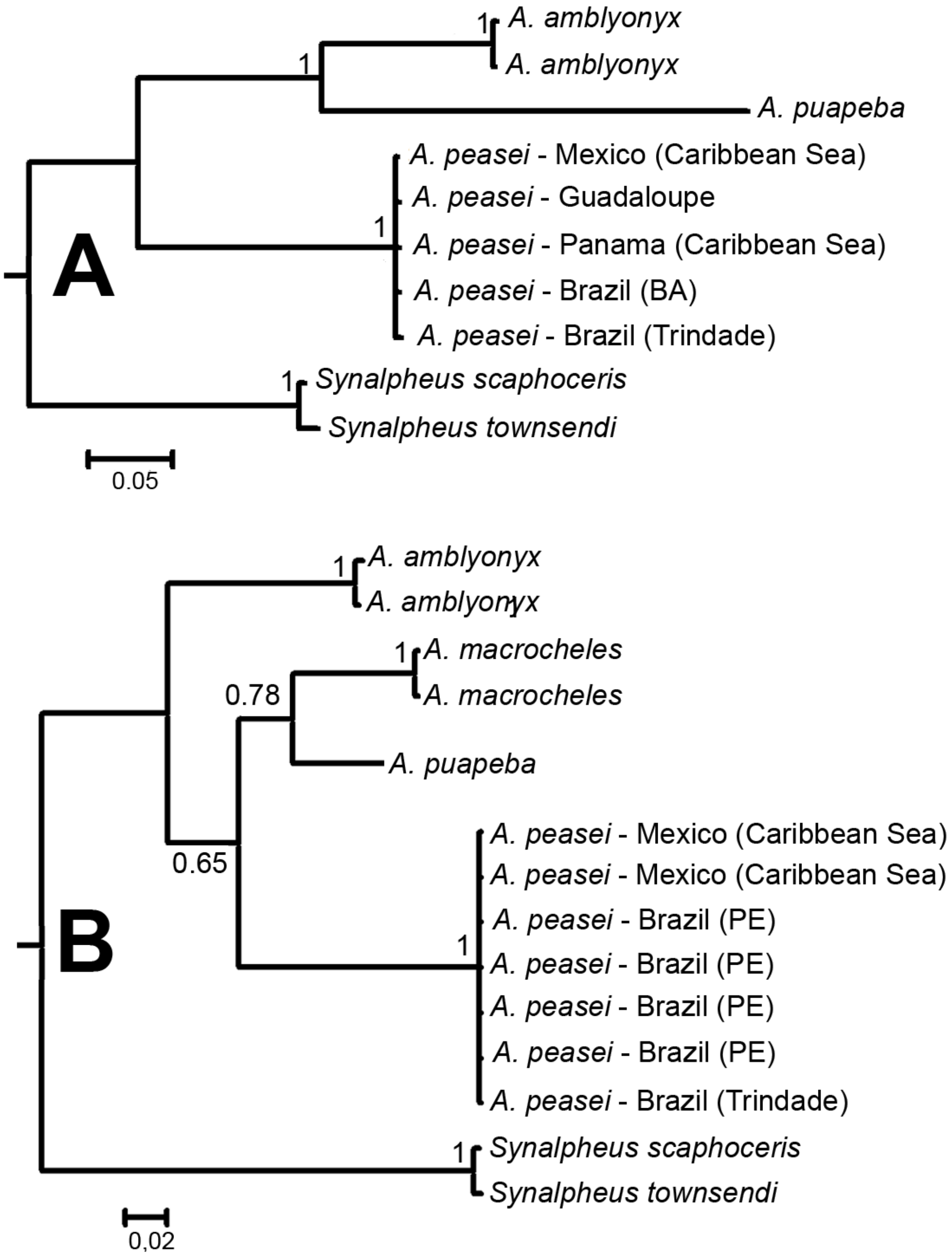

**FIGURE 4.** Phylogenetic trees of *Alpheus peasei* (Armstrong, 1940) and other species of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888. The trees were obtained using the Inference Bayesian analysis for (A) Cytochrome Oxidase I and (B) 16S mitochondrial genes. Numbers are posterior probabilities; values < 60% were not included.

## DISCUSSION

Specimens of *Alpheus peasei* formed a well-supported group, clearly separated from the congeners of the *Alpheus macrocheles* group (*A. macrocheles, A. amblyonyx* Chace, 1972 and *A. puapeba* Christoffersen, 1979). The molecular results agreed with the morphological ones, despite the observation of few morphological variations. The intraspecific genetic divergence was absent in both genes, whereas the interspecific divergence was high. Similarly, a low intraspecific divergence (0–0.08%) in the 16S gene was detected in the congeneric species *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013, *A. carlae* Anker, 2012, *A. estuariensis* Christoffersen, 1984, and *A. pontederiae* de Rochebrune, 1883 (Almeida *et al*. 2013). These results, coupled to the lack of morphological differences, support the hypothesis that individuals of *A. peasei* from its entire distribution range belong to a single taxon.

The phylogenetic trees of COI and 16S confirmed the values of genetic divergence and showed a consistent group, formed only by *A. peasei* specimens, supported by high posterior probabilities. Our results indicate the existence of gene flow between the northerwestern and southeastern Atlantic populations. Thus, there are no barriers for the gene flow and phenotypic plasticity (see morphological variability) may occur due to variation in environmental conditions (e.g., depth and substrate type).

For a long time, the estuaries of Orinoco and Amazon rivers were allegedly responsible for distribution gaps between the Caribbean Sea and South Atlantic Ocean in species such as *A. peasei* (Coelho & Ramos 1972; Briggs 1995). As such, the mouth of the Amazon River would be the main barrier for the propagation of corals in the north of Brazil (Leão *et al*. 2003). However, the only study about the distribution and diversity of corals in areas adjacent to the Amazon River mouth was conducted a long time ago by Laborel (1969; 1970). A recent evaluation revealed that the consolidated substrate of the Amazon River mouth extends for nearly 9500 km² (Moura *et al*. 2016). Thus, this region may be a connecting area for species associated with coral reefs (Moura *et al.* 2016) such as *A. peasei*. According to studies of reef fishes of families Serranidae and Carangidae (e.g., Floeter *et al.* 2008) and corals (e.g., Cordeiro *et al.* 2015), transgressions confirmed the connectivity between the Tropical Northwestern Atlantic and Tropical Southwestern Atlantic provinces. Since *A. peasei* is constantly associated with consolidated substrates such as corals, it would easily disperse through these areas. Limiting environmental factors, such as low salinity and high turbidity, would have no effect on its dispersion.

*Alpheus peasei* was one of the most abundant species in Trindade Island (Anker *et al.* 2016). Trindade Island and Martin Vaz Archipelago are located about 1200 km off the Brazilian coast and are the easternmost reef area of the Brazilian Biogeographic Province (Anker *et al.* 2016). These islands are under the main influence of the Brazil Current, which flows southwards along the Brazilian coast from 10°S to 38°S, reaching the Vitória-Trindade Seamounts Chain near 20.5°S (Stramma *et al.* 1990). These seamounts can act as stepping stones and promote the gene flow of *A. peasei* from continental waters, thus explaining its occurrence in Trindade. Although the larval stages of *A. peasei* (and of most of species of *Alpheus*) are not known (see Pescinelli *et al.* 2017 for a review), most marine animals have planktonic larvae that can be transported for long periods and large distances, and may even cross ocean barriers between continents (Thorson 1946, 1950; Scheltema 1988; Anger 2006). For instance, this phenomenon was recently demonstrated in the crab species *Sesarma rectum* Randall, 1840. Separated over 6000 km, its two populations are connected despite the presence of the strong physiological barrier created by the Amazon River freshwater plume (Buranelli & Mantelatto 2017).

Even though it is not possible to affirm that *A. peasei* has a continuous distribution, there is clearly a connectivity between the northwestern and southwestern Atlantic populations.

However, sampling in the North Brazil Shelf province and in other areas of the Brazilian coast are necessary to elucidate this question completely.

Our results extend the known distribution of *A. peasei* in the northwestern Atlantic (Barbados, Belize and Costa Rica) and provide a new record from the Brazilian coast (Pernambuco) (Fig. 3). In addition, the hypothesis of a species complex, or cryptic species, within *A. peasei* was rejected. There are at least two non-exclusive explanations for the gap (10°N − 2°S) seen in the geographic distribution of *A. peasei*: it may be an artifact due to the scarce samplings in the Equatorial Western Atlantic (Guyana, Suriname, French Guiana, and northern Brazil), and/or due to the passive dispersal by ocean currents during the larval development may carry them cross this gap and/or hamper the establishment there.

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ARTIGO II

# 3 MORPHOLOGY AND MOLECULAR EVIDENCES REVEALS HIDDEN PHYLOGENETIC DIVERSITY IN THE SNAPPING SHRIMP OF THE *Obesomanus* GROUP (CRUSTACEA: DECAPODA: ALPHEIDAE)

## ABSTRACT

The shrimps of the family Alpheidae include numerous complexes of cryptic species. Studies involving this problem made it possible to clarify the distribution of some species that primarily had a controversial geographical distribution. *Alpheus simus* is a shrimp that occurs in the western Atlantic, where its known distribution is disjoint: from Florida to the south of the Caribbean Sea and in Brazil, from Rio Grande do Norte to Bahia, a configuration that can indicate the existence of a complex of species. When examining a set of specimens identified as *A. simus* it was verified that the material from Bahia had different morphological characters, which resulted in the discovery and description of a new species of shrimp of the genus *Alpheus* genus, based on morphological and molecular evidence. The specimens were collected at the Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil. ***Alpheus* sp. nov.** belongs to the group *A. obesomanus* and is morphologically similar to *A. simus* (Atlantic northwest) and *A. saxidomus* (Eastern Pacific). However, it differs from these, mainly in stylocerite and scaphocerite length and by a large gap between cephalothorax and pleura of first abdominal somite. Molecular analysis using mitochondrial gene Cytochrome Oxidase subunit I confirms the existence of a new species derived from the species complex involving *A. simus* sensu stricto.

Key-words: Crustacea – cryptic species – Decapoda – *obesomanus* group

## INTRODUCTION

Cryptic species are defined when two or more species are classified as a single nominal species, because they are difficult to recognize using traditional systematic methods (Bickford *et al*., 2007). Occurrence of cryptic species in marine habitats is common (Knowlton, 1993) and has been documented in several groups such as polychaetes (Westheide & Schmidt, 2003), ascidians (Bock *et al*., 2012), cnidarians (Moura *et al*., 2008), mollusks (Vrijenhoek *et al*., 1994), fish (Colborn *et al*., 2001) and crustaceans (Knowlton, 1986). Inaccurate identifications involving cryptic species may result in equivocal investigations about behavior, ecology, physiology and species distribution (Knowlton, 1986).

Gaps in the distribution of some cryptic species of crustaceans have been the subject of studies to test the legitimacy of this distribution (e.g., Morrone & Lopretto, 1994; Santos & D'Incao, 2004; Jesse *et al*., 2009). In shrimps, the use of integrative taxonomy revealed an unknown biodiversity and elucidated the actual occurrence of some species with a wide geographic distribution, sometimes reported in different ocean basins (e.g., Williams *et al*., 2001; Anker & Pachelle, 2013; Hurt *et al*., 2013; Salgado-Barragán *et al*., 2014; 2017).

The caridean shrimps of the family Alpheidae Rafinesque, 1815 comprises more than 600 species (De Grave & Fransen, 2011). With a total of 313 valid species the genus *Alpheus* Fabricius, 1798 comprises the highest diversity among alpheids (De Grave & Fransen, 2011; Komai & Ohtomi 2018; Dehghani *et al.,* 2018). Species of *Alpheus* are an important component of benthic fauna in tropical and subtropical marine habitats and live from the intertidal zone to high depths (Chace, 1988; Anker *et al*., 2006). Those shrimps can be found under rocks, in dead coral crevices (Santos *et al*., 2012), sponges (Anker *et al*., 2012; Anker & Pachelle, 2014) and soft substrates such as mangroves and estuaries (Crosnier & Forest, 1966).

The western Atlantic *A. simus* Guérin-Méneville, 1856 [in Guérin-Méneville, 1855-1856] (type locality Cuba) belongs to *obesomanus* group, with currently 11 species grouping based on the following morphological characteristics:: absence of rostrum and orbital teeth; ocular peduncles devoid of processes; short antenna; major chela, inflated, presenting oval or cylindrical shape, with hammer-shaped dactylus; minor cheliped never with "balaeniceps" setae; second pereiopods are often elongated and asymmetrical (Anker, 2001). *Alpheus simus* is a rock boring shrimp, living endolithically in cavities of living and dead coral rocks (Grajal & Laughlin, 1984; Werding, 1990; Santos *et al*., 2012). The species occur from 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* Armstrong, 1949; Bezerra & Almeida, 2008; Santos *et al*., 2012). However, there is a substantial latitudinal gap in the species distribution which includes the North Brazil Shelf province (Spalding *et al*., 2007), from Curaçao to Rio Grande do Norte (Brazil) (approx. 16 degrees of latitude).

