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REVISÃO TAXONÔMICA E ANÁLISE FILOGENÉTICA DO COMPLEXO DE ESPÉCIES *Alpheus lobidens* (CRUSTACEA: DECAPODA: ALPHEIDAE)

Recife
2020

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

Área de concentração: Biologia Animal

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

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“Milho de pipoca que não passa pelo fogo continua a ser milho de pipoca, para sempre.”
(Alves, 1999, p.59-64).

RESUMO

Alpheus lobidens é um dos camarões-de-estalo mais comuns e largamente disseminado no Indo-Oeste Pacífico. A literatura tem apontado uma considerável variação morfológica e no padrão de coloração desta espécie, sugerindo que esta compõe um complexo de espécies crípticas. Além de *A. lobidens sensu stricto*, esse complexo também abrigaria *A. lobidens polynesica*, *A. inopinatus* e *A. buckupi*. Diante disso, o presente estudo teve como objetivo realizar uma revisão taxonômica do complexo de espécies *A. lobidens*, utilizando taxonomia tradicional e técnicas de biologia molecular. Para isso, foram examinados 190 espécimes obtidos, por empréstimo e visitas a coleções carcinológicas nacionais e internacionais, de forma a abranger a maior parte da distribuição geográfica reportada na literatura para as espécies. A análise morfológica externa foi baseada no exame de 68 caracteres. A análise molecular incluiu sequências parciais do gene mitocondrial 16S de nove indivíduos de *A. lobidens*, três de *A. buckupi*, um de *A. inopinatus* e oito indivíduos de outras espécies de Alpheidae. Os maiores valores de divergência genética (distância p) (19%) foram observados entre *A. lobidens sensu stricto* e *A. buckupi*, e entre *A. lobidens sensu stricto* e *A. lobidens sensu lato* da Austrália (Território do Norte). A menor divergência (12%) ocorreu entre *A. lobidens sensu stricto* e *A. lobidens sensu lato* das Ilhas Marshall. As análises morfológica e genética (inferência bayesiana e distância p) revelaram que *A. lobidens sensu stricto* é consistentemente distinto de *A. lobidens sensu lato*, *A. inopinatus* e *A. buckupi*. Com isso, a ocorrência de *A. lobidens sensu stricto* está atualmente restrita à localidade do tipo no Japão, e *A. inopinatus* e *A. buckupi* são taxa válidos. Não foram encontradas diferenças morfológicas consistentes nas populações de *A. lobidens sensu lato* examinadas. Contudo, as análises moleculares sugerem a existência de pelo menos seis linhagens em *A. lobidens sensu lato*, que apresentam considerável divergência genética. Esses resultados associados às correntes oceânicas, sugerem um fluxo gênico limitado entre essas linhagens, não deixando dúvidas quanto à validade das mesmas e demonstrando claramente a especiação críptica em *A. lobidens sensu lato*.

Palavras-chave: Caridea. Taxonomia integrativa. Divergência genética. 16S mtDNA.

ABSTRACT

Alpheus lobidens is one of the most common and widely spread snapping shrimps in the Indo-West Pacific. The literature has pointed out a considerable morphological and color variation of this species, suggesting that it composes a complex of cryptic species. In addition to *A. lobidens sensu stricto*, this complex would also include *A. lobidens polynesica*, *A. inopinatus* and *A. buckupi*. Therefore, the present study aimed to carry out a taxonomic revision of the *Alpheus lobidens* species complex, using traditional taxonomy and molecular biology techniques. For this, 190 specimens obtained by loan and visits to national and international carcinological collections were examined, along with most of the geographic distribution reported in the literature for the species. Morphological analysis was based on 68 characters. The molecular analysis incluided partial sequences of the mitochondrial 16S gene from nine individuals from *A. lobidens*, three from *A. buckupi*, one from *A. inopinatus* and eight individuals from other species of Alpheidae. The highest values of genetic divergence (p-distance) (19%) were observed between *A. lobidens sensu stricto* and *A. buckupi,* and between *A. lobidens sensu stricto* and *A. lobidens sensu lato* from Australia (Northern Territory). The lowest divergence (12%) occurred between *A. lobidens sensu stricto* and *A. lobidens sensu lato* from Marshall Islands. Morphological and genetic analyzes (Bayesian inference and distance p) revealed that *A. lobidens sensu stricto* is consistently distinct from A. *lobidens sensu lato*, *A. inopinatus* and *A. buckupi*. Thus, the occurrence of *A. lobidens sensu stricto* is currently restricted to the type locality in Japan, and *A. inopinatus* and *A. buckupi* are valid taxa. We could not find consistent morphological differences in the populations of *A. lobidens sensu lato* examined. However, molecular analyzes suggest the existence of at least six lineages in *A. lobidens sensu lato*, which show considerable genetic divergence. These results associated with ocean currents, suggest a limited gene flow between these lineages, leaving no doubt as to their validity and clearly demonstrating the cryptic speciation in *A. lobidens sensu lato*.

Keywords: Caridea. Integrative taxonomy. Genetic divergence. 16S mtDNA.

LISTA DE FIGURAS

Artigo Científico I

Artigo Científico II

LISTA DE TABELAS

Artigo Científico I

Artigo Científico II

SUMÁRIO

1 INTRODUÇÃO

A humanidade, desde a origem, busca identificar e classificar os seres vivos (FARBER, 2000; STEVENS, 2003). Com isso, acredita-se que a taxonomia seja uma das ciências mais antigas, visto que seu início se confunde com o surgimento do homem (SANTOS, 2008). Na Grécia clássica, com as produções de Aristóteles e Teofrasto, e na Renascença, com as obras de Gesner, Brunfels e Bock, foram criados os primeiros sistemas de classificação (STEVENS, 2003). Entretanto, considera-se que o primeiro trabalho a sistematizar de fato a classificação biológica, seja o *Systema Naturae* de Carl von Linné, publicado em 1758 (FARBER, 2000).

Lineu buscou classificar e nomear todos os animais, plantas e minerais, estabeleceu um sistema hierárquico de táxons e concebeu a nomenclatura binominal (DE QUEIROZ, 2005). O método lineano visava agrupar organismos que apresentassem um conjunto de características constantes, excluindo sempre características variáveis (KLEPKA; CORAZZA, 2018). Desde então, os taxonomistas passaram a adicionar e modificar as categorias elaboradas por Lineu, criando a hierarquia atual, e tornando este um dos sistemas mais influentes da história da biologia (STEVENS, 2003; SANTOS, 2008).

Com os estudos de Wallace (1858) e Darwin (1859), a evolução tornou-se o cerne da biologia (SANTOS, 2008). Então, a classificação da biodiversidade sofreu uma nova transformação, passando a levar em consideração as relações evolutivas entre organismos, além de esmerar-se em delimitar grupos monofiléticos, os quais reúnem todos os descendentes de um ancestral comum, que compartilham caracteres derivados resultantes do processo evolutivo (FARBER, 2000; STEVENS, 2003; SANTOS, 2008). À vista disso, a taxonomia tradicional baseada na morfologia, vem progredindo para uma taxonomia integrativa, que incorpora dados moleculares, biogeográficos, ecológicos, comportamentais, fisiológicos e embriológicos às análises (DAYRAT, 2005).

Esses diferentes tipos de dados têm permitido delinear e testar hipóteses de espécies por várias abordagens, promovendo uma compreensão abrangente da biodiversidade (AVISE; BALL, 1990; SITES; MARSHALL, 2003; DAYRAT, 2005). Um exemplo claro da sua contribuição, tem sido a resolução taxonômica de inúmeras espécies crípticas nos últimos anos (DAYRAT, 2005; PFENNINGER; SCHWENK, 2007). Essas são definidas na literatura como duas ou mais espécies, que apresentam baixos níveis de diferenciação morfológica e em contrapartida possuem diferentes trajetórias evolutivas (KNOWLTON, 1986; STRUCK et al., 2017).

A ocorrência de espécies crípticas, no sentido taxonômico, é muito comum em todos os táxons metazoários (BICKFORD et al., 2007; PFENNINGER; SCHWENK, 2007), incluindo os camarões Alpheidae Rafinesque, 1815 (ANKER, 2001; ALMEIDA et al., 2014). Em *Alpheus* Fabricius, 1798 e *Synalpheus* Spence Bate, 1888 diversos complexos de espécies crípticas têm sido revelados utilizando caracteres morfológicos e moleculares, principalmente do gene de RNA ribossômico mitocondrial 16S e o Citocromo Oxidase subunidade 1 (COI). Por exemplo, *Alpheus armillatus* H. Milne Edwards, 1837, *Alpheus formosus* Gibbes, 1850, *Alpheus cristulifrons* Rathbun, 1900 e *Synalpheus paraneptunus*, Coutière 1909 foram largamente reportados na literatura como espécies de ampla distribuição geográfica e após revisão utilizando os caracteres mencionados anteriormente, foram reconhecidas como táxons crípticos (ANKER, 2012; ANKER et al., 2008a, 2008b; ANKER; TÓTH, 2008). Isso sugere que esses gêneros ocultam uma biodiversidade ainda desconhecida e que sua importância evolutiva e ecológica ainda não foi completamente elucidada (ANKER et al., 2006).

Os camarões da família Alpheidae são um dos grupos mais numerosos e ecologicamente diversos entre os decápodos, com cerca de 600 espécies descritas distribuídas em 49 gêneros (ANKER et al., 2006; DE GRAVE; FRANSEN, 2011; ANKER, 2020). A maioria desses alfeídeos habita ambientes marinhos e estuarinos nas regiões tropicais e subtropicais, onde ocorrem do entremarés até grandes profundidades (CHACE, 1988; ANKER, 2003; ANKER et al., 2006). Os alfeídeos são estritamente bentônicos (ANKER et al., 2006) e geralmente apresentam estilo de vida livre, entretanto parte das espécies do grupo pode ser encontrada em associações simbióticas com diversos invertebrados marinhos (PATTON, 1966; KNOWLTON; KELLER, 1983; BOLTAÑA; THIEL, 2001; SILLIMAN et al., 2003; ANKER et al., 2007; 2008) e peixes gobiídeos (BRUCE, 1976; KARPLUS, 1987; ANKER et al., 2006; BAUER, 2004).

O gênero *Alpheus* é o mais expressivo dessa família, com 317 espécies válidas (DE GRAVE; FRANSEN, 2011; ANKER; PACHELLE, 2019; SCIOLI; ANKER, 2020; DE GRAVE et al., 2020). Este encontra-se dividido em sete grupos informais de espécies, ***macrocheles***, ***sulcatus***, ***diadema***, ***crinitus***, ***obesomanus***, ***brevirostris*** e ***edwardsi***, que remontam aos estudos de Coutière (1899; 1905). Estes grupos foram designados com base em caracteres morfológicos compartilhados, como semelhanças na região frontal e no primeiro par de pereiópodos (ANKER, 2001). Apesar destes não serem monofiléticos e apresentarem incontáveis exceções morfológicas dentro deles, esta subdivisão continua sendo considerada para o gênero (KIM; ABELE, 1988; WILLIAMS et al., 2001).

Dentre os grupos anteriormente citados, o ***edwardsi*** é o mais numeroso, com 110 espécies descritas, e morfologicamente mais heterogêneo (DE GRAVE; FRANSEN, 2011; ANKER; PACHELLE, 2019). Esse grupo apresenta espécies distribuídas em todo o mundo, além de ser notório por conter numerosos casos de complexos de espécies crípticas (ANKER, 2001). Um desses exemplos, é o complexo de espécies "*Alpheus lobidens*" que abarca possivelmente quatro espécies, sendo elas: *Alpheus lobidens* De Haan, 1849 (Indo-Pacífico, Mar Vermelho e Mar Mediterrâneo), *Alpheus lobidens polynesica* Banner & Banner, 1974 (Pacífico Ocidental), *Alpheus inopinatus* Holthuis & Gottlieb, 1958 (Indo-Pacífico Oeste, Mar Vermelho e Mar Mediterrâneo) e *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013 (Anfiatlântica) (ANKER, 2001; ALMEIDA et al., 2013). Essas se distribuem em estuários e manguezais, do entremarés até 10 m, escavando tocas sob rochas e cascalhos de coral, em fundos de areia e lama e podendo ser encontradas em associação com esponjas (ANKER, 2001; ALMEIDA et al., 2013; ANKER; DE GRAVE, 2016).

A ampla distribuição geográfica e a ocupação de uma grande gama de habitats, aliada a uma considerável variabilidade morfológica e de padrão de coloração (ANKER, 2001; ANKER; DE GRAVE, 2016), tem levantado dúvidas sobre a legitimidade de alguns registros prévios e, sobretudo sobre a validade de alguns dos táxons deste complexo. Tendo em vista toda a problemática apontada acima, faz necessária uma revisão aprofundada e integrativa do complexo *A. lobidens*.

1.1 HIPÓTESES TESTADAS

1. *Alpheus lobidens lobidens, A. lobidens polynesica, A. inopinatus* e *A. buckupi* são espécies taxonomicamente válidas.
2. A distribuição geográfica reportada para essas espécies é válida.
3. Existem táxons crípticos associados às espécies desse complexo.

1.2 OBJETIVOS

1.2.1 Objetivo geral

Revisar taxonomicamente o complexo de espécies "*Alpheus lobidens"*, utilizando taxonomia morfológica e técnicas de biologia molecular, para confirmar as espécies já descritas e identificar espécies crípticas.

1.2.2 Objetivos específicos

1. Testar a validade de *A. lobidens lobidens*, *A. lobidens polynesica*, *A. inopinatus* e *A. buckupi* com base na morfologia externa e dados moleculares;
2. Redescrever e ilustrar os caracteres morfológicos diagnósticos das espécies investigadas;
3. Analisar e confirmar a distribuição geográfica das espécies.

1.3 ESTRUTURAÇÃO DOS RESULTADOS

Os resultados desta tese estão estruturados em dois capítulos: 1- "Delimiting the snapping shrimp *Alpheus lobidens* De Haan, 1849 (Caridea: Alpheidae) based on morphological and molecular data", 2- "Multiple lineages and cryptic speciation in *Alpheus lobidens sensu lato* (Decapoda: Alpheidae) revealed by molecular diversity". Ambos estão escritos em língua inglesa seguindo as normas para publicação dos periódicos Zootaxa e Journal of Crustacean Biology, respectivamente

O capítulo 1, publicado na revista Zootaxa, objetivou delimitar o status taxonômico de *Alpheus lobidens* De Haan, 1849, com base em análises morfológicas e moleculares do material topotípico de Nagasaki (Japão). Por meio de comparações com espécies próximas, também testamos o status taxonômico de *A. inopinatus* Holthuis & Gottlieb, 1958 e *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013. O capítulo 2 buscou investigar a diversidade molecular das populações de *A. lobidens sensu lato*, ao longo de sua distribuição geográfica no Indo-Pacífico Oeste e verificar se a diversidade encontrada é suportada por características morfológicas.

