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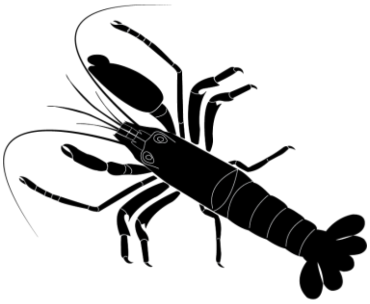
GUIDOMAR OLIVEIRA SOLEDADE

RESOLUÇÕES DA TAXONOMIA INTEGRATIVA NOS CAMARÕES-DE-ESTALO DO COMPLEXO DE ESPÉCIES “MACROCHELES” (*Alpheus macrocheles* (Hailstone, 1835)) (CRUSTACEA: DECAPODA: CARIDEA: ALPHEIDAE)



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

Área de concentração: Biologia Animal

Orientador: Prof. Dr. Alexandre Oliveira de Almeida.

Coorientador: Prof. Dr. Fernando Luís Medina Mantelatto.

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Aos meus pais, Guido e Marlene (*in memoriam*) por me darem força e sempre acreditarem que eu poderia alcançar meus objetivos, amo vocês,

Dedico

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RESUMO

O gênero *Alpheus*, atualmente composto por 313 espécies válidas, apresenta inúmeros complexos de espécies reconhecidos. Um destes complexos é o *Alpheus machocheles*, formado por 10 espécies distribuídas ao longo de toda região tropical. Neste grupo as principais problemáticas são a diferenciação entre *Alpheus macrocheles* e *A. amblyonyx* e a validação dos registros deste primeiro camarão na costa brasileira e no Caribe. Com isso, o objetivo da presente contribuição foi elucidar estas principais pendências dentro de uma abordagem integrativa envolvendo morfologia e genética. A grande maioria do material analisado foi proveniente de empréstimos em coleções nacionais e internacionais. Uma menor parcela dos espécimes foi obtida através de coletas de dragagem realizadas em 2017 ao largo de Recife, Nordeste do Brasil. Todo o material foi submetido a uma exaustiva análise morfológica. Um total de 42 caracteres foi analisado para cada espécie, incluindo região cefálica, abdome, leque caudal, e todo o conjunto de apêndices. Os principais caracteres diagnósticos foram elencados e devidamente ilustrados. A análise genética foi realizada pelo sequenciamento do gene mitocondrial 16S, através da reconstrução filogenética usando Inferência Bayesiana e do da divergência genética corrida, usando o modelo K81. Foram elencados caracteres morfológicos distintivos para a separação de *A. macrocheles* e *A. amblyonyx*. As principais diferenças concentram-se no tamanho do rostro, dáctilo do quelípodo menor, forma do dente molar da quela maior e ângulo distolateral do exópodo uropodal. Foram fornecidas redescrições morfológicas completas para ambas as espécies, com desenhos ilustrativos dos caracteres diagnósticos. Parte do material reportado para *A. macrocheles* na costa brasileira foi localizado e reexaminado. Estes espécimes apresentaram morfologia distinta de *A. macrocheles sensu stricto* e, portanto uma nova espécie para este complexo foi descrita. Estas resoluções geradas a partir dos dados morfológicos foram plenamente suportadas pela análise molecular aplicada. O padrão de coloração foi descrito para a nova espécie. Por fim, foi gerada uma chave de odentificação para as espécies pertencentes ao complexo de ocorrência no Atlântico.

Palavras-chave: Sistemática. Camarões carídeos. Alfeídeos. Morfologia. 16S. Espécies crípticas.

ABSTRACT

The *Alpheus* genus, currently composed of 313 valid species, presents numerous recognized species complexes. One of these is the *Alpheus machocheles* complex, formed by 10 species distributed throughout the tropical region. In this group the main problems are the differentiation between *Alpheus macrocheles* and *A. amblyonyx* and the validation of records of this first shrimp on the Brazilian and Caribbean coast. With this, the objective of the present contribution was to elucidate these main issueswithin an integrative approach involving morphology and genetics. The vast majority of the material analyzed comes from loans in national and international collections. A smaller portion of the specimens was obtained through dredging collections conducted in 2017 off Recife, Northeast Brazil. All the material was submitted to an exhaustive morphological analysis. A total of 42 characters were analyzed for each species, including cephalic region, abdomen, telson, uropods, and appendages. The main diagnostic characters were listed and the characteristics were illustrated. Genetic analysis was performed by sequencing the 16S mitochondrial gene through the Bayesian Inference analysis and the genetic divergence model K81. Morphological distinctive characters were listed for the separation of *A. macrocheles* and *A. amblyonyx*. The main differences are the size of the rostrum, the dactylus of the minor chelae, the shape of the molar tooth of the major chelae, and the distolateral angle of the uropodal exopod. Complete morphological redescriptions were provided for both species, with drawings illustrating the diagnostic characters. Part of the material reported for *A. macrocheles* on the Brazilian coast was located and reexamined. These specimens presented distinct morphology of *A. macrocheles sensu stricto* and therefore a new species for this complex was described based on this material of the Brazilian coast. These resolutions generated from the morphological data are fully supported by the applied molecular analysis. A differentiation based on the color pattern is also incorporated to distinguish this new species. Finally, an identification key was generated for the species belonging to the complex occurring in the Atlantic.

Keywords: Systematic. Caridean shrimps. Alpheids. Morphology. 16S. Cryptic species.

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1 INTRODUÇÃO

Um dos processos geradores de biodiversidade é denominado especiação críptica, o qual consiste numa rápida diversificação genética de linhagens podendo ocorrer ao nível simpátrico, mas, sendo bem comum em situações de alopatria. O mecanismo que medeia este processo é por vezes denominado de irradiação não adaptativa (GITTENBERGER, 1991) e não consiste de diferenciação expressiva ao nível morfológico. Isto tem implicações marcantes do ponto de vista sistemático podendo gerar confusões taxonômicas e erros de identificação.

Entre os camarões carídeos o reconhecimento de complexos de espécies crípticas vem historicamente aumentando. Em alguns casos, espécies no passado com ampla distribuição geográfica foram revisadas e identificadas como complexos envolvendo vários taxa crípticos. Tendo em vista a grande dificuldade do reconhecimento destes problemas taxonômicos apenas com o uso da taxonomia morfologia, abordagens envolvendo dados de coloração, informações ecológicas, comportamentais e dados moleculares vêm sendo aliados à morfologia num método que tem sido denominado taxonomia integrativa (e.g., ALMEIDA; TEROSSI; MANTELATTO, 2014; ANKER; HURT; KNOWLTON, 2008; BRACKEN-GRISSON; ROBLES; FELDER, 2014; CUNHA et al., 2017).

Camarões da família Alpheidae Rafinesque, 1815 são bons exemplos de como esta nova abordagem metodológica pode resolver problemas consistentes envolvendo complexos de espécies crípticas. Este grupo é um dos mais ricos em número de espécies (mais de 600 espécies descritas) da infraordem Caridea Dana 1852 (DE GRAVE; FRANSEN, 2011). Evidencias apontam a existência de biodiversidade críptica ainda desconhecida (ANKER et al., 2006). Neste táxon alguns complexos de espécies foram previamente identificados e solucionados, sobretudo, nos camarões-de-estalo dos gêneros *Alpheus* Fabricius 1798 [e.g., complexo "*cylindricus*" (ANKER; HURT; KNOWLTON, 2008); complexo "*armillatus*" (ANKER, 2012); complexo "*heterochaelis*" (ALMEIDA; TEROSSI; MANTELATTO, 2014); complexo "*floridanus*" (BRACKEN-GRISSON; ROBLES; FELDER, 2014)] e *Synalpheus* Spence Bate 1888 [complexos "*frizmuelleri*" e "*stimpsonii*" (HULTGREN; HURT; ANKER, 2014).

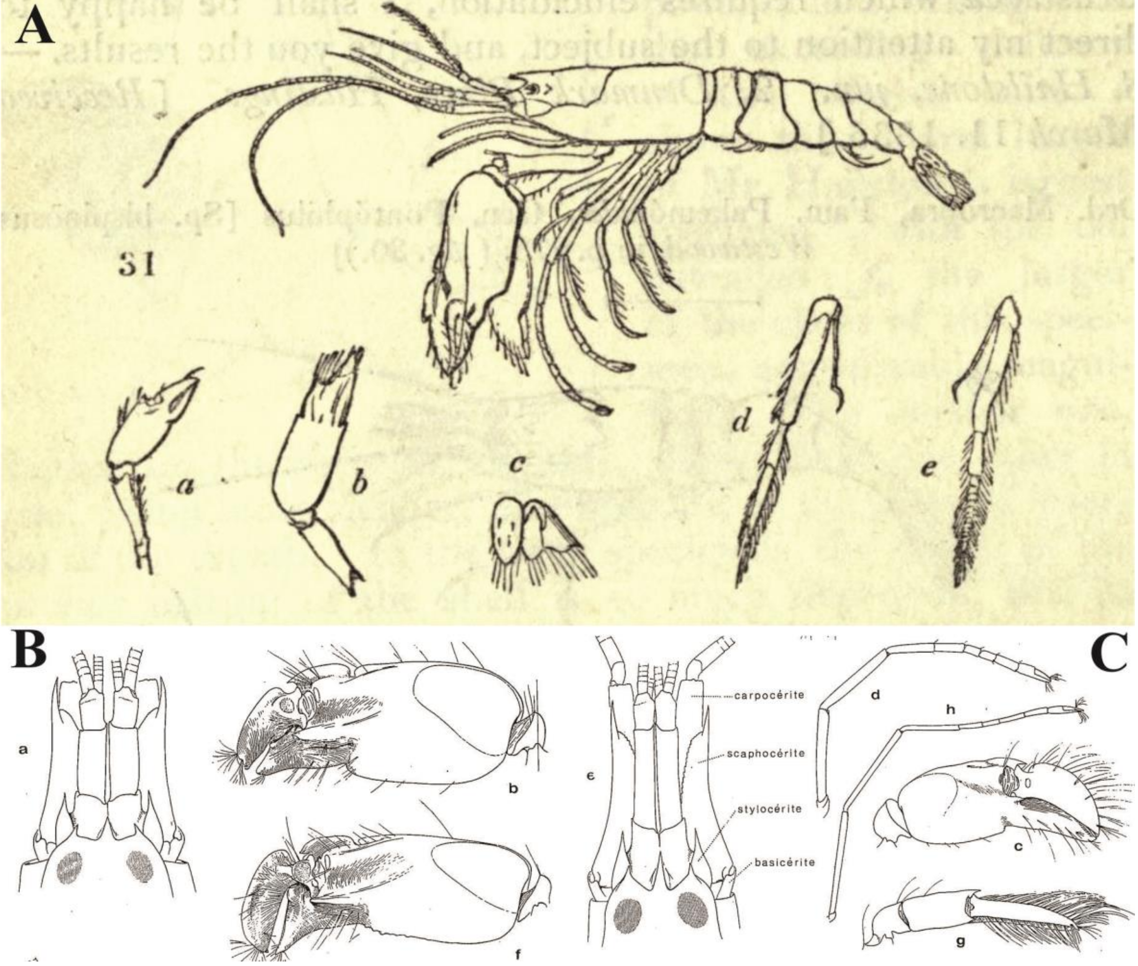
O mega diverso gênero *Alpheus* abriga atualmente 313 espécies válidas (DE GRAVE; FRANSEN, 2011; SALGADO-BARRAGÁN; AYÓN-PARENTE; ZAMORA-TAVARES, 2016) com uma diversidade estimada em mais de 400 espécies (ANKER, 2001). Estes camarões habitam todas as principais regiões do mundo, com exceção dos polos. Habitam uma ampla variedade de habitats, incluindo estuários, praias desabrigadas, recifes de corais, plataforma continental e águas profundas (ANKER et al., 2006; CHACE, 1988). No ambiente de água doce o gênero é atualmente representado apenas por *Alpheus cyanoteles* Yeo & Ng, 1996, com ocorrência restrita para a Malásia (YEO; NG, 1996).

Os camarões-de-estalo do gênero *Alpheus* apresentam hábito críptico, vivendo exclusivamente em habitações construídas e defendidas em um amplo espectro de substratos, desde tocas escavadas em ambiente lamoso a tocas escavadas em substrato arenoso sob rochas soltas do entremarés (NOLAN; SALMON, 1970). Alguns representantes são componentes da fauna endolítica, perfurando galerias dentro de estruturas coralíneas (KROPP, 1987). Os camarões deste grupo apresentam um vasto registro de associações com inúmeros outros grupos de animais marinhos, incluindo esponjas, anêmonas, briozoários, poliquetos, equinodermos e inclusive peixes (e.g., ANKER; HURT; KNOWLTON, 2008; KNOWLTON; MILLS, 1992; 1985; KNOWLTON; KELLER, 1985; KARPLUS, 1987).

Um dos inúmeros complexos reconhecidos no gênero é o que leva o nome da espécie *Alpheus macrocheles* (Hailstone, 1835) (sensu ANKER; DE GRAVE, 2012), que abriga atualmente dez espécies, sendo elas: *A. amblyonyx* Chace, 1972, *A. cedrici* Anker & De Grave, 2012, *A. lentiginosus* Anker & Nizinski, 2011, *A. macrocheles*, *A. platydactylus* Coutière, 1897, *A. pouang* Christoffersen, 1979 e *A. puapeba* Christoffersen, 1979, todas no Atlântico e *A. bellimanus* Lockington, 1877 e *A. rectus* Kim & Abele, 1988 do Pacífico Leste (ANKER; DE GRAVE, 2012). A única representante do Indo-Pacífico é *A. albatrossae* (Banner, 1953). Das quatro espécies que ocorrem no Atlântico Ocidental, apenas *A. amblyonyx*, *A. puapeba* e *A. pouang* apresentam registros confirmados na costa brasileira.

Nenhuma revisão taxonômica foi realizada neste complexo até o momento. O esforço de pesquisa taxonômica tem se limitado a diagnoses e comparações fornecidas nos trabalhos de descrições das espécies integrantes. Alguns destes táxons, como é o caso de *A. amblyonyx*, *A. puapeba* e *A. pouang* e da própria *A. macrocheles* são pouco ilustrados, sendo que para algumas os únicos desenhos publicados são os de suas descrições originais. O caso de *A. macrocheles* é ainda mais especial, tendo em vista que se trata da espécie mais registrada do grupo. Em contrapartida, estes registros na grande maioria carecem de informações taxonômicas adequadas e mesmo de ilustrações do material (ver SOLEDADE; ALMEIDA, 2013). A própria descrição desta espécie feita por Hailstone (1835) apresenta uma caracterização morfológica limitada e nenhuma comparação com espécies correlatas. As ilustrações deste trabalho também são bem simplistas (Fig. 1A), coerentes para o que geralmente se fornecia de detalhamentos para a época da descrição. Posteriormente Crosnier e Forest (1966) apresentaram desenhos pouco mais elaborados que os da descrição original, muito embora ainda bem limitados quanto a caracteres mais específicos (Fig. 1B,C).

Figura 1 – Ilustrações da morfologia geral de *Alpheus macrocheles* (Hailstone, 1835) para Hasting, Canal da Mancha (Reino Unido) fornecidas no artigo de descrição e para Conakry (Guiné) por Crosnier e Forest (1966).



Fonte: (A) Hailstone (1835) e (B,C) Crosnier e Forest (1966).

Alpheus amblyonyx foi descrita por Chace (1972) para o México, tendo como localidade tipo Quintana Roo. Contrariamente ao caso de *A. macrocheles*, a descrição de Chace é completa e detalhada, apresentando ilustrações e uma breve comparação de seus espécimes com o material de *A. macrocheles* do Atlântico Oriental. Em contrapartida, apesar de fornecer um conjunto de quatro caracteres distintivos entre estes camarões, o próprio autor chama a atenção para a extrema similaridade morfológica entre estas duas espécies. Posteriomente inúmeros registros envolvendo ambas as espécies foram feitos para a costa brasileira (e.g., CHRISTOFFERSEN 1979; RAMOS-PORTO 1979; COELHO; RAMOS 1980; COELHO FILHO 2006; SEREJO *et al.* 2007). Anker e De Grave apontaram os registros de *A macrocheles* para o Brasil como duvidosos, podendo corresponder a *A. amblyonyx* ou outra espécie do complexo. Soledade e Almeida (2013) compilaram os registros destas espécies para a costa brasileira. Estes autores mencionam que alguns destes registros são problemáticos por conta da ausência de informações morfológicas e ilustrações apropriadas. Estas questões envolvendo a imprecisão dos registros prévios levantam algumas principais dúvidas: (i) são as duas espécies válidas?; (ii) os registros prévios para o Brasil correspondem de fato a *A. macrocheles*?; (iii) existe uma provável nova espécie envolvida no material citado para a costa brasileira.

Tendo em vista toda a problemática apontada acima, sobretudo a carência de estudos com abordagens multidisciplinares do tema, torna-se necessária a revisitação ao material reportado como *A. macrocheles* e *A. amblyonyx*, bem como das demais espécies do complexo para fins comparativos. Como apontado acima, estudos envolvendo abordagens integrativas vêm sendo conduzidos, gerando dados conclusivos dentro de *Alpheus*. Desta forma, este tipo de abordagem integrativa é a mais apropriada para elucidar as questões relacionadas às confusões taxonômicas dentro do complexo de espécies *A. macrocheles*.

1.3 HIPÓTESES

(i). As diferenças observadas por Chace (1972) são robustas o suficiente para suportar a existência de duas espécies (*A. macrocheles* e *A. amblyonyx*);

(ii). Uma vez que seja existente a diferença entre estes dois táxons, o material do Atlântico ocidental não corresponde a *A. macrocheles*.

(iii). O material citado como *A. macrocheles* para a costa brasileira se trata de uma nova espécie do complexo.

1.2 OBJETIVOS GERAL

Revisar por meio da integralização de dados morfológicos e moleculares os taxa crípticos *Alpheus macrocheles* e *A. amblyonyx* pertencentes ao complexo de espécies *A. macrocheles* de distribuição circumtropical.

1.3 OBJETIVOS ESPECÍFICOS

- ✓ Checar a existência de diferenças morfológicas que suportem a separação de *A. macrocheles* e *A. amblyonyx*.
- ✓ Utilizar análise de DNA para verificar se as duas espécies são de fato distintas.
- ✓ Redescrever as espécies e descrever novos táxons se encontrados.
- ✓ Analisar e confirmar a distribuição geográfica de *A. macrocheles* no Atlântico Ocidental.

2 ESTRUTURA GERAL DA TESE

A presente tese foi estruturada em dois artigos, os quais correspondem a artigos científicos. O primeiro artigo versou sobre a comparação morfológica e genética entre *A. macrocheles* e *A. amblyonyx*. Neste manuscrito foi gerada uma redescrição de *A. macrocheles*, com a designação de um neótipo, além de uma completa redescrição morfológica de *A. amblyonyx*. No segundo manuscrito foi feita uma revisitação ao material previamente citado como *A. macrocheles* para a costa brasileira com o objetivo principal de verificar a validade de sua ocorrência no Atlântico Ocidental. Neste artigo foi gerada a descrição de uma nova espécie para o complexo, baseada em amostras coletadas no litoral brasileiro.

Toda a parte introdutória da tese está ajustada de acordo com as normas da ABNT, incluindo os elementos pré e pós-textuais, a Introdução Geral, Objetivos e a presente seção, bem como as Considerações Finais. Por outro lado, em toda a seção dos Artigos Científicos foram adotadas as normas específicas de cada periódico ao qual cada artigo será submetido. Os dois manuscritos foram incorporados à tese em suas versões definitivas de submissão e no idioma Inglês. Os artigos científicos I e II serão submetidos aos periódicos **Zootaxa** (Qualis B1) e **Systematics and Biodiversity** (Qualis A2), respectivamente. As respectivas normas de formatação do texto para submissão nestas duas revistas encontram-se nos seguintes endereços eletrônicos: http://www.mapress.com/j/zt/pages/view/forauthors e https://www.tandfonline.com/action/authorSubmission?show=instructions&journalCode=tsab20.

Para a realização deste estudo foi analisado material das seguintes coleções carcinológicas:

1. Museu de Oceanografia Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco (MOUFPE), Pernambuco, Brasil;
2. Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro, Brasil;
3. Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brasil;
4. Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, São Paulo, Brasil (CCDB);
5. Colección Nacional de Crustáceos, México (CNCR);
6. Muséum national d’Histoire naturelle, França (MNHN);
7. Netherlands Centre for Biodiversity Naturalis, Holanda (RMNH)

8. Oxford University Museum of Natural History, Reino Unido (OUMNH);
9. Senckenberg Naturmuseum Frankfurt, Alemanha (SNF);
10. University of Louisiana, Lafayette Zoological Collections, Lafayette, EUA (ULLZ).

Um total de 92 lotes identificados como espécies do complexo *A. macrocheles* foi examinado. Estes lotes representaram um montante de 192 espécimes, correspondentes a cinco espécies. Um total de 42 caracteres foi analisado para cada indivíduo, incluindo região cefálica, abdome, leque caudal, e todo o conjunto de apêndices. Esta lista foi baseada nos principais caracteres usados em descrições de espécies do gênero *Alpheus*, bem como características consideradas em chaves de identificação específicas para o grupo (e. g., CHACE, 1972; SOLEDADE; ALMEIDA, 2013). Variações entre fêmeas e machos também foram investigadas e descritas. A lista de caracteres avaliados encontra-se abaixo na Tabela 1.

Tabela 1– Lista de caracteres analisados nas espécies do complexo *Alpheus macrocheles* (Hailstone, 1835).