Based on previous information about distribution gaps of *A. simus*, the aim on this contribution is to test the hypothesis of existence of cryptic species in this taxon using morphological and molecular data.

## MATERIAL AND METHODS

### Morphological analysis

The material analyzed are 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); Museu de Zoologia da Universidade Estadual de Santa Cruz, Bahia, Brazil (UESC); Naturalis Biodiversity Centre, Leiden, the Netherlands (RMNH); National Museum of Natural History, Smithsonian Institution, United States of America (USNM); Muséum National d'Histoire Naturelle, France (MNHN) and Museo de Zoología de la Universidad de Costa Rica, Costa Rica (MZUCR). Abbreviations used: (m) meters, (P) pereiopod.

Additional material was collected in April 2012 and May 2013 at the Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil in fragments of the fire coral *Millepora alcicornis* Linnaeus, 1758. Samples were taken from the bottom of a reef bank at depths of 1–12 m through scuba diving. The sample procedure consisted in the use of hammer and chisel to remove the fragments attached to the colonies and some fragments of dead coral rubble were collected on the bottom. Both, after removal, were individually wrapped in tissue bags to avoid the escape of possible organisms. Knowing that some shrimps have an endolithic habit, in the laboratory the fragments obtained were carefully broken in order to find specimens. The specimens obtained were anesthetized with 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®.

### DNA extraction, PCR amplification and Sequencing

The methodological process followed the protocols proposed by Mantelatto *et al*. (2006; 2007; 2009) with adjustments when necessary. For DNA extraction, the pleonaltissue was placed in a 1.5 ml tube and then incubated for 24h in 600 μl lysis buffer and 10 μl Proteinase K (20 mg/ml) at 55°C in the dry bath. After 24h, the samples were taken from the dry bath and placed on ice for 10 minutes. The proteins were then separated by the addition of 200 μl of ammonium acetate (7.5M) previously to centrifugation. DNA was precipitated by the addition of 600 µl cold isopropanol (-20°C) followed by centrifugation; the resulting pellet (after 48 h of resting at -20°C) was washed with 15 µl of 70% ethanol, dried, and resuspended in 20 µl TE buffer. The concentrations of DNA obtained in the samples were quantified using the Nanodrop 2000 Spectrophotometer.

The region of the mitochondrial Cytochrome Oxidase I (COI) gene was amplified by Polymerase Chain Reaction (PCR) (Sambrook *et al*., 1989) using the primers COL6B2 (5'-ACAAATCATAAAGATATYGG-3') and COH6 (5'-TADACTTCDGGRTGDCCAAARAAYCA-3') (Mantelatto *et al*., 2016; Schubart & Huber, 2006, respectively). Reactions products were obtained in a 25 µl volume reaction containing distilled and deionized $H_2O$, PCR Buffer (10X), $MgCl_2$ (25 mM), betaine (5 M), DNTPs, primers, *Thermus aquaticus* polymerase and DNA previously extracted (50 ng) in a Veriti Thermal Cycler (Applied Biosystems) with specific thermal cycles for the primer set. The results of PCR reactions were observed in 1.5% agarose gel electrophoresis stained with Gel Red ™ and in a UVP Transilluminator M20 UV transilluminator. PCR products were purified with the SureClean® Purification Kit, the Big Dye® Terminator Cycle Sequencing (Applied Biosystems) was used in sequencing reaction. The sequencing took place in ABI 3100 Genetic Analyzar® automatic sequencers of the Departamento de Tecnologia da Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal, Universidade Estadual Paulista.

All sequences were confirmed by sequencing both strands. Editing and consensus were performed using the program BioEdit v7.0.9.0 (Hall, 1999). The DNA fragments obtained from the methodology employed were submitted to alignment in the BLAST system for comparison with the assembly of the NCBI database (http://blast.ncbi.ncbi.nlm.nih.gov/blast.cgi) aiming to confirmation of their respective identities. Some sequences of *Alpheus simus* and of other congeneric species of the *obesomanus* group were obtained from GenBank or Barcode of Life Data System v4 (BOLD) for comparison (Table 1). Sequences of the genus *Synalpheus* Spence Bate, 1888 retrieved from Genbank was used as outgroupt (Table 1).

Sequence alignment was performed in the MUSCLE (Multiple Sequence Comparison by Log- Expectation) (Edgar, 2004), available on the platform Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller *et al*., 2010). The substitution model best fit the data was calculated with jModelTest software (Darriba *et al*., 2012), implemented in the CIPRES platform, using Bayesian information criterion (BIC). MrBayes v3.2.6 (Ronquist *et al*., 2012), implemented in the platform CIPRES, was used to carried out the Bayesian Inference analysis with the parameters obtained in 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 races were performed and the convergence of races was analyzed using Tracer 1.6 software (Rambaut *et al*., 2014). The first 15% of trees and parameters were discarded (burn-in) and a final tree was generated in Tree Annotator software 1.8.4 (implemented in the BEAST package, Drummond *et al*., 2012). A posteriori probability values greater than 60% were reported. A matrix of genetic divergence was made by the Kimura 2 parameter model (K2P) (Kimura, 1980) in the MEGA v6 software (Tamura *et al*., 2013). Sequences resulting from this study will be deposited in GenBank.

**Table 1.** List of specimens of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888 used in genetic analyses with Cytochrome Oxidase I mtDNA.

| **Species** | **Locality** | **GenBank or BOLD** | **Reference** |
|---|---|---|---|
| *Alpheus armatus* Rathbun, 1901 | Caribbean Sea | KF131481 | Hurt *et al*. (2013) |
| *Alpheus formosus* Gibbes, 1850 | United States | KP254069 | Leray & Knowlton, (2015) |
| *Alpheus idiocheles* Coutière, 1905 | French Polynesia | MBMIA293-06 | |
| *Alpheus idiocheles* | French Polynesia | MBMIA294-06 | |
| *Alpheus immaculatus* Knowlton & Keller, 1983 | Caribbean Sea | KF131503 | Hurt *et al*. (2013) |
| *Alpheus lottini* Guérin-Méneville, 1838 | New Caledonia | KY746843 | Rouzé *et al*. (2017) |
| *Alpheus lottini* | New Caledonia | KY746854 | Rouzé *et al*. (2017) |
| *Alpheus malleator* Dana, 1852b | Panama-WA | FJ013923 | Hurt *et al*. (2009) |
| *Alpheus malleodigitus* (Spence Bate, 1888) | French Polynesia | MBMIA627-06 | |
| *Alpheus malleodigitus* | French Polynesia | MBMIA628-06 | |
| *Alpheus obesomanus* Dana, 1852b | French Polynesia | MBMIA360-06 | |
| *Alpheus obesomanus* | French Polynesia | MBMIA361-06 | |
| *Alpheus obesomanus* | French Polynesia | MBMIA402-06 | |
| *Alpheus polystictus* Knowlton & Keller, 1985 | Caribbean Sea | KF131508 | Hurt *et al*. (2013) |
| *Alpheus roquensis* Knowlton & Keller, 1985 | Venezuela | KF131529 | Hurt *et al*. (2013) |
| *Alpheus roquensis* | Venezuela | KF131530 | Hurt *et al*. (2013) |
| *Alpheus saxidomus* Holthuis, 1980 | Panama-EP | FJ013934 | Hurt *et al*. (2009) |
| *Alpheus saxidomus* | Panama-EP | FJ013932 | Hurt *et al*. (2009) |
| *Alpheus saxidomus* | Panama-EP | FJ013931 | Hurt *et al*. (2009) |

| | | | |
|---|---|---|---|
| *Alpheus saxidomus* | Panama-EP | FJ013930 | Hurt *et al*. (2009) |
| *Alpheus saxidomus* | Panama-EP | FJ013929 | Hurt *et al*. (2009) |
| *Alpheus saxidomus* | Panama-EP | FJ013934 | Hurt *et al*. (2009) |
| *Alpheus simus* Guérin-Méneville, 1855 | Panamá-WA | FJ013948 | Hurt *et al*. (2009) |
| *Alpheus simus* | Panama-WA | FJ013946 | Hurt *et al*. (2009) |
| *Alpheus simus* | Panama-WA | FJ013945 | Hurt *et al*. (2009) |
| *Alpheus* sp.nov. | Bahia | pendent | This study |
| *Alpheus* sp.nov. | Bahia | pendent | This study |
| *Alpheus* sp.nov. | Bahia | pendent | This study |
| *Synalpheus fritzmuelleri* Coutière, 1909 | Jamaica | KJ595081 | Hultgren *et al*. (2014) |
| *Synalpheus townsendi* Coutière, 1909 | São Paulo | KU313018 | Almeida *et al*. (2018) |

## RESULTS

### TAXONOMY

Family Alpheidae Rafinesque, 1815

Genus *Alpheus* Fabricius, 1798

***Alpheus* sp. nov.**

(Figs. 1–3)

*Thunor rathbunae*– Christoffersen, 1979: 355.

*Alpheus simus*–Bezerra & Almeida, 2008: 1; Santos *et al*., 2012: 154, fig. 4B; Soledade & Almeida, 2013: 105, fig. 6F; Almeida *et al*., 2016: 66.

*Type specimens:* Brazil, Bahia. **Holotype:** 1 female (CC 7.3 mm), 13.IV.2012, Porto Seguro, Parque Municipal Marinho Recife de Fora, colls. G.M. Reuss Strenzel, G.O. Soledade. P.S. Santos, L.M. Fernandes & I. Matos, on dead portions of *M. alcicornis*, MZUSP 36753. **Paratypes**: 1 female (CC 6.1 mm), 13.IV.2012, same data as holotype, MZUSP 36754; 1 female, 13.IV.2012, same data as holotype, on living portions of *M. alcicornis*, MOUFPE 18747; 1 female (CC 6.9 mm), 06.V.2013, Porto Seguro, Parque Municipal Marinho Recife de Fora, colls. G.M. Reuss Strenzel, G.O. Soledade, P.S. Santos, L.M. Fernandes & J.C. Viaggi, on living portions of *M. alcicornis*, MOUFPE 18748; 1 male (CC 4.2 mm), 06.V.2013, Porto Seguro, Parque Municipal Marinho Recife de Fora, colls. G.M. Reuss Strenzel, G.O. Soledade, P.S. Santos, L.M. Fernandes & J.C. Viaggi, on dead coral rubble, MOUFPE 18749; 1 male, 1 female, Santa Cruz Cabrália, Coroa Vermelha Beach, 22.III.2011, colls. P.S. Santos, G.O. Soledade, A.O. Almeida, salinity 36, on dead portions of

*M. alcicornis*, UESC 1411; 1 female, Porto Seguro, Mutá Beach, 25.IX.2011, colls. P.S. Santos, G.O. Soledade, A.G.L.M. Pedra, salinity 40, on dead portions of *M. alcicornis*, UESC 1503; 1 male, 1 ovigerous female, Bahia, Abrolhos Archipelago, Parcel de Paredes, 1982, MNRJ 15400; Rio Grande do Norte, 1 male, Maxaranguape, Parrachos de Maracajaú, 12.II.2004, coll. T.M. Garcia, 3–4 m, on *M. alcicornis*, UESC 995.

**Comparative material.** *Alpheus simus*: WESTERN ATLANTIC–**USA.** 1 ovigerous female, Florida, Looe Key Reef, 10.IX.1958, coll. E.L. Pierce, USNM 102355. **Mexico.** 8 males, 12 (10 ovigerous) females, 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, colls. R. Lemaitre, C.C. Tudge, D.L. Felder, J.M., Felder, S. Pecnick, 4.II.2011, USNM 1153629; 1 female, Carrie Bow Cay, in cavities under zoanthid, colls. D.L. Felder, J.M, Felder, S. de Grave, B. Thoma, E. Palacios Theil, S. Collier, 23.II.2009, USNM 1292514. **Costa Rica.** 1 male, 2 ovigerous females, Limón, Parque Nacional Cahuita, Ciesta Interna, coll. J. Cortés, 01.VI.1984, in coral reef, URC 2186–01. **Panama.** 2 females, Caribbean, Isla Grande, Off W. Point, colls. A. Anker, C. Hurt, 06.X.2005, in coral reef, MZUSP 33122. **Colombia.** 1 female, Cartagena, Playa Mohan Baru, MNHN 15651; 10 males, 16 females (15 ovigerous), Islas del Rosario, North of Isla Grande, coll. G.R. Navas, 14.IV.1991, 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, coll. C.C. Nutting, 18.V.1918, 146 m, USNM 68740; 3 males, 6 (3 ovigerous) females, Okra Reef, coll. C.C. Nutting, 13.V.1918, USNM 57937. **Netherlands Antilles.** 1 male, 1 female, Curaçao, Psicaderabaai, coll. J.C. den Hartog, 24.II.1972, RMNH.CRUS.D.30377.