As respectivas normas de formatação do texto para submissão nestas duas revistas encontram-se nos seguintes endereços eletrônicos:

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ARTIGO I: Publicado. Zootaxa, 4718 (3)

2 Delimiting the snapping shrimp *Alpheus lobidens* De Haan, 1849 (Caridea: Alpheidae) based on morphological and molecular data

Running title: Delimiting *Alpheus lobidens*

Abstract

Our aim was to delimit the taxonomic status of the snapping shrimp *Alpheus lobidens* De Haan, 1849, based on morphological and molecular analyses of the topotype material from Nagasaki (Japan). We provide a redescription, detailed illustrations, and molecular data. Through comparisons with close-related species, we also tested the taxonomic status of *A. inopinatus* Holthuis & Gottlieb, 1958 and *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013. We examined 74 specimens previously identified as *A. lobidens*, 84 specimens of *A. buckupi*, and 30 of *A. inopinatus*. The morphological analysis was based on the examination of 68 characters. The molecular analysis included mitochondrial gene sequences (16S) of 18 individuals: six *A. lobidens*, three *A. buckupi*, one *A. inopinatus*, and eight individuals of other species of Alpheidae. The morphological analysis revealed that *A. lobidens sensu stricto* is consistently distinct of *A. lobidens sensu lato*, *A. inopinatus* and *A. buckupi*. The genetic analyzes (Bayesian Inference and p-distance) corroborated the morphological results and showed a clear separation between them. The highest values of genetic divergence (p-distance) (19%) were observed between *A. lobidens sensu stricto* and *A. buckupi*, and between *A. lobidens sensu stricto* and *A. lobidens sensu lato* from Australia (Northern Territory). The lowest divergence (12%) occurred between *A. lobidens sensu stricto* and *A. lobidens sensu lato* from Marshall Islands. Based on our results, the occurrence of *A. lobidens sensu stricto* is currently restricted to the type locality in Japan, and *A. inopinatus* and *A. buckupi* are valid taxa. Delimiting *A. lobidens sensu stricto* is relevant since the name *A. lobidens* has been applied to cryptic species, resulting in a high unclear taxonomic state.

Keywords: Decapoda, alpheid, species complex, molecular systematics, 16S gene.

Introduction

Alpheus lobidens De Haan, 1849 is one of the most common and widespread snapping shrimps in the Indo-West Pacific. This species was described by De Haan (1849) based on a female collected by von Siebold and Bürger between 1823 and 1834, probably in Nagasaki, Japan, where von Siebold was assigned as resident physician and scientist of the Dutch army (Fransen *et al*. 1997). The holotype is deposited as a dry specimen in the Netherlands Center for Biodiversity Naturalis, Leiden, The Netherlands, and it is in poor conditions (Fig. 1). The holotype description, published in Latin, is short, uninformative, and lacks illustrations.

Alpheus lobidens entity is usually found under rocks, coral rubble, from mixed sand-rubble-rock bottoms to fine sand-silt and mud, and in burrows on mudflats, from the intertidal to 10 m of depth (Anker 2001; Anker & De Grave 2016). The species is apparently widely distributed in the Indo-West Pacific, from the Red Sea and South Africa to Japan, Australia, and also occurs in the Eastern and Western Mediterranean and in Hawaii (Anker 2001; Yang & Anker 2003; Anker & De Grave 2016). The diversity of habitats occupied by *A. lobidens* and its wide geographic range facilitated the development of studies concerning its ecology (Corfield & Alexander 1995; Dabbagh & Kamrani 2011; Jahanpanah & Savari 2013; Naderloo *et al*. 2013; Koyama *et al*. 2017), larval development (Yang *et al*. 2003), reproduction (Ansari & Maghsoodlou 2017) and behavior (Dabbagh *et al*. 2012).

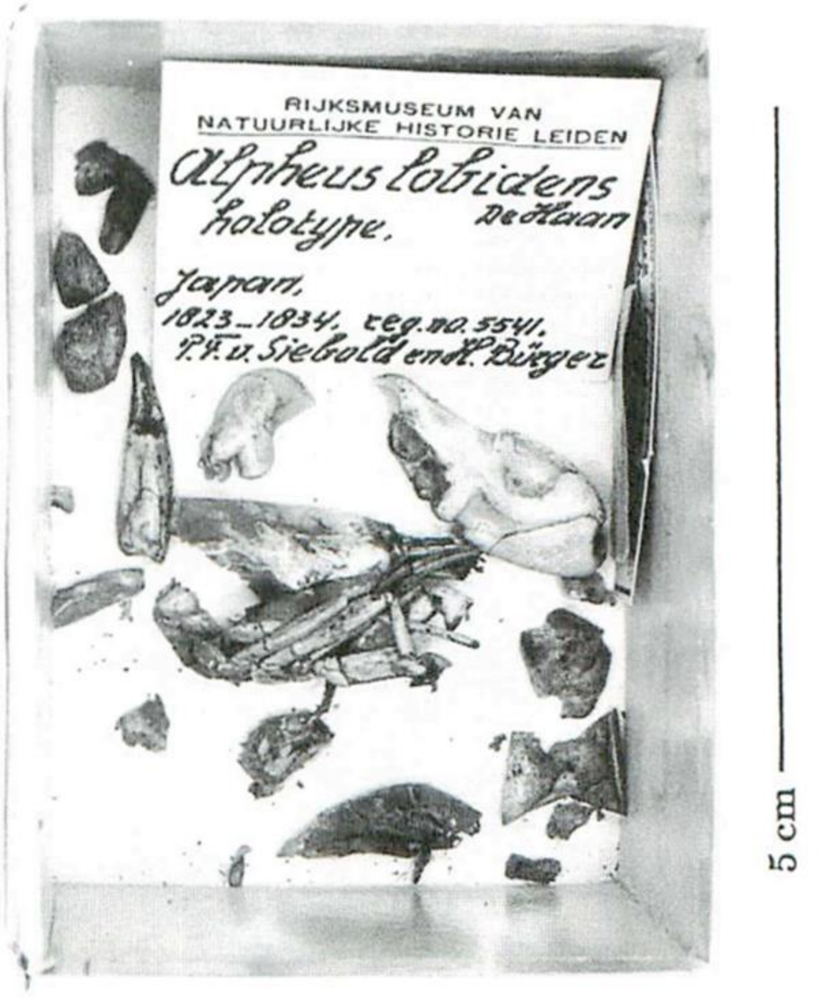

Figure 1. Holotype of *Alpheus lobidens* De Haan, 1849 deposited in the Netherlands Center for Biodiversity Naturalis, Leiden, Netherlands [from Yamaguchi & Baba 1993: 228, fig. 47].

Alpheus lobidens belongs to the ***edwardsi*** morphological group, which is characterized mainly by unarmed ocular hoods and presence of dorsal and ventral notches on the palm of the major chelae (Coutière 1905; Banner & Banner 1982). *Alpheus lobidens* can be distinguished from the other species of the ***edwardsi*** group by presenting the following combination of characters: rostrum sloping gradually into adrostral furrows; distolateral tooth of the scaphocerite distinctly overreaching the distal margin of the blade; major cheliped usually with subdistal tooth on flexor margin of merus; dactyl of minor chelae strongly sculptured and with "balaeniceps" setae in males; third pereiopod without strong distal tooth on flexor margin of merus and pereiopods 3 and 4 usually with a spiniform seta on ischium (Chace 1988; Yang & Anker 2003). However, these characters vary and most of them may appear in other species of the *A. lobidens* complex (see below).

Up to date there is a high taxonomic instability involving *A. lobidens*. Ortmann (1890), analyzing specimens from Japan, was the first to illustrate the minor cheliped in lateral view. Ortmann (1890) compared specimens of *A. lobidens* with the description of *A. strenuus* Dana, 1852 from Island of Tongatabu, observed the high morphological similarity between them, and suggested a possible synonymy. Coutière (1899) analyzed the holotype of *A. lobidens*, noticing its poor conditions; the author also observed the similarity with *A. strenuus* and with *A. crassimanus* Heller, 1865 from Nicobaren, and suggested *A. lobidens* as synonym of both species. De Man (1911), upon the analysis of the material from Amboina Island identified by Coutière (1897) as *A. lobidens,* suggested that the proposed synonymy between *A. strenuus*, *A. crassimanus* and *A. lobidens* could be valid but only a detailed review could confirm this hypothesis. Banner (1953), based on a literature review, considered *A. strenuus* and *A. crassimanus* as valid species, disagreeing with the synonymy proposed by Coutière (1899). Later, Banner & Banner (1974) performed a more detailed comparison between *A. crassimanus* and *A. lobidens* and found no reliable differences between them, revalidating part of the synonymy proposed by Coutière (1899). Additionally, Banner & Banner (1974) observed differences in the degree of development of the male minor chelae, and described two subspecies of *A. lobidens*: *A. lobidens lobidens*, represented by specimens from Malaysia, Thailand, Australia and the Red Sea, characterized by males with deep grooves on the palm of minor chelae; and *A. lobidens polynesica*, represented by Hawaiian specimens, characterized by males with subtle or absent grooves on the palm of the same structure.

Banner & Banner (1981) refuted the separation of *A. lobidens* into two subspecies and recommended that *A. inopinatus* Holthuis & Gottlieb, 1958 from Israel should be regarded as synonym of *A. lobidens*, based on the absence of distinctive morphological characters to distinguish them. Thus, at that time, *A. lobidens* was considered as a species with high morphological variability and a wide geographic distribution.

For many years, several opinions regarding the synonymy between *A. lobidens* and *A. inopinatus* have been published (Banner & Banner 1983; Bruce & Coombes 1997; Anker 2001; Yang & Anker 2003). Anker (2001) and De Grave & Fransen (2011) treated *A. lobidens* and *A. inopinatus* as valid. Additionally, Anker & De Grave (2016), when observing morphological characters and two different color patterns in specimens of *A. lobidens* from Singapore, reaffirmed that *A. lobidens* is a complex of cryptic species formed at least by *A. lobidens, A. lobidens polynesica* and *A. inopinatus*, but with the possibility of more species being involved.

Almeida *et al*. (2013) when describing the amphi-Atlantic *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013 observed its morphological similarity with members of the *A. lobidens* complex, including *A. inopinatus*, especially due to the major and minor chelae morphology. On the other hand, phylogenetic analyzes revealed a clear separation between specimens of *A. buckupi* and a specimen from New South Wales, Australia, identified as *A.* cf. *lobidens*. However, these results should be considered with caution, since the material from the type locality of *A. lobidens* was not analyzed at that time, and it is not possible to state the taxonomic identity of the Australian specimen.

In view of this scenario of high taxonomic uncertainty, delimiting *A. lobidens sensu* De Haan, 1849 represents the first step towards a better taxonomic resolution, before a broader revision of the complex can be accomplished. Thus, the aim of this study was to delimit *A. lobidens sensu* De Haan, 1849 and to redescribe this shrimp species based on topotypic material. We also provide detailed illustrations and compare its morphological and molecular characters with morphologically similar species. These comparisons also aimed to test the validity of *A. inopinatus* and *A. buckupi*.

Material and methods

Taxon sampling

Morphological characters

We examined 74 specimens previously identified as *A. lobidens*, including *A. lobidens polynesica*, obtained over most of its known geographical distribution. Additionally, 84 individuals of *A. buckupi* and 30 individuals of *A. inopinatus* were analyzed, as their morphology is highly similar to that of *A. lobidens*. The specimens analyzed are deposited in the crustacean collections of the following institutions: National Museum of Natural History, Smithsonian Institution, Washington DC, USA (NMNH), Florida Museum of Natural History, University of Florida, Gainesville, USA (UF), Netherlands Center for Biodiversity Naturalis, Leiden, The Netherlands (RMNH), Museu de Oceanografia, Universidade Federal de Pernambuco, Recife, Brazil (MOUFPE). Some specimens deposited at the MOUFPE collection have been previously deposited in the Collection of

Crustacea of the Universidade Estadual de Santa Cruz, Ilhéus, Brazil (MZUESC) (see Almeida *et al*. 2013).

Morphological data were obtained upon the examination of adults, although juvenile specimens were also included to provide an overview of the characters variability along ontogeny. In addition to the main diagnostic characters, other characters including those of mouthparts were explored, to provide more comparative data. Herein, the terminology of the mouthparts morphology and their setae follows Garm (2004), and the terminology of the other morphological characters follows McLaughlin (1980).

The sex was recognized based on the presence (male) of the *appendix masculina* on the endopod of the second pair of pleopods, or by the presence of embryos underneath the abdomen (females) (Bauer 2004). The carapace length of each specimen was measured from the tip of the rostrum to the posterior margin of the carapace. Measurements were taken with a digital caliper (accuracy of 0.01 mm). Specimens with carapace length smaller than the smallest ovigerous female examined in this study were considered as juveniles.

We assumed that the topotypes from Shimabara, Nagasaki, Japan (RMNH PEG 25134) correspond to *A. lobidens sensu stricto*, i.e., are conspecifics of the damaged holotype (see Fig. 1). All specimens morphologically different from the topotypes were treated as *A. lobidens sensu lato*. We included in the synonymy those studies that examined the holotype or topotypes (e.g. Banner & Banner 1974; 1981), and certain lists that refer to the holotype (e.g. Fransen *et al*. 1997; De Grave & Fransen 2011).

All drawings were prepared under a dissecting microscope equipped with a camera lucida. These were then scanned, digitally inked, and arranged on digital plates using the methods described by Coleman (2003; 2009).

Six sequences were generated from our own DNA extractions (Table 1), according to the methods described below. Sequences of nine specimens of other species of *Alpheus* Fabricius, 1798, retrieved from GenBank, were used to compare the genetic differences between *A. lobidens* and congenerics (Table 1). Two additional sequences of *Synalpheus* Spence Bate, 1888 were used as outgroups according to the phylogenetic relationship described in Anker *et al.* (2006).

Abbreviations used: (f)—female(s); (m)—male(s); (ovf) ovigerous females; (cl)—carapace length.

Table 1. List of specimens used in the genetic analysis. CCDB: Coleção de Crustáceos do Departamento de Biologia da FFCLRP/USP; MNHN: Muséum National d'Histoire Naturelle; MOUFPE: Museu de Oceanografia, Universidade Federal de Pernambuco; NMNH: National Museum of Natural History, Smithsonian Institution; NMV: Museum Victoria; OUMNH: Oxford University Museum of Natural History; RMNH: Netherlands Center for Biodiversity Naturalis; UF: Florida Museum of Natural History.