Estrutura	Caráter analisado
Região frontral da carapaça	
Rostro	Comprimento
Capuzes oculares	Forma dos dentes
Região entre o rostro e os capuzes	Forma das margens
Apêndices cefálicos	
Estilocerito	Comprimento em relação ao primeiro segmento antenular
Pedúnculo antenular	Relação de tamanho dos segmentos
Carena ventromesial do pedúnculo antenular	Tamanho e forma
Escafocerito	Forma
Dente distal do escafocerito	Comprimento em relação ao pedúnculo antenular
Superfície lateral do escafocerito	Côncava ou truncada

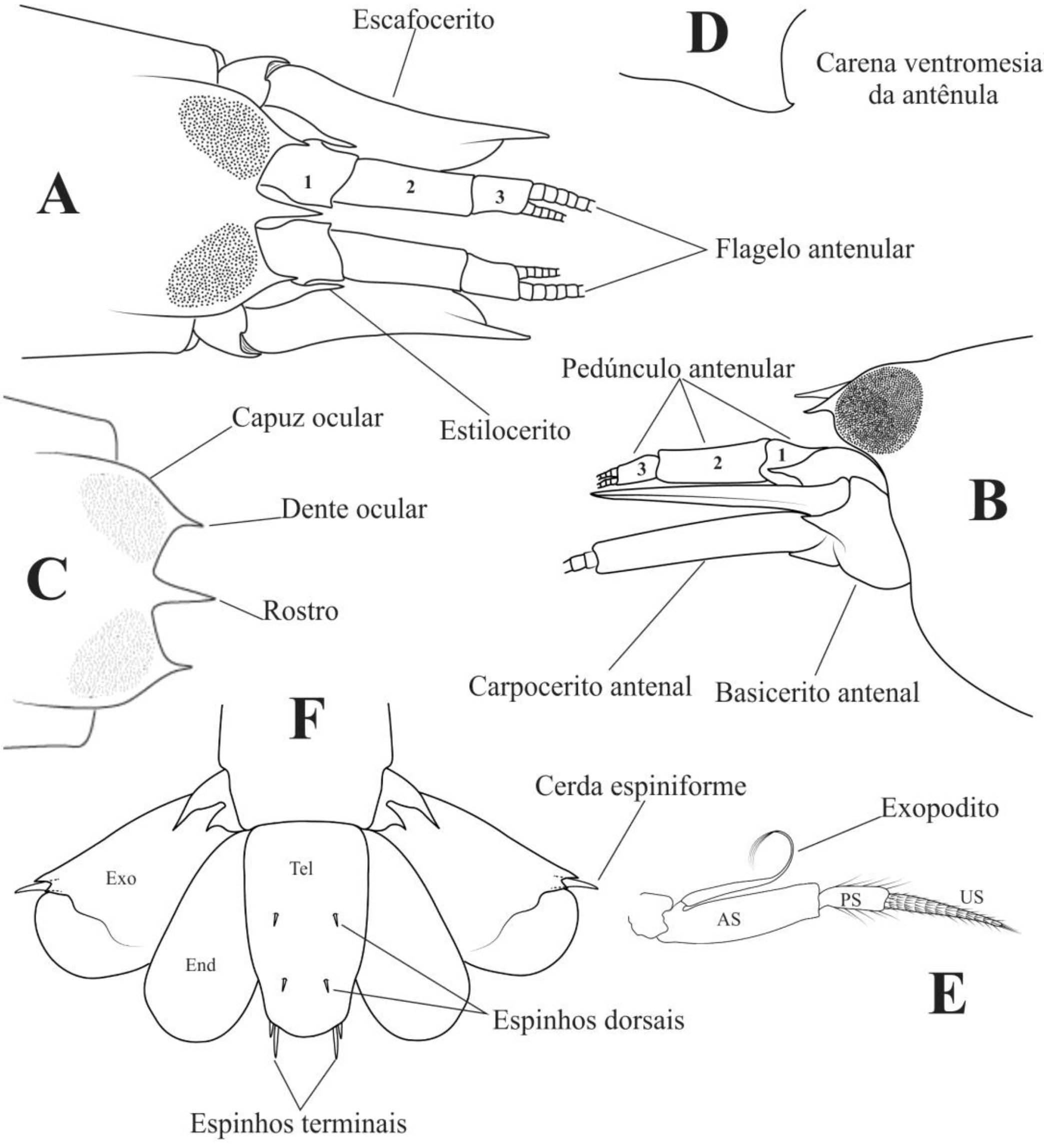
Apêndices Orais	
Terceiro maxilípodo	Comprimento e forma
Exópodo do terceiro maxilípodo	Comprimento em relação aos artículos do maxilípodo
Quelípodos (primeiro par de apêndices quelados)	
Superfície mesial do ísquio (ambos os quelípodos)	Número de cerdas espiniformes
Superfície mesial do mero (ambos os quelípodos)	Número de cerdas espiniformes
Ângulo distomesial do mero (ambos os quelípodos)	Presença de dente
Superfície distodorsal da palma (ambos os quelípodos)	Robustez e forma do dente
Dente distolateral da palma (ambos os quelípodos)	Robustez e forma do dente
Superfícies da palma da quela maior	Presença ou não de tubérculos
Endentação dorsal da quela maior	Largura e profundidade
Endentação ventral da quela maior	Largura e profundidade
Dedos da quela menor	Comprimento com relação à palma
Dáctilo da quela menor	Forma da margem dorsal
Pólex da quela maior	Forma da extremidade
Dáctilo da quela maior	Forma da margem distal
Plunger	Forma e nível de desenvolvimento
Pereiópodos (2-5)	
Quela de P2	Tamanho em relação ao último artículo do carpo
Dedos de P2	Tamanho em relação à palma
Ísquio de P3	Presença de cerda espiniforme

Ísquio de P4	Presença de cerda espiniforme
Ísquio de P5	Presença de cerda espiniforme
Própodo de P3	Número de cerdas espiniformes
Própodo de P4	Número de cerdas espiniformes
Própodo de P5	Número de cerdas espiniformes
Superfície extensora do dáctilo de P3	Com ou sem dentículo subterminal
Superfície extensora do dáctilo de P4	Com ou sem dentículo subterminal
Télson e Urópodos	
Espinhos dorsais do télson	Tamanho e ponto de inserção
Tamanho dos espinhos dorsais do télson	
Espinhos distais do télson	Relação de tamanho entre os pares
Superfície distal do télson	Forma
Superfície lateral do exópodo uropodal	Forma
Ângulo distolateral do exópodo uropodal	Número de dentes
Ângulo distolateral do exópodo uropodal	Número de cerdas espiniformes
Cerda espiniforme do exópodo uropodal	Comprimento em relação à superfície do exópodo

Fonte: Soledade (2019).

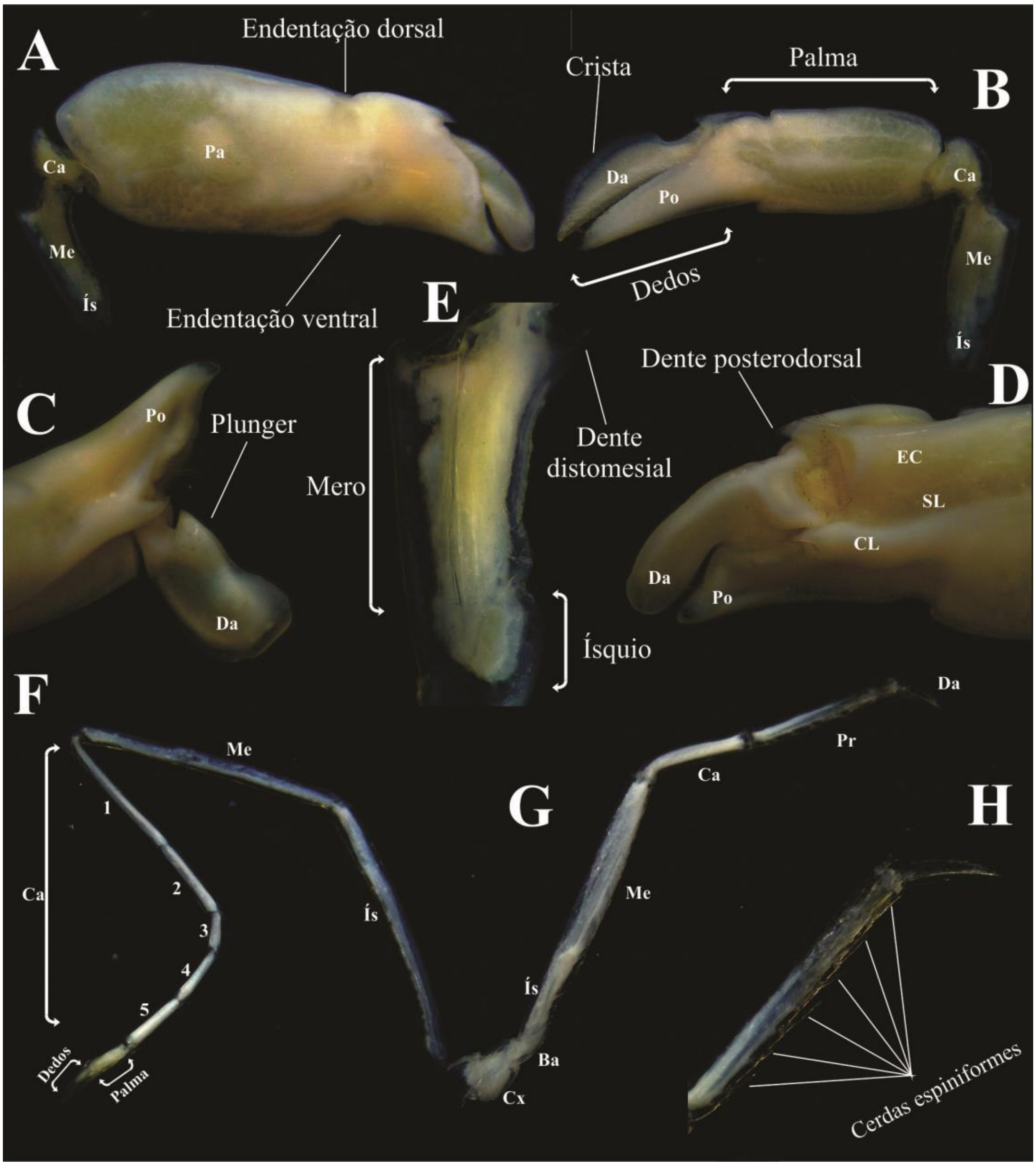
A partir deste conjunto de características foram identificados os principais caracteres diagnósticos usados para as comparações e ilustrações das espécies. Ilustrações das principais regiões corporais e dos apêndices considerados nas análises morfológicas desta tese são apresentadas nas Figuras 2 e 3.

Figura 2 – Morfologia geral dos camarões-de-estalo do gênero *Alpheus* Fabricius, 1798, principais caracteres de importância sistemática. (A) carapaça e apêndices cefálicos, vista dorsal; (B) o mesmo, vista lateral; (C) região anterior da carapaça, destaque do rostro e capuzes oculares; (D) carena ventromesial do pedúnculo antenular; (E) terceiro maxilípodo, vista lateral; (F) télson e urópodos, vista dorsal. Nas figuras (A) e (B) os números (1-3) representam os segmentos do pedúnculo antenular. Em (E), AS = antepenúltimo segmento, PS = penúltimo segmento e US = último segmento. Em (F), Tel = télson, Exo = exopodito e End = endopodito.



Fonte: Soledade (2019).

Figura 3 – Morfologia geral dos camarões-de-estalo do gênero *Alpheus* Fabricius, 1798, principais caracteres de importância sistemática. (A) quelípodo maior, vista mesial; (B) quelípodo menor, vista mesial; (C) quelípodo maior em vista lateroventral, destaque dos dedos; (D) o mesmo, vista laterodorsal; (E) detalhe do mero e ísquio do quelípodo maior; (F) segundo pereiópodo esquerdo, vista lasteral; (G) terceiro pereiópodo direito, vista lateral; (H) o mesmo, detalhe das cerdas espiniformes do própodo. Na figura (F) os números (1-3) representam os artículos do carpo. Ba = base, Ca = carpo, CL = crista lateral, Cx = coxa, Da = dáctilo, EC = elevação cilíndrica, Ís = ísquio, Me = mero, Pa = palma, Po = Pólex, Pr = própodo, SL = sulco lateral.



Fonte: Soledade (2019).

3 CONGRUENCE BETWEEN MORPHOLOGY AND MOLECULAR DATA SUPPORTS THE DISTINCTION BETWEEN THE SNAPPING SHRIMPS *Alpheus macrocheles* AND *A. Amblyonyx* (CARIDEA, ALPHEIDAE)

ABSTRACT

The snapping shrimp *Alpheus macrocheles* (Hailstone, 1835) is widely distributed across the Atlantic Ocean and was originally described from Hastings, England, based on a very concise description with limited morphological details and diagnostic illustrations. The morphologically similar *A. amblyonyx* Chace, 1972, type locality Quintana Roo, Mexico, is a western Atlantic taxon. The superficial description of *A. macrocheles* by Hailstone and the high similarity with *A. amblyonyx* has led to taxonomic confusion regarding the precise identification of these species. Thus, the objective of this study was to provide the redescription of *A. macrocheles* and a morphological characterization of *A. amblyonyx,* with detailed illustrations and morphological and molecular comparisons with congeners from the Atlantic Ocean. In total, 42 morphological characters were analyzed, in addition to a phylogenetic analysis of 16S ribosomal RNA (rRNA) gene sequences. A Bayesian Inference analysis recovered *A. macrocheles* and *A. amblyonyx* as distinct clades supporting the taxonomic distinction between them. The tree topology suggests that *A. macrocheles* is more closely related to *A. crockeri* (Armstrong, 1941) and *A. puapeba* (Christoffersen, 1979) than to *A. amblyonyx*, which forms the sister group to a well-supported clade containing these three species. This contribution conclusively distinguishes *A. macrocheles* and *A. amblyonyx* and points out the need for a comprehensive review involving all species of the larger *A. macrocheles* group.

Key words: Decapoda, cryptic species, 16S, genetic divergence, integrative taxonomy.

INTRODUCTION

The difficulty of solving taxonomic problems using only morphology is recurrent in the study of snapping shrimps of the genus *Alpheus* Fabricius, 1798. The genus, with 313 valid species (e.g., De Grave & Fransen 2011; Anker *et al.*, 2016; Salgado-Barragán *et al.* 2017; Komai & Ohtomi, 2018; Dehghani *et al.*, 2018) has the highest species richness of the family Alpheidae Rafinesque, 1814, which contains more than 600 valid species (De Grave & Fransen 2011). This genus contains numerous cryptic species complexes, several of which are still awaiting resolution (e.g., *A. packardii* Kingsley, 1880 and *A. paracrinitus* Miers, 1881). Recently, some potentially cryptic species complexes in *Alpheus* were resolved with integrative analyses utilizing both molecular and morphological data: e.g., *Alpheus armillatus* H. Milne Edwards, 1937 (Mathews 2006; Mathews & Anker 2009), *A. bouvieri* A. Milne-Edwards, 1878 (Anker *et al.* 2009), *A. hebes* Kim & Abele, 1988 (Anker *et al.* 2009), *A. heterochaelis* Say, 1818 (Almeida *et al.* 2014), *A. floridanus* Kingsley, 1878 (Bracken-Grissom *et al.* 2014) and *A. intrinsecus* Spence Bate, 1888 (Cunha *et al.* 2017). Molecular data have also been used as a complementary tool to describe new species of this genus. Recent examples include *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013, *A. petronioi* Almeida, Terossi & Mantelatto, 2014, *A. hephaestus* Bracken-Grissom & Felder, 2014, *A. roblesi* Bracken-Grissom & Felder, 2014 and *A. ulalae* Bracken-Grissom & Felder, 2014, all described after revisions of complexes of cryptic species.

The *Alpheus macrocheles* (Hailstone, 1835) species complex (sensu Anker & De Grave 2012) belongs to the informal *A. macrocheles* species group (sensu Coutière, 1905), which includes about 30 species distributed throughout the world that share the following set of characters: ocular hoods armed with sharp teeth; major chelae with notches on both the dorsal and ventral margins; lateral surface of the major chelae with strong and deep grooves and a well-developed cylindrical elevation, ending in an adhesive disc; fingers of the major chelae strongly twisted in lateral plane. The complex includes at least ten taxa (Anker & De Grave 2012): *Alpheus amblyonyx* Chace, 1972, *A. lentiginosus* Anker & Nizinski, 2011, *A. pouang* Christoffersen, 1979 and *A. puapeba* Christoffersen, 1979 (all in the western Atlantic Ocean), *A. cedrici* Anker & De Grave, 2012 (central Atlantic), *A. macrocheles* (amphi-Atlantic), *A. platydactylus* Coutière, 1897 (eastern Atlantic), two in *A. bellimanus* Lockington, 1877 and *A. rectus* Kim & Abele, 1988 (eastern Pacific), and *A. albatrossae* (Banner, 1953) (Indo-Pacific). These snapping shrimp inhabit the subtidal zone, most commonly in deeper areas (from 100 to up to 600 meters). However, several members of this species complex have been reported from shallow waters, such as *A. amblyonyx* (0–67 meters), *A. bellimanus* (0–300 meters), *A. macrocheles* (0–50 meters) and *A. puapeba* (12–175 meters) (Crosnier & Forest 1966; Anker & De Grave 2012; Almeida *et al.* 2018).

The *A. macrocheles* complex still lacks an appropriate taxonomic revision, since some of the species involved have very old and limited descriptions and have never been reexamined. One of the main taxonomic problems involves uncertainty about the distinction between *A. macrocheles* and *A. amblyonyx*. The former was originally described from Hastings, England (Hailstone 1835a) as a dubious *Hippolyte* Leach, 1814, and named *Hippólyte macrochèles*. Rathbun (1900) transferred the species to the genus *Alpheus*. Unfortunately, in Hailstone's description nothing is mentioned regarding the deposit of type material, which is not available at any of the major international museums, and is considered, lost. *Alpheus macrocheles* has been recorded in the Mediterranean Sea and both sides of the Atlantic Ocean, including the Central Atlantic (Ramos-Porto 1979; Manning & Chace 1990; d’Udekem d’Acoz 1999; Guterres *et al.* 2005; Souza *et al.* 2011). In Brazil, *A. macrocheles* has been reported from the Fernando de Noronha Archipelago and from Amapá to Espírito Santo States (see compilation by Soledade & Almeida 2013). Chace (1972) described *A. amblyonyx* based on material from Ascension Bay, Quintana Roo, Mexico. This species is restricted to the western Atlantic, being recorded from the Gulf of Mexico, Caribbean Sea to Espírito Santo, Brazil, including Atol das Rocas and Fernando de Noronha (see compilation by Soledade & Almeida 2013). The morphological similarity between these two species is remarkable. Chace (1972), describing *A. amblyonyx*, pointed out the resemblance with *A. macrocheles*, separating them mainly by differences in the rostrum and chelipeds, as well as other minor characteristics. The similarity between these two species and the apparent inconsistencies in the characters listed in the diagnosis of *A. amblyonyx,* have generated confusion and uncertainty about the validity of *A. amblyonyx* and also about the legitimacy of records of *A. macrocheles* from the western Atlantic.

The occurrence of *A. macrocheles* in the western Atlantic is uncertain. Records from the Brazilian coast were made mostly in checklists, without detailed illustrations or information regarding color pattern (e.g., Ramos-Porto 1979; Coelho & Ramos 1980; Guterres *et al.* 2005; Coelho *et al.* 2006; Coelho Filho 2006; Soledade & Almeida 2013). Anker & De Grave (2012) considered all such records of *A. macrocheles* to be dubious, perhaps representing some other species within the complex, such as *A. amblyonyx*. After the short original description of *A. macrocheles,* more detailed drawings of eastern Atlantic specimens of *A. macrocheles* were provided by Crosnier & Forest (1966). However, these illustrations were limited to the frontal region and the two pairs of chelae, making it difficult to compare with western Atlantic specimens. This history of confusion regarding these taxa raises the question: is *A. amblyonyx* morphologically and genetically distinct of *A. macrocheles*? With this in mind, our objective was to reexamine these two species, based on a combined analysis of morphological – including a redescription for *A. macrocheles* and new morphological characterization of *A. amblyonyx* – and molecular data.

MATERIAL AND METHODS

The specimens of all species analyzed were loaned from the following institutions / collections: Museu Nacional do Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu de Oceanografia Professor Petrônio Alves Coelho (MOUFPE), Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo, Brazil (CCDB / FFCLRP / USP), Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico (CNCR), Muséum national d'Histoire naturelle, France (MNHN), Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands (RMNH), Oxford University Museum of Natural History (OUMNH) , Senckenberg Naturmuseum Frankfurt, Germany (SNF) and University of Louisiana, Lafayette Zoological Collection, Lafayette, USA (ULLZ). In total, 42 characters were analyzed for each species, including those in the cephalic region, abdomen, caudal fan, and appendages. Variations between females and males were also analyzed. The main diagnostic characters were listed and illustrated. Material of some additional species of the *A. macrocheles* species complex from the Atlantic Ocean (*A. platydactylus*, *A. pouang* and *A. puapeba*) was analyzed as comparative material. We also included a specimen of *A. crockeri* (Armstrong, 1941) of Cape Verde, a member of the *A. macrocheles* group in the analysis. In the case of species for which no specimens were obtained for analysis, morphological characters extracted from the original descriptions were used.

All genetic sequences of the ingroup were generated in this study. Sequences of two species of *Synalpheus* Spence Bate, 1888 obtained from Genbank were used as outgroups in the analysis (Table 1).

Table 1. List of specimens used for genetic analysis. CCDB: Coleção de Crustáceos do Departamento de Biologia de FFCLRP/USP; CNCR: Colección Nacional de Crustáceos, Mexico; MNHN: Muséum national d'Histoire naturelle, France; RMNH: Netherlands Centre for Biodiversity Naturalis; OUMNH: Oxford University Museum of Natural History; UF: Florida Museum of Natural History; ULLZ: University of Louisiana at Lafayette Zoological Collection.