*Alpheus saxidomus*: 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, coll. W.L. Schmitt, 11.II.1933, USNM 237094; 2 males, 1 ovigerous female, Isabela Island, Tagus Cove, 14.II.1934, USNM 237089; 2 males, Espanola

Island, in *Pavona* sp., 17.XII.1934, USNM 237095. **Costa Rica.** 1 male, Nicoya, Playa Montezuna, colls. F.L.M. Mantelatto, I.S. Werthman, I. Miranda, M. Terossi, P. Hernáez, CCDB 3491. **Panama.** 3 males, 3 ovigerous females, Secas Islands, coll. W.L. Schmitt, 4.II.1935, USNM 237075; 1 male, Secas Islands, coll. W.L. Schmitt, 4.II.1935, 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, dredge, 37 m, 14.II.1934, USNM 237079; 1 female, Choco, Ensenada de Utria, coll. G. Ramos, 28.VIII.1984, USNM 259390; 1 male, 1 female, Málaga Bay, under rocks, G. Ramos, 25.II.1983, USNM 244242.

**Diagnosis:** Rostrum and orbital teeth absent. Stylocerite shorter than half length of visible part of first antennular segment. Antenna unarmed. Scaphocerite short, rounded, without distal spine in females, reaching proximal margin of carpocerite; presence of distal spine in males and overreaching proximal margin of carpocerite. Large gap between cephalothorax and pleura of first abdominal somite.

**Description:** (based on female holotype, Brazil, Bahia, Parque Municipal Marinho Recife de Fora, Porto Seguro, 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 deeply. Eyes well pigmented, completely covered by ocular hoods in dorsal and lateral views (Fig. 1A-C).

Pleonal somites smooth; posteroventral margin of pleurae from 1–5 rounded, sixth pleura semi-triangular, without articulated plate; large gap between cephalothorax and pleura of first abdominal somite; cardiac notch well-developed. (Fig. 1D). Telson (Fig. 1E, F) tapering distally, proximal region about 4.2 times wider than distal; without dorsal spiniform setae; pair of tiny spiniform setae near to lateral margin of telson than midline; distal margin of telson narrow and straight; with three pairs of spiniform posterolateral setae, lateral about 2 times as long as mesial and 1.3 times as long as inner, anal tubercles well-developed. Uropods (Fig. 1E) with bifid protopods, each lobe ending in two rounded tip; exopod longer than endopod; diaeresis absent; lateral margin of exopod slightly convex proximally and straight distally; with one stout adjacent tooth, separated by slender distolateral dark-colored spiniform setae, overreaching distal margin of exopod; noticeably longer than adjacent tooth.

Second antennal segment about 4 times longer than first and third segment. Stylocerite short and rounded distally, not reaching half of the visible part of first antennular segment. Antenna unarmed. Scaphocerite short, rounded, without distal spine in the female, reaching proximal margin of the carpocerite; distal spine presence in the male and overreaching proximal margin of the carpocerite; blade absent in both. Carpocerite smaller than half of second antenular segment (Fig. 1A-C).

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 largest than both laciniae, extremities rounded and lateral margin convex. First maxilliped (Fig. 1J) palp approximately 3.5 times longer than narrow, truncated tip; 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, when extended forward, overreaching more than half of second antennal segment; last segment 1.6 times longer than penultimate; and with many transverse rows of stiff setae; antepenultimate segment slightly longer than last; exopod extends beyond the distal end of penultimate segment and ends with long setae; epipod present. Pleurobranch and epipod present from pereiopods first to fourth.

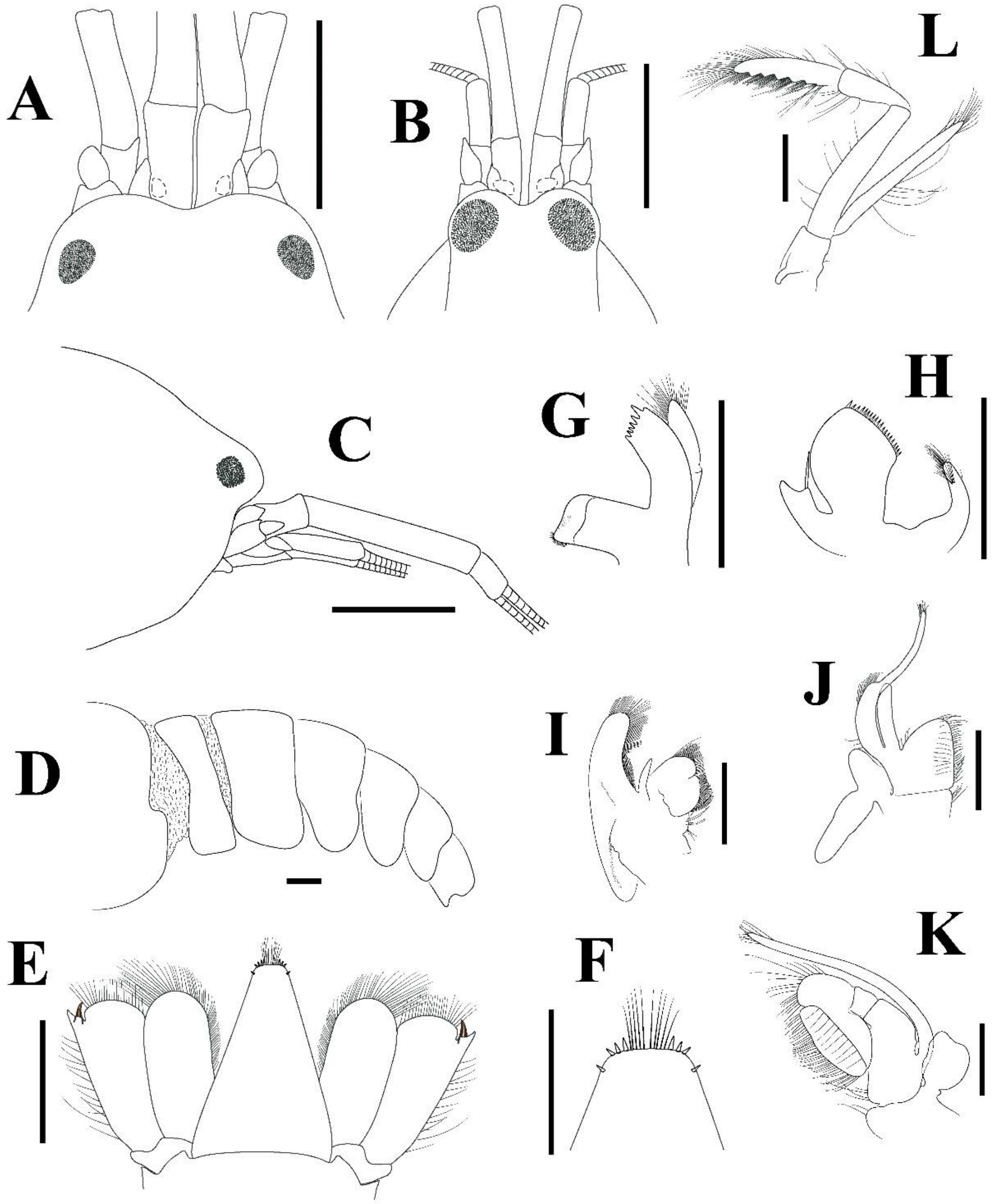

**FIGURE 1.** ***Alpheus*** **sp. nov.** Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil: A, C-F, female holotype (MZUSP 36753); B, male paratype (MOUFPE 18749); G-L, female paratype (MZUSP 36754, dissected); (A) frontal region and cephalic appendages, dorsal view; (B) same, male dorsal view; (C) frontal region and cephalic appendages, lateral view; (D) posterior region of carapace and abdomen, 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.

The left and right first pereiopods very unequal. Major cheliped female (Fig. 2A-C) long palm, about 5.7 times as long as dactylus and 3.2 times as long as greatest height; greatest height is in the proximal third of palm, gradually narrows anteriorly dorsal view with shallow furrow, smooth mesial and lateral view with deep furrow on distal third on both sides, ends with distal upper lobe; truncated lobe distoventral, sometimes denticle (Fig. 2D).

Major cheliped male (Fig. 2C) relatively slenderer and more cylindrical. Dactylus such as female, but palm is about 4.8 times as long as dactylus, almost 3.7 times as long as its greatest height; height is practically the same over the full length of palm, which is not inflated in basal part as in female. In other aspects there are no conspicuous differences in the major chelipeds of two sexes. Dactylus strongly curved and hammer-shaped, ends in a blunt rounded apex directed down over tip of pollex. Pollex shorter than dactylus (about half), has numerous long, rigid setae at distal margin. Carpus short, cup-shaped, being 5.8 times (in the female) and 6.4 times (in the male) palm length, reaching less than half the length of merus, as long as ischium. Ischium short, stout and unarmed. There are no spines or teeth visible in any of the cheliped segments (Fig. 2A-C).

Minor cheliped (Fig. 3E) simple, slender fingers; approximately 1.5 palm length. Fingertips sharp, curved, obscurely bifid (Fig. 2F). Fingers in no sex with "balaeniceps" setae. Palm cylindrical, without teeth or grooves, about 4 times longer than higher. Carpus cup-shaped, about 3.4 and merus 1.1 times palm length. Ischium very short, visibly shorter than carpus. Segments without teeth or spines.

Second pereiopod slender (Fig. 2G), right visibly shorter than left. Fingers short and simple, approximately 1.3 times palm length. Carpus about 4 times longer than chela; five-segmented, 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. Ischium short, about 3 times merus length.

Third (Fig. 2H) and fourth (Fig. 2J) pereiopods long, similar in shape and length; Dactylus slender and simple; propodus about 5 times longer than dactylus and with 4 strong spines in posterior margin and one distal pair; carpus visibly longer than propodus; merus 1.5 times longer than propodus, without ventrodistal tooth. Ischium, merus and carpus unarmed.

Fifth pereiopod (Fig. 2I) shorter than P3 and P4; If stretched, dactylus exceeds first antennular segment; propodus about 6 times longer than dactylus; with 1 ventral spiniform setae and transverse rows of setae on lateral margin; carpus about 1.2 times propodus length; merus visibly shorter than propodus; ischium, merus and carpus unarmed.

Pleopods with sparse setae on lateral margin of protopodite; endopod and exopod with densely setose edges; first pleopod (in female) with short endopod and distal margin ornamented with setae; first pleopod (in male) short and narrow. Second pleopod in male with wide *appendix masculina*; longer than inner appendix, ornamented with numerous setae.