Species	**Locality**	**Catalogue Number**	**GenBank**	**Reference**
Alpheus angulosus McClure, 2002	Ascension Bay, Quintana Roo, Mexico	NMNH 135891	JX286600	Almeida *et al.* (2013)
Alpheus armillatus H. Milne Edwards, 1837	Baby Beach, Aruba	—	FJ528477	Mathews & Anker (2009)
Alpheus buckupi Almeida, Terossi, Araújo-Silva & Mantelatto, 2013	Lagarto Beach, São Tomé and Príncipe	OUMNH.ZC. 2011-06.005	JX286604	Almeida *et al.* (2013)

Alpheus buckupi	Timbó River, Paulista, Pernambuco, Brazil	MOUFPE 19791	JX286603	Almeida *et al.* (2013)
Alpheus buckupi	Tassimirim Beach, Boipeba Island, Cairu, Bahia, Brazil	MOUFPE 19500	JX286605	Almeida *et al.* (2013)
Alpheus carlae Anker, 2012	Maramata Beach, Cachoeira River, Ilhéus, Bahia, Brazil	MOUFPE 19795	JX286602	Almeida *et al.* (2013)
Alpheus estuariensis Christoffersen, 1984	Paripe River, Itamaracá, Pernambuco, Brazil	MOUFPE 19794	JX286607	Almeida *et al.* (2013)
Alpheus heterochaelis Say, 1818	Whitney Marine Laboratory, Florida, USA	UF 23208	JX286610	Almeida *et al.* (2013)
Alpheus inopinatus Holthuis & Gottlieb, 1958	Haifa, Israel	RMNH 18313	MN617767	Present study

Alpheus lobidens De Haan, 1849	Moorea, Society Islands, French Polynesia	UF 15757	MN617768	Present study
Alpheus lobidens	Darwin, Northern Territory, Australia	UF 19966	MN617769	Present study
Alpheus lobidens	Darwin, Northern Territory, Australia	UF 19984	MN617770	Present study
Alpheus lobidens	Lennox Head, New South Wales, Australia	NMV J 21615	JX286611	Almeida *et al.* (2013)
Alpheus lobidens	Shimabara, Nagasaki, Japan	RMNH PEG 25134	MN617771	Present study
Alpheus lobidens	Marshall Islands, Majuro Atoll	UF 13776	MN617772	Present study
Alpheus petronioi Almeida, Terossi & Mantelatto, 2014	Estuary of the Mojuim River, São Caetano de Odivelas, Pará, Brazil	CCDB 4509	KF667545	Almeida *et al.* (2014)
Synalpheus pandionis Coutière, 1909	Curlew Reef, Belize	-	HQ435468	Hultgren & Duffy (2011)

Synalpheus plumosetosus				
Macdonald, Hultgren & Duffy, 2009	Dairy Bull, Discovery Bay, Jamaica	-	HQ435472	Hultgren & Duffy (2011)

DNA extraction, amplification, and sequencing

DNA was extracted from the abdomen using the Qiagen DNeasy® Blood and Tissue Kit, following the manufacturer's protocol. The DNA amplification process followed the protocols of Schubart *et al.* (2000), with modifications according to Mantelatto *et al.* (2006). Partial fragments (~ 600 bp) of 16S mtDNA were amplified by PCR (Polymerase Chain Reaction) (Sambrook *et al*. 1989) in a Veriti Applied Biosystems® Thermocycler (Applied Biosystems, Foster City, CA, USA) using the primers 1472 (5'-AGATAGAAACCAACCTGG-3') and 16L2 (5'-TGCCTGTTTATCAAAAACAT-3') (Crandall & Fitzpatrick 1996; Schubart *et al*. 2002). PCR cycles started with denaturation for 5 min at 95°C, followed by 40 cycles of 1 min at 95°C, 45 s at 46−48°C, and 1 min at 72°C, and a final extension step of 3 min at 72°C. Amplicons were visualized after electrophoresis in 1.0 % agarose gel stained with GelGreen. The amplicons were purified using the Exosap-it Purification Kit following the manufacturer's instructions and sequenced on an ABI 3100 Genetic Analyzer® automated sequencer (Applied Biosystems) of the company ACTGene Molecular Analyzes (Porto Alegre/RS). Both DNA strands were sequenced, and the consensus sequence was obtained using the program Bioedit 7.0.9.0 (Hall 1999). DNA sequences were compared to the NCBI database using BLAST (http://blast.ncbi.ncbi.nlm.nih.gov/blast.cgi) to confirm their identities.

The sequences were aligned with MUSCLE (Edgar 2004), using the default configuration, through the Cyberinfrastructure for Phylogenetic Research (CIPRES) website (Miller *et al*. 2010). After aligning and trimming, the 16S gene sequences consisted of 551 base pairs. The best replacement model was selected according to the Bayesian Information Criterion (BIC) criterion, among the 88 alternatives given by the jModelTest program (version 2.1.4) (Darriba *et al*. 2012). The Bayesian inference was performed using the program MRBayes (version 3.2.2) (Ronquist *et al*. 2012) implemented in the CIPRES with the parameters obtained in jModelTest (model TPM3uf + G with nucleotide frequencies A = 0.2852, C = 0, 1028, G = 0.2457, T = 0.36663, substitution rates AC = 0.1693, AG = 6.2075, AT = 1, CG = 0.1693, CT = 6.2075, GT = 1, and gamma distribution = 0.20). In the analysis we sampled one tree every 1,000 generations of 20,000,000 generations, starting with a random tree. The convergence of the parameters and probabilities of the runs were verified in the Tracer 1.6.0 program (Rambaut *et al*. 2014). To summarize the later distribution, the maximum credibility tree was retrieved from the total of subsequent trees and the support values from the tree annotated in the treeAnnotator program 1.8.2 (Drummond *et al*. 2012). Of the total trees (and parameters) the first 15% of the traces were discarded (burn-in). Only *A posteriori* probability values higher than 80% were reported. The matrix of genetic divergences was calculated based on the p-distance using MEGA v5 (Tamura *et al*. 2011).

Results

Taxonomic section

Family Alpheidae Rafinesque, 1815

Genus *Alpheus* Fabricius, 1798

Alpheus lobidens De Haan, 1849

Alpheus lobidens De Haan, 1849: 179; Ortmann 1890: 474, pl. 36, fig. 13; Coutière 1899: 14, 293, 486; Balss 1914: 41 (in part); Banner & Banner 1981: 29–34, fig. 4 (in part); Anker 2001: 165, 204, 205; De Grave & Fransen 2011: 385.

Alpheus lobidens lobidens Banner & Banner 1974: 430–432 (in part); Yamaguchi & Baba 1993: 228, fig. 47; Fransen *et al*. 1997: 35.

Type material. Damaged; dry and not examined (Netherlands Center for Biodiversity Naturalis, Leiden, The Netherlands [RMNH.CRUS.D.5541], (Fig. 1).

Material examined. **Japan.** *Topotypes*, 8 m (cl 5.4–11.0 mm) (one specimen used in genetic analysis), 5 f (5.8–10.6 mm), 8 ovf (cl 4.9–10.6 mm) (RMNH PEG 25134), Ariake Bay Coast, near Mizuho, N.W., Shimabara, Nagasaki, Japan, 08.ix.1968, coll. T. Sakai & L.B. Holthuis.

Comparative material examined.

Alpheus buckupi Almeida, Terossi, Araújo-Silva & Mantelatto, 2013. **Brazil.** 1 m (cl 5.3 mm), 1 f (cl 5.6 mm) (MOUFPE 19471), Pará, São Caetano de Odivelas, Mojuim River, 16.xi.2012, coll. A.O. Almeida, P.S. Santos & G.O Soledade; 1 m (cl 9.3 mm), 1 f (cl 9.1 mm), 1 ovf (cl 9.4 mm) (MOUFPE 19472), Piauí, Luís Correia, 28.xii.2013, coll. A.O. Almeida; 1 m (cl 5.7 mm), 2 f (cl 7.9, 9.1 mm), 1 ovf (cl 9.4 mm) (MOUFPE 19473), Piauí, Luís Correia, 28.xii.2013, coll. A.O. Almeida; 1 m (cl 7.2 mm), 1 f (cl 5.4 mm) (MOUFPE 19474), Pernambuco, Santa Cruz Channel, 19.v.2015; 1 m (cl 9.3 mm), 1 f (cl 7.2 mm) (MOUFPE 19475), near Santa Cruz Channel, 19.v.2015, coll. A.O. Almeida;

1 m (cl 6.5 mm) (MOUFPE 19476), near Santa Cruz Channel, 19.v.2015, coll. A.O. Almeida; 8 m (cl 3.8–9.4 mm), 6 f (cl 5.2–12.2 mm), 6 ovf (cl 4.7–8.6 mm) (MOUFPE 19477, cited in Almeida *et al*. 2013 as MZUESC 1367), Pernambuco, Ilha de Itamaracá, Paripe River, 01.ix.2008, coll. R.J.C. Paiva & F.S. Santana; 5 m (cl 7.6–11.5 mm), 2 ovf (cl 9.4, 10.0 mm) (MOUFPE 19478), Pernambuco, Ilha de Itamaracá, Paripe River, 19.v.2015, coll. A.O. Almeida *et al*.; 4 m (cl 4.3–6.9 mm), 3 f (cl 3.7–7.6 mm), 3 ovf (cl 4.0–6.0 mm) (MOUFPE 19479), Pernambuco, Ilha de Itamaracá, Paripe River, 19.v.2015, coll. A.O. Almeida *et al*.; 1 m (cl 7.2 mm) (MOUFPE 19480), Pernambuco, Ilha de Itamaracá, Paripe River, 04.viii.2015, coll. A.O. Almeida *et al*.; 1 ovf (cl 7.5 mm) (MOUFPE 19481), Pernambuco, Ilha de Itamaracá, Paripe River, 04.viii.2015, coll. A.O. Almeida *et al*.; 1 m (cl 10.3 mm) (MOUFPE 19482, cited in Almeida *et al*. 2013 as MZUESC 1368), Pernambuco, Olinda, Casa Caiada Beach, 18.viii.2008, coll. F.S. Santana; 1 ovf (cl 10.8 mm) (MOUFPE 19483, cited in Almeida *et al*. 2013 as MZUESC 1369), Pernambuco, Recife, confluence between Pina and Capibaribe rivers, 08°04'12.5"S 34°52'19.11"W, 13.vii.2007, coll. A.O. Almeida & R.J.C. Paiva; 1 m (cl 7.9 mm), 2 ovf (cl 6.3, 6.8 mm) (MOUFPE 19484), Pernambuco, Cabo de Santo Agostinho, Praia do Paraíso, 16.ii.2007, coll. Almeida *et al*.; 1 m (cl 7.9 mm) (MOUFPE 19485), Pernambuco, Cabo de Santo Agostinho, Praia do Paraíso, 02.vi.2015, coll. Classe de Invertebrados II; 1 f (cl 4.3 mm) (MOUFPE 19486), Pernambuco, Ilha de Santo Aleixo, 19.iv.2007; 1 m (cl 8.4 mm), 1 ovf (cl 8.1 mm) (MOUFPE 19487, cited in Almeida *et al*. 2013 as MZUESC 1520), Bahia, Baía de Todos os Santos, PROAMB, Poço Dom João, Station 12, 07.ix.2002; 6 m (cl 4.5–6.3 mm), 5 f (4.7–6.2 mm) (MOUFPE 19488), Bahia, Cairú, Ilha de Boipeba, 19.viii.2012, coll. A.O. Almeida, P.S. Santos & G.O. Soledade; 1 m (cl 6.8 mm), 1 f (cl 5.3 mm) (MOUFPE 19500, cited in Almeida *et al*. 2013 as MZUESC 1521), Bahia, Cairu, Ilha de Boipeba, Praia de

Tassimirim, 13°34'49.6"S 38°54'49.4"W, 19.v.2011, coll. A.O. Almeida, P.S. Santos & G.O. Soledade; 1 m (cl 7.2 mm), 1 f (cl 5.1 mm), 1 ovf (cl 8.5 mm) (MOUFPE 19490), Bahia, Cairu, Ilha de Boipeba, Praia de Moreré, 20.v.2011, coll. A.O. Almeida, P.S. Santos & G.O. Soledade; 1 m (cl 10.1 mm), 1 f (cl 10.8 mm) (MOUFPE 19491, cited in Almeida *et al*. 2013 as MZUESC 1522), Bahia, Itacaré, Contas River, 14.viii.2011, coll. G.O. Soledade; 1 ovf (cl 11.4 mm) (MOUFPE 19492, cited in Almeida *et al*. 2013 as MZUESC 1523), Bahia, Ilhéus, Malhado Beach, 07.viii.2012, coll. Almeida *et al*.; 1 f (cl 6.5 mm) (MOUFPE 19493), Bahia, Ilhéus, Cachoeira River, Av. Lomanto Jr., 28.viii.2012, coll. Almeida *et al*.; 1 ovf (cl 5.8 mm) (MOUFPE 19494), Bahia, Ilhéus, Cachoeira River, Praia da Maramata, 20.viii.2009, coll. Almeida *et al*.; 2 m (cl 10.1, 10.2 mm) (MOUFPE, 19495 cited in Almeida *et al*. 2013 as MZUESC 1524), São Paulo, Ilhabela, Engenho d'Água Beach, iii.2000 – ii.2002, coll. E.C. Mossolin.

Alpheus inopinatus Holthuis & Gottlieb, 1958. **Israel.** 1 m (cl 8.49 mm), 1 ovf (cl 5.3 mm) (RMNH.CRUS.D. 18314), Haifa, Tel Shikmona, Marine Fisheries Research Station, 15.x.1956; *topotype*, 2 m (cl 9.0, 9.2 mm) (one specimen used in genetic analysis), 6 ovf (cl 5.9–9.7 mm) (RMNH.CRUS.D. 18313), Haifa, Tantura, 03.v.1962, coll. A. Ben-Turia, E. Gilat & L.B. Holthuis; **Pakistan.** 4 m (cl 6.3–13.3 mm) (one specimen used in genetic analysis), 1 f (cl 8.3 mm) (NMNH 173981), west of Astola Island, 285 km west of Karachi, 27.xi.1963, coll. International Indian Ocean Expedition; 7 m (cl 9.6–15.7 mm), 2 f (cl 9.2, 11.6 mm), 2 ovf (cl 8.8, 10.2 mm) (RMNH.CRUS.D. 29945), Karachi, Manora Island, 01.i.1974-31.xii.1974, coll. S. Barkati; **India.** 1 ovf (cl 8.7 mm) (RMNH.CRUS.D. 16989), Mumbai, Maharashtra State, Ratnagiri, Marine Biological Research Station, 02.xii.1959, coll. K.N. Sankolli; 1 f (cl 9.0 mm)

(RMNH.CRUS.D. 16990), Mumbai, Maharashtra State, fishing village near Ratnagiri, 31.xii.1959, coll. K.N. Sankolli.