Species	**Locality**	**Catalogue number**	**GenBank**	**References**
Alpheus amblyonyx Chace, 1972	Gulf of Mexico	ULLZ 6615	Pendent	Present study
Alpheus amblyonyx	Quintana Roo, Mexico	CNCR 21271	Pendent	Present study
Alpheus amblyonyx	Belize	ULLZ 16584	Pendent	Present study
Alpheus amblyonyx	Guadeloupe	MNHN 12026	Pendent	Present study
Alpheus amblyonyx	French Antilles	UF 32400	Pendent	Present study
Alpheus crockeri (Armstrong, 1941)	Cape Verde	OUMNH 2014-01-0030	Pendent	Present study
Alpheus macrocheles (Hailstone, 1835)	Azores, Portugal	RMNH.Crus.D.51342	Pendent	Present study
Alpheus macrocheles	Azores, Portugal	OUMNH 2002-09-0003	Pendent	Present study

Alpheus macrocheles	Canary Islands	RMNH.Crus.D.51363	Pendent	Present study
Alpheus puapeba Christoffersen, 1979	Rio de Janeiro Brazil	MNRJ 21836	Pendent	Present study
Synalpheus cf. *brevicarpus* Herrick, 1891	Ubatuba, São Paulo, Brazil	CCDB 3419	KF667548	Almeida *et al.* (2014)
Synalpheus fritzmuelleri Coutière, 1909	Gulf of Mexico	ULLZ 7136	EU868642	Bracken *et al.* (2009)

DNA extraction, amplification and sequencing were conducted at the University of São Paulo (USP) and the University of Louisiana at Lafayette (ULL). DNA extractions conducted at USP followed the protocols of Mantelatto *et al.* (2009; 2018). The DNA was extracted from abdominal muscle tissue and then incubated for 24 h in 600 μl of lysis buffer and 200 μl of Proteinase K 500 μl / ml at 65°C; the proteins were separated by the addition of 200 μl of ammonium acetate (7.5 M) prior to centrifugation. The DNA was precipitated by the addition of 600 μl of cooled isopropanol (-20°C) followed by centrifugation; the resulting pellet (after 48 h rest at -20°C) was washed with 70% ethanol, dried and resuspended in 20 μl TE buffer. DNA extractions conducted at ULL were done using the Qiagen DNeasy ® Blood and Tissue Kit (Cat. No. 69504) following the manufacturer's instructions. The concentrations of DNA obtained in the samples were quantified using a spectrophotometer Nanodrop 2000c$^{®}$.

A ~550 base pair region of the 16S large ribosomal subunit gene was amplified from the extracted DNA through PCR (Polymerase Chain Reaction) (Sambrook *et al.* 1989) using the primers: 1472 (5’-AGATAGAAACCAACCTGG-3’) and 16SL2 (5’-TGCCTGTTTATCAAAAACAT-3’) (Schubart *et al.* 2000). PCR reactions performed at USP were done in 25μl volumes containing 5M betaine, 10X PCR buffer, primers, 25mM $MgCl_2$, 200μM dNTPs, deionized water, 1 unit *Taq* polymerase and 1 μl of extracted genomic DNA. PCR reactions performed at ULL were done in 25μl volumes containing 1 unit DreamTaq ™ hot start DNA polymerase (Cat. No. EP1701), 2.5μl DreamTaq™ 10X sequencing buffer, 0.2mM dNTPs, 1μM each primer and roughly 30ng of genomic template DNA.

DNA amplification at USP was performed in a Veriti 96-Well Thermal Cycler® (Applied Biosystems) with specific thermal cycles for the utilized set of primers. DNA amplification at ULL was performed using a Stratagene RoboCycler® Gradient 96 Thermocycler with thermal cycles for the utilized set of primers. PCR products were visualized using gel electrophoresis with 1% agarose gel and photographed with a SX520 Canon® digital camera on a UV 302 Kasvi® Transilluminator. PCR products were purified using the SureClean® Purification Kit following the manufacturer’s instructions. Cycle sequencing reactions were performed in 20μl volumes using Big Dye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) following the manufacturer’s instructions. Sequencing was performed on ABI 3100 Genetic Analyzers® at the Departamento de Tecnologia da Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal, Universidade Estadual Paulista, Jaboticabal, São Paulo, Brazil and in the department of biology at the University of Louisiana at Lafayette, Lafayette, LA, USA.

Sequences were confirmed by sequencing both strands. Sequence assembly was performed using the programs Bioedit 7.0.9.0 (Hall 2005) and Sequencher 4.7 (GeneCodes, Ann Arbor, MI, USA).

The sequences were aligned using MUSCLE (Edgar 2004), with standard parameters, available on the platform Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller *et al.* 2010).

An analysis was performed using jModelTest (Darriba *et al.* 2012), implemented on CIPRES, to find out which substitution model best fit the data, using the Bayesian information criterion (BIC). Bayesian inference analysis was carried out in the software MrBayes v3.2.6 (Ronquist *et al.*, 2012), implemented on CIPRES, using parameters obtained from jModelTest. In the analysis, one tree was sampled for every 1,000 generations of 20,000,000 generations, starting with a randomly generated tree. Four independent runs were performed and the convergence of runs was analyzed using Tracer 1.6 (Rambaut *et al.* 2014). The first 20% of trees and parameters were discarded as burn-in and a final tree was generated in Tree Annotator 1.8.4 (implemented in BEAST, Drummond *et al.* 2012). Posterior probability values greater than 95% were reported. Genetic distance matrix was constructed in MEGA version 5 (Tamura *et al.* 2011) based on the substitution model selected by jModelTest.

The results section includes synonymy, material examined, comparative material, distribution, redescription, morphological variation, remarks and genetics. In the synonymy, the records where part of the species was reanalized were considered valid. Records were also considered as valid in the synonymy where illustrations or any description of the material analyzed were provided. The redescription was based on all of the material examined. The geographical distribution is based only on the localities included in the material examined and in the records where it was possible to rely on the accuracy of the identification of the species. The map was built with a template of the software Diva-Gis 7.5 (Hijmans *et al.* 2001). Finally, the following abbreviations were used in this study: F = female; OVF = ovigerous female; M = male; NI = sex unidentified; Exp = expedition.

RESULTS

Systematics

Infraorder Caridea Dana, 1852

Family Alpheidae Rafinesque, 1815

Alpheus macrocheles (Hailstone, 1835b)
(Figs. 1–3)

Hippólyte rùbra Hailstone, 1835a: 272; Fig. 31. [off Hastings, England]; Westwood, 1835: 274.

Hippólyte macrochèles Hailstone, 1835b: 395. [*nomen novum* for *Hippólyte rùbra* Hailstone, 1835a].

Alpheus macrocheles (Hailstone, 1835)–Rathbun 1900; Crosnier & Forest 1966, p. 218–219, fig. 2 a–d; d'Udekem d'Coz 1999.

Non *Alpheus macrocheles* (Hailstone, 1835)–Rathbun 1901, p. 105; Zimmer 1913, p. 386, fig. F; Coelho & Ramos 1972, p. 149; 1980, p. 135; 1995, p. 116; Ramos-Porto 1979, p. 118, fig. 1, plates 1–6; 1980; Coelho *et al.* 1980, p. 55; 1986, p. 84; Fausto Filho 1980, p. 113; Manning & Chace 1990, p. 15; Ramos-Porto *et al.* 1996, p. 219; Guterres *et al.* 2005, p.233; Coelho *et al.* 2006, p. 51; Coelho Filho 2006, p. 8; Alves *et al.* 2008, p. 49; Souza *et al.* 2011; p. 47; Soledade & Almeida 2013, p. 101.

Non *Crangon macrocheles* (Hailstone, 1835)–Schmitt, 1935, p. 142.

Type material. EAST ATLANTIC – France, Roscoff. Neotype, 1 M, Roscoff, Bretagne, France, 12.X.1972, RMNH.Crus.D.29789.

Additional material examined. MEDITERRANEAN – **Spain.** 1 F, Cabo Norfeo, 1940, RMNH.Crus.D.5982; 1 OVF, Cadaquez, X.1947, RMNH.Crus.D.5983; **Croatia.** 1 OVF, Ístrien, 4 m, VII.1882, SNF 14050. EAST ATLANTIC – **France.** 1 F, Roscoff, RMNH.Crus.D.34508; 1 M, Guéthary, 27.X.1947, RMNH.Crus.D.5981; **Azores.** 1 M, 1 NI, Exp. #5.142, 108–118 m, 38°35’N 28°33’W, 7.VI.1981, RMNH.Crus.D.51342 (**genetic voucher**); 1 NI, Faial Island, 15 m, 38.522919°N, 28.627468°W 9.IX.2001, OUMNH 2002-09-03 (**genetic voucher**); **Madeira.** 1 M, Cais de Porto Novo, under stones, 18.VIII.1993, RMNH.Crus.D.42706; **Morocco.** 1 F, 33°50’N 07°07’W, 25.I.1956, RMNH.Crus.D.34495; 1 M, Témara, 1952, RMNH.Crus.D.34496; 1 M, Témara, 1954, RMNH.Crus.D.34497; **Canary Islands.** 1 M, #4.070, Southeast of Lanzarote, 41–50 m, sand and calcareous algae, 28°56’N 13°33’W, 20.V.1980, RMNH.Crus.D.51363 (**genetic voucher**); **Cape Verde.** 1 OVF, 3 NI, “Tydeman” Cancap–VI, Cape Verde islands Exp., #6.109, off Santa Luzia, 55–80 m, calcareous algae, 16°44’N 24°46’W, 16.VI.1982, RMNH.Crus.D.51345; 1 M, Tarrafal Bay, 1959, MNHN 3163; **Angola.** 3 F (2 OVF), 1 M, Cuanza River, 9°20’S 13°0’E, 31.I.1949, RMNH.Crus.D.7821.

Type locality. EAST ATLANTIC – England, Hasting (Hailstone 1835b).

Distribution. MEDITERRANEAN SEA – Spain and Croatia; EAST ATLANTIC – England, France, Azores, Morocco, Madeira, Canary Islands, Cape Verde, Angola (Hailstone 1835a; Holthuis 1951; Crosnier & Forest 1966; d’Udekem d’Acoz 1999; this study).

Diagnosis. Rostrum reaching halfway up the length of the first segment of the antennular peduncle; scaphocerite with blade reaching little beyond distal end of second article of antennular peduncle; distal tooth distinctly overreaching distal limit of antennular peduncle. Minor cheliped with ischium armed with 1 or 2 spiniform setae; ventromesial margin of the merus with 7 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; Dactylus with broad crest on extensor margin. Major cheliped with ischium armed with 3 spiniform setae; ventromesial margin of the merus with 7 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; dactylus flattened, laterally twisted, dorsally convex and strongly bulbous distally; plunger reduced to small tooth in proximal portion. Second pereiopod elongated, slender; ischium slightly longer than merus; carpus with 5 articles with ratio approximately equal to 2: 1.5: 1: 1: 1.5. Distolateral margin of uropodal exopod with one strong and sharp lateral tooth adjacent to long spiniform setae.

Redescription. Carapace smooth, frontal margin with strong rostrum, ocular hoods with well-developed teeth originating from the anterior margin of hoods; rostrum slightly flat in dorsal view, distinctly longer than broad, distally tapering and ending in sharp point, without setae, reaching halfway up the length of the first segment of the antennular peduncle; margin between orbital teeth and rostrum V-shaped (Fig. 1A, B); orbital process present. Pterygostomial angle rounded, not anteriorly protruding (Fig. 1B); cardiac notch deep. Abdominal somites with posteroventral margins broadly rounded, those of fifth segment slightly angular; sixth somite without articulated plate in posterolateral margin.

Eyes with well-developed corneas; ocellar beak projecting anteriorly, acute, visible in lateral view. Antennular peduncle moderately slender; stylocerite with acute tip reaching beyond distal limit of first article of antennular peduncle; ventromesial carina well-developed, triangular in shape, with small pointed tooth (Fig. 1C); second article of antennular peduncle much longer than visible part of first article, about 3 times longer than broad (Fig. 1A); lateral flagellum with groups of aesthetascs extending to article 10. Antennal basicerite with acute lateral tooth; carpocerite slightly exceeds distal end of scaphocerite and antennular peduncle; lateral margin of scaphocerite slightly concave, ending in strong lateral tooth overpassing distal margin of blade (Fig. 1A); blade reaching little beyond distal end of second article of antennular peduncle; distal tooth distinctly overreaching distal limit of antennular peduncle. Mouthparts as illustrated. Third maxilliped slender; coxa with lateral plate slightly truncated distally; exopod reaching beyond distal limit of antepenultimate article when extended; antepenultimate article somewhat flattened, approximately 4 times longer than broad, ventral surface sparsely setose; penultimate article approximately 3 times longer than broad, slightly broadened distally and densely setose; ultimate article disarmed, distally tapering, with dense rows of long setae (Fig.1I).

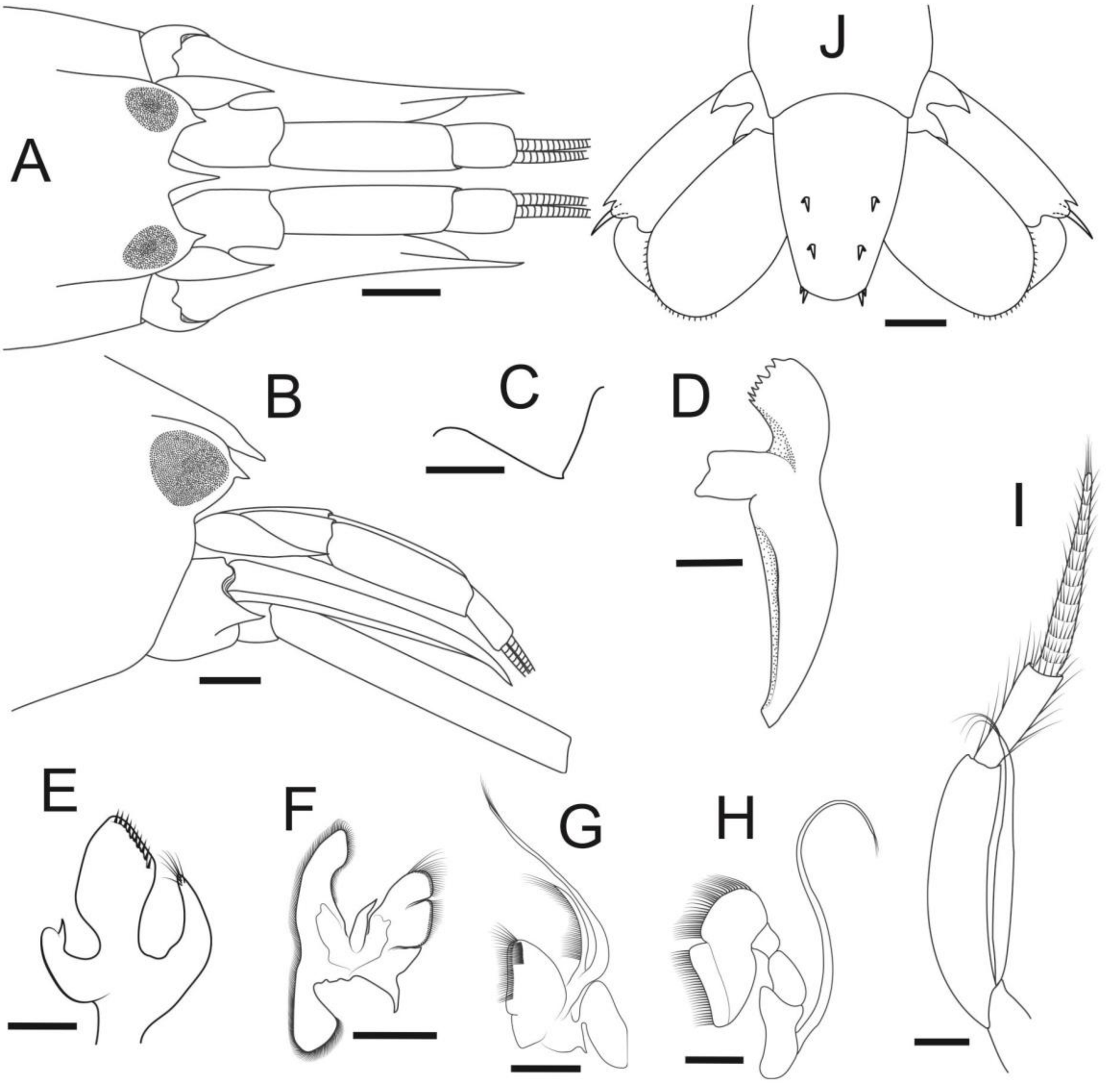


Figure 1. *Alpheus macrocheles* (Hailstone, 1835), neotype male specimen from Roscoff, France, RMHN.Crus.D.29789. (A) Carapace and cephalic appendages, dorsal view (setae omitted); (B) same, lateral view; (C) ventromesial carina of the antenular peduncle; (D) left mandible, mesial view; (E) first maxilla, lateral view; (F) second maxilla, lateral view; (G) first maxilliped, lateral view; (H) second maxilliped, lateral view; (I) third maxilliped, lateral view; (J) telson and uropods, dorsal view (setae omitted). Scale Bars: (A, B, I, J) = 1 mm; (C–H) = 0.5 mm.

Minor cheliped with short and stout ischium; distomesial margin broad, subtriangular in cross-section, armed with 1 or 2 spiniform setae; ventrolateral surface unarmed; merus with ventromesial margin slightly convex, ending in small acute tooth, with 7 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; carpus cup-shaped; chelae strongly compressed, palm with grooves and notches from distal half of lateral surface; mesial surface convex and devoid of depressions or grooves; lateral surface with low crest starting at about middle of palm and ending in acute distolateral tooth; ventral surface smooth, ending in well-defined notch; dorsal margin also smooth, with sub-cylindrical elevation ending distally in small adhesive disk; distomesial surface with high ridge ending in strong sharp tooth; fingers as long as palm; pollex lightly excavated on cutting edge; dactylus slightly flattened and twisted laterally, with broad crest on extensor margin, with small adhesive disk proximally (Fig. 2C, D).

Major cheliped with ischium short and robust, ventromesial surface with 3 small spiniform setae; merus robust, not elongated, about 2 times longer than wide, sub- triangular in cross section; ventrolateral margin disarmed; ventromesial margin straight, with 7 small spiniform setae, ending in robust and sharp tooth; carpus very short, cup-shaped, slightly compressed; lateral surface with low crest starting at approximately 0.6 of length of palm, ending in distolateral sharp tooth, slightly directed laterally; linea impressa well-marked; mesial surface convex, devoid of sculptures and grooves; ventral surface with rounded smooth shoulder a slightly projecting into adjacent deep notch; notch extends transversely to groove on mesial surface; dorsal margin with sub-cylindrical elevation ending distally in large adhesive disk; distomesial surface with deep transversally notched crest ending in sharp tooth; distal third of ventral margin of palm with strong and long setae extending to distomesial margin of palm; pollex shorter than dactylus, strongly curved laterally, cutting edge slightly excavated and with small rounded tooth in proximal portion; dactylus flattened, laterally twisted, dorsally convex and slightly bulbous distally; plunger reduced to small tooth in proximal portion (Fig. 2A, B).

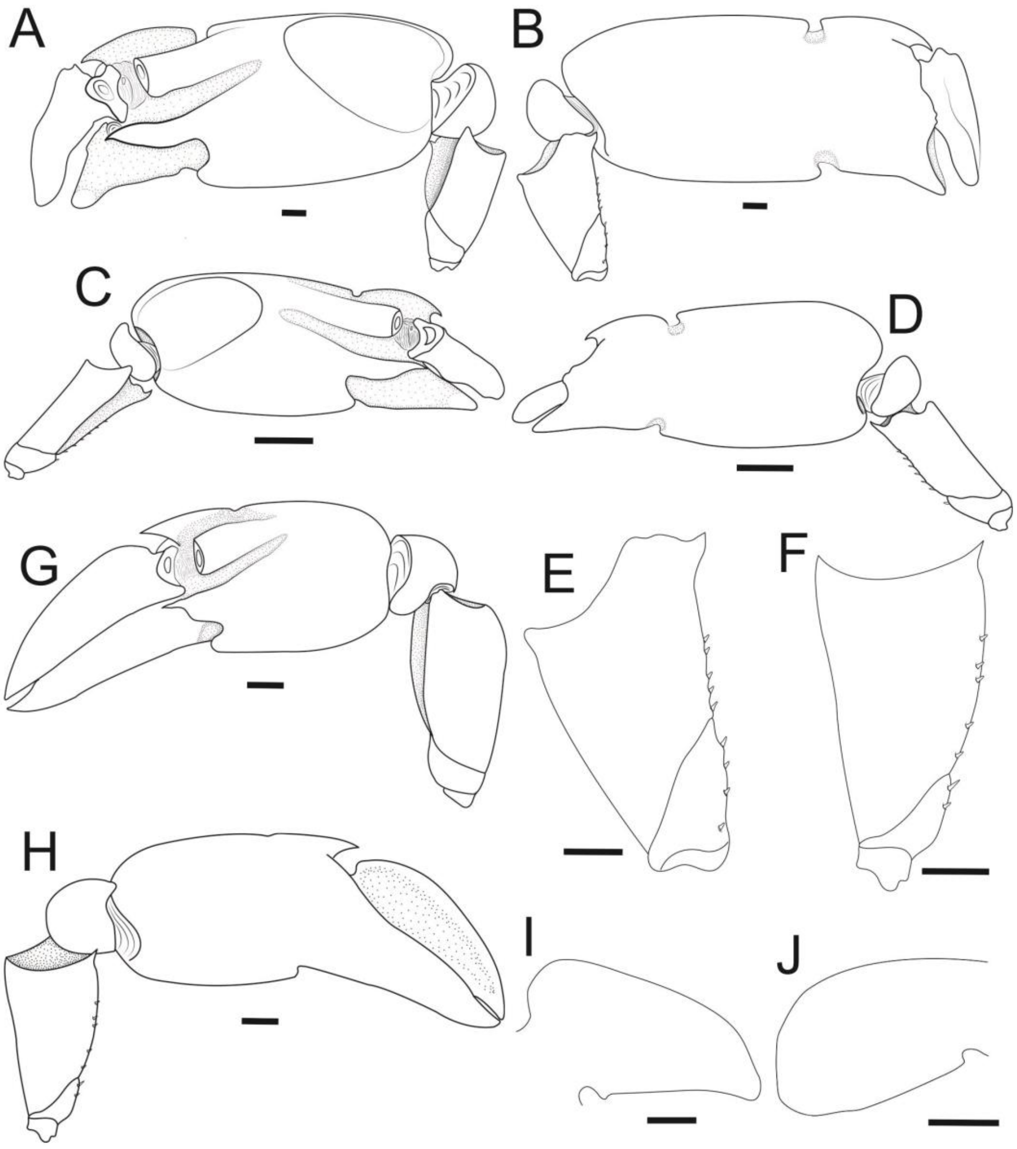


Figure 2. *Alpheus macrocheles* (Hailstone, 1835), (A, B, E) neotype male specimen from Roscoff, France, RMHN.Crus.D.29789; (G, H, F) female specimen from Roscoff France, RMHN 34508; (C, D, J), male specimen of the Azores, RMNH.Crus.D.51342: (A, C) major cheliped in lateral view; (B, D) same, in mesial view; (E, F) Detail of the spiniform setae in the ischium and propodus of the major and minor chelae, respectively; (G) cheliped minor lateral view; (H) same, mesial view; (I, J) dactylus of the major chelae in mesial view, detail of the plunger. Scale Bars = 1 mm in (A–H) and 0.5 mm in (I, J).