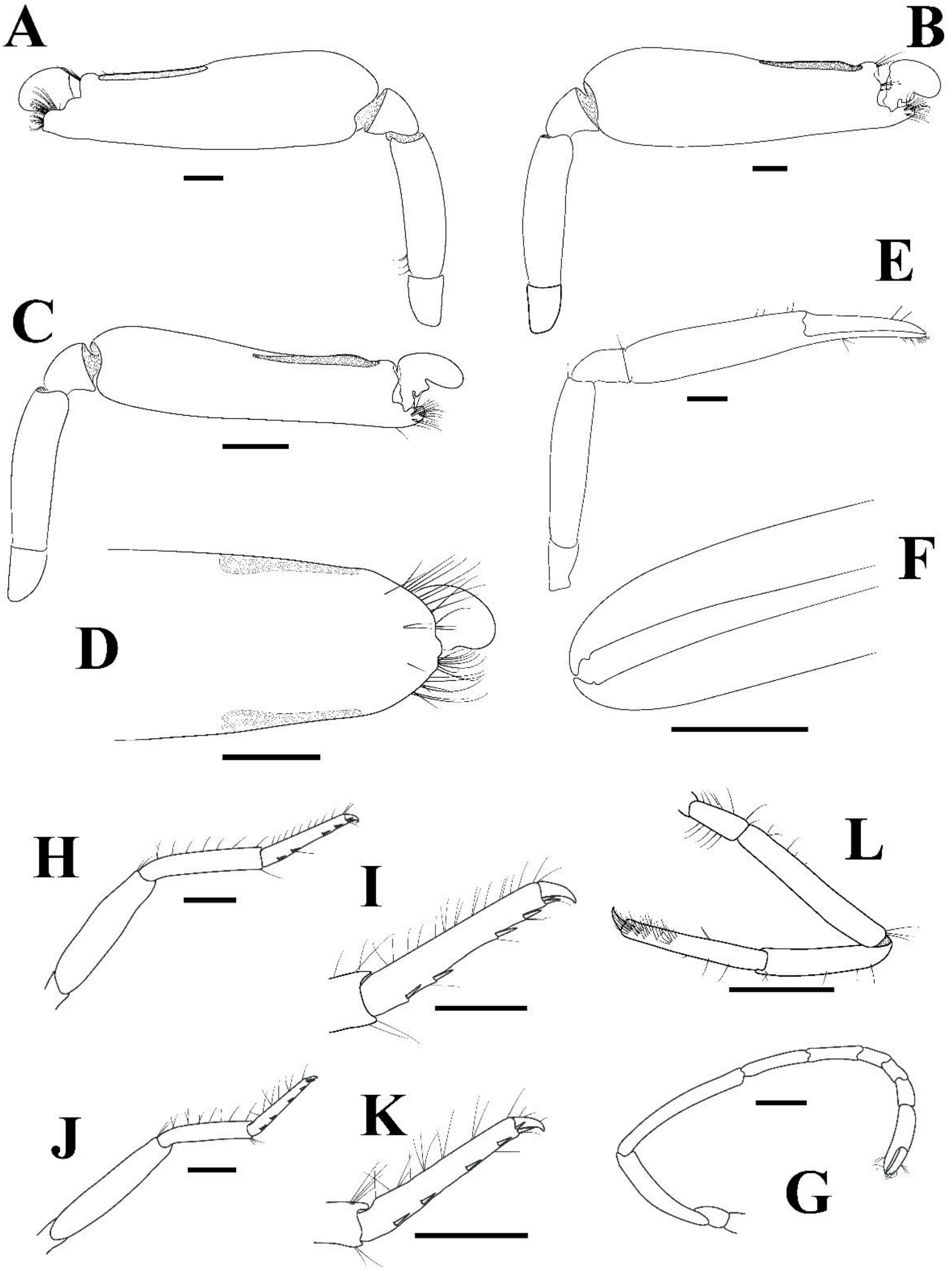

**FIGURE 2.** ***Alpheus*** **sp. nov.** Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil: A, B, D-J, female holotype (MZUSP 36753); C, male (MOUFPE 18749). (A) major chela, mesial view; (B) same, lateral view (C) male major chela, lateral view; (D) detail of major chela, ventral view; (E) minor chela, lateral view; (F) minor chela, detail of tip of fingers, ventral view; (G) second pereiopod, lateral view; (H) third pereiopod, lateral view; (I)

same, detail of dactylus and propodus; (J) fourth pereiopod, lateral view; (K) same, detail of dactylus and propodus; (L) fifth pereiopod, lateral view. Scale bars = 1 mm.

**Morphological variation.** The scaphocerite in females presented two forms: (1) reaching about half length of first antennular segment, with a short distal tooth and very reduced blade; (2) shorter that half length of first antennular segment, without distal tooth (Fig. 1A). Scaphocerite elongate in males, slightly overreaching the distal margin of the first antennular segment, with a small distal tooth (Fig. 1B) and a little developed blade. The number of ventral spiniform setae on propodus of the pereiopods 3 and 4 ranged from four to six (more frequently four). The number of distolateral spiniform setae on uropodal exopod ranged from one to two (more frequently one). The female's eyes are smaller than male and the distance between the eyes is visibly larger in female than male.

Differences between characters in the new species and other two near, have been observed (Table 2).

**Table 2.** Characters useful for separation of *Alpheus* sp. nov. and morphologically similar species of *Alpheus* Fabricius, 1798. *****Mostly based on comparative material cited above and ******based on comarative material, illustrations and description provied by Holthuis, 1980.

| Characters/Species | *Alpheus* sp. nov | *Alpheus simus* (mostly | *Alpheus saxidomus* |
|---|---|---|---|
| Rostrum | Absent | Absent | Absent or vestigial |
| Relative length of the second antennular segment | Around 4 times as long as visible part of frst | Around 3 times as long as visible part of frst | Around 2.5 times as long as visible part of frst |
| Propodus spines (not included in this count is the distal pair) | 4 to 6 | 3 or 4 | 5 or 6 |
| Shape of distolateral spiniform seta of uropodal exopod | Slender | Slender | Stout |
| Colour of distolateral spiniform seta uropodal exopod | Dark brown or black and uncoloured | Uncoloured | Dark brown or black |
| Diaeresis | Absent | Absent | Present |
| Depth | 1-12m | 2-146 m | 02-12 m |
| Distribution | Eastern Pacific | South Florida to Caribbean Sea | Northwestern Brazil |

**Color pattern.** Body semi-transparent, some specimens with reddish chromatophores, mainly on cephalothorax (Fig. 3A); palm, distal margin of chelipeds and second pereiopod pale yellowish, P2 also shows dark yellow coloration on articulations (Fig. 3B). Was also observed dark-brown, black or not pigmented distolateral spiniform setae in the uropodal exopod.

**FIGURE 3.** ***Alpheus* sp. nov.** Parque Municipal Marinho do Recife de Fora, Porto Seguro, Bahia, Brazil: (A) specimen retrieved from a dead coral fragment.; (B) color pattern.

**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 of living and dead coral of the fire coral *Millepora alcicornis* and coral rubble (Fig. 3A, B); depth range 1–12 m.

## Genetic and Phylogenetic analyses

The best-fitted substitution model, selected with a corrected Bayesian information criterion, was: GTR+I+G assuming the nucleotide frequencies A = 0.3622, C = 0.2670, G = 0.0996, T = 0.2712, replacement rates AC = 0.0899, AG = 6.8412, AT = 0.2764, CG = 0.3997, CT = 3.6794, GT = 1, substitution model variable sites followed a gamma distribution with shape parameter = 0.5590, invariable sites = 0.4880;

The topology obtained by the Bayesian Inference analysis (Fig. 4) showed a clear separation of the specimens of ***Alpheus* sp. nov.** from the other analyzed species. This analysis included other species of the *A. obesomanus* group, with morphological similarities to the new species, such as *A. malleodigitus*, *A. obesomanus*, *A. idiocheles*, *A. simus* and *A. saxidomus*.

Therefore, the genetic analysis corroborated the morphological results and confirmed the validity of ***Alpheus* sp. nov.**. The intraspecific genetic divergence was null. The estimated interspecific variation between specimens of ***Alpheus* sp. nov.** and other species of *Alpheus* ranged from 11.4 to 23.6% Finally, the close morphological resemblance and genetic differences between *A. simus* (12.9 to 14.6%), *A. saxidomus* (11.4 to 12.4%) and ***Alpheus* sp. nov.**, indicate that they are cryptic taxa.

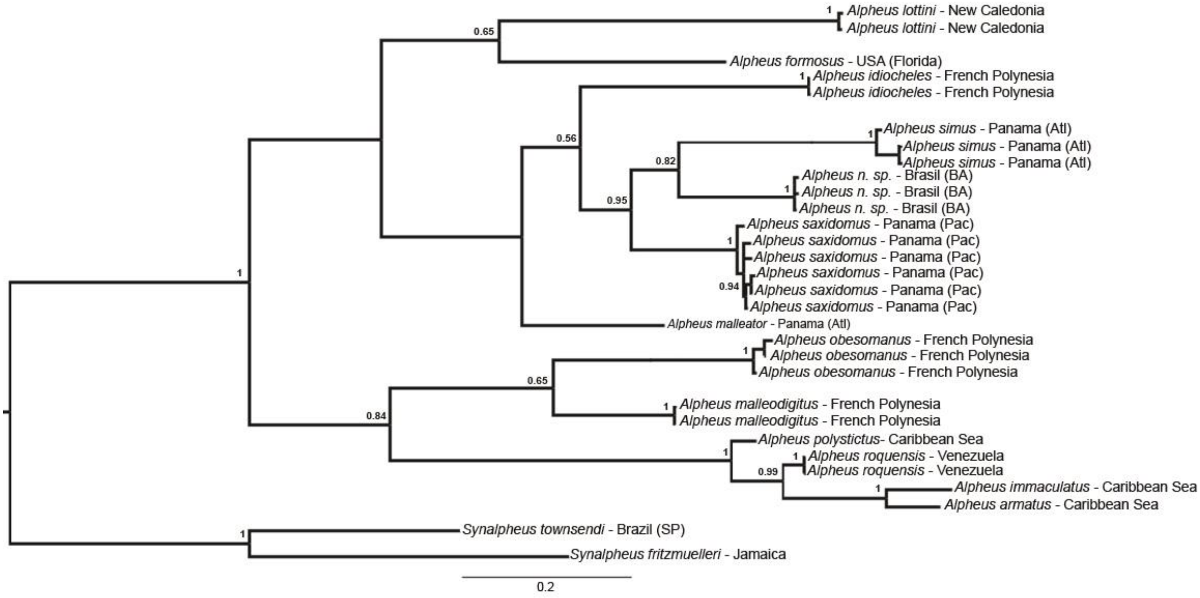

**FIGURE 4.** Phylogenetic tree of ***Alpheus* sp. nov.** and other species of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888, using the Inference Bayesian analysis for Cytochrome Oxidase I. Numbers are support values for posterior probabilities; values < 60% were not included. Abbreviations: USA, United States of America; BA, Bahia; Atl, Atlantic Ocean; Pac, Pacific Ocean.

## DISCUSSION

The analysis of 54 morphological characters associated with molecular analysis confirms the similarities among ***Alpheus* sp. nov.** (northwestern Atlantic), *A. simus* (southwestern Atlantic) and *A. saxidomus* (eastern Pacific), confirming the existence of a complex of species involving such species.

***Alpheus* sp. nov.** differs from *A. simus* and *A. saxidomus* by the narrow and elongated anterior part of epipod of the first maxilliped, aprox. 3 times as long as broad [vs. 2 times as long as broad in *A. simus* and aprox. 2.5 times as long as broad in *A. saxidomus*]. The scaphocerite in ***Alpheus* sp. nov.** reaches or is slightly shorter half length of the visible part of the first antennular article and absence of blade [vs. scaphocerite elongate, reaching half length of the second antennular segment and presence of blade in *A. simus* and *A. saxidomus*]. ***Alpheus* sp. nov.** has a large gap between cephalothorax and pleura of first abdominal somite [vs. absence of gap in *A. simus* and absence or presence of a small gap in *A. saxidomus*].

Additionally, ***Alpheus* sp. nov.** differs form *A. saxidomus* by the presence of three pairs of posterolateral spiniform setae on telson (vs. two pairs in *A. saxidomus*); spiniform setae absent on dorsal surface of telson (vs. two pairs in *A. saxidomus*). The new species shares with *A. saxidomus* spiniform setae on the propodus of the fifth pereiopod and with *A. simus* the absence of diaeresis on the exopod of the uropod. No sexual dimorphism was found in spiniform setae in the uropodal exopod (male with shorter and broader setae than female) as observed in *A. saxidomus* (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) matches very well with ***Alpheus* sp. nov.**.

The new species formed a well-supported group, with distinct separation among the congeners belonging to the *A. obesomanus* group, *A. simus*, *A. saxidomus*, *A. malleodigitus*, *A. obesomanus* and *A. idiocheles*. The intraspecific variation among all specimens of the genus *Alpheus* ranged from 0 to 0.5. Furthermore, ***Alpheus* sp. nov.** is genetically distinct (COI gene) from the species that are morphologically more related (*A. simus* and *A. saxidomus*) supporting the establishment of the new species (Fig. 4).

Several studies using the gene COI have been revealed its potential for the validation of species and the recognition of cryptic biodiversity (e.g. Williams *et al*., 2001; Anker *et al*., 2008; Hurt *et al*., 2009; Hultgren *et al*., 2014). The phylogenetic tree generated by Bayesian Inference analysis showed a clear separation of the specimens of ***Alpheus* sp. nov.** from the other analyzed species. The genetic distances estimated among the specimens of ***Alpheus* sp. nov.** and other species of *Alpheus* ranged from 11.4 to 23.6. Although ***Alpheus* sp. nov.** is morphologically very similar to *A. simus*, the new species is also genetically similar to *A. saxidomus* (Fig. 4). The genetic divergence between ***Alpheus* sp. nov.** and *A. simus* (12.9–14.6) was slightly larger than the divergence between the new species and *A. saxidomus* (11.4–12.4).