Alpheus lobidens De Haan, 1849 *sensu lato*. **Madagascar.** 1 m (6.8 mm) (specimen used in genetic analysis) (UF 14424), Nosy Be, west off point of Hellville, 13°25'09.7"S 48°15'37.9"E, NBE-1686, MGNW-24, 17.v.2008, coll. G. Bakary, H. Bruggemenn, F. Michonneau, G. Paulay & T. Werner; **Seychelles.** 3 m (cl 7.6–8.7 mm), 5 fov (cl 7.5–10.7 mm) (NMNH 173982), Aldabra Atoll, Lagoon, southeastern end of Ile Picard, 9°22'40.1"S 46°14'39.8"E, International Indian Ocean Expedition, R/V Anton Bruun, station HA-16, 03.xii.1964, coll. H.A. Fehlmann; **Saudi Arabia.** 1 m (cl 7.2 mm) (specimen used in genetic analysis) (UF 37050), Thuwal, King Abdullah University of Science and Technology, south beach, 22°17'31.7"N 39°05'24.0"E, BDJRS-2805, SAFA-027, iii..2013, coll. A. Anker, J. Moore & P. Norby; **India.** 1 m (cl 5.0 mm), 1 f (cl 4.0 mm), 1 fov (cl 7.1 mm) (NMNH 173979), Tamil Nadu, Mandapam Camp, Church Area, R/V Te Veja, 14.ii.1964, coll. J.S. Garth; **Thailand.** 2 m (cl 6.0, 6.8 mm) (NMNH 213629), Phuket Island, Fishery Station, Fifth Thai Danish Expedition, R/V Gallardo, 08.ii.1966; **China.** 1 m (cl 8.0 mm), 1 fov (cl 9.3 mm) (NMNH 173753), Guangdong, Hong Kong, Port Shelter, Rocky Bay, station 3 B, 19.v.1965, coll. A.J. Bruce; 1 m (cl 8.1 mm), 1 fov (cl 8.6 mm) (NMNH 173754), Guangdong, Hong Kong, Mirs Bay, Kat O Chau, station 11 B, 07.viii.1965, coll. A.J. Bruce; 1 m (cl 8.5 mm) (NMNH 173755), Guangdong, Hong Kong, Mirs Bay, Sha Taukah, Stirling Inlet, station 16B, 18.iv.1965, coll. D. Eggleston; **Philippines.** 1 fov (cl 10.6 mm) (NMNH 221999), Zambale, Luzon Island, Subic Bay, 14°45'00.0"N 120°12'00.0"E, Philippines Expedition, Albatross R/V, 07.i.1908, coll. United States Fish Commission; 1 m (cl 9.7 mm), 1 f (cl 9.5 mm) (NMNH 213628), Palawan, Cuyo Islands, San Carlos, 10°48'00.0"N 121°02'34.8"E, Smithsonian

Philippines Expedition, Sting Ray V R/V, station SP-11-3, 23.v.1978, coll. Smithsonian Oceanographic Sorting Center; **Australia**. 1 m (cl 9.8 mm), 1 fov (cl 10.1 mm) (specimen used in genetic analysis) (UF 19966), Northern Territory, Darwin area, Fannie Bay, Vesteys Beach near Northern Territory Museum, 12°26'13.0"S 130°49'56.0"E, AUS-165, Anker-092, 16.iii.2009, coll. A. Anker & C. Watson; 1 m (cl 7.4 mm), 1 fov (cl 7.6 mm) (UF 19972), Northern Territory, Darwin area, Fannie Bay, Vesteys Beach near Northern Territory Museum, 12°26'13.0"S 130°49'56.0"E, AUS-091, Anker-092, 16.iii.2009, coll. A. Anker & C. Watson; 1 m (cl 10.8 mm) (specimen used in genetic analysis) (UF 19984), Northern Territory, Darwin area, Fannie Bay, Vesteys Beach near Northern Territory Museum, 12°26'13.0"S 130°49'56.0"E, AUS-163, Anker-092, 16.iii.2009, coll. A. Anker & C. Watson; 1 m (cl 7.5 mm) (UF 16624), Queensland, Lizard Island, off Bird Island, 14°41'34.1"S 145°28'00.5"E, AUST-0151, AUST-ST-004, 8.ii.2009, coll. A. Anker & R. Lasley; 4 fov (cl 6.5–7.8 mm) (NMNH 123602), Queensland, Port Curtis, 26.i.1961, coll. J.M. Moulton; 2 m (cl 7.6, 8.2 mm) (NMNH 123602), west side of Facing Island, Curtis Harbor, Queensland, 26.i.1961, coll. J.M. Moulton; 1 m (cl 8.9 mm) (UF 18721), Queensland, Moreton Bay, south of Stradbroke Island, south of Dunwich, 27°30'14.7"S 153°24'20.5"E, AUS-046, AA-AUST-05, 12.iii.2009, coll. A. Anker & S. De Grave; 1 m (cl 8.5 mm), 1 fov (cl 8.9 mm) (UF 18722), Queensland, Moreton Bay, south of Stradbroke Island, south Dunwich, 27°30'14.7"S 153°24'20.5"E, AUS-047, AA-AUST-05, 12.iii.2009, coll. A. Anker & S. De Grave; 1m (cl 8.4 mm) (UF 18723), Queensland, Moreton Bay, south of Stradbroke Island, south Dunwich, 27°30'14.7"S 153°24'20.5"E, AUS-050, AA-AUST-05, 12.iii.2009, coll. A. Anker & S. De Grave; 1 f (cl 6.3 mm) (UF 27805), Western Australia, Ningaloo Reef, South Lefroy Bay, 15 km north of Ningaloo Station, 22°33'14.3"S 113°39'38.3"E, AUST-7281, NR10-026, 19.v.2010, coll. R. Lasley; 1 fov (cl 4.8 mm) (UF 27809), Western Australia, Ningaloo Reef, South Lefroy

Bay, 15 km north of Ningaloo Station, 22°33'14.3"S 113°39'38.3"E, AUST-7285, NR10-026, 19.v.2010, coll. R. Lasley; **Marshall Islands.** 1 m (cl 5.7 mm) (specimen used in genetic analysis), 1 f (cl 5.2 mm) (UF 13776), Majuro Atoll, Kolalen, channel (eastern end of the island), 7°09'28.5"N 171°12'51.8"E, FM-St-MAJ08-11, 8.iv.2008, coll. F. Michonneau & K. Sun; **Hawaii.** 1 f (cl 4.7 mm) (UF 8728), Hawaiian Islands, Oahu Island, Kaneohe Bay, Coconut Island, 21°26'07.0"N 157°47'19.6"W, BOAHU-112, GP-Loc-855, 28.ii.2006, coll. G. Paulay; 1 f (cl 4.5 mm) (UF 27342), Mariana Islands, Guam Island, 13°30'00.0"N 144°48'00.0"E, GUOK10-0306, GUOK10-St-AA04, 14.vi.2010, coll. A. Anker; 1 fov (cl 6.1 mm) (UF 27344), Mariana Islands, Guam Island, Agat, 13°30'00.0"N 144°48'00.0"E, GUOK10-0311, GUOK10-St-AA01, 13.vi.2010, coll. A. Anker; **French Polynesia.** 1 fov (cl 6.8 mm) (UF 15755), Society Islands, Moorea Island, off Nihimaru River estuary, 17°31'58.8"S 149°54'16.2"W, BMOO_3081, MIB_069, 18.x.2008, coll. A. Anker; 1 m (cl 7.1 mm) (specimen used in genetic analysis) (UF 15757), Society Islands, Moorea Island, off Nihimaru River estuary, 17°31'58.8"S 149°54'16.2"W, BMOO_3083, MIB_069, 18.x.2008, coll. A. Anker; 1 f (cl 4.4 mm) (UF 15768), Society Islands, Moorea Island, off Nihimaru river estuary, 17°31'58.8"S 149°54'16.2"W, BMOO_3222, MIB_069, 18.x.2008, coll. A. Anker; 1 fov (cl 5.9 mm) (UF 15851), Society Islands, Moorea Island, Afareaitu, Paorea Point, 17°32'55.0"S 149°47'04.9"W, BMOO_3519, MIB_076, 19.x.2008, coll. J. Poupin.

Alpheus lobidens polynesica Banner & Banner, 1974. **Hawaii.** *Paratypes*, 1 m (cl 6.6 mm), 1 f (cl 6.6 mm) (NMNH 155375), Oahu Island, Kaneohe Bay, 21°26'23"N 157°48'29"W, station BH-4.

Redescription (based on material from Shimabara, Nagasaki, Japan, RMNH PEG 25134). Carapace smooth, free of teeth or tubercles on midline, laterally not compressed (Fig. 2*B*); rostrum triangular, with acute tip reaching approximately mid-length of first article of antennular peduncle (Fig. 2*A*); rostral carina sharply delimited between orbital hoods, extending to posterior margin of orbital hoods, not broadening posteriorly (Fig. 2*A*); adrostral furrows moderately deep, not abruptly delimited posteriorly (Fig. 2*A*); orbital hoods inflated dorsally, distally rounded, unarmed (Fig. 2*A*); pterygostomial angle rounded (Fig. 2*B*); cardiac notch well-developed.

Eyes totally concealed in lateral, dorsal, and frontal views; cornea well-developed, rounded (Fig. 2*A*, *B*); ocellar beak protruding dorsally between eyes, apically rounded (Fig. 2*B*); antennular peduncle moderately slender (Fig. 2*A*); stylocerite distally acute, reaching distal margin of first article of antennular peduncle (Fig. 2*A*); ventromesial carina of first article with triangular tooth, distal margin concave and acute (Fig. 2*C*); visible part of first article as long as wide; second article longest, two times as long as wide; third article as long as wide, 0.4 times length of second article (Fig. 2*A*); lateral antennular flagellum with row of aesthetascs starting at 15th article, antenna with basicerite armed with robust acute distolateral tooth (Fig. 2*B*); carpocerite stout, reaching distinctly beyond end of antennular peduncle and tip of distolateral tooth of scaphocerite (Fig. 2*B*); scaphocerite with lateral margin slightly concave; blade broad, separated from distolateral tooth by deep cleft running about 1/3 length of blade (Fig. 2*A*); distolateral tooth well-developed, clearly overreaching distal margin of blade and end of antennular peduncle (Fig. 2*A*, *B*).

Mandible with 2-segmented palp; simple setae on all segments; apical setae longer; molar and incisor processes well-developed; incisor process with 9 teeth on both mandibles; fifth tooth is the largest one; molar process subdivided in 3 cusps: less-developed and broadened cusp flanked by two more developed cusps (Fig. 2*D*). First maxilla with coxa with scattered setae; 2 rows of spiniform setae at apical area; ventral surface with few setae; dorsal surface of basis with many setae, scattered at base and more numerous on apex; endopod bilobated; medial lobe with spiniform seta projected forward (Fig. 2*E*). Basis of second maxilla with two well-developed endites bearing numerous simple setae on apex; endopod unsegmented, about half the length of scaphognathite; scaphognathite well-developed, with setae all around edge (Fig. 2*F*). Basis and coxa of first maxilliped with numerous simple setae at external edge, invading dorsal side; endopod slightly exceeding the distal margin of exopodal lobe, exopod with numerous simple setae at apex (Fig. 2*G*). Second maxilliped with endopod with five segments; propodus and dactylus strongly expanded, with numerous setae at edge directed posteriorly covering mouth appendages; exopod with flagellum similar to flagellum of first maxilliped, with simple setae on apex (Fig. 2*H*). Third maxilliped relatively thin, noticeably longer than antennular peduncle and carpocerite when extended; lateral plate with subacute tip; ischium and merus fused, narrow, flat, showing few setae; carpus with about three times length of ischium and merus, smooth lateral margin, with few setae; propodus and dactylus fused with smooth lateral margin, with several bands of setae; exopod reaching beyond distal margin of carpus, with long and flexible setae on posterior margin (Fig. 2*I*).

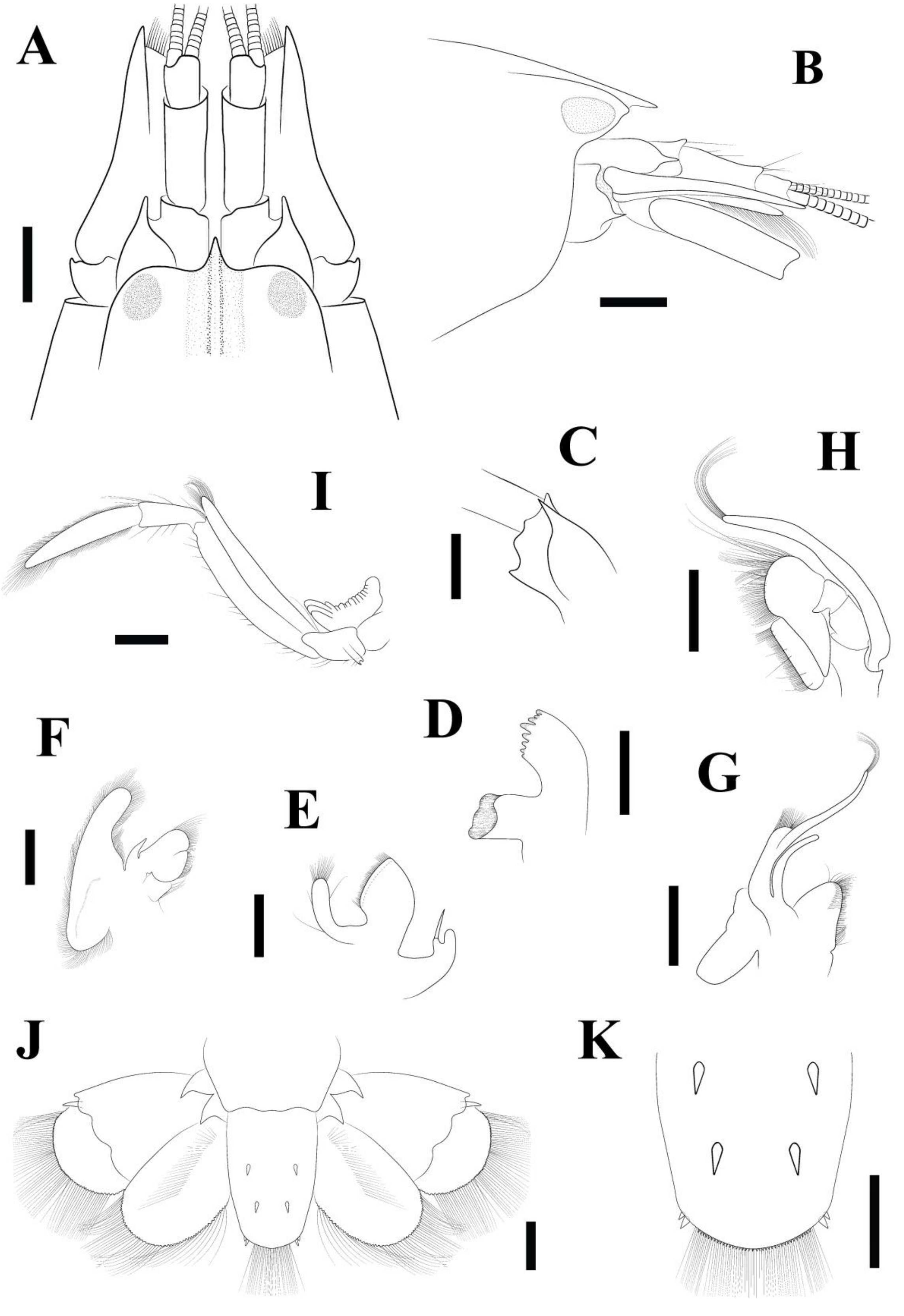

Figure 2. *Alpheus lobidens* De Haan, 1849, male, Ariake Bay Coast, Shimabara, Nagasaki, Japan, RMNH PEG 25134, topotype. (A) frontal region and cephalic appendages, dorsal view; (B) same, lateral view; (C) tooth on ventromesial carina of first

article of antennular peduncle, lateral view; (D) mandible, lateral 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; (K) detail of telson, dorsal view. Scale bars: A, B, D–J, 1 mm; C, K, 0.5 mm.