Second pereiopod elongated, slender; ischium slightly longer than merus; carpus with 5 articles with ratio approximately equal to 2: 1.5: 1: 1: 1.5; chelae not ornamented, fingers as long as palm, with small tufts of setae (Fig. 3A). Third pereiopod with ischium armed with strong spiniform setae on ventrolateral surface; merus 5 times longer than broad, without tooth at distoventral angle; carpus slender, about half length of merus; propodus about 1.2 times longer than carpus, with about 9 robust spiniform setae along ventral margin and 1 pair of spiniform setae near to articulation with dactylus; dactylus slightly shorter than half length of propodus, conical, slightly curved, ending in sharp tip; extensor margin with 1 subdistal denticle (Fig. 3B). Fourth pereiopod similar to third in shape and proportion of articles, but slightly less robust; ischium armed with strong spiniform setae on the ventrolateral surface; propodus with about 7 robust spiniform setae along the ventral margin and 1 pair of spiniform setae near to articulation with the dactylus (Fig. 3C). Fifth pereiopod more slender than third and fourth (Fig. 3D); merus slightly longer than carpus; ischium with 1 spiniform setae; propodus with about 7 spiniform setae along ventral margin and 9 well-developed distolateral setal brushes. Pleopods with sparse setae on lateral margin of protopod; endopods and exopods with edges densely setose; first pleopod very reduced, distal margin of endopod with setae; second pleopod in male with *appendix masculina* subequal in length to *appendix interna*, not reaching distal margin of endopod, with numerous rigid setae at distal end; uropod with lateral lobe of protopod ending in strong and sharp tooth; diaeresis sinuous. Distolateral margin with one strong and sharp lateral tooth adjacent to long spiniform setae; endopod with row of small spiniform setae along distal margin (Fig. 1I). Telson subretangular, tapering to posterior margin; proximal margin 2.0 times broader than distal margin; lateral margins slightly convex; dorsal surface with 2 pairs of spiniform setae, first pair located at half-length of telson, second pair located approximately 0.7 of length of telson;

posterior margin broadly convex, with 2 pairs of spiniform setae, mesial pair about 3 times size of lateral pair (Fig. 1J); anal tubercles well-developed.

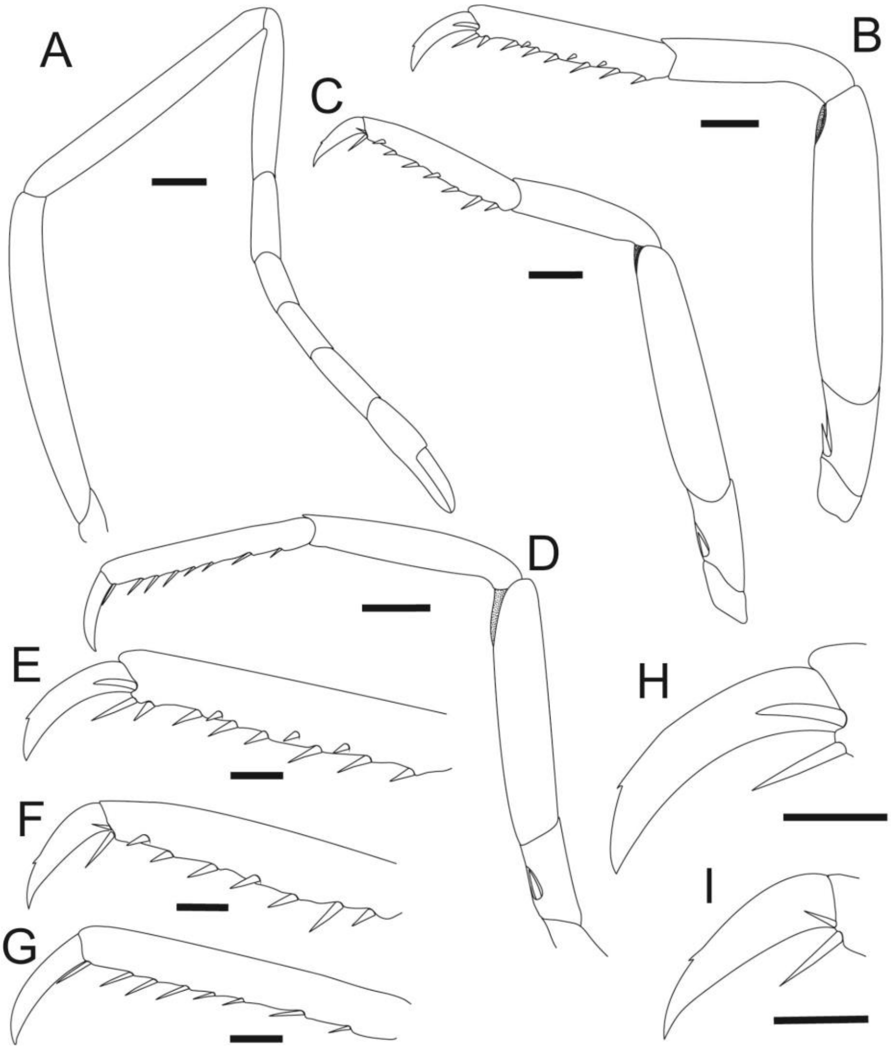


Figure 3. *Alpheus macrocheles* (Hailstone, 1835), neotype male specimen from Roscoff, France, RMHN.Crus.D.29789. (A) second pereiopod, lateral view; (B) third pereiopod, lateral view; (C) fourth pereiopod, lateral view; (D) fifth pereiopod, lateral view; (E–G) third–fifth pereiopods, detail of the propodus; (H, I) third and fourth pereiopods, detail of the dactylus. Scale bars = 1 mm in (A–D) and 0.5 mm in (E–I).

Morphological variation. The main differences observed between the sexes were more sculptured palms of major chelae in males, dactylus of major chelae with extremities less angular and more bulbous in females and presence of spiniform setae on the ventrolateral surface of the ischium of the fifth pereiopod only in males. The shape of the dactylus of the major chelae also varied among males from different localities, and may be more or less bulbous at the distal end (see Fig. 2). Variations were also observed in chelipeds and pereiopods 3–5 (see Table 2).

Table 2. Morphological variation in diagnostic characters of the snapping shrimp *Alpheus macrocheles* (Hailstone, 1835) and *Alpheus amblyonyx* Chace, 1972.

Character	Number of spiniform setae			
	Alpheus macrocheles (Hailstone, 1835) (n= 23)		*Alpheus amblyonyx* Chace, 1972 (n= 12)	
	Variation	Predominance	Variation	Predominance
Mesial margin of merus of major cheliped	4–7	7	6–7	without predominance
Mesial margin of merus of minor cheliped	5–9	7	4–8	6
Mesial margin of ischium of major cheliped	1–4	3	3–4	3
Mesial margin of ischium of minor cheliped	1–3	3	1–4	without predominance
Ventral margin of propodus of third pereiopod	7–11	8	6–9	9
Ventral margin of propodus of fourth pereiopod	7–10	9	6–10	10
Ventral margin of propodus of fifth pereiopod	5–10	7	6–8	8
Rows of setae on propodus of fifth pereiopod	6–11	without predominance	8–10	10

***Alpheus amblyonyx* Chace, 1972**

(Figs. 4–6)

Alpheus amblyonyx Chace, 1972: 59; fig. 16. [Near center of Arrecife Nicchehabin, Baía de la Ascensión, Territorio de Quintana Roo, Mexico]–Christoffersen 1979: 302, fig. 1 (in part); Abele & Kim 1986: 197, 208, 209, figs. b–d; Martínez-Iglesias *et al*. 1997: 403, fig. 2; 356; Serejo *et al.* 2007: 198; Alves *et al.* 2008: 48; Souza *et al*. 2011: 46; Soledade & Almeida 2013: 94 (in part); Anker *et al*. 2016: 14, fig. 2.

Type material. 1 OVF, Mexico, Quintana Roo, Bahía de la Ascención, #52–60, USNM 135356 (Not examined).

Material analyzed. WEST ATLANTIC – **Mexico.** 1 NI, Quintana Roo, Southwest of the Chinchorro Reef, 28.VIII.1990, CNCR 21271 (**topotype, genetic voucher);** 1 NI, Gulf of Mexico, 34–36 m, R/V Pelican, Box Dredge 14.XI.2005, 022°6.78'N 91°26.43'W, ULLZ 6615 (**genetic voucher**); **Belize.** 1 OVF, Stann Creek, Carrie Bow Cay, 16.80251°N, 88.081747°W, 3–4 m, 28.IV.2015, ULLZ 16584 (**genetic voucher**); 1M, Same locality, 04.IV.2007, ULLZ17432; 1OVF, Same Locality, 21.IV.2015, ULLZ16509, **Guadeloupe.** 1 M, KARUBENTHOS, #GB20, 16 m, 18.v.2012, MNHN 12112; 1 OVF, KARUBENTHOS, #GB24, 16 m, 18.v.2012, MNHN 12026 (**genetic voucher**); **French Antilles.** 1 OVF, Chicot, windward side of Tintamarre Island, 12–20 m, 23.IV.2012, UF 32400 (**genetic voucher**); **Brazil.** 1 OVF, Espírito Santo, REVIZEE Benthos #34, 20°24’10”S 39°55’35”W, Coll. R/V Astro Garoupa, 50 m, dredge, 15.VII.2001, MNRJ 17471; 1 OVF, Trindade Island, Ilha da Racha, 20°30’26.5”S– 29°20’40.0”W , 32 m, under rocks, 30.I.2012, MZUSP 30317; 1 OVF, Trindade Island, Ilha da Racha, 20°30’26.5”S– 29°20’40.0”W , 25 m, under rocks, 12.XI.2014, MZUSP 30262; 1 OVF, off Rio de Janeiro, REVIZEE Benthos #Y1, Coll. R/V Astro Garoupa, 60 m, dredge, 11.VI.2002, MNRJ 17467.

Type locality. WEST ATLANTIC – Mexico, Quintana Roo, Bahía de la Ascensión (Chace 1972).

Distribution. WESTERN ATLANTIC–Gulf of Mexico, Yucatan Peninsula, Florida, Caribean Sea, Brazil (Ceará to Espírito Santo, North Chain Seamounts, Fernando de Noronha, Atol das Rocas, Vitória-Trindade Seamount Chain, Trindade & Martin Vaz Archipelago) (Chace 1972; Abele & Kim 1986; Christoffersen 1979; Martínez-Iglesias *et al*. 1997; Soledade & Almeida 2013 and references therein; Anker *et al*. 2016; present study).

Diagnosis. Rostrum almost reaching distal margin of first segment of antennular peduncle; scaphocerite slightly, with blade reaching half of second article of antennular peduncle; distal tooth reaching distal limit of antennular peduncle. Minor cheliped with ischium armed with 4 spiniform setae; ventromesial margin of the merus with 6 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; Dactylus without crest on extensor margin. Major cheliped with ischium armed with 3 spiniform setae; ventromesial margin of the merus with 6 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; dactylus flattened, laterally twisted, dorsally convex and strongly bulbous distally; plunger developed, with anterior surface distinctly angular. Second pereiopod elongated, slender; ischium slightly longer than merus; carpus with 5 articles with ratio approximately equal to 3: 2: 1: 1.3: 1.5. Distolateral margin of uropodal exopod with 1 mesial and 1 lateral teeth adjacent to spiniform setae.

Redescription. Carapace smooth, frontal margin with strong rostrum, ocular hoods with well-developed teeth originating from the anterior margin of hoods; rostrum slightly flat in dorsal view, distinctly longer than broad, distally tapering and ending in sharp point, without setae, almost reaching distal margin of first segment of antennular peduncle; margin between orbital teeth and rostrum V-shaped (Fig. 4A, B); orbital process present. Pterygostomial angle rounded, not anteriorly protruding (Fig. 4B); cardiac notch deep. Abdominal somites with posteroventral margins broadly rounded, those of fifth segment slightly angular; sixth somite without articulated plate in posterolateral margin.

Eyes with well-developed corneas; ocellar beak projecting anteriorly, acute, visible in lateral view. Antennular peduncle moderately slender; stylocerite with acute tip reaching distal limit of first article of antennular peduncle; ventromesial carina well-developed, triangular in shape, with small pointed tooth (Fig. 4C); second article of antennular peduncle much longer than visible part of first article, about 2 times longer than broad (Fig. 4A); lateral flagellum with groups of aesthetascs extending to article 10. Antennal basicerite with acute lateral tooth; carpocerite slightly exceeds distal end of scaphocerite and antennular peduncle; lateral margin of scaphocerite slightly concave, ending in strong lateral tooth overpassing distal margin of blade (Fig. 4A); blade reaching half of second article of antennular peduncle; distal tooth reaching distal limit of antennular peduncle. Mouthparts as illustrated by Chace (1972). Third maxilliped slender; coxa with lateral plate slightly truncated distally; exopod reaching beyond distal limit of antepenultimate article when extended; antepenultimate article somewhat flattened, approximately 4 times longer than broad, ventral surface sparsely setose; penultimate article approximately 3 times longer than broad, slightly broadened distally and densely setose; ultimate article disarmed, distally tapering, with dense rows of long setae (Fig.4I).

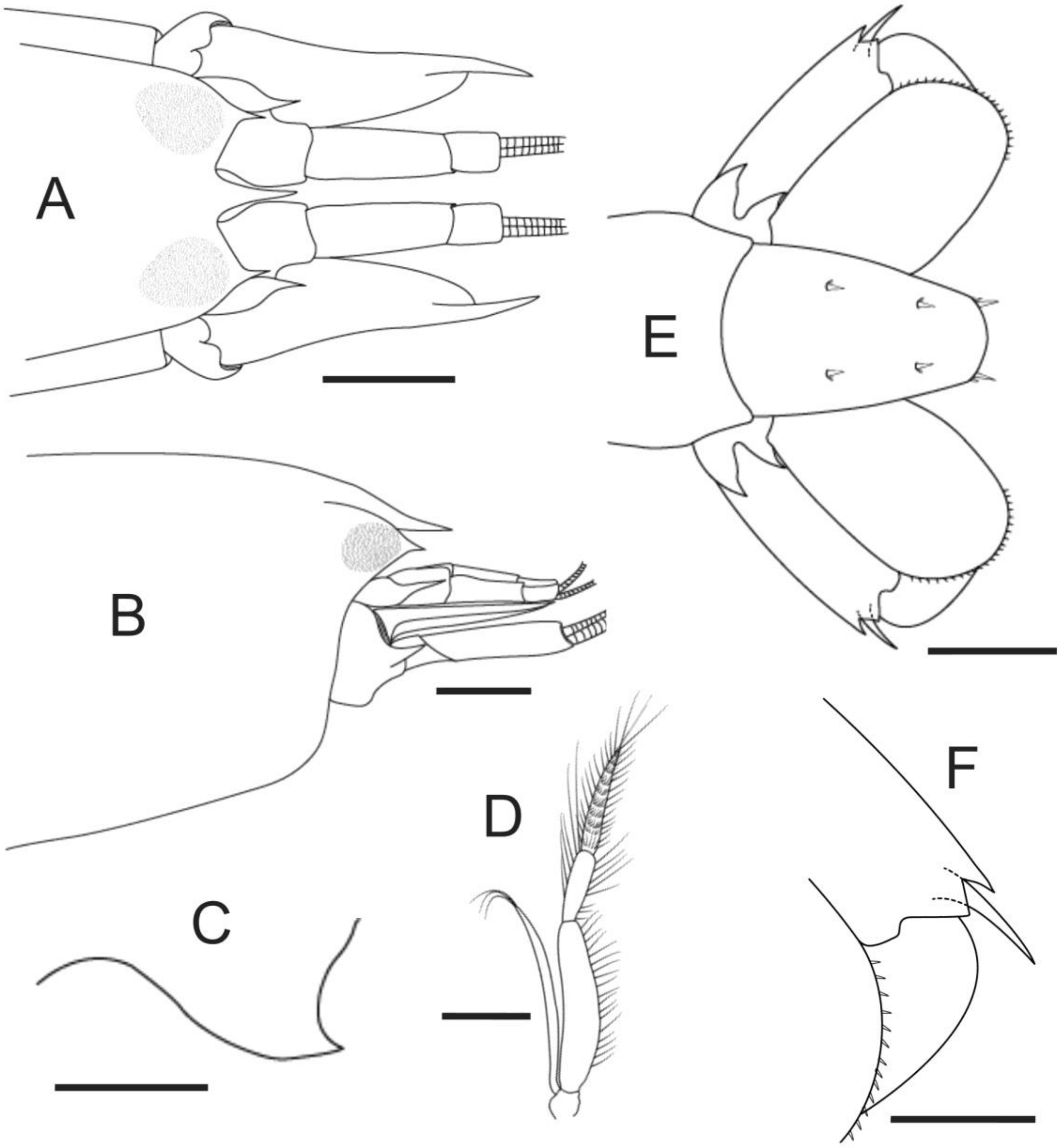


Figure 4. *Alpheus amblyonyx* Chace, 1972, male specimen from Quintana Roo, Mexico, CNCR 21271. (A) Carapace and cephalic appendages, dorsal view (setae omitted); (B) same, lateral view; (C) ventromesial carina of the antenular peduncle; (D) third maxilliped, lateral view; (E) telson and uropods, dorsal view (setae omitted); (F) uropod, detail of the final margin of endopod. Scale Bars: (A, B, D, E, F) = 1 mm; (C) = 0.5 mm.

Minor cheliped with short and stout ischium; distomesial margin broad, subtriangular in cross-section, armed with 4 spiniform setae; ventrolateral surface unarmed; ventromesial margin of merus slightly convex, ending in small acute tooth, with 6 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; carpus cup-shaped; chelae strongly compressed, palm with grooves and notches from distal half of lateral surface; mesial surface convex and devoid of depressions or grooves; lateral surface with low crest starting at about middle of palm and ending in acute distolateral tooth; ventral surface smooth, ending in well-defined notch; dorsal margin also smooth, with sub-cylindrical elevation ending distally in small adhesive disk; distomesial surface with high ridge ending in strong sharp tooth; fingers as long as palm; pollex lightly excavated on cutting edge; dactylus slightly flattened and twisted laterally, without crest on extensor margin, with small adhesive disk proximally (Fig. 5C, D).

Major cheliped with ischium short and robust, ventromesial surface with 3 small spiniform setae; merus robust, not elongated, about 2 times longer than wide, sub- triangular in cross section; ventrolateral margin disarmed; ventromesial margin straight, with 6 small spiniform setae, ending in robust and sharp tooth; carpus very short, cup-shaped, slightly compressed; lateral surface with low crest starting at approximately 0.6 of length of palm, ending in distolateral sharp tooth, slightly directed laterally; linea impressa well-marked; mesial surface convex, devoid of sculptures and grooves; ventral surface with rounded smooth shoulder a slightly projecting into adjacent deep notch; notch extends transversely to groove on mesial surface; dorsal margin with sub-cylindrical elevation ending distally in large adhesive disk; distomesial surface with deep transversally notched crest ending in sharp tooth; distal third of ventral margin of palm with strong and long setae extending to distomesial margin of palm; pollex shorter than dactylus, strongly curved laterally, cutting edge slightly excavated and with small rounded tooth in proximal portion; dactylus flattened, laterally twisted, dorsally convex and strongly bulbous distally; plunger developed, with anterior surface distinctly angular (Fig. 5A, B).

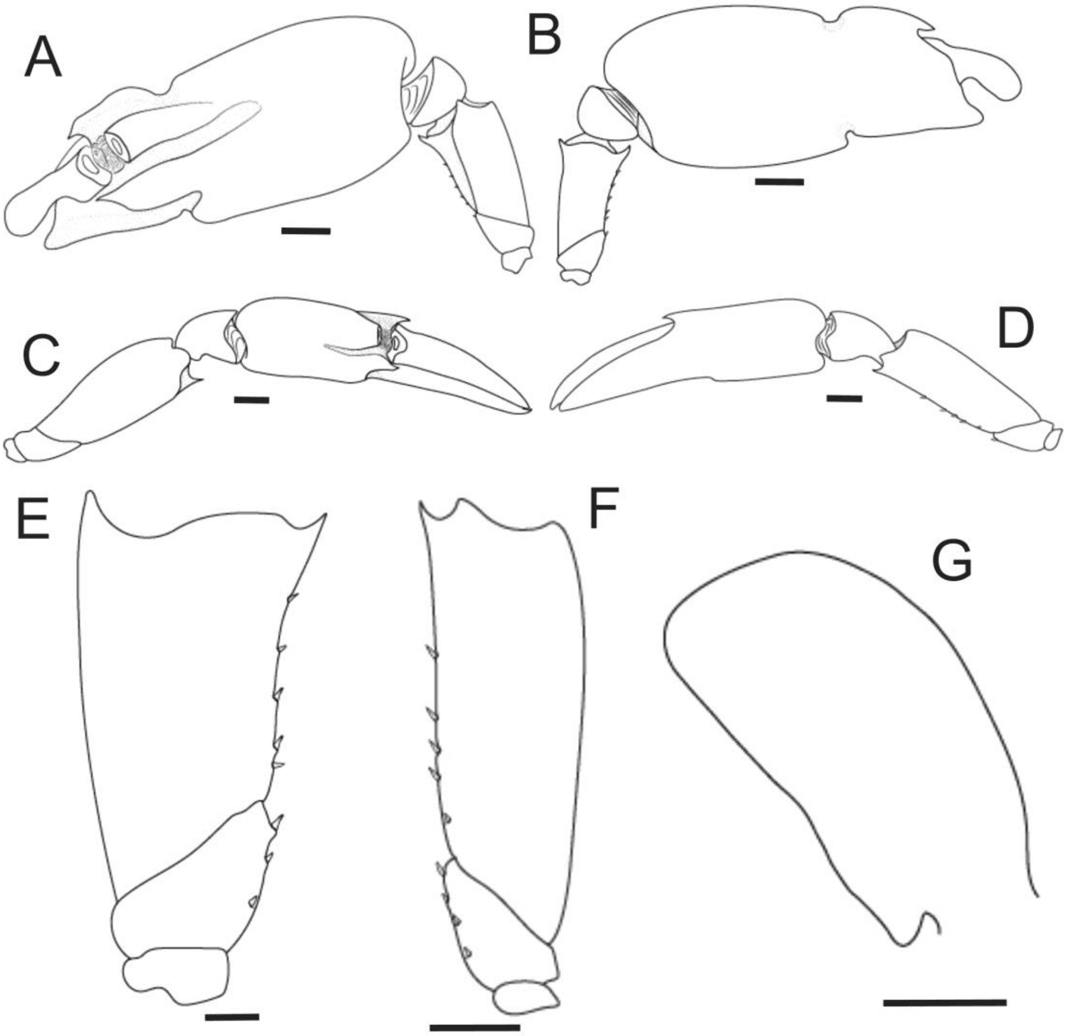


Figure 5. *Alpheus amblyonyx* Chace, 1972, ovigerous female specimen from Guadeloupe, MNHN 12112. (A) major cheliped in lateral view; (B) same, in mesial view; (C) cheliped minor lateral view; (D) same, in mesial view; (E, F) Detail of the spiniform setae in the ischium and propodus of the major and minor chelae, respectively; (G) dactylus of the major chelae in mesial view, detail of the plunger. Scale Bars: (A–E) = 1 mm; (F, G) = 0.5 mm.