Previous studies involving the transisthmian *A. simus* from the Caribbean and *A. saxidomus* Pacific coast have demonstrated they were sibling species (Knowlton *et al.* 1993; Knowlton & Weigt, 1998; Williams *et al.* 2001). Geographical isolation of *A. simus* in the Caribbean may be due to particular oceanographic conditions found in the North Brazil Shelf province (Spalding *et al*., 2007). The presence of soft substrate and the low salinity of the water (Coelho & Ramos, 1972) influenced by the Orinoco, Tocantins and Amazonas Rivers Basins may act as geographic barrier to the dispersion. The freshwater effluents of those rivers in the Guyana region covers an area of approx. 2700 km and this high volume modify the salinity of the coastal zone (Collette & Rützler, 1977). Even with the record of an extensive hard-bottom mosaic with approximately 9500 km$^2$, extending from French Guiana, presence of the coral *Millepora* cf. *alcicornis* and dead corals in the mouth of the Amazon River by Moura *et al*. (2016), the abiotic factors on this region may not bring favorable conditions for a continuous distribution of ***Alpheus* sp. nov.** and *A. simus* in the western Atlantic. Furthermore, these evidences grant the genetic isolation and absence of gene flow among of the populations of the Caribbean Sea and Brazil.

Excluding Brachyura, the fauna of crustaceans in coral reefs is still little known (Amaral & Jablonski, 2005), evidencing the importance of studies on fauna surveys in this environment. Although alpheid shrimps are not on the list of endangered crustacean species in Brazil (Almeida *et al*., 2016), coastal areas, among them coral reefs, are refuges for a high diversity of animals and are more vulnerable to anthropic action (Amaral & Jablonski, 2005), deserve attention due to the risk of species extinction before they are even discovered.

Therefore, there is relevance in using multidisciplinary approaches to elucidate possible taxonomic inconsistencies and to emphasize areas that contain unique genetic diversity that may be lost in the near future (Burnham & Dawkins, 2013). Finally, our results confirmed the hypothesis of existence of a complex species involving *A. simus* sensu stricto, *A. saxidomus* e ***Alpheus* sp. nov.,** and present the current known distribution of the three coral rock-boring alpheids (Fig. 5).

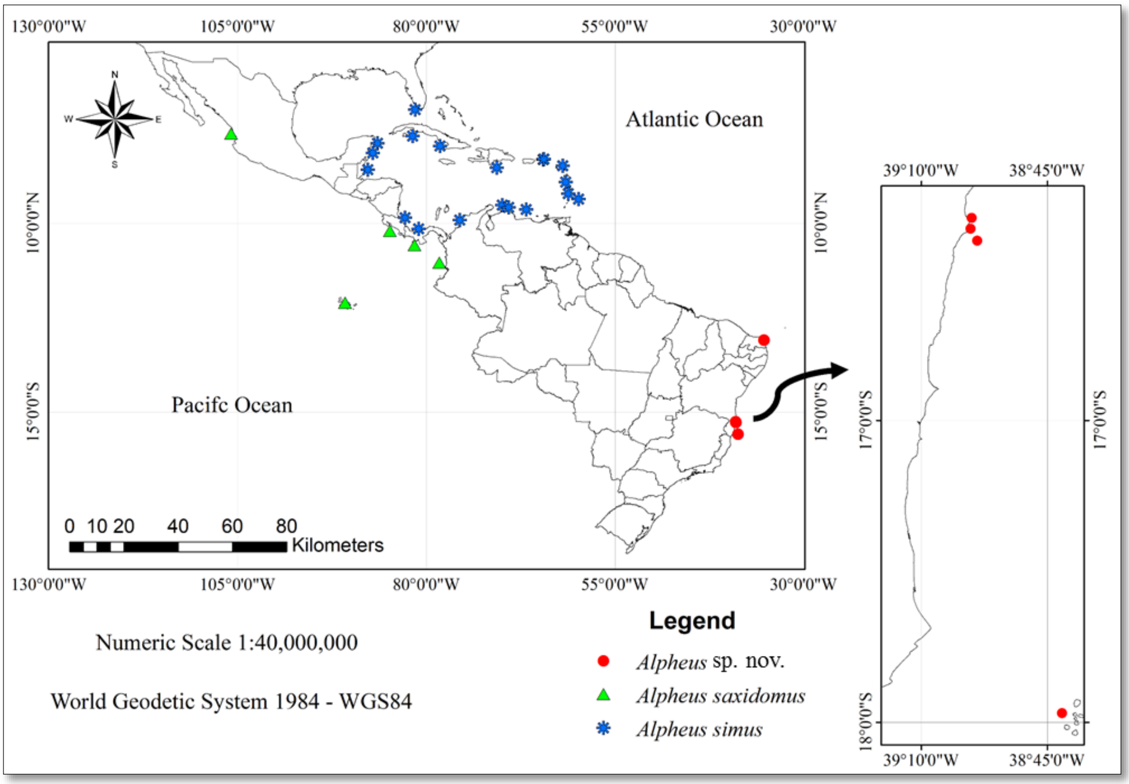

**FIGURE 5.** Presently known distribution of the shrimps ***Alpheus* sp. nov.**, *A. saxidomus* (Holthuis, 1980) and *A. simus* Guérin-Méneville, 1856, based on the material examined and literature records.

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## ARTIGO III

# 4 INTEGRATIVE TAXONOMY OF TWO DISJOINT SPONGE-DWELLING SNAPPING SHRIMPS (ALPHEIDAE: *Synalpheus*) WITH EVIDENCE OF ONGOING SPECIATION

## ABSTRACT

Synalpheus dardeaui *and* Synalpheus ul *are distributed from Caribbean Sea to Brazil. This wide distribution, together with the disjunct nature of populations, makes these taxa a candidate for cryptic speciation processes. To test this, were analyzed specimens throughout the known distribution in the Western Atlantic, including the type-locality and type-series. These animals undergo to exhaustive morphological analysis and a total of 54 morphological characters were studied in addition to genetic analyzes using the gene mitochondrial Cytochrome Oxidase I. Morphological and molecular data support that both species belong to the* gambarelloid *group and are clearly separated from other congeners. The morphological analysis was supported by the topology obtained through Bayesian Inference, showing that* S. dardeaui *formed a clade with subdivisions, separated in* S. dardeaui *from Caribbe and Brazil.* Synalpheus ul *constitutes a well-supported clade without subdivisions. Morphological variations were observed among specimens of* S. dardeaui *from Brazil and the Caribbean region, suggesting a process of speciation in progress. However, these observations should be processed with precaution, as it may be only population variation. No consistent morphological and molecular variation was found in the species studied, for this reason, the hypothesis of the existence of species complex was refuted. However, it is confirmed that there is connectivity between the populations of* S. ul *in the northwest and southwest of the Western Atlantic. In addition, we found new records for* S. ul *and* S. dardeaui *on the Brazilian coast, in the states of Pernambuco and Rio de Janeiro, respectively*. Key-words: *gambarelloides* group, Molecular, COI, Caribbean, Western Atlantic.

## INTRODUCTION

Shrimps of the family Alpheidae Rafinesque, 1815 are one of the most diverse groups of marine decapods with more than 600 described species worldwide (De Grave & Fransen, 2011). With 169 described species, *Synalpheus* Spence Bate, 1888 is the second most diverse alpheid genus (De Grave & Fransen, 2011; Anker *et al.*, 2017). Species of *Synalpheus* live in association with sponges, cnidarians, echinoderms, and some species can present eusociality (Duffy, 1996; Hultgren & Duffy, 2012; Hultgren *et al.*, 2014).

One of the most remarkable morphological groups within *Synalpheus* is *Synalpheus gambarelloides* (Nardo, 1847), characterized by a dense brush of bristles on the dactyl of the minor chela (Coutière, 1909). With more than 60 species described (Anker *et al*., 2012), all these shrimps are obligatory symbionts of demosponges, found in channels and chambers of their hosts (e.g., Dardeau, 1984; Ríos & Duffy, 2007; Macdonald *et al*., 2009; Hultgren *et al*., 2010), feeding on sponge tissue and organic matter drawn of the feeding currents of the host (Duffy, 1996; Hultgren & Duffy, 2010). Some of them live in truly eusocial groups (e.g., Duffy, 1996, 1998; Chak *et al*., 2017), with colonies of up to several dozen individuals with only single female breeding (Duffy, 1998).

The taxonomic uncertainties involving these shrimps are significant due to small body size, cryptic habit and difficulty in identification due the similar morphology shared by many species of the genus (Duffy & Macdonald, 1999). Because the abbreviated larval development which may lead to geographically isolated populations and eventually to speciation (Duffy, 1996), Anker *et al.* (2012) suggest that Brazilian material of *Synalpheus,* especially species of *S. gambarelloides* group, must be compared genetically and morphologically with the Caribbean / Florida material.

Among the species of *gambarelloides* group that have been recorded from Brazil are *S. dardeaui* (Ríos & Duffy, 2007) and *S. ul* (Ríos & Duffy, 2007), both presenting morphological and/or phylogenetic relationships with the *S. pandionis* species complex (which includes *S. pandionis* Coutière, 1909, *S. yano,* (Ríos & Duffy, 2007) *S. hoetjesi* Hultgren, Macdonald & Duffy, 2010) (Ríos & Duffy, 2007; Hultgren *et al.*, 2010). *Synalpheus dardeaui* (type locality Twin Cays, Belize) has been recorded in Belize, Panama, Curaçao, Florida, Brazil (Bahia) and possibly North Carolina (Ríos & Duffy, 2007 as *Zuzalpheus dardeaui*; Hultgren *et al*., 2010; Anker *et al.*, 2012; Oliveira *et al.*, 2015). The species can be found in shallow reefs and mangrove roots with an abundance of sponges *Spheciospongia vesparium* and *Lissodendoryx colombiensis* (Ríos & Duffy 2007; Anker *et al.*, 2012).

*Synalpheus ul* (type locality Sandbores, Belize) has been recorded in Belize, Panama, Jamaica, Curaçao, Barbados and Brazil (Alagoas and Bahia) (Ríos & Duffy, 2007 as *Zuzalpheus ul*; Almeida *et al*., 2007 as *Synalpheus* cf. *pandionis*; Macdonald *et al*., 2009;

Hultgren *et al.*, 2010; 2011; Almeida *et al.*, 2012; Anker *et al.*, 2012). The species is found in shallow subtidal reefs and associated rubble and seagrass (Anker *et al.*, 2012), most common in chambers of the several sponges as *Hymeniacidon caerulea Agelas clathrodes*, *Xestospongia proxima* (currently *Neopetrosia proxima*) and *Calyx podatypa* (Ríos & Duffy, 2007; Hultgren *et al.*, 2011; Anker *et al.*, 2012).

We carried out an integrative analysis using morphological and molecular data for both species with the aim of answering the following question: Does *S. dardeaui* and *S. ul* occur in the Caribbean and Brazil or there is other species involved in in these cases?

## MATERIALS AND METHODS

Specimens of *S. dardeaui* and *S. ul* were obtained in loan from the following crustacean collections: Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade Estadual de Santa Cruz, Bahia, Brazil (UESC); Naturalis Biodiversity Centre, Leiden, the Netherlands (RMNH); National Museum of Natural History, Smithsonian Institution, United States of America (USNM); Muséum National d'Histoire Naturelle, France (MNHN). The identification of the material was based on Ríos & Duffy (2007). We analyzed a total of 57 morphological characters in all specimens examined. The sequences used in this study were generated from our own extractions and others, including those from species belonging to the *S. pandionis* species complex, were retrieved from GenBank in order to make the analysis more consistent (Table 1).