Major male cheliped with short, stout ischium; merus slightly excavated ventrally; ventrolateral margin straight, with blunt distal end; ventromesial margin also straight, ending in strong tooth distally (Fig. 3*A*, *C*); carpus short, cup-shaped (Fig. 3*A*–*C*); chela somewhat compressed; fingers closing in same plane as palm; palm with dorsal and ventral margins convex, with broad transverse grooves; dorsal and ventral grooves extending to mesial and lateral surfaces as deep depressions, latter extending posteriorly; dorsal shoulder rounded, slightly overhanging groove; ventral groove broad, oblique, deep, also extending mesially and laterally as well-delimited deep depressions, latter not extending posteriorly; ventral shoulder rounded, slightly protruding; lateral and mesial surfaces mostly smooth; *linea impressa* well-marked; mesial surface ending bluntly distally (Fig. 3*A*, *B*); fingers compressed, less than half palm length (Fig. 3*A*, *B*); pollex with tip curved upward, with V-shaped notch on cutting edge anterior to deep fossa; proximal mesial surface surrounding fossa forming obtuse angle, fringed with rows of setae; dactylus overreaching slightly beyond pollex, with rounded tip, cutting edge with stout plunger (Fig. 3*A*, *B*, *D*); adhesive disks conspicuous (Fig. 3*B*, *D*). Female major cheliped similar in shape, but proportionally smaller than that of male.

Minor male cheliped with ischium short and stout (Fig. 3*E*, *F*); merus proportionally longer than that of major cheliped, slightly excavated ventrally (Fig. 3*E*, *F*); ventrolateral and ventromesial margins as in major cheliped; tooth on distal portion of ventromesial margin generally smaller than that of major cheliped; carpus short, cup-shaped (Fig. 3*E*, *F*); chela roughly cylindrical in transverse section; palm sculpturing resembling that of major cheliped, with dorsal and ventral margins slightly convex, with transverse grooves (Fig. 3*E*, *F*); dorsal and ventral grooves also extend to mesial and lateral surfaces as deep depressions, latter extending posteriorly; dorsal shoulder rounded, not overhanging groove; ventral groove not as broad and deep as that of major cheliped; ventral shoulder rounded, not protruding; lateral and mesial surfaces mostly smooth; *linea impressa* well-marked; dorsomesial angle of palm with blunt tooth (Fig. 3*E*); fingers as long as palm, with conspicuous rows of balaeniceps setae, cutting edges sharp, tip curved (Fig. 3*E*, *F*); dactylus expanded laterally, with dorsal disk similar to adhesive disk of dactylus of major cheliped, and conspicuous carina on proximal region (Fig. 3*F*); female minor cheliped slenderer than that of males; palm inconspicuously sculptured; dorsal and ventral grooves absent; *linea impressa* weakly marked (Fig. 3*G*, *H*); fingers as long as palm, without balaeniceps setae, cutting edges blade-like, tip curved (Fig. 3*G*, *H*); dactylus not expanded laterally, without proximal carina on dorsal margin, but with inconspicuously marked disk, similar to that of male minor chela (Fig. 3*G*, *H*).

Second pereiopod slender, ischium and merus subequal in length; carpus five-segmented, first segment longest; segment ratio (proximal to distal) subequal to 4: 2.5: 1: 1: 2; chela simple, fingers slightly longer than palm and bearing tufts of curved setae distally (Fig. 3*I*). Third and fourth pereiopods similar in shape and length, both with ischium armed with spiniform seta on ventrolateral surface (Fig. 3*J*, *K*); merus longer than propodus, about four times as long as wide, distoventral margin unarmed; carpus unarmed, about half of merus length and slightly shorter than propodus length (Fig. 3*J*, *K*); propodus with about 10 strong spiniform setae along ventral margin, plus one distal pair of spiniform setae near dactylus; dactylus around 2.2 propodus length, simple, conical, slightly curved, acute distally (Fig. 3*J*, *K*). Fifth pereiopod with ischium and merus unarmed; merus slender, about six times as long as wide; carpus about 3/4 merus length (Fig. 3*L*); propodus slightly longer than carpus, with six spiniform setae along ventral margin plus one distal pair of spiniform setae near dactylus; distolateral surface with cleaning brush consisting of about 16 transverse rows of short setae; dactylus similar in shape to that of third and four pereiopods, proportionally slightly longer, corresponding to almost 3 times propodus length (Fig. 3*L*).

Abdominal segments smooth, glabrous; ventral and posterior margins of pleurae 1–4 broadly rounded and pleura 5 forming angle of approximately 90° with rounded tip; sixth pleura without articulated plate; protopod pleopods free of spines; male pleopod 2 with *appendix masculina* slightly shorter than *appendix interna*; preanal plate with rounded tip.

Telson broad, tapering distally, approximately 1.2 times as long as wide at base (Fig 2*J*); lateral margins slightly sinuous; dorsal surface slightly convex, without median groove, with two pairs of spiniform setae inserted at some distance from lateral margins, first pair slightly anterior to mid-length, second pair conspicuously posterior to telson mid-length (Fig. 2*J*, *K*); posterior margin broadly rounded, fringed with spinules (short spiniform setae) and long setae, posterolateral angle each with two pairs of spiniform setae, lateral seta approximately 1/2 length of mesial seta (Fig. 2*J*, *K*); anal tubercles well-developed.

Uropods with bifid protopods, each lobe ending in acute tooth (Fig. 2*J*); exopod slightly longer than endopod; distolateral spiniform setae slender, distinctly shorter than posterior margin of exopods, not pigmented; exopodal diaeresis with two slightly lobes separated by median notch; distolateral tooth acute, approximately 1/2 length of distolateral spiniform seta (Fig. 2*J*).

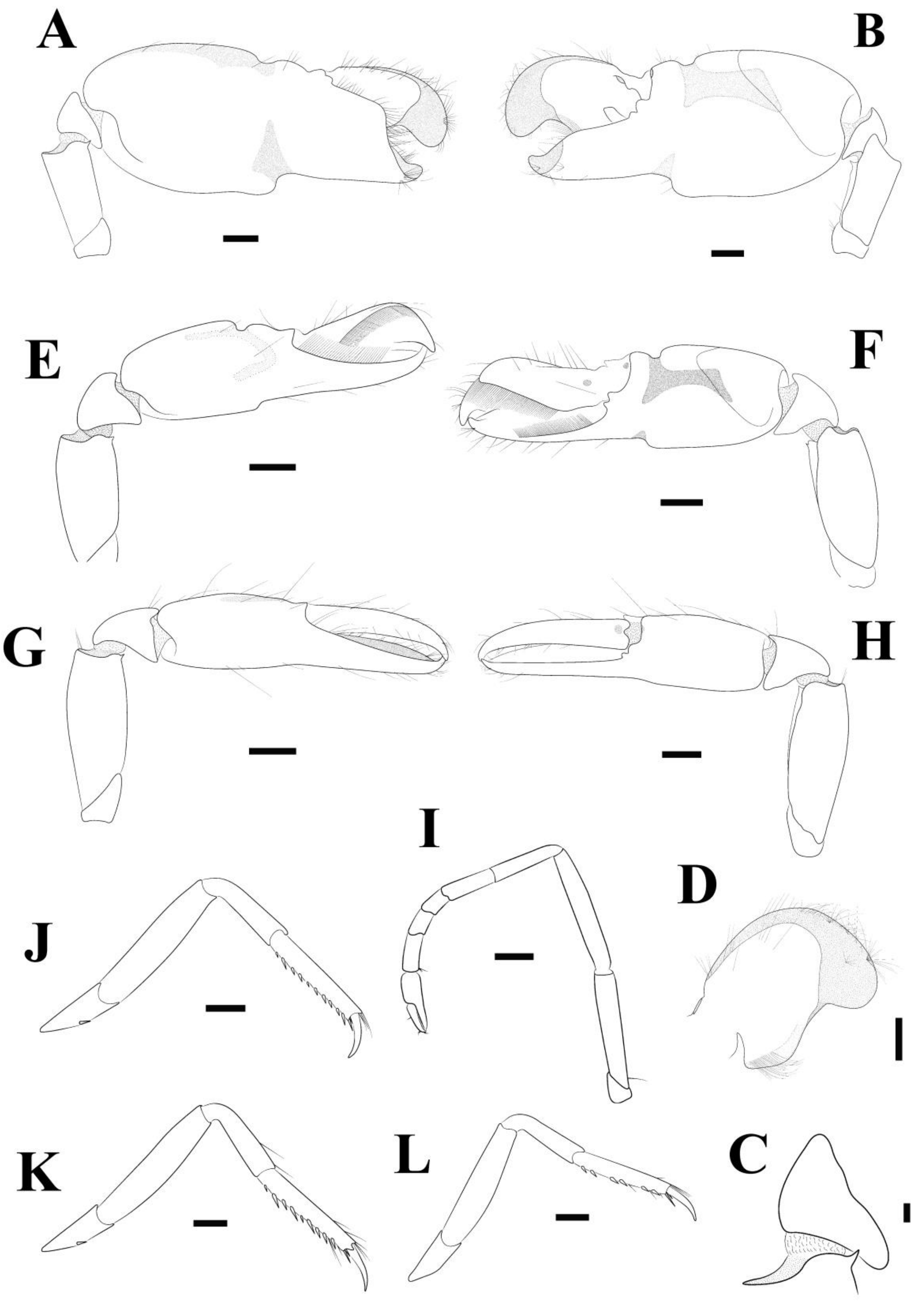

Figure 3. *Alpheus lobidens* De Haan, 1849, male (A–F, I–L) and female (G, H) from Ariake Bay Coast, Shimabara, Nagasaki, Japan, RMNH PEG 25134, topotype. (A) major cheliped, mesial view; (B) same, lateral view; (C) detail of major cheliped merus, mesial

view; (D) major cheliped dactylus, lateral view; (E) minor male cheliped, mesial view; (F) same, lateral view; (G) minor female cheliped, mesial view; (H) same, lateral view; (I) second pereiopod, lateral view; (J) third pereiopod, lateral view; (K) fourth pereiopod, lateral view; (L) fifth pereiopod, lateral view. Scale bars: A, B, E–L, 1 mm; C, D, 0.5 mm.

Morphological variation. Minor cheliped slenderer and palm less conspicuously sculptured in females than in males (Fig. 3*G*, *H*). The distal tooth of the ventromesial margin of the minor chelae merus is usually well-developed; however, sometimes it may be less developed in both sexes.

Distribution. Japan — Nagasaki (De Haan 1849; present study).

Genetic data

The Bayesian analysis performed with the 16S gene recovered a very well-supported phylogeny (Fig. 4). *Alpheus lobidens sensu stricto* (topotype from Japan) is clearly separated of *A. lobidens sensu lato* (from Australia, French Polynesia and Marshall Islands), *A. buckupi*, and *A. inopinatus*.

A considerable genetic divergence (p-distance), ranging from 12% to 19%, was observed between *A. lobidens sensu stricto* (topotype from Japan), *A. lobidens sensu lato*, *A. buckupi* and *A. inopinatus*: the highest values were observed between *A. lobidens sensu stricto* and *A. buckupi*, and between *A. lobidens sensu stricto* and *A. lobidens sensu lato* from Australia (Northern Territory). The lowest divergence was observed between *A. lobidens sensu stricto* and *A. lobidens sensu lato* from Marshall Islands. The divergence between *A. lobidens sensu stricto* and other species of *Alpheus* (*A. lobidens sensu lato*, *A. buckupi* and *A. inopinatus* excluded) ranged from 16% (*A. estuariensis* Christoffersen, 1984 and *A. heterochaelis* Say, 1818) to 22% (*A. angulosus* McClure, 2002).