Second pereiopod elongated, slender; ischium slightly longer than merus; carpus with 5 articles with ratio approximately equal to 3: 2: 1: 1.3: 1.5; chelae not ornamented, fingers as long as palm, with small tufts of setae (Fig. 6A). Third pereiopod with ischium armed with strong spiniform setae on ventrolateral surface; merus 4 times longer than broad, without tooth at distoventral angle; carpus slender, about half length of merus; propodus about 1.5 times longer than carpus, with about 9 robust spiniform setae along ventral margin and 1 pair of spiniform setae near to articulation with dactylus; dactylus slightly shorter than half length of propodus, conical, slightly curved, ending in sharp tip; extensor margin with 1 subdistal denticle (Fig. 6B). Fourth pereiopod similar to third in shape and proportion of articles, but slightly less robust; ischium armed with strong spiniform setae on the ventrolateral surface; propodus with about 7 robust spiniform setae along the ventral margin and 1 pair of spiniform setae near to articulation with the dactylus (Fig. 6C). Fifth pereiopod more slender than third and fourth (Fig. 6D); merus slightly longer than carpus; ischium with 1 spiniform setae; propodus with about 8 spiniform setae along ventral margin and 10 well-developed distolateral setal brushes. Pleopods with sparse setae on lateral margin of protopod; endopods and exopods with edges densely setose; first pleopod very reduced, distal margin of endopod with setae; second pleopod in male with *appendix masculina* subequal in length to *appendix interna*, not reaching distal margin of endopod, with numerous rigid setae at distal end; uropod with lateral lobe of protopod ending in strong and sharp tooth; diaeresis sinuous. Distolateral margin of uropodal exopod with 1 mesial and 1 lateral teeth adjacent to spiniform setae; endopod with row of small spiniform setae along distal margin (Fig. 4F). Telson subretangular, tapering to posterior margin; proximal margin 2.0 times broader than distal margin; lateral margins slightly convex; dorsal surface with 2 pairs of spiniform setae, first pair located at half-length of telson, second pair located approximately 0.7 of length of telson; posterior margin broadly convex, with 2 pairs of spiniform setae, mesial pair about 3 times size of lateral pair (Fig. 4E); anal tubercles well-developed.

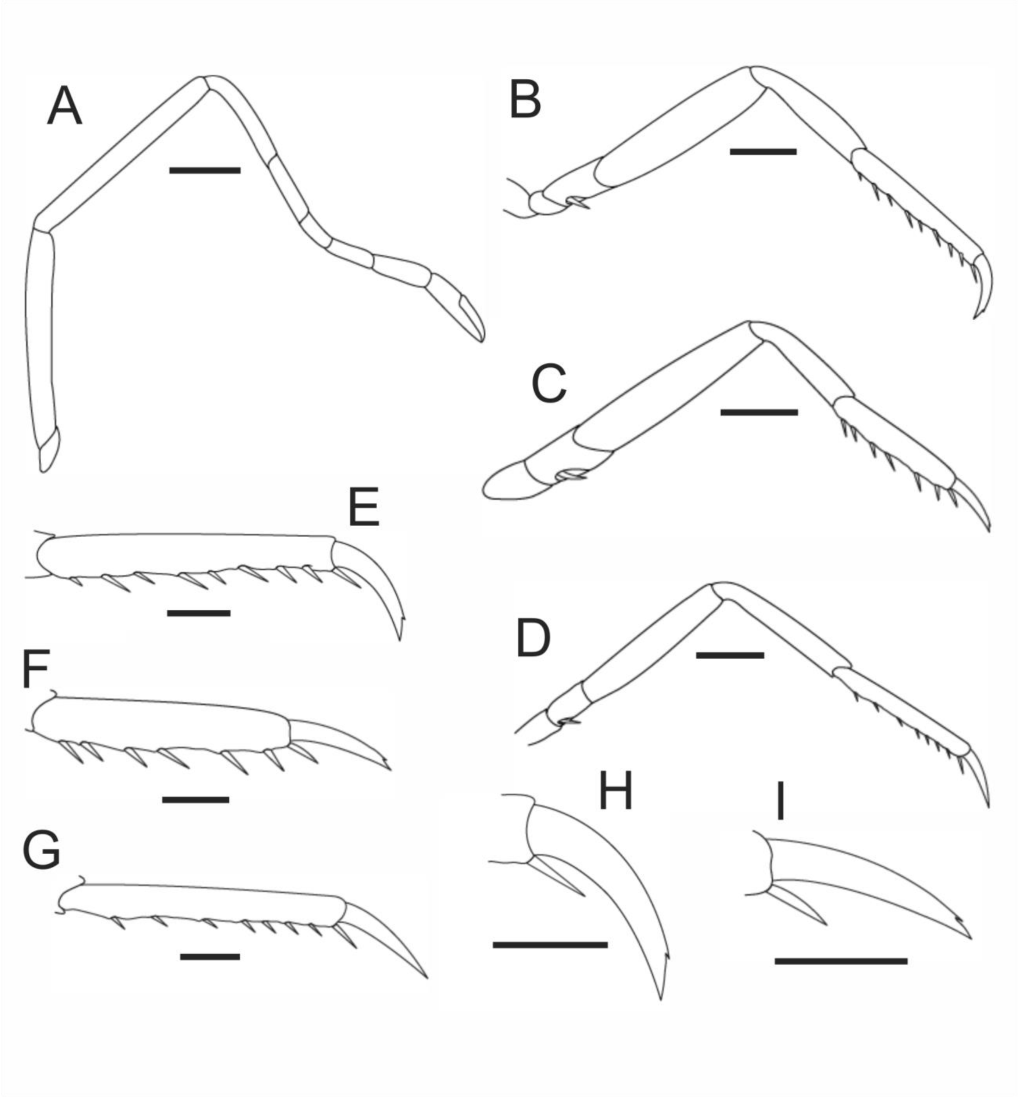


Figure 6. *Alpheus amblyonyx* Chace, 1972, ovigerous female specimen from Guadeloupe, MNHN 12112. (A) second pereiopod, lateral view; (B) third pereiopod, lateral view; (C) fourth pereiopod, lateral view; (D) fifth pereiopod, lateral view; (E–G) third–fifth pereiopods, detail of the propodus; (H, I) third and fourth pereiopods, detail of the dactylus. Scale bars = 1 mm in (A–D) and 0.5 mm in (E–I).

Morphological variation. Little morphological variation has been observed (see Table 2). No consistent differences between sexes have been observed.

Comparative material analyzed. *Alpheus crockeri*. EAST ATLANTIC – **Cape Verde.** 1 NI, São Vicente Island, 01.X.2013, OUMNH 2014-01-30 (**genetic voucher**).

Alpheus pouang. WEST ATLANTIC – **Brazil.** 1 M (**Holotype**), off São Paulo, R/V Wladimir Besnard #1019, 23°39'S 43°37'W, 120–121 m, mud and sand, 27.V.1970, MZUSP 4543; 1 F, 1 M, off Rio Grande do Sul, GEDIP I #330, 34°35'S 52°00'W, sand, 30.VI.1968, MNRJ 4388.

Alpheus puapeba: WEST ATLANTIC – **Brazil.** 1 OVF (**Paratype**), off Rio de Janeiro, R/V Wladimir Besnard #1632, 23°33'S 44°11'W, 72 m, 17.XII.1971, MZUSP 31525; 1 OVF, off Rio de Janeiro, HAB 2 #66, 23°11'15.741"S 41°37'17.184"W, trawl, continental shelf of the Campos Basin, 26.IV.2008, MNRJ 21836; 1 M, Rio de Janeiro, Ilha Grande, #302, 49 m, 16.II.1968, MNRJ 4387; 1 F, 1 M, HAB 1, #66, trawl, 98.7 m, 26.IV.2008, MNRJ 21836 (**genetic voucher**); 4 F, 10 M, off Santa Catarina, #61 – CB102, 27°07'S 42°03'W,100 m, 01.VI.1987, MZUSP 31900.

Alpheus platydactylus: WEST ATLANTIC – **Azores.** 1 OVF, 1 NI, # 5.010, 26.V.1981, RMNH.Crus.D.51229; 2 OVF, # 5.129, 06.VI.1981, RMNH.Crus.D.51237; **Canary Islands.** 1 OVF, 1 M, # 4.07, 20.I.1980, RMNH.Crus.D.51238; 2 F (1 OV), # 4.17, 09.I.1980, RMNH.Crus.D.51239; **Cape Verde.** 2 F (1 OV), 1 M, "Tydeman" Cancap-VII, # 7.122, 01.IX.1986, RMNH.Crus.D.51240.

Morphological remarks. *Alpheus macrocheles* and *A. amblyonyx* can be separated from all species of the *A. macrocheles* species complex of the Atlantic Ocean by the presence of a subterminal denticle on the extensor margin of the dactylus of pereiopods 3 and 4. The main differences between *A. macrocheles* and *A. amblyonyx* are: the shorter rostrum in *A. macrocheles*, reaching half the length of the proximal segment of antennular peduncle (Fig. 7A) vs. reaching the distal end of the proximal segment in *A. amblyonyx* (Fig. 7F); second segment of the antennular peduncle about 2X length of the third in *A. macrocheles* (Fig. 7A) vs.1.5X in *A. amblyonyx* (Fig. 7F); dactylus of the minor chelae with crest on the extensor margin in *A. macrocheles* (Fig. 7C), vs. dactylus cylindrical in cross-section, without crest on the dorsal surface in *A. amblyonyx* (Fig 7H); molar tooth reduced and flat, only with a small denticle in *A. macrocheles* (Fig. 7D, E), vs. well developed in *A. amblyonyx*, with anterior margin angled (Fig. 7I); distolateral margin of the uropodal exopod with only one acute tooth bordering laterally the spiniform setae and a broad lobe medially to this setae in *A. macrocheles* (Fig. 7B), vs. distolateral margin of the uropodal exopod with two acute teeth being one of them mesial to the spiniform setae in *A. amblyonyx* (Fig. 7G).

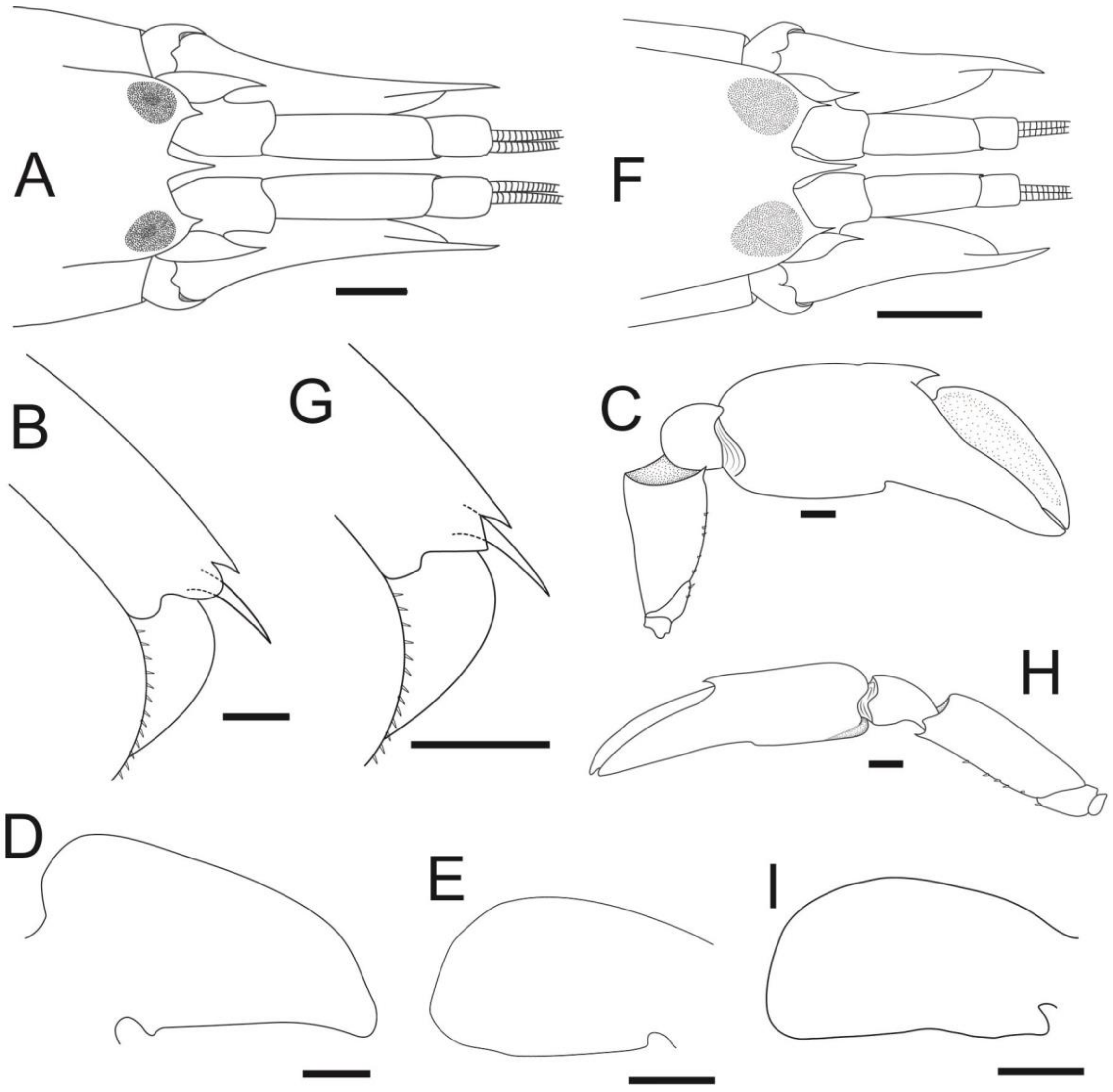


Figure 7. Main diagnostic characters between *Alpheus macrocheles* (Hailtone, 1834) (A–E) and *Alpheus amblyonyx* Chace, 1972 (F–I). (A, F) carapace and cephalic appendages, dorsal

view (setae omitted); (B, G) uropodal exopod, detail of the distolateral angle; (C, H) cheliped minor lateral view; (D, E, I) dactylus of the major chelae in mesial view, detail of the plunger. Scale bars = 1 mm in (A–C, F, G) and 0.5 mm in (D, E, I).

Molecular Analysis. A total of 10 new 16S rRNA gene sequences were obtained from species of the *A. macrocheles* species complex in the present study (see Table 1). The substitution model that best fit the data was the TPM3uf + I (= K81) assuming the nucleotide frequencies A = 0.2812, C = 0.1185, G = 0.2601, T = 0.3402, replacement rates AC = 0.1431, AG = 4.6735, AT = 1, CG = 0.1431, CT = 4.6735, GT = 1, and invariable sites = 0.54.

The topology generated from the Bayesian Inference Analysis shows the presence of two main clades, clearly separating the specimens of *A. macrocheles* and *A. amblyonyx* (Fig. 8). In the first clade *A. crockeri* (Cape Verde) is placed as a sister group of *A. puapeba* (Brazil) + *A. macrocheles* (Azores and Canary Islands), in the second clade are the specimens of *A. amblyonyx*, including the topotypic material (Quintana Roo, Mexico). In both clades the groupings are well supported by the posterior probability values (Fig. 8).

The values of interspecific genetic distance (K81 model) ranged from 14% (*A. macrocheles* X *A. puapeba*) to 29% (*A. amblyonyx* X *A. crockeri*). There was no intraspecific genetic divergence among specimens of *A. macrocheles* or *A. amblyonyx*. The two species of interest (*A. macrocheles* and *A. amblyonyx*) had a genetic distance of 19%.

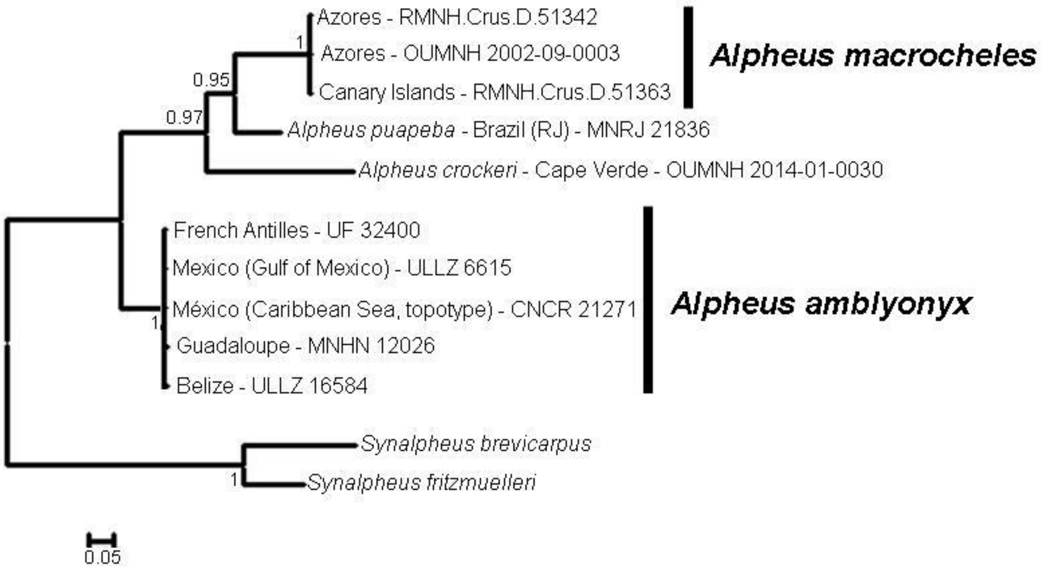


Figure 8. Bayesian Inference Tree of 16S gene among specimens of cryptic taxa *Alpheus macrocheles* (Hailstone, 1835) and *Alpheus amblyonyx* Chace, 1972 and other snapping shrimp of the genus *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888.CNCR: Colección Nacional de Crustáceos, Mexico; MNHN: Muséum national d'Histoire naturelle, France; RMNH: Netherlands Centre for Biodiversity Naturalis; OUMNH: Oxford University Museum of Natural History; UF: Florida Museum of Natural History; ULLZ: University of Louisiana at Lafayette Zoological Collection. Numbers close to nodes represent posterior probabilities.

DISCUSSION

Here we present a new characterization of *A. macrocheles* and *A. amblyonyx* and a conclusive evidence of the differentiation between these cryptic species. Chace (1972) listed some characters regarding *A. amblyonyx,* (i) long rostrum, (ii) dactylus of the major cheliped with bulbous distal extremity; (iii) notch of the mesiodistal margin of the palm of the major cheliped, widened and less defined; and (iv) the dactylus of the minor cheliped without a strong crest on the dorsal margin and without defined ventral notch on the palm. These characters are, in part, useful for the distinction between the species, at least (i) and (iv), but we observed intraspecific variation in characters (ii) and (iii) and therefore these characters are not fully valid for the separation of taxa. However, as mentioned above, consistent morphological characters that can be used to differentiate these two species do exist (see Table 2 and Figures 7).

The genetic data also confirm the separation of these two species. Phylogenetic analyses showed that the analyzed specimens of *A. macrocheles* from the eastern Atlantic formed a distinct group from *A. amblyonyx* from the Caribbean Sea and Gulf of Mexico (including the topotypic specimen). *Alpheus macrocheles* form a well-supported clade with *A. puapeba* from the Brazilian coast. This grouping is somewhat surprising considering that the two species are morphologically distinct. Christoffersen (1979), in the description of *A. puapeba*, made comparisons only with *A. platydactylus*, also part of the *A. macrocheles* species complex. However, *A. puapeba* and *A. macrocheles* were morphologically distinct, and the genetic distance between them was also high (14%).