**TABLE 1.** Specimens of *Synalpheus* Spence Bate, 1888 used in genetic analyses. CCDB: Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil; MNHN: Muséum National d'Histoire Naturelle, France; RMNH: Naturalis Biodiversity Centre, Leiden, the Netherlands. COI: Cytochrome Oxidase I.

| **Species** | **Locality** | **Catalogue number** | **GenBank** | **Reference** |
|---|---|---|---|---|
| *Synalpheus dardeaui*<br>(Ríos & Duffy, 2007) | Panama | RMNH.CRUS.D. 54881 | - | This study |
| *Synalpheus dardeaui* | Panama | MNHN-IU-2010-4126 | - | This study |

| | | | | |
|---|---|---|---|---|
| *Synalpheus dardeaui* | Panama | - | KJ595066 | Hultgren *et al.* (2014) |
| *Synalpheus dardeaui* | Panama | - | KJ625036 | Hultgren *et al.* (2014) |
| *Synalpheus dardeaui* | Brazil, Bahia | - | - | This study |
| *Synalpheus goodei* Coutière, 1909 | Belize | - | KJ477698 | Hultgren *et al.* (2014) |
| *Synalpheus hoetjesi* Hultgren, MacDonald & Duffy, 2010 | Barbados | - | GQ424431 | Hultgren *et al.* (2010) |
| *Synalpheus hoetjesi* | Barbados | - | GQ424432 | Hultgren *et al.* (2010) |
| *Synalpheus pandionis* Coutière, 1909 | Belize | - | KJ595126 | Hultgren *et al.* (2014) |
| *Synalpheus ul* (Ríos & Duffy, 2007) | Barbados | - | KJ625044 | Hultgren *et al.* (2014) |
| *Synalpheus ul* | Panama | - | KJ477705 | Hultgren *et al.* (2014) |
| *Synalpheus ul* | Panama | - | KJ595160 | Hultgren *et al.* (2014) |
| *Synalpheus ul* | Brazil, Bahia | - | - | This study |
| *Synalpheus yano* (Ríos & Duffy, 2007) | Belize | - | KJ595161 | Hultgren *et al.* (2014) |
| *Synalpheus yano* | Panama | - | KJ595162 | Hultgren *et al.* (2014) |
| *Synalpheus minus* (Say, 1818) | Brazil, São Paulo | CCDB 4877 | KU313016 | Almeida *et al.* 2018 |

For genetic analyses, DNA extraction and amplification were performed using the protocols proposed by Mantelatto *et al*., (2006; 2007; 2009) adjusted when necessary. Total genomic DNA was extracted from the muscle tissue of the pleon. The tissue was transferred in a 1.5 ml tube and then incubated for 24 h in 600 µl lysis buffer and 10 µl Proteinase K (20 mg / ml) at 55°C in the dry bath. After 24 h, the activity of Proteinase K was to inactivate by placed the sampled on dry ice for 10 minutes. Then the proteins were separated by the addition of 200 µl ammonium acetate (7.5 M) before centrifugation. DNA was precipitated by the addition of 600 µl of cold absolute isopropanol (-20°C) followed by centrifugation; the resulting pellet (after 48 hours of rest at -20ºC) was washed with 15µl 70% ethanol, dried and resuspended in 20 µl of TE buffer. The concentrations of DNA obtained in the samples were quantified, using the Spectrophotometer Nanodrop 2000.

The mitochondrial gene Cytochrome OxidaseI (COI) was amplified by the Polymerase Chain Reaction (PCR) (Sambrook *et al.*, 1989) using the primers COIAL2o (5´-ACGCAACGATGATTATTTTCTAC-3´) e COIAH2m (5´-GACCRAAAAATCARAATAAATGTTG-3´) (Mantelatto *et al.*, 2016). PCR products were obtained in a Thermocycler Veriti (Applied Biosystems) with specific thermal cycles for the primer set with a total reaction volume of 25 µl containing distilled and deionized $H_2O$, PCR Buffer (10X), $MgCl_2$ (25 mM), betaine (5M), DNTPs, primers, *Thermus aquaticus* polymerase previously extracted DNA (50 ng). The results were observed in electrophoresis with 1.5% agarose gel stained with GelRed ™ and a UV transilluminator Transilluminator UVP ® M20. PCR products were purified with the SureClean ® Purification kit. Sequencing occurred using the Big Dye ® Terminator sequencing reaction Cycle Sequencing (Applied Biosystems) in ABI 3100 Genetic automatic sequencers Analyzar ® of the Departamento de Tecnologia da Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal, Universidade Estadual Paulista. Both strands were sequenced and a consensus sequence was obtained with Bioedit program 7.0.9.0 (Hall 1999). DNA fragments obtained were submitted to alignment in the BLAST system for comparison with the assembly of the NCBI database (http://blast.ncbi.ncbi.nlm.nih.gov/blast.cgi) aiming to confirmation of their respective identities. Some sequences were retrieved from Genbank for comparison.

The alignment of the sequences was performed in the software MUSCLE (Multiple Sequence Comparison by Log- Expectation) (Edgar 2004), available on the platform Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller *et al.*, 2010). jModelTest software (Darriba *et al.*, 2012), implemented in the CIPRES platform, was used to find out which replacement substitution model best fit the data, using Bayesian information criterion (BIC). Bayesian inference analysis was carried out in the software MrBayes v3.2.6 (Ronquist *et al.*, 2012), implemented in the platform CIPRES, with the parameters obtained in 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 races were performed and the convergence of races was analyzed using Tracer 1.6 software (Rambaut *et al.*, 2014). The first 20% of trees and parameters were discarded (burn-in) and a final tree was generated in Tree Annotator software 1.8.4 (implemented in the BEAST package, Drummond *et al.*, 2012). A posteriori probability values greater than 60% were reported. A genetic divergence matrix was created using the

Kimura 2 parameter model (K2P) (Kimura 1980) in the MEGA v6 software (Tamura *et al.*, 2013).

## RESULTS

### SYSTEMATICS

Family Alpheidae Rafinesque, 1815

Genus *Synalpheus* Spence Bate, 1888

*Synalpheus dardeaui* (Ríos & Duffy, 2007)

(Figure 1)

*Synalpheus* '*pandionis* giant' – Morrison *et al.,* 2004: p. 568; Macdonald *et al*., 2006: p. 170.

*Zuzalpheus dardeaui* Ríos & Duffy, 2007: p. 18, figs 3–6, pl. 2.

*Synalpheus dardeaui* – Anker & Tóth, 2008: p. 17; Duffy & Macdonald, 2010: p. 579; Hultgren *et al.*, 2010: p. 229; De Grave & Fransen, 2011: p. 405; Anker *et al.*, 2012: p. 34, figs 22, 23; Oliveira *et al.*, 2015: p. 1, fig. 4.

MATERIAL EXAMINED:

Holotype: 1 male, Belize, Twin Cays, 26.iv.2001, depth: 1–2 meters, in *Lissodendoryx colombiensis*, USNM 1019038.

Allotype: 1 ovigerous female, same data as holotype, USNM 1019039. Paratypes: 1 male, 1 ovigerous female, Twin Cays, 02.xii.1999, depth: 2 meters, in *Lissodendoryx colombiensis*, USNM 1019040.

Other material:

Panama. 11 males, 2 sex not indentified, Caribbean coast, Bocas del Toro, Isla Colón, A. Anker, 8.viii.2008, RMNH.CRUS.D.54879; 1 male, 1 ovigerous female, Caribbean coast, Bocas del Toro, Isla Colón, A. Anker & J.A. Baeza, RMNH.CRUS.D.54881; 2 males, 2 females (1 ovigerous), Caribbean coast, Bocas del Toro, A. Anker. 8.viii.2008, in several sponges, RMNH.CRUS.D.54882; 1 male, Bocas del Toro, Isla Colón, Punta Caracol, 11.viii.2008, MNHN-IU-2010-4126; 1 male, Bocas del Toro, viii.2008, MNHN-IU-2010-4128. Brazil. 2 males, Bahia, Porto Seguro, Parque Municipal Marinho do Recife de Fora (16º23'0"S

38º59’0’W), 10 meters, colls. P.S. Santos, G.O. Soledade, L.M. Fernandes, J.C. Viaggi, G.M. Reuss-Strenzel, 6.v.2013, MZUESC 1567; 4 males, 2 ovigerous female, Rio de Janeiro, Arraial do Cabo, 1994, MNRJ 27640.

**Description.** For detailed description and illustrations see Ríos & Duffy (2007).

**Type locality.** Belize, Carrie Bow Cay.

**Distribution.** Western Atlantic: possibly in North Carolina (Ríos & Duffy, 2007); Florida (Florida Keys), Belize (Carrie Bow Cay), Panama (Bocas del Toro), Curaçao and Brazil (Bahia: Porto Seguro; Rio de Janeiro: Arraial do Cabo) (Ríos & Duffy, 2007; Hultgren *et al.*, 2010; Anker *et al.*, 2012; Oliveira *et al.*, 2015; this study).

**Color in life.** Body semitransparent, pale brown to orange-brown, with some small reddish chromatophores; major cheliped distally olive-brown; ovaries and freshly laid eggs orange-yellow (see Ríos & Duffy, 2007: pl 2; Anker *et al*. 2012: 35, Fig. 22A-C).

**Ecology.** Typically found in heterosexual pairs. Predominantly in association with sponges such as *Spheciospongia vesparium* and *Lissodendoryx colombiensis* (Ríos & Duffy, 2007; Hultgren *et al.*, 2010; Anker *et al.*, 2012); 0.5–10 meters (more commonly) up to 65 meters (Ríos & Duffy, 2007; Hultgren *et al.*, 2010; Almeida *et al*., 2012; Anker *et al.*, 2012).

**Remarks.** Two specimens of the lot RMNH.CRUS.D.54879 and one of the lot RMNH.CRUS.D.54882 (parasitized by bopyrid isopod). Were compared specimens from Bahia (MZUESC 1567) and Belize (RMNH. CRUS.D. 54881) Oliveira *et al.* (2015) reported some differences on orbital teeth, degree of development of the scaphocerite blade and number of distolateral teeth adjacent to spiniform seta of uropodal exopod, when compared Brazilian and Caribbean material. In the specimens from Bahia (MZUESC 1567) and Belize (RMNH. CRUS.D. 54881) we find the same differences in the first two characters, the orbital teeth are not so elongated (Figure 1A) *vs.* slender (Figure 1D); long and broad (Figure 1A) *vs.* short and narrow (Figure 1D) scaphocerite blade, and new differences as ventral margin of second abdominal somite rounded (Figure 1B) *vs.* with acute angle (Figure 1E); cutting edge of dactylus of major cheliped with a notch followed by a tubercle (Figure 1C) *vs*. cutting edge of dactylus of major cheliped without notch and tubercle (Figure 1F).

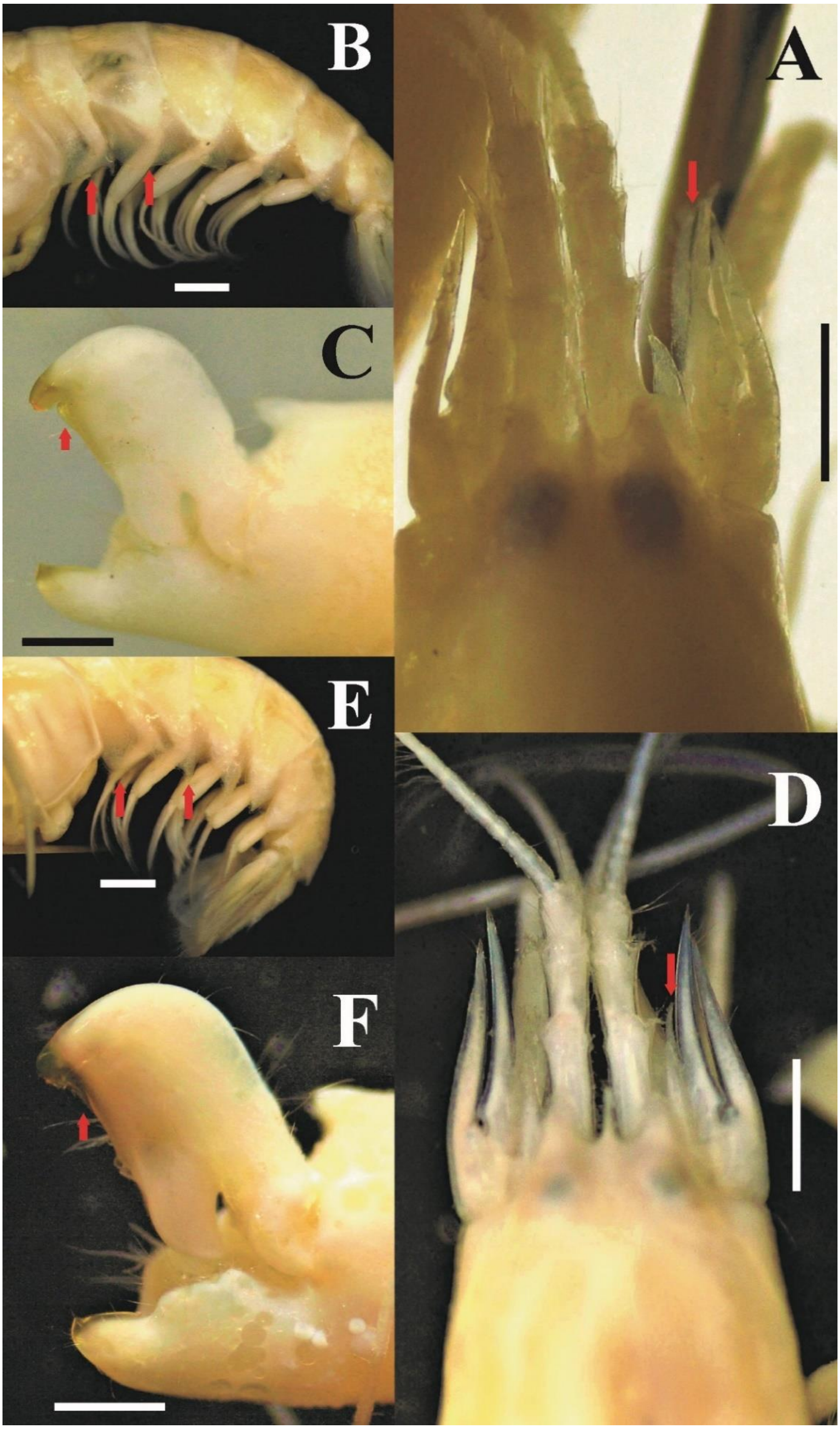

**Fig 1.** *Synalpheus dardeaui* (Ríos & Duffy, 2007): male from Bahia (MZUESC 1567) (A–C); male from Belize (RMNH.CRUS.D.54881) (D–F): (A, D) cephalic appendages, dorsal view,

red arrow indicates scaphocerite blade; (B, E) abdomen, lateral view, red arrow indicates ventral margin of first and second abdominal somite; (C, F) major chela, distal portion, lateral view, red arrow indicates presence and absence of tubercle, respectively. Scale bars = 1 mm.