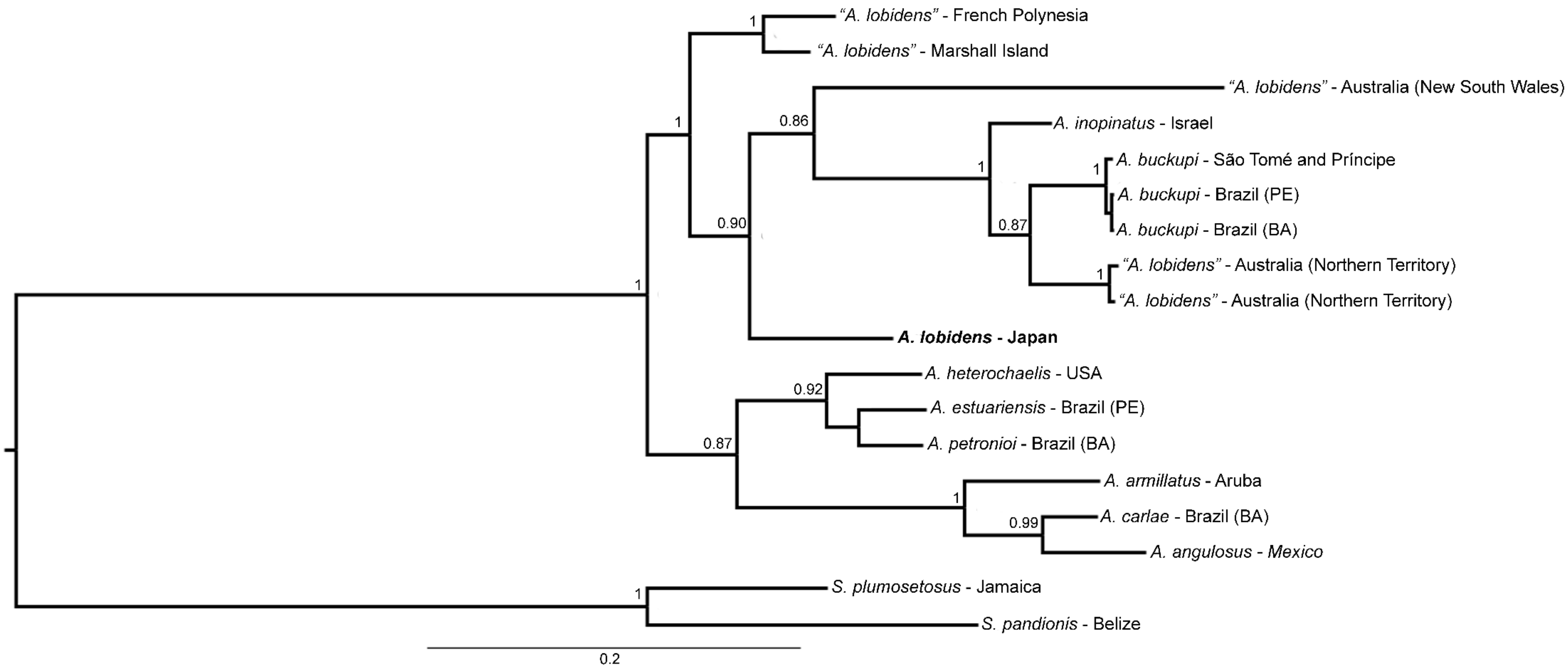

Figure 4. Bayesian tree of *Alpheus lobidens sensu stricto* (bold), *Alpheus lobidens sensu lato* (" ") and other species of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888, based on 16S DNA sequence data. Numbers next to the nodes represent posterior probabilities. Probabilities <80% are not shown. Locality abbreviations: PA, Pará; PE, Pernambuco; BA, Bahia.

Discussion

Alpheus lobidens sensu stricto can be distinguished from *A. lobidens sensu lato* by the rostrum reaching mid-length of first article of antennular peduncle [*vs*. not reaching or exceeding mid-length of the first article of antennular peduncle in *A. lobidens sensu lato*]; ventromesial carina of the first article of antennular peduncle with triangular tooth, distal margin concave and acute in *A. lobidens sensu stricto* [*vs*. tooth ending rounded, anterior margin slightly concave in *A. lobidens sensu lato*]; exopod of third maxilliped reaching beyond distal margin of carpus in *A. lobidens sensu stricto* [*vs*. reaching half of carpus length in *A. lobidens sensu lato*].

Banner & Banner (1974) described *A. lobidens polynesica* based on individuals from Hawaii whose minor cheliped palm notches were absent or inconspicuous. However, in our analysis, absent or inconspicuous notches were also observed in individuals of *A. lobidens sensu lato* from the Indo-Western Pacific. In fact, we observed a high variation on the sculpturing of the minor chela in *A. lobidens sensu lato*, probably due to the diversity of source localities and the high number of individuals analyzed here resulted. Thus, we recommend that *A. lobidens polynesica* should be included in *A. lobidens sensu lato* until a complete review of the *A. lobidens* complex is accomplished (see Table 2).

Table 2. Current taxonomic status of species related to *Alpheus lobidens* De Haan, 1849

Species	**Status**	**Reference**
Alpheus buckupi Almeida, Terossi, Araújo-Silva & Mantelatto	Valid	Present study
Alpheus crassimanus Heller, 1865	Treated as *A. lobidens sensu lato* by Anker & De Grave (2016); status unknown	Anker & De Grave (2016)
Alpheus inopinatus Holthuis & Gottlieb, 1958	Valid	Present study
Alpheus lobidens polynesica Banner & Banner, 1974	Included in *Alpheus lobidens sensu lato*; status remain unknown	Anker & De Grave (2016); present study
Alpheus strenuus Dana, 1852	Species complex	Anker (2001); Anker & De Grave (2016)

Alpheus lobidens sensu stricto is morphologically similar to *A. inopinatus* and *A. buckupi*, especially regarding the configuration of the major and minor chelipeds. However, *A. lobidens* differs from *A. inopinatus* by the short term stylocerite 0.4 times wider than long (Fig. 5*A*) [*vs*. 0.5 times longer than wide in *A. inopinatus* (Fig. 5*C*)]; by the presence of a distal tooth on the ventromesial margin of the major (Fig. 6*A*, *B*) and minor cheliped merus (Fig. 7*A*, *B*) [absent in *A. inopinatus* (Figs. 6*C*, *D*; 7*C*, *D*)]; by the palm of major cheliped 1.8 times longer than wide (Fig. 6*A*, *B*) [*vs*. 1.5 times longer than wide in *A. inopinatus* (Fig. 6*C*, *D*)]; by the palm of minor cheliped 1.4 times longer than wide (Fig. 7*A*, *B*) [*vs*. 1.2 times longer than wide in *A. inopinatus* (Fig. 7*C*, *D*)]; by the less setose palm and fingers of the minor cheliped (Fig. 7*A*, *B*) [*vs*. very setose in *A. inopinatus* (Fig. 7*C*, *D*)]; and by the presence of a transverse U-shaped groove on the palm of the male minor chela (Fig. 7*A*, *B*) [*vs*. absent in *A. inopinatus* (Fig. 7*C*, *D*)]. The significant genetic divergence between the specimen of *A. lobidens sensu stricto* from Japan and the specimen of *A. inopinatus* from Israel, plus the morphological differences described above, clearly support the validity of *A. inopinatus* (see Table 2).

Alpheus lobidens sensu stricto differs from *A. buckupi* by having shallower adrostral furrows (Fig. 5*A*) [*vs*. deeper adrostral furrows in *A. buckupi* (Fig. 5*C*)]; ventromesial carena of the first antennular article with a small triangular tooth on the ventromesial surface in the shape of a shark fin (Fig. 2*C*) [*vs*. triangular tooth with rounded end in *A. buckupi*; see Almeida *et al*. 2013, p. 442, fig. 1*D*]; by the more rounded distal tip of the pollex and dactylus (Fig. 6*A*, *B*) [*vs*. distal tip of the pollex and dactylus acute in *A. buckupi* (Fig. 6*E*, *F*)]; and by the more curved and less developed plunger (Fig. 3*D*) [*vs*. stout plunger in *A. buckupi*; see Almeida *et al*. 2013, p. 443, fig. 2*H*].

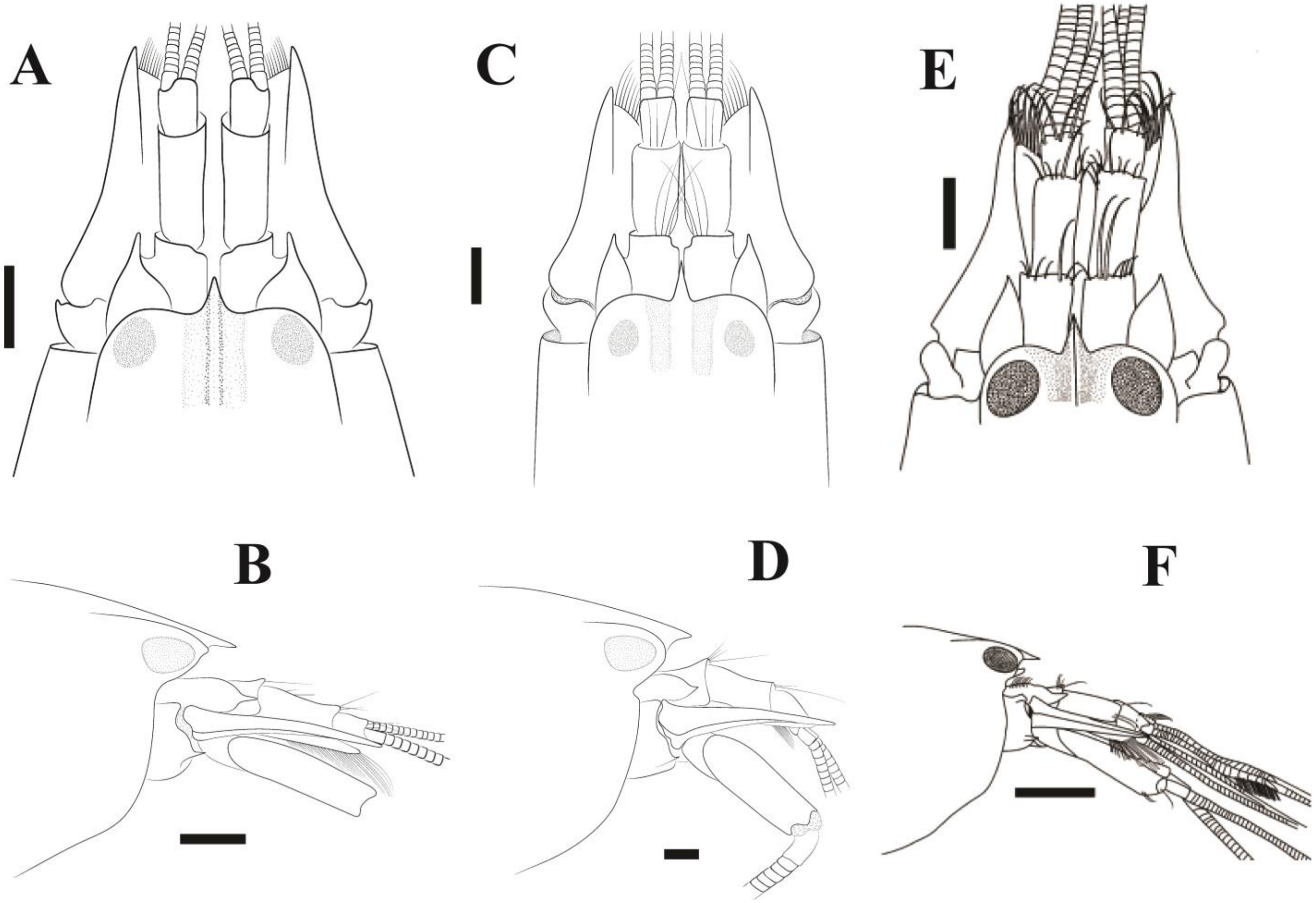

Figure 5. Frontal region and cephalic appendages, dorsal view (A, C, E) and lateral view (B, D, F): (A–B) *Alpheus lobidens* De Haan, 1849, male (RMNH PEG 25134), topotype; (C–D) *Alpheus inopinatus* Holthuis & Gottlieb, 1958, male (RMNH.CRUS.D. 18313); (E–F) *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013, male (MZUSP 27548) [from Almeida *et al*. 2013, Fig. 1A, C]. Scale bars = 1 mm.

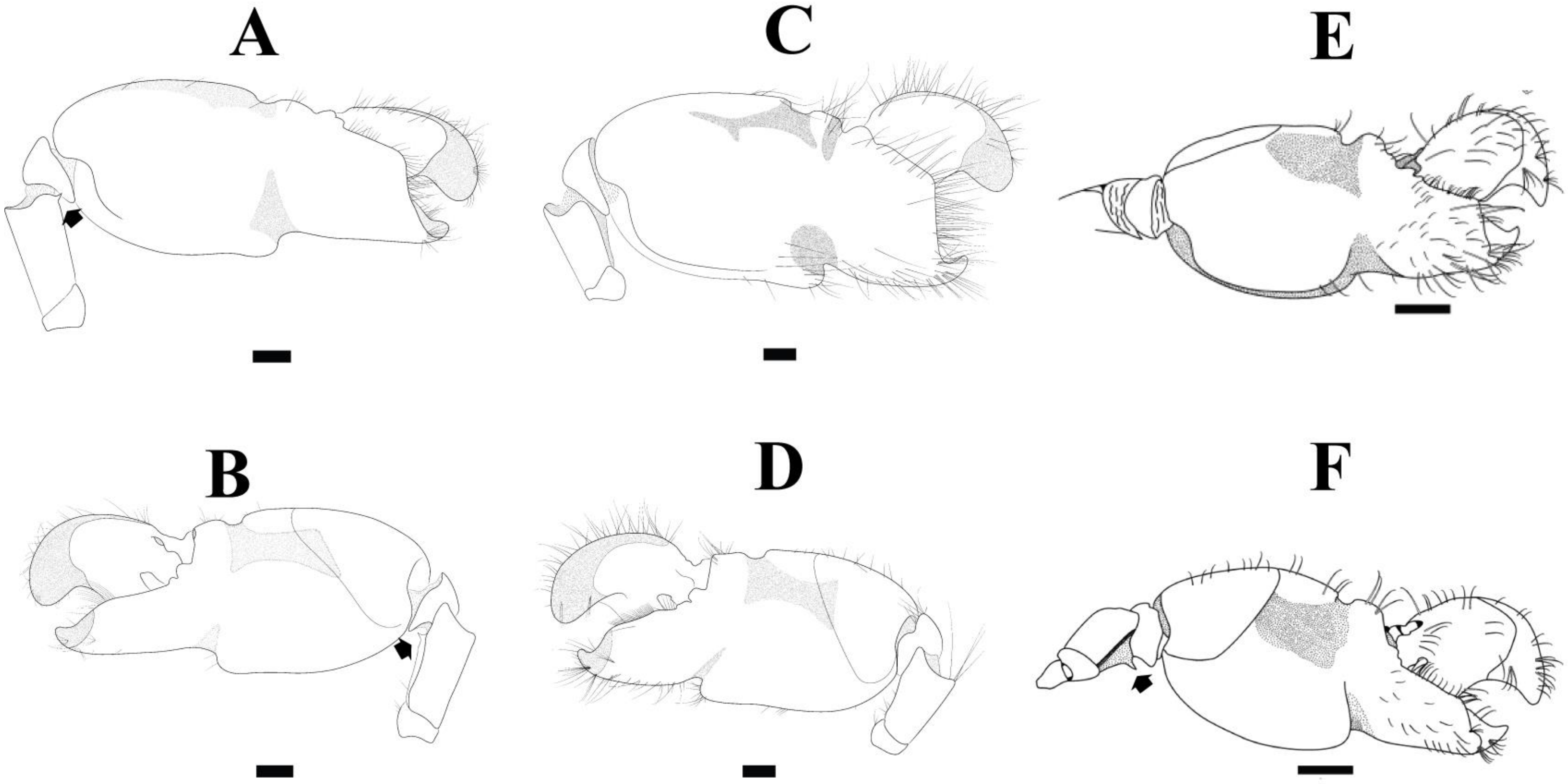

Figure 6. Major cheliped, mesial view (A, C, E) and lateral view (B, D, F): (A–B) *Alpheus lobidens* De Haan, 1849, male (RMNH PEG 25134), topotype; (C–D) *Alpheus inopinatus* Holthuis & Gottlieb, 1958, male (RMNH.CRUS.D. 18313); (E–F) *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013, male (MZUSP 27548) [see Almeida *et al*. 2013, Fig. 2A, B]. Arrows indicate tooth on ventrolateral margin of merus Scale bars = 1 mm.