The genetic distance between the pair of *A. amblyonyx* - *A. macrocheles* (19%) was much greater than the highest intraspecific distance obtained among the species analyzed. The interspecific variation of genetic distance found (14 to 29%) is consistent with the variation obtained in molecular comparisons of 16S in *Alpheus* (Mathews *et al*. 2002; Mathews 2006; Almeida *et al*. 2013; 2014). It is also important to highlight here those future analyses that incorporate molecular data for other species within the complex (e.g., *A. pouang*, *A. lentiginosus*, *A. platydactylus*, *A. cedrici*) may improve the resolution of these phylogenetic relationships. Our results refute the notion of *A. amblyonyx* as the sister of *A. macrocheles*. Current molecular data indicate that these two species are only cryptically similar taxa. Their morphological similarity may be due to the retention of ancestral character states or morphological convergence. Similar results were observed between the pair of cryptic species

A. heterochaelis and *A. petronioi* (Almeida *et al.* 2014) based on phylogenetic analysis of 16S gene sequences.

The type locality of *A. macrocheles* is Hastings, southern England, located near the eastern limit of English Channel (Fig. 9). As previously mentioned, the holotype of this shrimp is not available in any of the world's great biological collections. This material was probably lost or may not have actually been deposited by Hailstone (1835) in some international museum of reference. Because of all the taxonomic problems involved with the *A. macrocheles* complex, the best thing to do would be to obtain material from the type locality for the designation of a neotype. Although, specimens from the Hastings were unavailable to us during this study, we assume that material from Roscoff, France (about 800 km from the locality type), located near the western limit of the English Channel belongs to *A. macrocheles s. str*. (Fig. 9). Therefore, we deem absolutely valid here the designation of a neotype based on this French material, generating a robust definition of what is characterized as *A. macrocheles s. str*..Those specimens agree with all other material here treated under *A. macrocheles*.

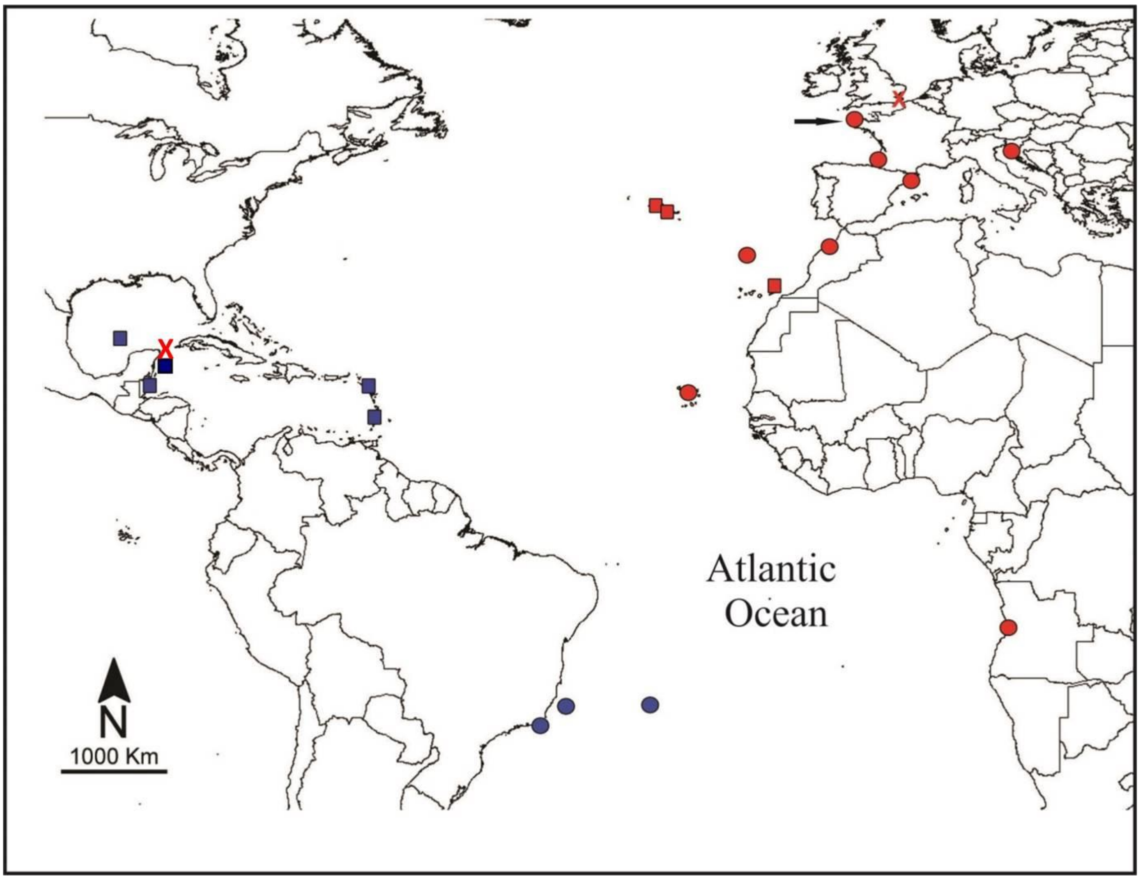


Figure 9. Localities of origin of the specimens of *Alpheus macrocheles* (Hailstone, 1835) (red) and *Alpheus amblyonyx* Chace, 1972 (blue) used in the morphology analyses (solid circles), or for both morphology and genetics (solid squares). Type localities are indicated with a letter X. The black arrow indicates the location of the neotype.

Our revision does not support the occurrence of *A. macrocheles* in the western Atlantic. The material examined in this study does not belong to this species. The other records in the western Atlantic (e.g., Antilles) were not considered to define the geographic distribution of this species due to the inability to confirm the specific identity of the organisms recorded in those studies. As discussed by Soledade & Almeida (2013), most of these records provide little or no morphological description and have no illustrations of the diagnostic characters. Unfortunately, many of the specimens reported from the Brazilian coast have not been deposited in formal carcinological collections or the whereabouts of the specimens were not specified in the published records. The material cited by Guterres *et al.* (2005), for example, could not be located in MZUSP. When examining lots deposited in MOUFPE collection, some of the few specimens in good condition strongly resembled *A. amblyonyx*. Another set of specimens identified as *A. macrocheles* is morphologically distinct of both *A. macrocheles* and *A. amblyonyx*. These few specimens also do not match any other described species within the *A. macrocheles* complex, and probably belongs to a new species.

On the other hand, *Alpheus amblyonyx* seems to be widely distributed in the western Atlantic (Fig. 9). The Brazilian material presents morphological similarity with the Caribbean material, including that from the type locality. However, there are uncertainties about some previous records (see Soledade & Almeida 2013; Anker *et al*. 2016). For example, the material reported by Christoffersen (1979) from Bahia, Brazil, shows significant morphological variation regarding to the shape of the dactylus of the minor chelae. This author, at that time, attributed these differences to the large size of his specimens in relation to Chace’s material (1972). Unfortunately, in this case the material is not accessible; however when analyzing the illustrations of Christoffersen (1979), we noticed that his material probably contained more than one species (*A. amblyonyx* and a potential new species). In addition, other records in some checklists present the same problem discussed above for *A. macrocheles* (lack of morphological account, absence of illustrations and material not deposited in formal collections) (e.g., Coelho *et al*. 2002; Coelho Filho 2006; Serejo *et al*. 2006, 2007; Souza *et al*. 2011). In the most recent record of *A. amblyonyx* from the Brazilian coast, Anker *et al.* (2016) reported differences in the color pattern compared to Caribbean material. The analysis of this material did not yield any significant morphological difference compared to topotype material of *A. amblyonyx*. Despite this, a broader study with the inclusion of a larger number of specimens covering the Caribbean and the Brazilian coast may reveal if there is at least one new species related to *A. amblyonyx*.

Thus, based on our analyses morphological and molecular *A. amblyonyx* and *A. macrocheles* are in fact distinct, and *A. macrocheles* seems to be restricted to the eastern Atlantic. On the other hand, a broader analysis of the *A. macrocheles* group (*sensu* Coutière, 1905) is needed. The main conclusions of the present study, as well as the morphological and molecular data provided here, represent a good starting point for a future comprehensive approach.

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4 INTEGRATIVE TAXONOMY REVEALS A NEW CRYPTIC SHRIMP OF THE *Alpheus macrocheles* (HAILSTONE, 1835) COMPLEX (CARIDEA, ALPHEIDAE) IN THE WESTERN ATLANTIC

Running title. Integrative taxonomy reveals a new cryptic shrimp

ABSTRACT

Among the numerous complexes of cryptic species found in the highly diverse genus *Alpheus*, the *Alpheus macrocheles* (Hailstone, 1835) complex is one of those that persist without a complete taxonomic resolution. Of the seven species distributed in the Atlantic, four are recorded from the Brazilian coast. One of the species with the highest number of records is *A. macrocheles*, which in contrast, has its occurrence on the Brazilian coast invalidated due to the inexistence of detailed illustrations and appropriate morphological comparisons in previous records of occurrence. Therefore, the objective of this contribution is to describe a new species of the *Alpheus macrocheles* complex for the Brazilian coast. By locating and reviewing this previously quoted material to Brazil, we identify conclusive morphological differences in material of *A. macrocheles* from East Atlantic, which allowed for the establishment of a new species. Additional specimens were collected off Recife, northeastern Brazil by means of dredging at depths of 50 to 80 meters, in the bottoms of calcareous algae, rhodolites and sponges. This study involved an exhaustive analysis of morphological characters that was combined with color pattern and a genetic analysis of Bayesian Inference with the use of the 16S mitochondrial gene. Illustrations of the diagnostic characters and comparisons with the other species of the complex for the Atlantic are provided.

Key-words: Alpheid, Brazilian coast, Molecular biology, Morphology, New species, 16S, snapping shrimp.

INTRODUCTION

The highly diverse genus *Alpheus* Fabricius, 1798, with 313 valid species throughout the world (De Grave & Fransen, 2011; Komai & Ohtomi, 2018; Dehghani *et al.*, 2018), was previously subdivided into seven informal morphological groups (see Coutière 1905). This infrageneric division has been followed in several subsequent taxonomic works (Banner 1953; Crosnier & Forest 1966; Kim & Abele 1988). In contrast, molecular data show that some of these morphological groups may not be monophyletic (Williams *et al.* 2001). Within the genus *Alpheus*, molecular evidences have pointed to the existence of high cryptic biodiversity (e.g., Williams *et al.* 2001; Anker *et al*. 2006; Mathews & Anker 2009). Many cryptic species complexes have been resolved using integrative taxonomy methods, which utilize both genetic and morphological data (e.g., Anker *et al.* 2009; Almeida *et al.* 2014; Bracken-Grisson *et al.* 2014; Cunha *et al.* 2017). Despite these numerous revisions, some unresolved taxonomic issues still persist in *Alpheus*, such as cases of morphologically indistinguishable species (e.g., *A. paracrinitus* Miers, 1881- *A. rostratus* Kim & Abele, 1988) and cases of morphologically variable species with broad biogeographic ranges, raising suspicions of potential cryptic species (e.g., *A. packardii* Kingsley, 1880).

One taxonomically unresolved caseis the *Alpheus macrocheles* (Hailstone, 1835) morphological group, which currently includes 33 valid species distributed worldwide. The species in this group share a, diagnostic major cheliped morphology (chela strongly twisted and compressed, with plane of dactylar articulation deviating from the plane perpendicular to the dorsal margin, often resulting in a pair of distinct grooves on the lateral face of the chela).The group nominated as *A. macrocheles* species complex includes 10 species (sensu Anker and De Grave 2012): *Alpheus amblyonyx* Chace, 1972, *A. lentiginosus* Anker & Nizinski, 2011, *A. pouang* Christoffersen, 1979 and *A. puapeba* Christoffersen, 1979 in the Western Atlantic; *A. cedrici* Anker & De Grave, 2012 in the Central Atlantic; *A.*

macrocheles in the Eastern and Western Atlantic; *A. platydactylus* Coutière, 1897 in the Eastern Atlantic; *A. bellimanus* Lockington, 1877 and *A. rectus* Kim & Abele, 1988 in the Eastern Pacific; and *A. albatrossae* Banner, 1953 in the Indo-West Pacific.

The main taxonomic problem within this complex was the confusion involving *A. amblyonyx* and *A. macrocheles*. *Alpheus macrocheles* was described from Hastings, located in the English Channel. This snapping shrimp has been broadly recorded along the Mediterranean Sea and both sides of the Atlantic, including some oceanic islands (Holthuis 1951; Crosnier & Forest 1966; d'Udekem d'Acoz 1999). In Brazil, the species has been recorded from Amapá to Espírito Santo (see Soledade & Almeida 2013). *Alpheus amblyonyx* Chace, 1972 was described for Quintana Roo, Mexico, being distributed until the Espírito Santo, Brazil (including Atol das Rocas, Fernando de Noronha and Trindade Island and Martin Vaz Archipelago) (Chace, 1972; Soledade & Almeida, 2013; Anker *et al*., 2016). However, these species have recently been separated based on morphological and molecular data (Soledade *et al.*, chapter 1). These authors also refuted the validity of the records of *A. macrocheles* for the Brazilian coast.

When examined a series of specimens identified as *A. macrocheles* collected from Brazil deposited in the MOUFPE collection, subtle differences from the Eastern Atlantic material of *A. macrocheles* were observed. The material analyzed was also distinct from *A. amblyonyx*, indicating the existence of a new cryptic species. Therefore, our objective is to describe a new cryptic species in the *A. macrocheles* species complex from the Brazilian coast, [utilizing an integrative approach that combines morphological and molecular data.

MATERIALS & METHODS

Specimens deposited in the following institutions / collections were used: Museu de Oceanografia Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco

(MOUFPE), Museu Nacional do Rio de Janeiro (MNRJ), Coleção de Crustáceos do Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (CCDB), Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México, Ciudad de México, Mexico (CNCR), Muséum National d'Histoire Naturelle, France (MNHN), Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands (RMNH). Additional specimens were collected during two expeditions carried out off Recife, state of Pernambuco, northeastern Brazil, to obtain fresh material from the *A. macrocheles* complex. The material was dredged between 50 and 65 meters deep on mud, sand, calcareous algae and coral rubble bottoms. The specimens obtained were deposited in the MOUFPE, CCDB and MNRJ crustacean collections.

We carried out a detailed morphological analysis, using a set of 42 characters distributed throughout the body. The morphological characters were photographed through a stereomicroscope with an image capture system. Illustrations were generated from these images through vectorization in the Adobe Illustrator® program, showing the morphology of thespecimens examined.

Molecular sequence data were generated during this study or were retrieved from Genbank (Table 1). All sequence data of the new species are original to this study.

Whole genomic DNA was extracted from abdomen tissue using the Qiagen DNeasy® Blood and Tissue Kit (Cat. No. 69504) following the manufacturer's instructions.

Table 1. List of specimens used in the genetic analysis. CCDB: Coleção de Crustáceos do Departamento de Biologia de FFCLRP, Universidade de São Paulo, Brazil; CNCR: Colección Nacional de Crustáceos, Mexico; MNHN: Muséum National d'Histoire Naturelle, France; MNRJ: Museu Nacional do Rio de Janeiro, Brazil; MOUFPE: Museu de Oceanografia Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco, Brazil; RMNH: Netherlands Centre for Biodiversity Naturalis, The Netherlands; OUMNH: Oxford University Museum of Natural History, United Kingdom; UF: Florida Museum of Natural History, USA; ULLZ: University of Louisiana, Lafayette Zoological Collections, USA.

Taxon	**Locality**	**Catalogue number**	**GenBank**	**Reference**
Alpheus amblyonyx Chace, 1972	Mexico (Gulf of Mexico)	ULLZ 6615	pendent	Soledade *et al.* (submitted)
Alpheus amblyonyx	Quintana Roo, Mexico	CNCR 21271	pendent	Soledade *et al.* (submitted)
Alpheus amblyonyx	Belize	ULLZ 16584	pendent	Soledade *et al.* (submitted)
Alpheus amblyonyx	Guadeloupe	MNHN 12026	pendent	Soledade *et al.* (submitted)
Alpheus amblyonyx	French Antilles	UF 32400	pendent	Soledade *et al.* (submitted)
Alpheus crockeri (Armstrong, 1941)	Cape Verde	OUMNH 2014-01-00330	pendent	Soledade *et al.* (submitted)

Alpheus macrocheles (Hailstone, 1835)	Azores, Portugal	RMNH 51342	pendent	Soledade *et al.* (submitted)
Alpheus macrocheles	Azores, Portugal	OUMNH 2002-09-0003	pendent	Soledade *et al.* (submitted)
Alpheus macrocheles	Canary Islands, Spain	RMNH 51363	pendent	Soledade *et al.* (submitted)
Alpheus puapeba Christoffersen, 1979	Rio de Janeiro, Brazil	MNRJ 21836	pendent	Soledade *et al.* (submitted)
Alpheus **spec. nov.**	off Recife, Brazil	MOUFPE 13703	pendent	Present study
Alpheus **spec. nov.**	off Recife, Brazil	MOUFPE 19470	pendent	Present study
Alpheus **spec. nov.**	off Recife, Brazil	MZUSP 39146	pendent	Present study
Alpheus **spec. nov.**	off Recife, Brazil	CCDB 6120	pendent	Present study
Synalpheus cf. *brevicarpus* Herrick, 1891	Ubatuba, São Paulo, Brazil	CCDB 3419	KF667548	Almeida *et al.* (2014)
Synalpheus fritzmuelleri Coutière, 1909	Gulf do Mexico	ULLZ 7136	EU868642	Bracken *et al.* (2009)

A ~550 base pair region of the 16S small ribosomal subunit gene was amplified from the extracted DNA through PCR (Polymerase Chain Reaction) (Sambrook *et al.* 1989) using the primers: 1472 (5'-AGATAGAAACCAACCTGG-3') and 16SL2 (5'-TGCCTGTTTATCAAAAACAT-3') (Crandall & Fitzpatrick 1996; Schubart *et al*. 2002). PCR reactions were done according protocol of Mantelatto *et al.* (2009, 2018), in 25µl volumes containing 5M betaine, 10X PCR buffer, primers, 25mM $MgCl_2$, 200µM dNTPs, deionized water, 1 unit *Taq* polymerase and 2 µl of extracted genomic DNA, and reactions were performed in a Veriti 96-Well Thermal Cycler® (Applied Biosystems) with specific thermal cycles for the utilized set of primers (melting temperature of 48°). PCR products were visualized using gel electrophoresis with 1.2% agarose gel on a Transilluminator. PCR products were purified using the Exo-sap® Purification Kit following the manufacturer's instructions. Cycle sequencing reactions were performed in 20µl volumes using Big Dye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) following the manufacturer's instructions. Sequencing was perfmormed on an ABI 3100 Genetic Analyzers® at the ACTGENE - Analises Moleculares Ltda – ME, Porto Alegre, Brazil and on an ABI 3130xl Genetic Analyzer at the University of Louisiana at Lafayette, Lafayette, LA, USA. Sequences were confirmed by sequencing both forward and reverse. Sequence assembly was performed using the program Bioedit 7.0.9.0 (Hall 2005).

The sequences were aligned using MUSCLE (Edgar 2004), with standard parameters, available on the platform Cyber infrastructure for Phylogenetic Research (CIPRES) (Miller *et al.* 2010).

An analysis was performed using jModelTest (Darriba *et al.* 2012), implemented on CIPRES, to find out which substitution model best fit the data, using the Bayesian information criterion (BIC). Bayesian Inference analysis was carried out in the software MrBayes v3.2.6 (Ronquist *et al.* 2012), implemented on CIPRES, using parameters obtained from jModelTest. In the analysis, one tree was sampled for every 1,000 generations of 20,000,000 generations, starting with a randomly generated tree. Four independent runs were performed and the convergence of runs was analyzed using Tracer 1.6 (Rambaut *et al.* 2014). The first 15% of trees and parameters were discarded as burn-in and a final tree was generated in Tree Annotator 1.8.4 (implemented in BEAST, Drummond *et al.* 2012). Posterior probability values greater than 95% were reported. A genetic distance matrix was constructed in MEGA version 5 (Tamura *et al.* 2011) based on the substitution model selected by jModelTest.

Abbreviations: F – female; OVF – ovigerous female; M – male; NI – sex not identified; Exp – Expedition; Revizee – Program for the Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone; m – meters.

RESULTS

SISTEMATICS

Family Alpheidae Rafinesque, 1815

Genus *Alpheus* Fabricius, 1798

Alpheus spec. nov.

(Figs. 1–4)

Alpheus macrocheles – Ramos-Porto 1979, p. 118, Figs. 1–6 [not *Alpheus macrocheles* (Hailstone, 1835)]

Non *Alpheus macrocheles* – Coelho & Ramos 1972, p. 149; Fausto Filho & Sampaio Neto 1976, p. 67; Fausto Filho 1980, p. 113; Coelho & Ramos-Porto 1980, p. 135; 1995, p. 116; Coelho *et al.* 1980, p. 55; 1986, p. 84; Fausto Filho 1980, p. 113; Ramos-Porto *et al.* 1996, p. 219; Christoffersen 1998, p. 359; Barros & Pimentel 2001, p. 21; Guterres *et al.* 2005, p. 231, fig. 1; Coelho *et al.* 2006, p. 51; Coelho Filho 2006, p. 8; Alves *et al.* 2008, p. 49; Souza *et al.* 2011, p. 47; Almeida *et al.* 2012, p. 27; Soledade & Almeida 2013, p. 101.

Holotype: WESTERN ATLANTIC – Brazil. Pernambuco: 1 M, off Recife, REC I, draga 4, 8°08'51.5"S 34°34'08.0"W, 65 m, in aglomerations of sponges, rhodolites and calcareous algae, 07.II.2018, MOUFPE 19470 (**genetic voucher**).

Paratypes: WESTERN ATLANTIC – Brazil. Amapá: 3 M, Exp. GEOMAR. II 116, 81.5 m, calcareous algae, 13.IX.1970, MOUFPE 8848. Pará: 1 M, 1 OVF, Exp. GEOMAR II 2441, 1970, MOUFPE 8855; 1 M, 1 OVF, Exp. GEOMAR II 2528, 60 m, 1971, MOUFPE 8836. Maranhão: 1 F, Tutóia, R/V Almirante Saldanha 1732A, 69 m, calcareous algae, 30.X.1967, MOUFPE 8829; 9 NI, R/V Almirante Saldanha 1750, 52 m, calcareous algae, 06.XI.1967, MOUFPE 8830; 1 M, 1 F, São Luis, R/V Almirante Saldanha 1875, 49 m, calcareous algae, 23.IV.1968, MOUFPE 8831; 1 NI, Tutóia, R/V Almirante Saldanha 1813, 83 m, calcareous algae, 28.XI.1967, MOUFPE 8837; 1 F, R/V Almirante Saldanha, #1751, 44 m, calcareous algae, 06.XI.1967, MOUFPE 8845; 1 M, R/V Almirante Saldanha, #1750, 52 m, calcareous algae, 06.XI.1967, MOUFPE 8847. Off Ceará. 1 M, seamounts of the North Chain, Revizee NE III #75A, 54 m, calcareous algae, 07.VI.1998, MOUFPE 13703 (**genetic voucher**); 1 M, Revizee NE III #72A, 2°4'48"S 38°12'0"W, 08.VI.1998, MOUFPE 13647 (**genetic voucher**). Pernambuco: 1 M, PE. 31–33 m, calcareous algae, 07.III.1969, MOUFPE 8826; 2 M, Pesq. IV, #5, 54 m, 12.VI.1971, MOUFPE 8856; 1 F, off Recife, REC I, draga 6, 8°09'06.8"S 34°34'28.4"W, 53 m, in a rhodolite crevice, 07.II.2018, CCDB 6120 (**genetic voucher**); 1 OVF, off Recife, REC I, draga 3, 8°08'44.2"S 34°34'23.2"W, 55 m, in a rhodolite crevice, 07.II.2018, MZUSP 39146 (**genetic voucher**).