*Synalpheus ul* (Ríos & Duffy, 2007)
(Figures 2–4)

*Zuzalpheus ul* Ríos & Duffy, 2007: 63, figs 27–30, pl. 3.

*Synalpheus ul*—Macdonald *et al.*, 2009: 50; Hultgren *et al.*, 2010: 234, 251, fig. 9A–F, pl. 6A–D; Almeida *et al.*, 2012: 19, figs 6–8; Anker *et al.*, 2012: 73–75, figs 47–49.

*Synalpheus* cf. *pandionis*—Almeida *et al.*, 2007, in part: 15, figs 3, 4 (not *S. pandionis* Coutière 1909.

*Synalpheus yano*—Macdonald *et al.*, 2009: 51, pl. 6A, B [not S. *yano* (Ríos & Duffy, 2007), see Hultgren & Duffy, 2010: p. 3].

MATERIAL EXAMINED:

Holotype: 1 male, Belize, The Pinnacles (Sand Bores), Southwest of Carrie Bow Cay, 30.iv.2001, depth: 2 m, in *Hymeniacidon caerulea*, USNM 1019053.

Allotype: 1 ovigerous female, same data as holotype, USNM 1019054.

Other material:

1 male, 1 ovigerous female, Panama, Caribbean coast, Isla Grande, A. Anker, 23.iv.2006, RMNH.CRUS.D.54853; 6 males, Caribbean coast, Bocas del Toro, Isla Colón, A. Anker, 8.viii.2008, RMNH.CRUS.D.54854; 1 female, Bocas del Toro, Isla San Cristobal, Punta Coco, 29.x.2005, MNHN-IU-2010-4157. Brazil. 2 males, 1 ovigerous female, 1 sex not identified, Pernambuco, Suape Bay, 22.viii.2008; 2 males, Pernambuco, Praia dos Carneiros, colls. G.L. Bochini, A.M. Cunha, P.S. Santos, G.O. Soledade, 28.viii.2017, in artificial refuge (ERA); 1 male, Bahia, Camamu Bay, trawl, St. 4 (13°54’06”S; 39°00’22”W), 30.x.2004, MZUESC 709; 1 male, 1 ovigerous female, Bahia, Porto Seguro, Recife de Fora, colls. P.S. Santos, G.O. Soledade, L.M. Fernandes, J.C. Viaggi, G.M. Reuss-Strenzel, on dead coral rubble, St. 3,

12.iv.2012, MZUESC 1598; 1 male, Bahia, Porto Seguro, Recife de Fora, colls. P.S. Santos, G.O. Soledade, L.M. Fernandes, J.C. Viaggi, G.M. Reuss-Strenzel, on dead coral rubble, St. 3, 05.v.2013, MZUESC 1694.

**Description.** For detailed description and illustrations see Ríos & Duffy (2007); for illustrations of the Brazilian material see Almeida *et al.* (2012).

**Type locality.** Belize, Carrie Bow Cay.

**Distribution.** Western Atlantic: Belize (Carrie Bow Cay), Panama (Bocas del Toro, San Blas Islands, Porvenir, Aguadargana), Jamaica (Discovery Bay), Dominican Republic (Bayahibe), Barbados, Curaçao, and Brazil (Pernambuco, Alagoas, Bahia) (Ríos & Duffy, 2007; Macdonald *et al.*, 2009; Hultgren *et al.*, 2010; Almeida *et al.*, 2012; Anker *et al.*, 2012; this study).

**Color in life.** Body semitransparent with small reddish chromatophores and palm of major cheliped; dactylus and pollex pale green; some specimens with a more intense orange background (Anker *et al*., 2012).

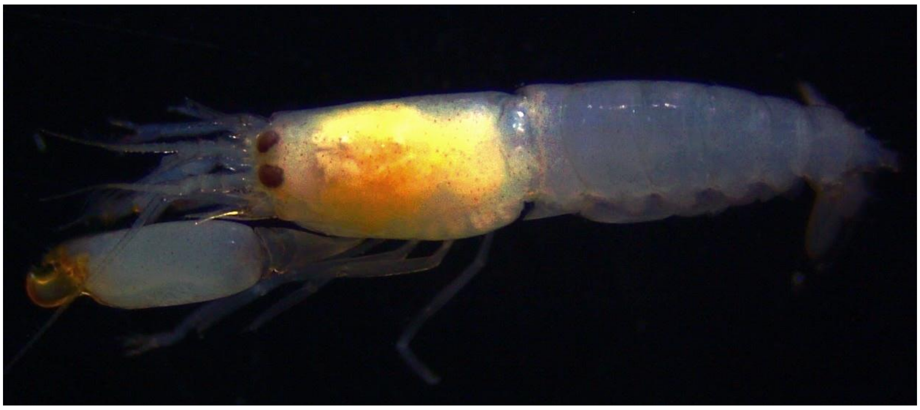

**Fig 2.** *Synalpheus ul* (Ríos & Duffy, 2007): male from Praia dos Carneiros, Pernambuco, northeastern Brazil. Photo: Gabriel Bochini.

**Ecology.** Typically found in heterosexual pairs; predominantly in association with sponges such as *Hymeniacidon caerulea, Hyattella intestinalis*, *Calyx podatypa* (Laubenfels, 1934), *Lissodendoryx colombiensis*, *Lissodendoryx* sp., *Agelas* cf. *clathrodes*, *Xestospongia subtriangularis* (Duchassaing, 1850), *Xestospongia* sp., and unknown sponge (Almeida *et al*., 2012), as well as in shallow reefs and rubble-seagrass (Anker *et al*., 2012), usually in shallow water (1–3 meters) (Ríos & Duffy, 2007; Macdonald *et al*., 2009; Hultgren *et al*., 2010; Anker *et al*., 2012).

**Remarks.** No consistent morphological differences were found between specimens from the Caribbean Sea and Brazil (Figures 3A-F, 4A-F). For details on morphological differences between *S. ul* and *S. pandionis* (see Almeida *et al*., 2012). Even though the known morphological similarity between *S. ul*, *S. hoetjesi* and *S. yano*, these species are phylogenetically distinct (Hultgren *et al*., 2010; this study (Figure 5)). Specialized in inhabiting sponges, this is the first occurrence of the species in artificial shelter refuge on material from Praia de Carnerios Pernambuco.

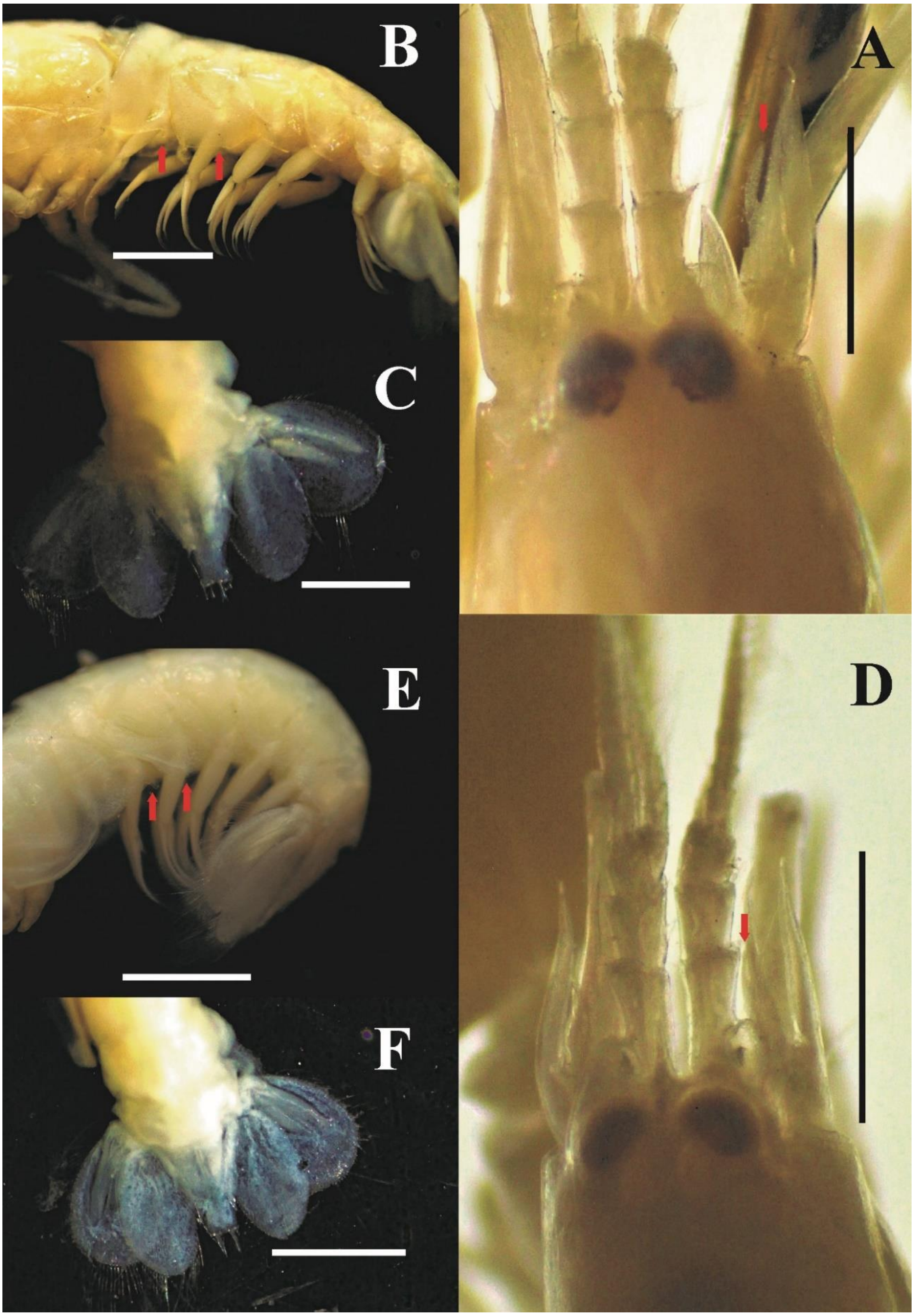

**Fig 3.** *Synalpheus ul* (Ríos & Duffy, 2007): male from Bahia (MZUESC 709) (A–C); male from Belize (RMNH.CRUS.D.54854) (D–F): (A, D) cephalic appendages, dorsal view, red arrow indicates scaphocerite blade; (B, E) abdomen, lateral view, red arrow indicates ventral

margin of first and second abdominal somite; (C, F) telson and uropods, dorsal view. Scale bars = 1 mm.