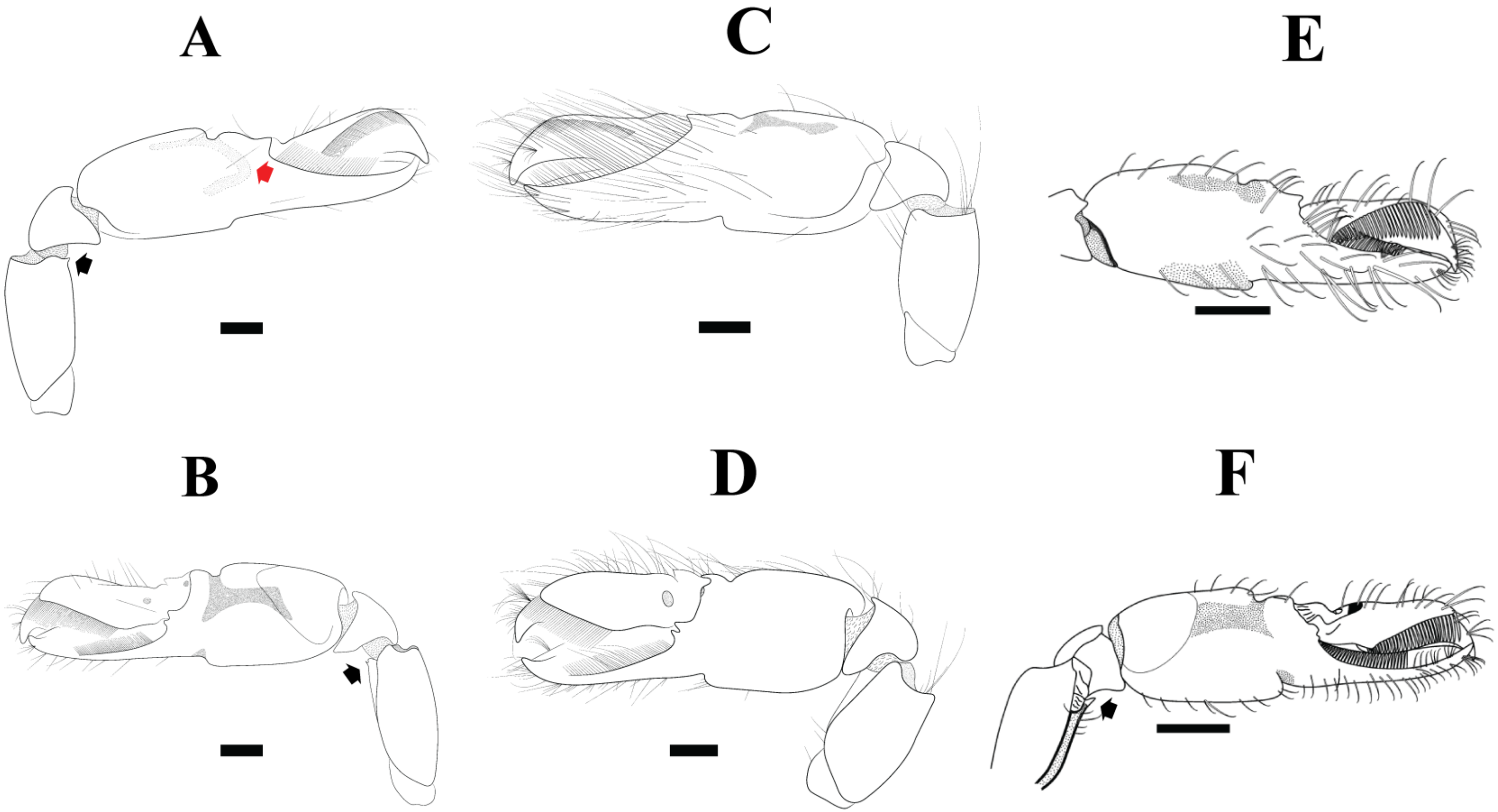

Figure 7. Minor cheliped, mesial view (A, C, E) and lateral view (B, D, F): (A–B) *Alpheus lobidens* De Haan, 1849, male (RMNH PEG 25134); (C–D) *Alpheus inopinatus* Holthuis & Gottlieb, 1958, male (RMNH.CRUS.D. 18313); (E–F) *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013, male (MZUSP 27548) [see Almeida *et al*. 2013, Fig. 2E, F]. Black arrows indicate tooth on ventrolateral margin of merus; red arrow indicates transverse U-shaped groove on palm. Scale bars = 1 mm.

The V-shaped notch on the cutting edge of the pollex and the degree of development of the distal tooth on the ventromesial margin of major and minor chelipeds were suggested by Almeida *et al*. (2013) as a means to differentiate *A. buckupi* and *A.* cf. *lobidens* from Australia (here regarded as *A. lobidens sensu lato* based on genetic analyses). In this study, these characters were not informative because their degree of development varied in *A. buckupi* and in *A. lobidens sensu lato*. Nevertheless, despite the high morphological similarity between these species, there are morphological characters that allow their distinction (see Table 2).

The phylogenetic reconstruction showed a clear separation between *A. lobidens sensu stricto* from Japan (topotypes) and the specimens previously identified as *A. lobidens* (Fig. 4). Consequently, the occurrence of *A. lobidens sensu stricto* is, to date, restricted to the type locality in Japan. Our analysis recovered other lineages of *A. lobidens sensu lato* and indicated a considerable genetic divergence between them. This observation confirms the hypothesis, previously raised in the literature (Anker 2001; Anker & De Grave 2016), that the taxonomic entity recognized as *A. lobidens* is, in fact, a complex of cryptic species. It is worth mentioning that the specimens previously identified as *A. lobidens* do not group in a single clade. Instead, in the tree they appear closely related with *A. buckupi* and *A. inopinatus*, demonstrating that the current diversity of this group is still far from being well-known.

To conclude, it is possible to state that the morphological and genetic data analyzed here allowed the delimitation of *A. lobidens sensu stricto*. This definition is relevant since the name *A. lobidens* has been applied to cryptic species, which obviously resulted in a high taxonomic confusion. Most of the previous records of *A. lobidens* should be treated with caution, since they may correspond to *A. lobidens sensu stricto, A. lobidens sensu lato, A. inopinatus* or *A. buckupi*. In addition, it is necessary to evaluate the morphological and molecular diversity within *A. lobidens sensu lato*, given that, apparently, there were several undescribed species among the specimens studied here, and their taxonomic status should be elucidated.

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ARTIGO II: A ser encaminhado à revista Journal of Crustacean Biology

3 Multiple lineages and cryptic speciation in *Alpheus lobidens sensu lato* (Decapoda: Alpheidae) revealed by molecular diversity

Running title: Genetic diversity of *Alpheus lobidens sensu lato*

ABSTRACT

The complex of species related to *Alpheus lobidens sensu lato* is one of the groups most common and widespread snapping shrimps in the Indo-West Pacific, that presents a wide range of morphological variations. Moreover, little is known about the species that compose it and their phylogenetic relationships. Therefore, the objective of the present study was to investigate the phylogenetic relationships between individuals of *A. lobidens sensu lato*, throughout their geographical distribution in the Indo-West Pacific and to verify whether these are supported by morphological characteristics. The material analyzed was obtained by loans from national and international crustacean collections. Molecular data were obtained through protocols the amplification and sequencing of 16S mtDNA, from nine individuals from *A. lobidens,* three from *A. buckupi*, one from *A. inopinatus* and eight individuals from other species of Alpheidae. The genetic analyzes (p-distance and Bayesian Inference) suggest considerable genetic divergence the existence in at least six lineages of *A. lobidens sensu lato*. Other species of *Alpheus* were positioned among the lineages of *A. lobidens sensu lato,* demonstrating that *A. lobidens sensu lato* does not form a monophyletic group. The morphological characters analyzed do not allow the lineages of *A. lobidens sensu lato* to be separated into isolated species. However, the high rates of intraspecific molecular divergence, associated to ocean currents, suggests a limited gene flow between these lineages, leaving no doubt as to the

validity of themselves. It is possible that such morphological differences exist, but they were not detected by traditional taxonomic methods. New studies applying more sensitive methods to detect structural differences, such as geometric morphometry and scanning electron microscopy image could help to define the species of this complex.

Key Words: Caridea, cryptic species, Pacific Ocean, snapping shrimp, 16S mtDNA.

INTRODUCTION

Accentuated intraspecific morphological differences may be the result of genetic divergence between individuals and/or phenotypic plasticity, being the basic elements of speciation (Ridley, 2006). However, some species accumulate genetic differences without consistent morphological divergence, being called cryptic species (Mathews *et al.*, 2002). Cryptic speciation is very common in all metazoan taxa, reflecting both limitations of applied taxonomy and divergence in habitat, life history, and chemical recognition systems without phenotypic disparity (Knowlton, 1986; Bickford *et al.*, 2007; Heethoff, 2018; Struck *et al.*, 2018)

Several investigations have demonstrated the existence of many cryptic lineages in the Alpheidae Rafinesque, 1815, mainly in the genera *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888, suggesting that they hide a high cryptic biodiversity, which has not yet been fully understood (Williams *et al.*, 2001; Mathews, 2006; Mathews & Anker, 2009; Hultgren *et al.*, 2014; Hultgren & Brandt, 2015). One such case that needs review is that of *Alpheus lobidens* De Haan, 1849. This species occurs in the Indo-West Pacific, from the Red Sea and South Africa to Japan, Australia, Hawaii and Eastern and Western Mediterranean (Anker, 2001; Yang & Anker, 2003; Anker & De Grave, 2016) and occupy a wide range of habitats, occurring under rocks, coral rubble and in burrows on sand and mud bottoms, from the intertidal to 10 m of depth (Anker, 2001; Anker & De Grave, 2016).

Moreover, this species has high morphological variability, which supports its separation in the subspecies *A. lobidens lobidens* and *A. lobidens polynesica* (Banner & Banner, 1974), what results in taxonomic doubts/misidentification mainly when compared to *Alpheus inopinatus* Holthuis & Gottlieb, 1958 (for more details see Cunha *et al*., 2020). Considering this, for a long time, the taxonomic identity of *A. lobidens* and its geographical distribution was doubtful.

Thus, Cunha *et al*. (2020) delimited and redescribed *A. lobidens sensu* De Haan, 1849, based on morphological and molecular data. Additionally, *A. lobidens sensu* De Haan, 1849 was compared with morphological similar species, *A. inopinatus* and *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013. Furthermore, *A. lobidens* from Japan (topotype) and sequences obtained from other localities were genetically different. Thus, *A. lobidens sensu* De Haan, 1849 became restricted to Japan and the other three recovered strains were treated as *A. lobidens sensu lato* (Cunha *et al*., 2020).

However, Cunha *et al*., 2020 were unable to describe all the diversity present in *A. lobidens sensu lato*. Other important points of the geographical distribution previously reported for *A. lobidens* needed to be analyzed, since they could produce/discover new strains. Thus, the objective of the present study was to investigate the phylogenetic relationships between individuals of *A. lobidens sensu lato*, throughout their geographical distribution in the Indo-West Pacific and to verify whether these are supported by morphological characteristics.

MATERIAL AND METHODS

The dataset generated by Cunha *et al*. (2020) was used in this study. Additionally, three specimens of *A. lobidens sensu lato* according to Cunha *et al.* (2020) were obtained from the following collections: National Museum of Natural History, Smithsonian Institution, Washington DC, USA (NMNH) and Florida Museum of Natural History, University of Florida, Gainesville, USA (UF) (Table 1). Molecular analyzes were performed at the Laboratory of Carcinology, Federal University of Rio Grande do Sul (UFRGS). Tissue extraction, PCR amplification, product cleaning and sequencing were conducted following protocols described by Cunha *et al*. (2020). All sequences were confirmed by sequencing both filaments (foward and reverse directions). Parts not readable at the beginning of the sequences were omitted. All generated sequences were submitted to GenBank.

Specimens of *A. lobidens sensu lato* from nine localities (three from the Indian Ocean, three from Pacific Ocean and one from Red Sea, Mediterranean Sea and Timor Sea) (Table 1) were used to assess the genetic data. In addition, we used ten specimens from eight other species of *Alpheus* Fabricius, 1798, as sister group, to compare the genetic divergence among *A. lobidens sensu lato* and congeners (Table 1). Two additional sequences of *Synalpheus* Spence Bate, 1888 were used as out-groups according to the phylogenetic relationship proposed by Anker *et al*. (2006). The sequences were aligned with MUSCLE (Edgar, 2004), with standard configurations, using the *Cyberinfrastructure for Phylogenetic Research* (CIPRES) website (Miller *et al*., 2010). Alignment of the 16S mtDNA sequences consisted of 552 base pairs. The best replacement model was selected according to the Bayesian Information Criterion (BIC), among the 88 alternatives available by the jModelTest program (version 2.1.4) (Darriba *et al*., 2012).