Comparative material analyzed. *Alpheus amblyonyx*: WESTERN ATLANTIC – Mexico. 1 NI, Quintana Roo, Southeast of Arrecife Chinchorro, 28.VIII.1990, CNCR 21271 (**genetic voucher**); Guadeloupe. 1 M, KARUBENTHOS, #GB20, 16 m, 18.V.2012, MNHN 12112 (**genetic voucher**); 1 OVF, KARUBENTHOS, #GB24, 16 m, 18.V.2012, MNHN 12026 (**genetic voucher**). *Alpheus macrocheles*: EASTERN ATLANTIC – France. 1 F, Roscoff, RMNH.Crus.D.34508; 1 M, Roscoff, RMNH.Crus.D.29789; 1 M, Guéthary, 27.X.1947, RMNH.Crus.D.1869; Azores. 1 M, 1 NI, Exp. #5.142 108–118 m, 7.VI.1981, RMNH.Crus.D.51342 (**genetic voucher**); Morocco. 1 F, 33°50'N 07°07'W, 25.I.1956, RMNH.Crus.D.34495; 1 M, Témara, 1952, RMNH.Crus.D.34496; 1 M, Témara, 1954, RMNH.Crus.D.34497; Madeira. 1 M, Cais de Porto Novo, under rocks, 18.VIII.1993, RMNH.Crus.D.42706; Canary Islands. 1 M, #4.070, southeast of Lanzarote, 41–50 m, sand and calcareous algae, 20.V.1980, RMNH.Crus.D.51363 (**genetic voucher**); Cape Verde. 1 OVF, 3 NI, "Tydeman" Cancap–VI, Cape Verde islands Exp., #6.109, off Santa Luzia, 55–80 m, calcareous algae, 16°44'N 24°46'W, 16.VI.1982, RMNH.Crus.D.51345; 1 M, Tarrafal Bay, 1959, MNHN 3163; Angola. 3 F (2 OVF), 1 M, Cuanza River, 31.I.1949, RMNH.Crus.D.7821.

Diagnosis. Rostrum almost reaching well beyond half the length of first segment of antennular peduncle; scaphocerite slightly, with blade reaching half of second article of antennular peduncle; distal tooth reaching distal limit of antennular peduncle. Minor cheliped with ischium armed with 4 spiniform setae; ventromesial margin of the merus with 7 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; Dactylus with strong crest on extensor margin. Major cheliped with ischium armed with 4 spiniform setae; ventromesial margin of the merus with 5 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; dactylus flattened, laterally twisted, dorsally convex and slightly bulbous distally; plunger developed, with anterior surface distinctly angular. Second pereiopod elongated, slender; ischium slightly longer than merus; carpus with 5 articles with ratio approximately equal to 4:

2: 1: 1.5: 2; Distolateral margin of uropodal exopod with 1 mesial and 1 lateral teeth adjacent to spiniform setae.

Description. Carapace smooth, frontal margin with strong rostrum; ocular hoods with well-developed teeth originating from anterior margin of hoods (Fig. 1A); rostrum slightly flat in dorsal view, distinctly longer than broad, distally tapering and ending in acute point; rostrum without setae, reaching well beyond half the length of the first segment of the antennular peduncle (Fig. 1B); margin between orbital teeth and rostrum U-shaped with slightly rounded angle (Fig. 1A); orbital process present. Pterygostomial angle rounded, not anteriorly protruding (Fig. 1B); cardiac notch deep. Abdominal somites with posteroventral margins broadly rounded, those of fifth segment slightly angular; sixth somite without articulated plate in posterolateral margin.

Eyes with well-developed corneas; ocellar beak projecting anteriorly, acute, visible in lateral view. Antennular peduncle moderately slender; stylocerite with acute tip reaching distal limit of first article of antennular peduncle; ventromesial carina well-developed, triangular in shape, with small acute tooth (Fig. 1C); second article of antennular peduncle much longer than visible part of first article, approx. 3X longer than broad, 2X size of the third article (Fig. 1A, B); lateral flagellum with groups of aesthetascs extending to article 10. Antenna with basicerite ending in sharp ventrolateral tooth; carpocerite slightly exceeds distal end of scaphocerite and antennular peduncle; scaphocerite with lateral margin slightly concave, ending in strong lateral tooth surpassing distal margin of blade (Fig. 1A); blade reaches the middle of the third article of the peduncle antenular; The distal tooth distinctly exceeds the end of the peduncle. Mouthparts as illustrated (Fig. 1D–H). Third maxilliped slender; coxa with lateral plate slightly truncated distally; exopod reaching beyond distal limit of antepenultimate article when extended; antepenultimate article somewhat flattened, approximately 4 times longer than broad, ventral surface sparsely setose; penultimate article approx. 3 times longer than broad, slightly broadened distally and densely setose; ultimate article disarmed, distally tapering, with dense rows of long setae (Fig.1I).

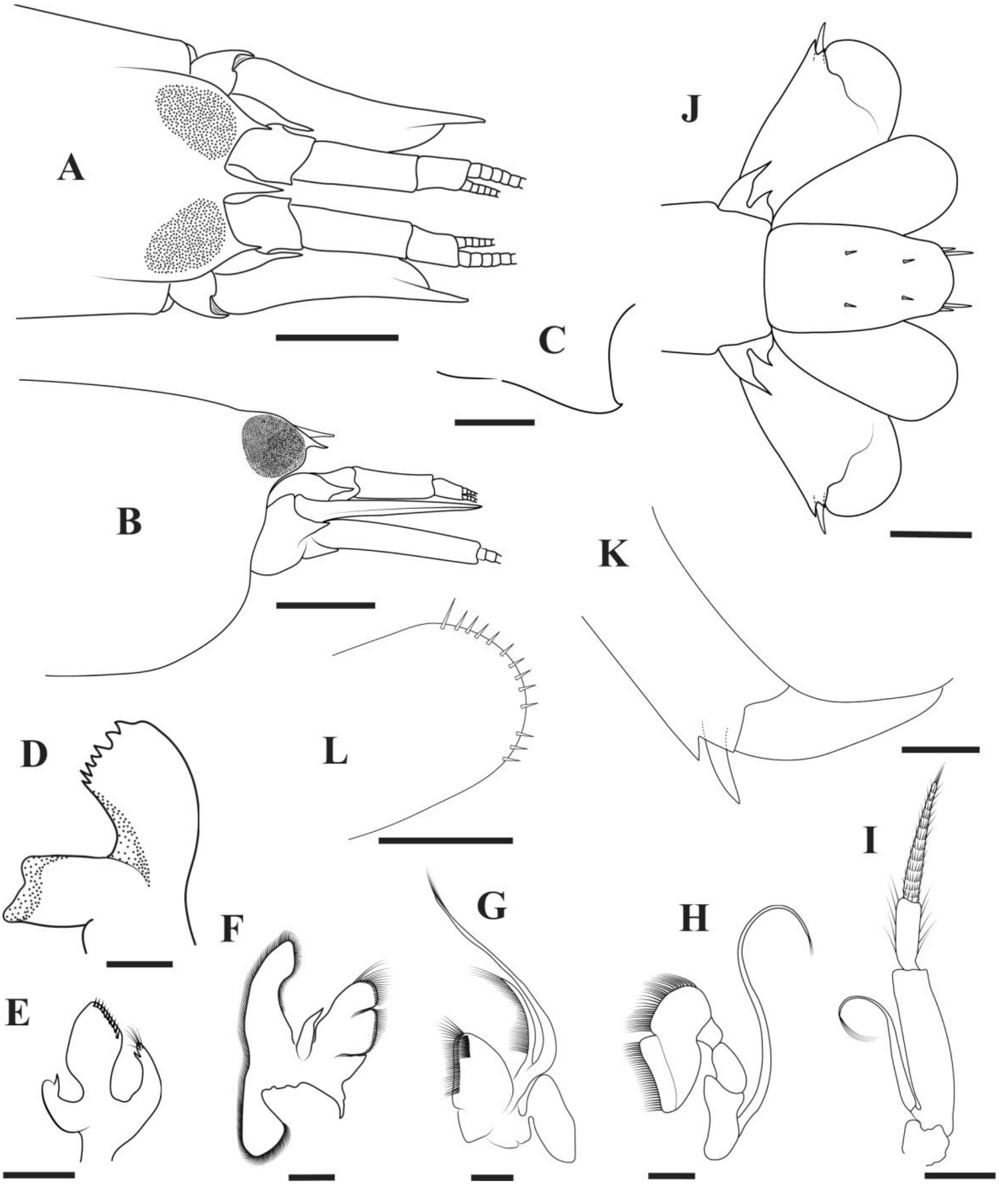

Figure 1. *Alpheus* **spec. nov.** from off Recife, state of Pernambuco, northeastern Brazil: (A–D) holotype, male (MOUFPE 19470); (E–M) paratype, male (MOUFPE 13703, dissected). Carapace and cephalic appendages, dorsal view (setae omitted); (B) same, lateral view; (C) ventromesial carina of the antenular peduncle; (D) left mandible, mesial view; (E) first

maxilla, lateral view; (F) second maxilla, lateral view; (G) first maxilliped, lateral view; (H) second maxilliped, lateral view; (I) third maxilliped, lateral view; (J) telson and uropods, dorsal view (setae omitted); (K) uropod, detail of the distolateral angle of the exopod; (L) uropod, detail of the final margin of endopod. Scale Bars: (A, B, J, M) = 1 mm; (C–I, L) = 0.5 mm.

Major cheliped with ischium short and robust, ventromesial surface with 4 small spiniform setae; merus robust, not elongated, approx. 2X longer than wide, sub- triangular in cross section; ventrolateral margin disarmed; ventromesial margin straight, with 5 small spiniform setae, ending in robust and sharp tooth; carpus very short, cup-shaped, slightly compressed; lateral surface with low crest (inferior crest) starting at 0.6 of length of palm, ending in distolateral sharp tooth, slightly directed laterally; linea impressa well-marked; mesial surface convex, devoid of sculptures and grooves; ventral surface with rounded smooth shoulder a slightly projecting into adjacent deep notch; notch extends transversely to groove on mesial surface (inferior groove); dorsal margin with sub-cylindrical elevation ending distally in large adhesive disk; distomesial surface with deep transversally notched crest (superior crest) ending in sharp tooth; distal third of ventral margin of palm with strong and long setae extending to distomesial margin of palm; pollex shorter than dactylus, strongly curved laterally, cutting edge slightly excavated and with small rounded tooth in proximal portion; dactylus flattened, laterally twisted, dorsally convex and slightly bulbous distally; plunger developed, with sharply angled anterior surface (Fig. 2A, B, E, F).

Minor cheliped with short and stout ischium; distomesial margin armed with 4 spiniform setae; broad, subtriangular in cross-section; ventrolateral surface disarmed; ventromesial margin slightly convex, ending in small acute tooth, with 7 spiniform setae similar in size and shape, spaced almost equidistantly along length of mesial surface of merus; carpus cup-shaped; chelae strongly compressed, palm with grooves and notches from distal half of lateral surface; mesial surface convex and devoid of depressions or grooves; lateral surface with low crest (inferior crest) starting at about middle of palm and ending in acute distolateral tooth; ventral surface smooth, ending in well-defined notch; dorsal margin also smooth, with sub-cylindrical elevation ending distally in small adhesive disk; distomesial surface with high ridge ending in strong sharp tooth (superior crest); fingers as long as palm; pollex lightly excavated on cutting edge; dactylus slightly flattened and twisted laterally, with broad crest on extensor margin, with small adhesive disk proximally (Fig. 2C, D, G).

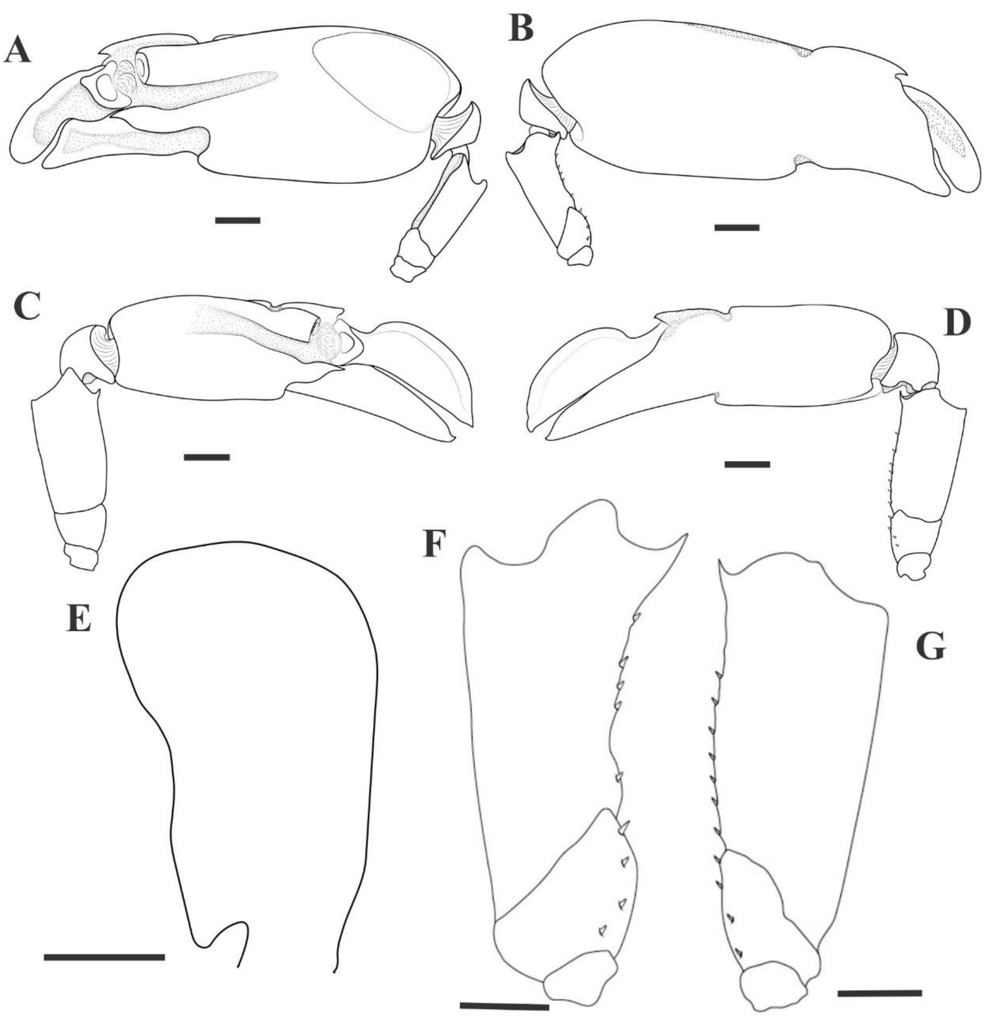

Figure 2. *Alpheus* **spec. nov.** from off Recife, state of Pernambuco, northeastern Brazil: paratype male, Pernambuco (MOUFPE 13703, dissected). (A) major cheliped in lateral view; (B) same, in mesial view; (C) cheliped minor lateral view; (D) same, in mesial view; (E) dactylus of the major chelae in mesial view, detail of the plunger; (F, G) Detail of the spiniform setae in the ischium and propodus of the major and minor chelae, respectively. Scale Bars: (A–E) = 1 mm; (F, G) = 0.5 mm.

Second pereiopod elongate, slender; ischium slightly longer than merus; carpus with 5 articles with ratio approximately equal to 4: 2: 1: 1.5: 2; chelae not ornamented, fingers as long as palm, with small tufts of setae (Fig. 3A). Third pereiopod with ischium armed with strong spiniform setae on ventrolateral surface; merus 5 times longer than broad, without tooth at distoventral angle; carpus slender, about half length of merus; propodus approx. 1.2 times longer than carpus, with about 9 robust spiniform setae along ventral margin and 1 pair of spiniform setae near to articulation with dactylus (Fig. 3B, E); dactylus slightly shorter than half length of propodus, conical, slightly curved, ending in sharp tip; extensor margin with 1 subdistal denticle (Fig. 3H). Fourth pereiopod similar to third in shape and proportion of articles, but slightly less robust; ischium armed with strong spiniform setae on the ventrolateral surface; propodus with about 8 robust spiniform setae along the ventral margin and 1 pair of spiniform setae near to articulation with the dactylus (Fig. 3C, F); extensor margin with 1 subdistal denticle (Fig. 3I). Fifth pereiopod more slender than third and fourth (Fig. 3D); merus slightly longer than carpus; ischium with 1 spiniform setae; propodus with about 8 spiniform setae along ventral margin and 9 well-developed distolateral setal brushes (omitted) (Fig. 3G).

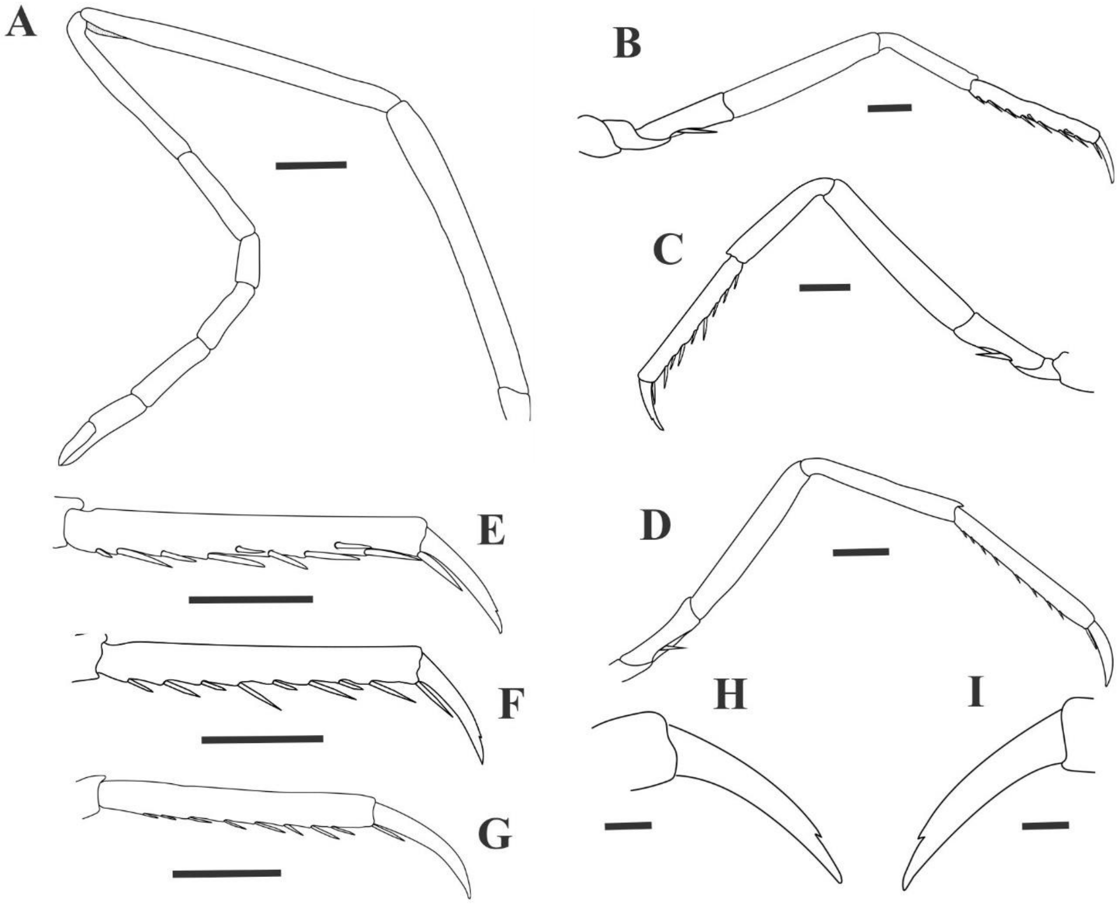

Figure 3. *Alpheus* **spec. nov.** from off Recife, state of Pernambuco, northeastern Brazil: paratype, male, Pernambuco (MOUFPE 13703, dissected). (A) second pereiopod, lateral view; (B) third pereiopod, lateral view; (C) fourth pereiopod, lateral view; (D) fifth pereiopod, lateral view; (E–G) third–fifth pereiopods, detail of the propodus; (H, I) third and fourth pereiopods, detail of the dactylus. Scale bars: (A–G) = 0.5 mm; (H, I) = 0.25 mm.

Pleopods with sparse setae on lateral margin of protopod; endopods and exopods with edges densely setose; first pleopod very reduced, distal margin of endopod with setae; second pleopod in male with *appendix masculina* subequal in length to *appendix interna*, not reaching distal margin of endopod, with numerous rigid setae at distal end; uropod with lateral lobe of protopod ending in strong and sharp tooth (Fig. 1J); diaeresis sinuous. Distolateral margin with 2 strong and sharp tooth adjacent to long spiniform setae (Fig. 1K);

endopod with row of spiniform setae along distal margin, the mesial more developed than the lateral ones (Fig. 1L). Telson subretangular, tapering to posterior margin; proximal margin 2.0 times broader than distal margin; lateral margins slightly convex; dorsal surface with 2 pairs of spiniform setae, first pair located at half-length of telson, second pair located approximately 0.7 of length of telson; posterior margin broadly convex, with 2 pairs of spiniform setae, mesial pair about 3 times size of lateral pair (Fig. 1J); anal tubercles well-developed.