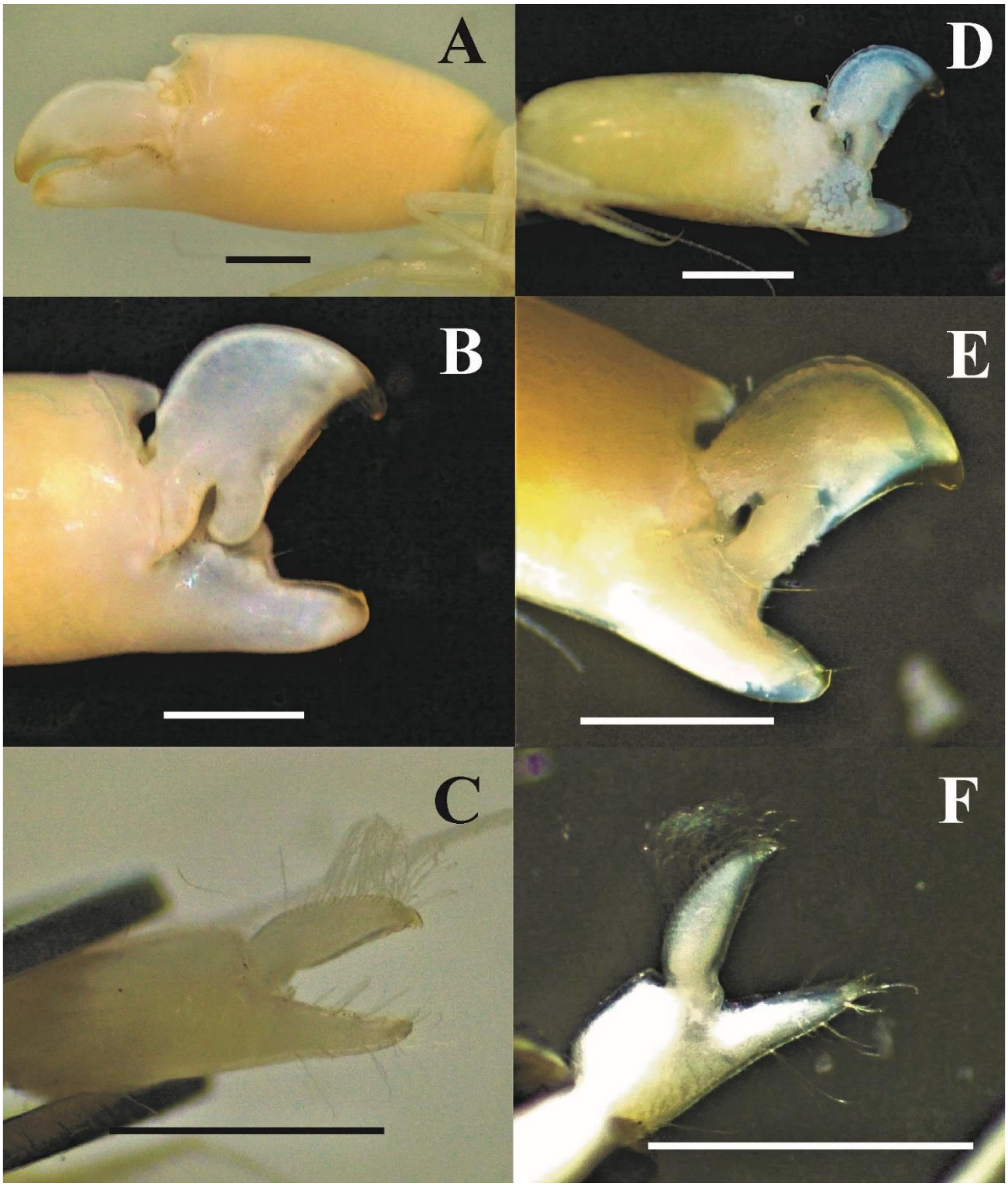

**Fig 4.** *Synalpheus ul* (Ríos & Duffy, 2007): male from Bahia (MZUESC 709) (A–C); male from Belize **(**RMNH.CRUS.D.54854) (D–F): (A, D) major chela, lateral and mesial view, respectively; (B, E) major chela, distal portion, lateral view; (C, F) minor chela, lateral view. Scale bars = 1 mm.

## PHYLOGENETIC ANALYSIS AND GENETIC DISTANCE

The best-fitted substitution model, selected with a corrected Bayesian information criterion were: COI - TIM2+G assuming the nucleotide frequencies A = 0.2844, C = 0.2210, G = 0.1859, T = 0.3087, replacement rates AC = 5.4563, AG = 11.0989, AT = 5.4563, CG = 1, CT = 45.8478, GT = 1, substitution model variable sites followed a gamma distribution with shape parameter = 0.2090. The topology obtained by the Bayesian Inference analysis (Figure 5) show that *S. dardeaui* formed a clade with a subdivision between specimens from Panama and one specimen from Braziland *S. ul* formed a well-supported clade with no subdivisions and both were clearly separated from other congeneric species belonging to the *gambarelloides* group. In these cases, the groups were well supported by the values of posterior probabilities. The intraspecific divergence of *S. dardeaui* and *S. ul* were 0 to 2.8% and 0 to 0.2%, respectively. The estimated interspecific variation between *S. dardeaui* specimens and other *Synalpheus* species group ranged from 5.1 to 20.5%. The estimated interspecific variation between *S. ul* specimens and other *Synalpheus* species group ranged from 10.3 to 20.2%.

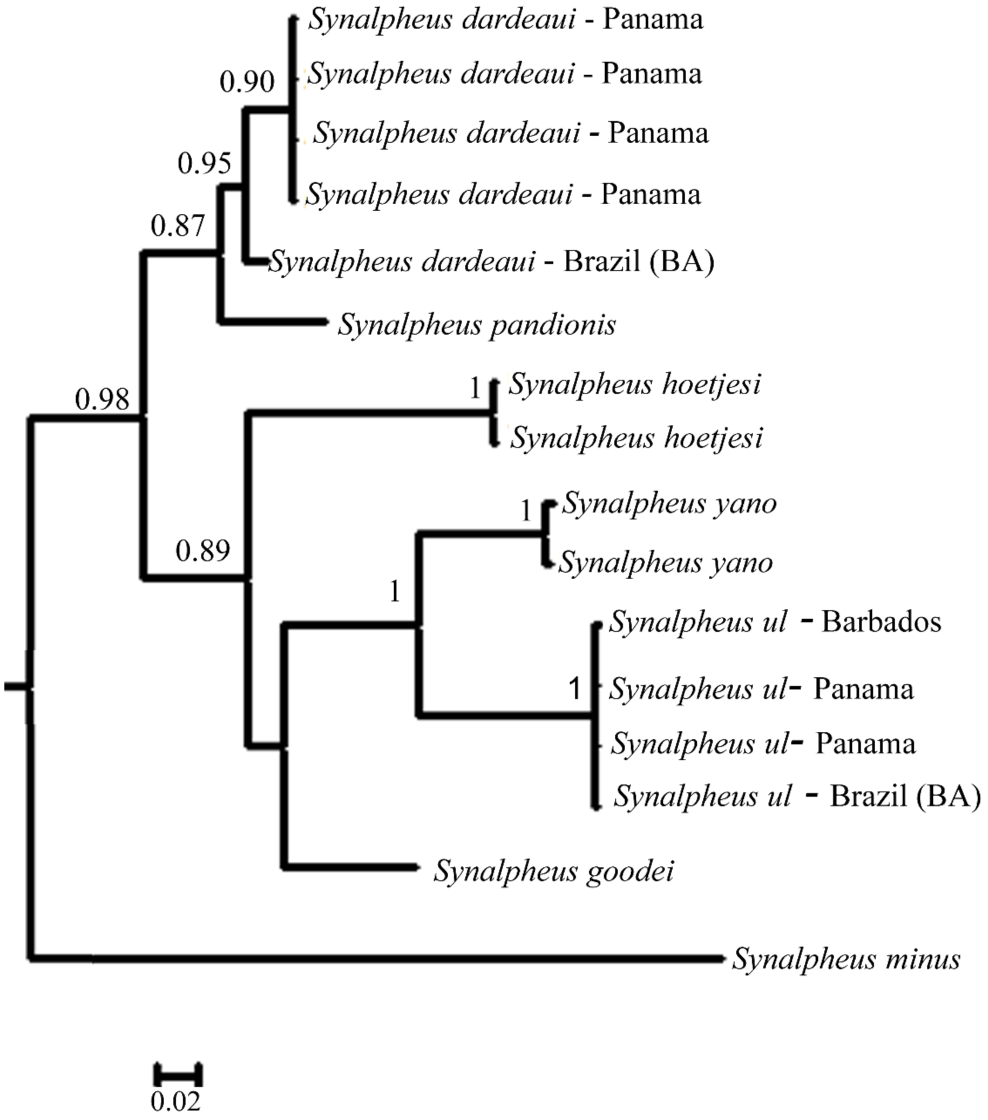

**Fig 5.** Phylogenetic tree of *Synalpheus* Spence Bate, 1888, using the Inference Bayesian analysis of COI gene sequences. Numbers are support values for posterior probabilities; values < 60% were not included.

## DISCUSSION

Molecular and morphological data do not support the definition of a species complex involving any of the species studied. *Synalpheus ul* formed a well-supported group, with distinct separation among other species of *Synalpheus* included in the analysis, including those of the *S. pandionis* complex. The recovered sister group relationship between *S. ul* and *S. yano* has also been observed by Hultgren & Duffy (2011).

In *S. dardeaui,* a low genetic distance (2.8%) was observed among the specimens of Brazil and those from the Caribbean Sea (Panama). This value may be attributed to a population variation among the localities. However, consistent morphological differences were observed, suggesting the occurrence of reproductive isolation or ongoing speciation between these populations. Other possible explanation for the morphological differences observed between Caribbean and Brazilian material aredifferences in host use by *S. dardeaui* in both areas. In the Caribbean, *S. dardeaui* is found more frequently associated to the sponges *Spheciospongia vesparium* and *Lissodendoryx colombiensis* (Ríos & Duffy, 2007; Hultgren *et al*., 2010; Anker *et al*., 2012), whereas in Brazil, the only host for *S. dardeaui* so far identified was *Ircinia* cf. *strobilina* (Oliveira *et al*., 2015). Host specificity and speciation has been reported in four cryptic species of *Synalpheus* (Duffy, 1996). Moreover, Hurt *et al*. (2013) reported five species of the genus *Alpheus* obligatory commensal of marine anemones, demonstrating a high degree of fidelity and ecological specificity regarding hosts. Our results indicated a sister group relationship between *S. dardeaui* and *S. pandionis*, which is in agreement the results by Hultgren *et al*. (2010).

Abiotic factors such as temperature and salinity may limit the dispersion between the Caribbean Sea and Brazil (Coelho & Ramos, 1972). However, it is known that species living in pairs have swimming larvae capable of long-distance dispersal (Duffy & Macdonald, 2010) and this mechanism could act differently in the two species analyzed. In addition, these species are known to be obligate symbionts of sponges, and often specialized in a species, so the distribution and abundance of their host sponges can to influence the occurrence of their symbionts (Hultgren *et al*., 2010) and demonstrates the necessity of more researches involving sponge dwelling snapping shrimps.

Obtaining 16S sequences in a near future would be important for confirming or refuting the recognition of *S. dardeaui* from Brazil as a new species, with *S. dardeaui* becoming a species complex. On the other hand, we confirm that there is connectivity between the populations of *S. ul* do Caribbean Sea and Brazil and our results provide the expansion of the distribution of *S. dardeaui* and *S. ul* in the southwestern Atlantic to Rio de Janeiro and Pernambuco, respectively.

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Mendes de Conservação da Biodiversidade), Nº. 24408-1 MMA/IBAMA/SISBIO for AOA and of the Porto Seguro city hall.

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# 5 CONCLUSÃO

Apresentando uma abordagem integrativa, concatendando dados morfológicos e moleculares, a presente tese traz novos resultados sobre padrões distribucionais de quatro espécies de Alpheidae. Os resultados para *Alpheus peasei* confirmam que há conectividade entre as populações do Atlântico Norte e Sul e, através do material examinado foi possível registrar novas ocorrências o limite de distribuição no noroeste do Atlântico (Barbados, Belize e Costa Rica) e uma nova ocorrência para a costa brasileira (Pernambuco). Ao examinar os espécimes atribuídos à *Alpheus simus*, verificou-se que havia um novo táxon. *Alpheus* sp.n. foi descrita e possui até o momentp, distribuição restrita no Atlântico Sul Ocidental (Rio Grande do Norte e Bahia). Em *Synalpheus ul* e *Synalpheus dardeaui* não foram encontradas variações morfológicas e moleculares sólidas. Mas, confirma-se que há conectividade entre a população caribenha e do Atlântico Sul Ocidental. Além disso, nossos resultados trazem a expansão da distribuição de *S. dardeaui* e *S. ul* no Atlântico Sul Ocidental para o Rio de Janeiro e Pernambuco, respectivamente.

Finalmente, a hipótese da existência de um complexo de espécies foi refutada para *A. peasei* e *S. ul*. Porém, constatou-se a existência do complexo de espécies envolvendo *Alpheus* sp.n., *A. simus* sensu stricto e *A. saxidomus*. Além disso, há indícios de novo táxon envolvendo indivúduos de *S. dardeaui* do Brasil e do Caribe.

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