Color in life. Body predominantly reddish; carapace more uniformly reddish (Fig. 4D, E); abdomen reddish with whitish transverse bands (Fig. 4G); whitish spots on the lateral portions of the abdominal segments (Fig. 4G). Palms of major chelipeds reddish, with three typical transverse white patches on both lateral and mesial surfaces; spots more defined on the mesial surface (Fig. 4F). Fingers of both major and minor chelipeds reddish. Telson and uropods strongly reddish (Fig. 4G); protopods of uropods whitish (Fig. 4G). Pereopods (2–5) slightly reddish (Fig. 4D–F).

Habitat. On sand calcareous algae, rhodolites and sponges, at depths from 33 to 90 m (Fig. 4A–C) (Ramos-Porto 1979; present study).

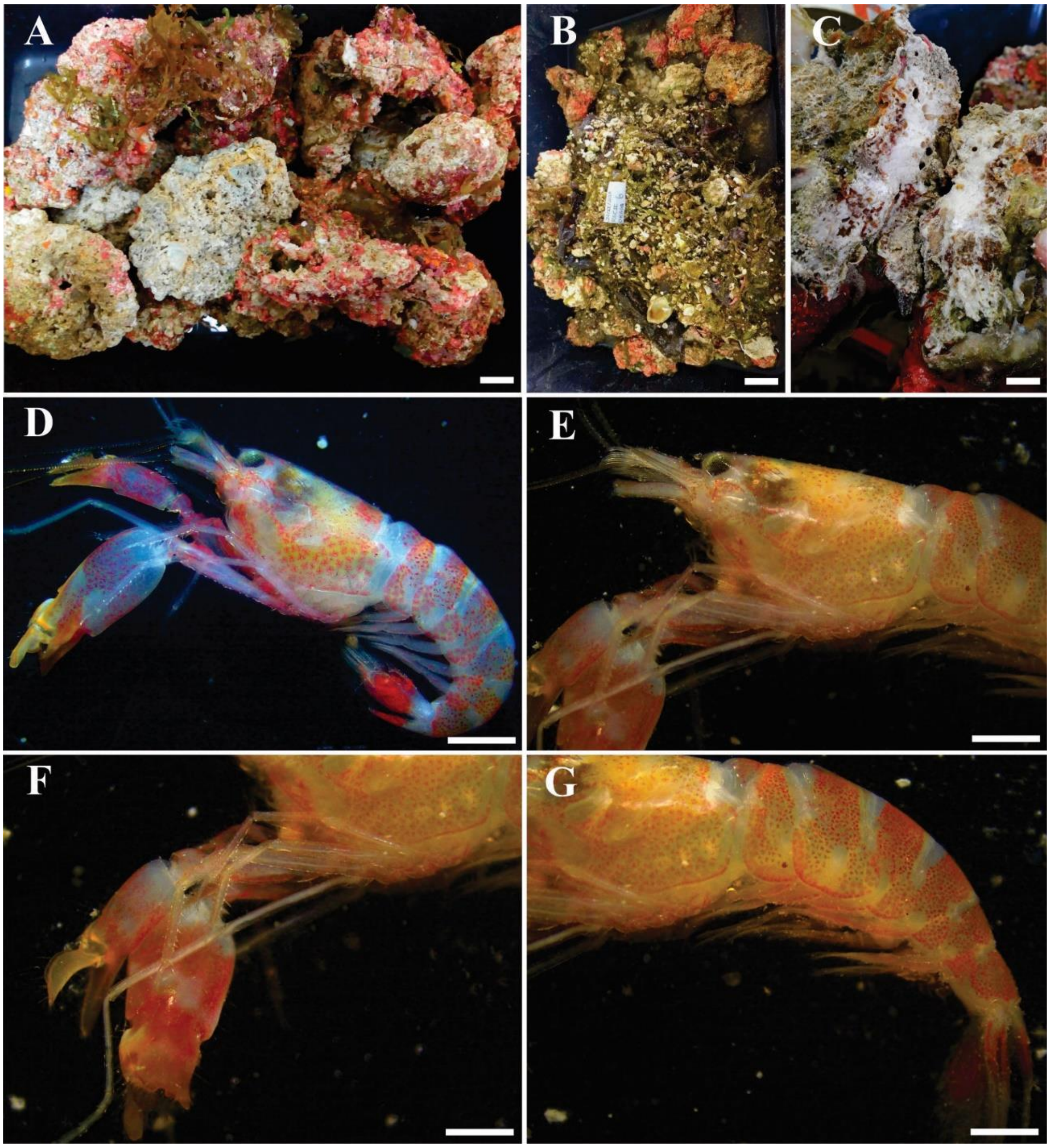

Figure 4. *Alpheus* **spec. nov.** from off Recife, state of Pernambuco, northeastern Brazil: substrates where the specimens were obtained (A–C) and color pattern in life of the species (D–G). (A) external appearance of rhodolith fragments; (B) rhodolith, calcareous algae, sponges and sandy sediment clusters; (C) detail of a fragment of rhodolith broken in half, showing crevices from which specimens were retrieved; (D) body color pattern, lateral view; (E–G), coloration of carapace, chelipeds and abdomen, respectively. Scale Bars: (A–C) = 2 cm; (D–G) = 1 mm.

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

Type locality. Western Atlantic, Brazil, state of Pernambuco, off Recife, approximately 20 nautical miles from the coast (8°08'51.5"S 34°34'08.0"W).

Molecular analysis. The best-fit substitution model, selected with a corrected Bayesian information criterion, was TPM3uf+I, assuming the nucleotide frequencies A = 0.2847, C = 0.1194, G = 0.2561, T = 0.3398, replacement rates AC = 0.0010, AG = 4.5910, AT = 1, CG = 0.0010, CT = 4.5910, GT = 1, proportion of invariable sites = 0.5410. The Bayesian Inference analysis (Fig. 5) clearly shows the separation of the species into two clades, one being formed only by the *A. amblyonyx* specimens and another clade presents the new species as the sister group of *A. crockeri*, *A. puapeba* and *A. macrocheles*.

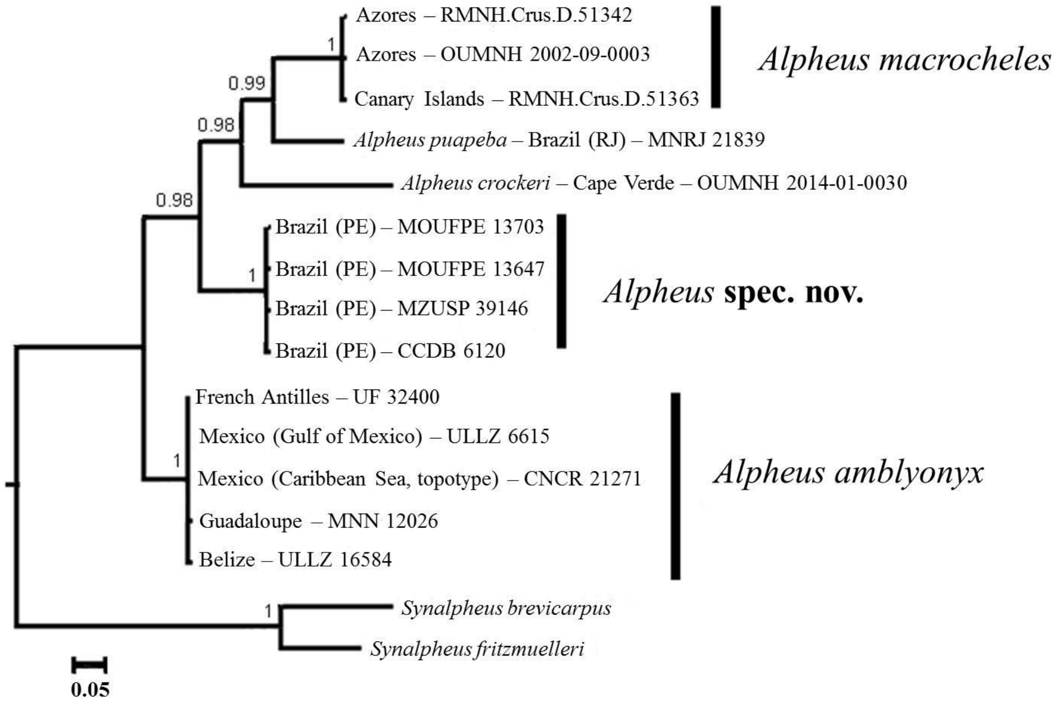

Figure 5. Bayesian Inference Tree of the 16S gene with specimens of *Alpheus* **spec. nov.** and other species from the *A. macrocheles* complex and *Synalpheus* Spence Bate, 1888. Numbers close to nodes represent posterior probabilities.

The values of genetic divergence support these results (Table 2). *Alpheus* **spec. nov.** presents about 15.9–22.9% of divergence with the other species according to the TPM3 model. *Alpheus* **spec. nov.**, as well as *A. amblyonyx* and *A. macrocheles*, shows null intraspecific divergence.

Tabela 2. Matrix of genetic divergence of the 16S gene between *Alpheus* **spec. nov.** from off Recife, state of Pernambuco, northeastern Brazil, and species from *"macrocheles"* species complex and *Synalpheus* Spence Bate, 1888, built with the K81 model. The numbering prior to localities represents the number of specimens used in the analysis for each taxon.

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

DISCUSSION

Alpheus **spec. nov.** can be separated from other representatives of the *A. macrocheles* complex of the Atlantic by means of morphology, genetics and coloration. *Alpheus ramosportoae* **spec. nov.** can be distinguished from most species in the complex by the presence of a subdistal denticle on the extensor margin of the dactylus of the pereiopods 3–4, a character it shares only with *A. macrocheles* and *A. amblyonyx* (Fig. 3H, I). Furthermore, *Alpheus* **spec. nov.** is distincty from of *A. cedrici* and *A. puapeba* by the presence of a strong crest on the extensor surface of the dactylus of the minor cheliped (vs. absent in *A. cedrici* and *A. puapeba*) and by the presence of two teeth on the distolateral margin of the uropodal exopod (vs. only 1 in *A. cedrici* and *A. puapeba*). The new species can be distinguished from *A. platydactylus* by the presence of a developed plunger on the cutting edge of the dactylus of the major cheliped (vs. plunger absent in *A. platydactylus*) (for comparison, see Fig. 2E and Crosnier & Forest 1966, p. 219, fig. 2F) and by the absence of tubercles along the ventral surface of the palm of major chelae (vs. tubercles present along the ventral surface of the palm in *A. platydactylus*).

Alpheus **spec. nov.** differs from *A. pouang* by the presence of a well-defined and broad ventral notch on the palm of the major cheliped (vs. ventral notch rudimentary in *A. pouang*) (for comparison, see Fig. 2A, B and Christoffersen 1979, p. 327, fig. 15J). The new species can be distinguished from *A. lentiginosus* by two main characteristics: the presence of well-defined plunger on the cutting edge of the dactylus of the major cheliped (vs. plunger rudimentary in *A. lentiginosus*) (for comparison, see Fig. 2E and Anker & Nizinski 2011, p. 51, fig. 1G) and the absence of an subdistal denticle in the flexor surface of the dactylus of the pereiopods 3–5 in the new species (vs. subdistal denticle present in *A. lentiginosus*) (for comparison, see Fig. 3H, I and Anker & Nizinski 2011, p. 52, fig. 2C, E). Below is a complete identification key for the Atlantic species of the complex.

Key for identification of the species of the complex *Alpheus macrocheles* from the Atlantic

1. Dactylus of the pereiopods 3–4 with a subdistal denticle on the extensor margin……………………………………………………………………………………….2

1’. Dactylus of the pereiopods 3–4 without subdistal denticle on the extensor margin……………………………………………………………………………………….4

2. Distolateral margin of the uropodal exopod with 1 mesial tooth and 1 lateral tooth flanking the spiniform setae; Major chelae with plunger developed, with anterior surface distinctly angular………………………………………...3

2’. Distolateral margin of the uropodal exopod with 1 acute lateral tooth and 1 mesial lobe flanking the spiniform setae; Major chelae with plunger rudimentary and flat, with only a small tooth on the anterior surface....……………………………………*Alpheus macrocheles*

3. Dactylus of the minor chelae with strong crest on the extensor margin; Distal tooth of the scaphocerite distinctly exceeds the distal end of the antennular peduncle……..*Alpheus* **spec. nov.**

3’. Dactylus of the minor chelae without crest on the extensor margin; Distal tooth of the scaphocerite reaches the distal end of the antennular peduncle……..*Alpheus amblyonyx*

4. Dactylus of the minor chelae with strong crest on the extensor margin…………………………………………………………………………….…5

4’. Dactylus of the minor chelae without crest on the extensor margin……………………………………………………………………………………….7

5. Major chelae with tubercles along the ventral surface of the palm ………………...*Alpheus platydactylus*

5’. Major chelae without tubercles along the ventral surface of the palm……………………………………………………………………………………………6

6. Pleopodal protopods armed with row of the spiniforms setae; Major chelae with broad dorsal and ventral notches ……………………………………….....................*Alpheus cedrici*

6’. Pleopodal protopods disarmed of the spiniforms setae; Major chelae with narrow dorsal and ventral notches ………………………………………………………….*Alpheus puapeba*

7. Major chelae with plunger developed; Dactylus of the pereiopods 3–5 without subdistal denticle in the ventral surface………………………………………………….*Alpheus pouang*

Alpheus **spec nov.** differs from *A. amblyonyx* and *A. macrocheles* based on several morphological characters (Table 3). The most conspicuous difference with *A. amblyonyx* is the presence of a strong crest on the extensor surface of the dactylus of the minor cheliped in *Alpheus* **spec. nov.** (vs. extensor surface of the dactylus of the minor cheliped without crest) (for comparison, see Fig. 2C, D and Chace 1972, p. 60, fig. 16L, M, Y, V). This feature is shared with *A. macrocheles* (see Crosnier & Forest 1966, p. 219, fig. 2C). Other differences between *Alpheus* **spec. nov.** and *A. amblyonyx* are: second article of antennular peduncle two times length of the third (vs. second article less than 1.5 times the size of the third in *A. amblyonyx*) and distal tooth of the scaphocerite overreaching the distal margin of the antennular peduncle (vs. reaching the final margin of the antennular peduncle in *A. amblyonyx*) (see Table 3). *Alpheus* **spec. nov.** differs from *A. macrocheles* by the more elongate rostrum, reaching well beyond half of the first article of antennular peduncle (vs. reaching the half of the first article of antennular peduncle in *A. macrocheles*), a well developed plunger of the dactylus of the major cheliped (vs. rudimentary and flat, with a small tooth on the anterior surface in *A. macrocheles*) and the presence of two well defined teeth on the distolateral margin of the uropodal exopod (vs. with 1 acute lateral tooth and 1 mesial lobe in *A. macrocheles*) (Table 3).

Table 3. Characters useful for separation between *Alpheus* **spec. nov.** from off Recife, state of Pernambuco, northeastern Brazil and *Alpheus amblyonyx* Chace, 1972 and *Alpheus macrocheles* (Hailstone, 1835).

Characters	*Alpheus amblyonyx* Chace, 1972	*Alpheus macrocheles* (Hailstone, 1835)	*Alpheus* **spec. nov.**
Relative length of rostrum to first article of antennular peduncle	Nearly reaches distal margin	Reaches halfway	Reaches well beyond halfway
Length ratio of second and third antennular peduncle articles	1.5 times	2.0 times	2.0 times
Size of stylocerite in relation to first article of antennular peduncle	Reaches the distal end	Reaches beyond the distal end	Reaches the distal end
Scaphocerite in relation to third article of antennular peduncle	Reaches halfway	Reaches the distal end	Reaches halfway
Distal tooth of the scaphocerite in relation to antennular peduncle	Reaches the distal end	Distinctly exceeds	Distinctly exceeds
Distolateral margin of the uropodal exopod	With 1 mesial tooth and 1 lateral tooth flanking the spiniform setae	With 1 acute lateral tooth and 1 mesial lobe flanking the spiniform setae	With 1 mesial tooth and 1 lateral tooth flanking the spiniform setae
Strong crest on the extensor margin of the dactylus of the minor chelae	Absent	Present	Present
Dactylus of the major chela	Tip strongly bulbous	Tip slightly bulbous	Tip strongly bulbous
Plunger	Developed, with anterior surface distinctly angular	Rudimentary and flat, with only a small tooth on the anterior surface	Developed, with anterior surface distinctly angular

The genetic analysis reinforced the separation of *Alpheus* **spec. nov.** from *A. amblyonyx* and *A. macrocheles*. The four specimens of *Alpheus* **spec. nov.** included in the Bayesian phylogenetic analysis formed a sigle clade distinct from the other species included. Pairwise genetic distances obtained in this analysis (15.9% between *Alpheus* **spec. nov.** and *A. amblyonyx*; 18.3% between *Alpheus* **spec. nov.** and *A. macrocheles*) are consistent with the values used for the separation of cryptic lineages within the genus *Alpheus* (Mathews *et al*. 2002; Mathews 2006; Almeida *et al*. 2013; 2014).

The new species shows marked differences in color pattern from specimens of *A. amblyonyx* [Guadeloupe and Panamá] and *A. macrocheles* [Spain (Mediterranean Coast) and Madeira] (see Anker & De Grave 2012), especially in the abdominal banding pattern. In *A. amblyonyx* and *A. macrocheles* the abdomen is uniformly reddish (see Anker & De Grave 2012, p. 7, fig. 4 A-D). The color pattern of the chelipeds of *Alpheus* **spec. nov.** somewhat resembles that observed in a specimen of *A. amblyonyx* from Guadeloupe. Both have conspicuous white patches on the mesial surface of the palm; however, in the specimen of *A. amblyonyx* the spots are more developed and well defined. *Alpheus amblyonyx* and *A. macrocheles* appear to have no whitish spots on the pleurae of the abdominal segments.

The fact that specimens of *Alpheus* **spec. nov.** were previously identified as *A. macrocheles* raises suspicion about the legitimacy of previous records of *A. macrocheles* on the Brazilian coast (e.g., Coelho & Ramos 1972; Ramos-Porto 1979; Coelho *et al.* 1986; Fausto Filho 1980; Ramos-Porto *et al.* 1996; Guterres *et al.* 2005). Unfortunately, most of the material previously reported from Brazil was not deposited in reference collections and could not be located. As mentioned above, these records lack illustrations of morphological characters and detailed morphological accounts. The only exception is the records by Ramos-Porto (1979), where a small diagnosis is given and a comparison is made with material of *A. amblyonyx* from the Caribbean. Illustrations are also provided in this contribution (Figures 1-

6). Part of Ramos-Porto's material (e.g., material from the Expeditions GEOMAR II-III and NORTE\NORDESTE I-II) was located in the Museu de Oceanografia Professor Petrônio Alves Coelho. Most of this material corresponds to *Alpheus* **spec. nov.**. From a total of 15 lots analyzed by Ramos-Porto (1979), only a female from Amapá (GEOMAR II 114, 12.IX.1970) was not found. The specimens of the other lots, with a few exceptions, are in good condition for analysis, including the three specimens illustrated by Ramos-Porto (1979) and matched the characteristics of the new species. Finally, none of the specimens of the *A. macrocheles* complex examined by us correspond to *A. macrocheles s. str.*. Previous records of *A. macrocheles* from Brazil are doubtful (see synonymy). Taking into account that the Ramos-Porto's (1979) material corresponds to *Alpheus* **spec. nov.**, we have several pieces of evidence supporting that most of those records correspond to *Alpheus ramosportoae* **spec. nov.**. Based on our parallel ongoing contribution (Soledade *et al.* chapter 1) and on the present findings, we propose that *A. macrocheles* is restricted to the Eastern Atlantic.

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5 CONSIDERAÇÕES FINAIS

A presente tese levantou dados importantes relacionados ao complexo de espécies crípticas *A. macrocheles* sob o ponto de vista taxonômico. A partir de uma abordagem integrativa que envolveu dados morfológicos, genéticos e de coloração foram geradas informações para a resolução de duas das principais problemáticas reconhecidas entre os camarões deste grupo. Entre as principais conclusões deste trabalho está a diferenciação morfológica e genética entre *A. macrocheles* e *A. amblyonyx*, embasada pela análise de material proveniente do lado oriental do Atlântico (para a primeira espécie) e material caribenho e da costa brasileira (para *A. amblyonyx*). Atrelado a isto, foram gerados aqui uma redescrição de *A. macrocheles*, com a designação de um neótipo. Isto gera estabilidade taxonômica ao grupo, uma vez que sana o problema de inexistência de material tipo para este camarão. Além disso, foi gerada uma completa caracterização morfológica para *A. amblyonyx*, incluindo desenhos diagnósticos e comparações com *A. macrocheles* e os demais representantes do complexo para o Atlântico.

Um segundo principal avanço deste estudo, foi a reexaminação do material de *A. macrocheles* citado para o Brasil que se encontrava acessível e devidamente depositado em coleções. Isto possibilitou a descoberta de um novo camarão críptico intimamente relacionado a *A. macrocheles* e *A. amblyonyx*. Esta nova espécie se apresenta geneticamente distinta destes dois camarões e, quanto à morfologia, é também distinta de todas as demais espécies do complexo. Este achado é mais um indício de que *A. macrocheles* muito provavelmente não ocorra do lado oeste do Atlântico. Acreditamos, portanto, que os registros prévios para este camarão tratam-se de identificações errôneas, e que correspondam na verdade a esta nova espécie.

Por fim, as três principais hipóteses não fora rejeitadas a partir dos nossos resultados: (i) *Alpheus amblyonyx* e *A. macrocheles* são de fato espécies válidas; (ii) *A. macrocheles* muito provavelmente não ocorra no Atlântico Ocidental; (iii) uma nova espécie foi descrita com base em material citado previamente como *A. macrocheles* para costa brasileira. Alem disso, nossos dados abriram um leque de possibilidades e apontou alguns pontos em que o conhecimento sobre este grupo ainda requer avanços. O principal deles é uma filogenia global (morfológica e molecular) envolvendo todo o grupo *Alpheus macrocheles* (senso Coutière 1905), o qual atualmente abriga cerca de 30 espécies no mundo inteiro. Apenas um estudo desta magnitude poderá elucidar as relações de parentesco dentro deste enorme grupo de espécies intimamente relacionadas quanto à morfologia.

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