The Bayesian inference was performed using the program MRBayes (version 3.2.2) (Ronquist *et al*., 2012) implemented in the CIPRES with the parameters obtained in jModelTest (model TPM3uf + G with nucleotide frequencies A = 0.2852, C = 0.1028, G = 0.2457, T = 0.36663, substitution rates AC = 0.1693, AG = 6.2075, AT = 1, CG = 0.1693, CT = 6.2075, GT = 1, and gamma distribution = 0.20). In the analysis, we sampled one tree every 1000 generations of 20,000,000 generations, starting with a random tree. The convergence of the parameters and probabilities of the races were verified in the Tracer 1.6.0 program (Rambaut *et al*., 2014). To summarize the later distribution, the maximum credibility tree was retrieved from the total of subsequent trees and the support values from the tree annotated in the treeAnnotator program 1.8.2 (Drummond *et al*., 2012). Of the total trees (and parameters), the first 15% of the races were discarded (burn-in). *A posteriori* probability values higher than 60% were reported. The matrix of genetic divergences was calculated based on the p distance using MEGA v5 (Tamura *et al*., 2011).

According to the phylogenetic relationships based on molecular data proposed by Cunha *et al*. (2020) and this study, were analyzed only adult morphological characters to verify the morphological support for the clades obtained.

Table 1. List of specimens used in the genetic analysis. CCDB: Crustacean Collection of the Department of Biology, Faculty of Philosophy, Sciences and Letters of Ribeirão Preto, University of São Paulo, Ribeirão Preto, Brazil; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MOUFPE: Museu de Oceanografia Prof. Petrônio Alves Coelho, Universidade Federal de Pernambuco; NMNH: National Museum of Natural History, Smithsonian Institution, Washington DC, USA; NMV: Museum Victoria, Melbourne, Australia; OUMNH: Oxford University Museum of Natural History, Oxford, United Kingdom; RMNH: Netherlands Center for Biodiversity Naturalis, Leiden, The Netherlands; UF: Florida Museum of Natural History, Gainesville, USA.

Species	**Locality**	**Catalogue Number**	**GenBank**	**Reference**
Alpheus angulosus McClure, 2002	Ascension Bay, Quintana Roo, Mexico	NMNH 135891	JX286600	Almeida *et al.* (2013)
Alpheus armillatus H. Milne Edwards, 1837	Baby Beach, Aruba	—	FJ528477	Mathews & Anker (2009)
Alpheus buckupi Almeida, Terossi, Araújo-Silva & Mantelatto, 2013	Lagarto Beach, São Tomé and Príncipe	OUMNH.ZC. 2011-06.005	JX286604	Almeida *et al.* (2013)
Alpheus buckupi	Timbó River, Paulista, Pernambuco, Brazil	MOUFPE 19791	JX286603	Almeida *et al.* (2013)

Alpheus buckupi	Tassimirim Beach, Boipeba Island, Cairu, Bahia, Brazil	MOUFPE 19500	JX286605	Almeida *et al.* (2013)
Alpheus carlae Anker, 2012	Maramata Beach, Cachoeira River, Ilhéus, Bahia, Brazil	MOUFPE 19795	JX286602	Almeida *et al.* (2013)
Alpheus estuariensis Christoffersen, 1984	Paripe River, Itamaracá Island, Pernambuco, Brazil	MOUFPE 19794	JX286607	Almeida *et al.* (2013)
Alpheus heterochaelis Say, 1818	Whitney Marine Laboratory, Florida, USA	UF 23208	JX286610	Almeida *et al.* (2013)
Alpheus inopinatus Holthuis & Gottlieb, 1958	Haifa, Israel	RMNH 18313	MN617767	Cunha *et al*. (2020)
Alpheus lobidens De Haan, 1849	Mayotte, France	MNHN-IU-2009-1485	KP725485	Aznar-Cormano *et al.* (2015)
Alpheus lobidens	Mayotte, France	MNHN-IU-2012-1082	KP725486	Aznar-Cormano *et al.* (2015)
Alpheus lobidens	Nosy Be Island, Madagascar	UF 14424	pendent	Present study
Alpheus lobidens	Thuwal, Saudi Arabia	UF 37050	pendent	Present study
Alpheus lobidens	Island of Astola, Pakistan	NMNH 173981	pendent	Present study
Alpheus lobidens	Shimabara, Nagasaki, Japan	RMNH PEG 25134	MN617771	Cunha *et al*. (2020)
Alpheus lobidens	Marshall Islands, Majuro Atoll	UF 13776	MN617772	Cunha *et al*. (2020)
Alpheus lobidens	Darwin, Northern Territory, Australia	UF 19966	MN617769	Cunha *et al*. (2020)
Alpheus lobidens	Darwin, Northern Territory, Australia	UF 19984	MN617770	Cunha *et al*. (2020)

Alpheus cf. *lobidens*	Lennox Head, New South Wales, Australia	NMV J 21615	JX286611	Almeida *et al.* (2013)
Alpheus lobidens	Moorea, Society Islands, French Polynesia	UF 15757	MN617768	Cunha *et al*. (2020)
Alpheus petronioi Almeida, Terossi & Mantelatto, 2014	Estuary of the Mojuim River, São Caetano de Odivelas, Pará, Brazil	CCDB 4509	KF667545	Almeida *et al.* (2014)
Synalpheus pandionis Coutière, 1909	Curlew Reef, Belize	-	HQ435468	Hultgren & Duffy (2011)
Synalpheus plumosetosus Macdonald, Hultgren & Duffy, 2009	Dairy Bull, Discovery Bay, Jamaica	-	HQ435472	Hultgren & Duffy (2011)

RESULTS

The molecular data obtained suggest the existence of at least nine lineages within the *A. lobidens* complex [*A. buckupi* + *A. inopinatus* + *A. lobidens sensu stricto* (topotype of Japan) + six lineages of *A. lobidens sensu lato*] (Fig. 1). One clade includes *A. buckupi* (Atlantic), *A. inopinatus* (Israel) and three Indo-Pacific lineages of *A. lobidens sensu lato* [1) Mayotte + Madagascar; 2) Pakistan + Mayotte + Saudi Arabia; 3) northern Australia). More external to this clade is a lineage of *A. lobidens sensu lato* from southeastern Australia. As a sister group of this large clade is a clade formed by *A. lobidens sensu stricto* and two lineages of *A. lobidens sensu lato* from the central Pacific (Marshall Islands and French Polynesia) (Fig. 1). The presence of *A. buckupi* and *A. inopinatus* positioned among the lineages of *A. lobidens sensu lato*, demonstrate that *A. lobidens sensu lato* does not form one monophyletic, but at least six separated group.

A considerable genetic distance for the 16S gene was observed among the six lineages within the *A. lobidens sensu lato*, ranging from 7.9% (French Polynesia X Marshall Islands) to 22.1% (French Polynesia X southeastern Australia; Marshall Islands X southeastern Australia; northern Australia X French Polynesia) (Table 2). Moreover, the estimated genetic distances between samples of "*A. lobidens*" and other analyzed species of *Alpheus*, that do not belong to the *A. lobidens* complex, ranged from 10 to 28.6%.

The morphological comparison of the lineages of *A. lobidens sensu lato* recovered have shown high variability in the scaphocerite length, length of the fingers of the major cheliped, the shape of the dactylus of the major cheliped, the degree of development of the major and minor cheliped grooves and the reach of distolateral spiniform seta of the uropod in the different populations of *A. lobidens sensu lato*. Despite this, these characters do not allow the lineages to be separated into isolated species.

Figure 1. Bayesian tree of *Alpheus lobidens sensu stricto* (triangle), *Alpheus lobidens sensu lato* (" ") and other species of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888, based on 16S mtDNA sequence data and map with origin of the analysed samples. Numbers at nodes represent posterior probabilities. Numbers <60% are not shown. Locality abbreviations: PE, Pernambuco; BA, Bahia.

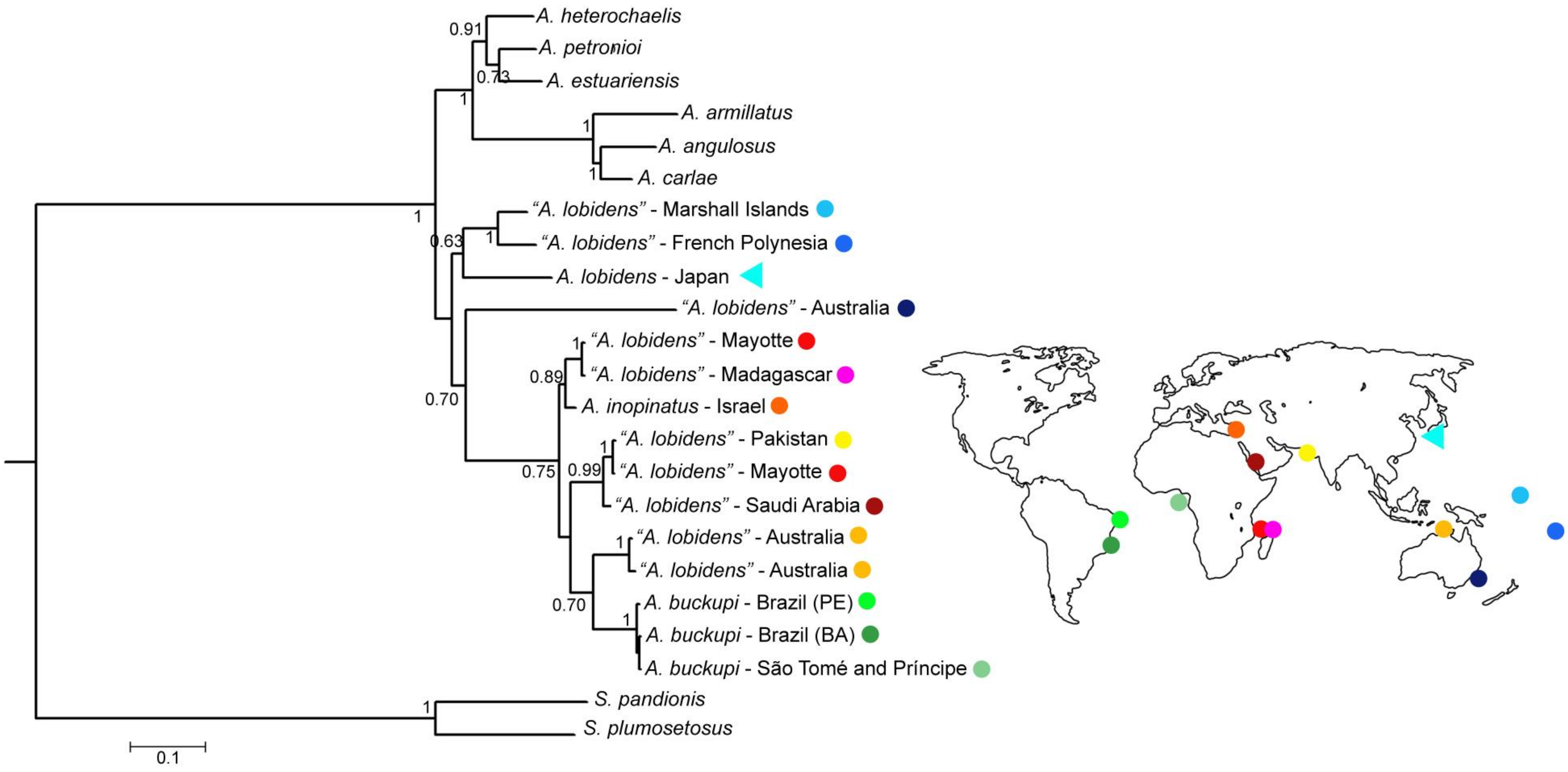

Table 2. Matrix of genetic divergence (p-distance %) of the 16S mtDNA between some specimens of *Alpheus lobidens sensu stricto* (bold), *Alpheus lobidens sensu lato* (" ") and other species of *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888. Locality abbreviations: PE, Pernambuco; BA, Bahia.

Specimens	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
1. *A. buckupi* (Brazil-PE and BA, São Tomé and Príncipe)	0.0														
2. *A. inopinatus* – Israel	14.3	-													
3. ***A. lobidens*** **– Japan**	21.4	15.7	-												
4. “*A. lobidens*” – southeastern Australia	20.0	20.7	20.0												
5. *“A. lobidens”* – French Polynesia	23.6	17.1	17.1	22.1	-										
6. *“A. lobidens”* – Marshall Islands	21.4	17.1	15.0	22.1	7.9	-									
7. *“A. lobidens”* – northern Australia	12.1	12.1	20.7	21.4	22.1	19.3	-								

8. *“A. lobidens”* – northern Australia	12.1	12.1	20.7	21.4	22.1	19.3	0.0	-							
9. *“A. lobidens”* – Saudi Arabia	13.6	10.7	17.9	18.6	20.0	17.9	12.9	12.9	-						
10. *“A. lobidens”* – Mayotte	13.6	11.4	20.0	20.7	19.3	17.9	13.6	13.6	2.9	-					
11. *“A. lobidens”* – Pakistan	13.6	11.4	20.0	20.7	19.3	17.9	13.6	13.6	2.9	0.0	-				
12. *“A. lobidens”* – Mayotte	13.6	7.9	16.4	20.7	20.0	18.6	11.4	11.4	13.6	14.3	14.3	-			
13. *“A. lobidens”* – Madagascar	12.9	7.1	15.7	20.0	19.3	17.9	10.7	10.7	12.9	13.6	13.6	0.7	-		
14. Other *Alpheus* spp.	21.4–25.0	18.6–29.3	14.3–26.4	19.3–27.1	17.1–23.6	17.9–25.7	21.4–28.6	21.4–28.6	17.1–28.6	17.1–27.9	17.1–27.9	22.1–27.1	21.4–26.4	10.0–24.3	
15. *Synalpheus* spp.	27.9–28.6	28.6–30.7	30.7–31.4	32.9–35.7	28.6	29.3–31.4	30.0–30.7	30.0–30.7	32.1–32.9	30.7–32.1	30.7–32.1	30.7–31.4	30.0–30.7	27.9–35.0	23.6

DISCUSSION

The formation of a clade including *A. buckupi* (Atlantic), *A. inopinatus* (Israel) and three Indo-Pacific lineages of *A. lobidens sensu lato* [1) Mayotte + Madagascar; 2) Pakistan + Mayotte + Saudi Arabia; 3) northern Australia] shows the close relationship between those species. This dates to the Miocene, about 20 million years ago, a period in which the beginning of diversification of Alpheidae shrimps is suggested, based on the fossil record (Hyžný *et al*., 2017). At that time, the tectonic plates movements gradually opened and closed gateways, blocking the circulation of the global equatorial flow of warm ocean waters, making it difficult for marine organisms to disperse and promoting adaptive radiation (Potter & Szatmari, 2009).

The genetic distance values found among lineages exceed the average intraspecific genetic distance detected in other species of *Alpheus*, in studies based on the 16S mtDNA (Mathews *et al*., 2002; Mathews, 2006; Almeida *et al*., 2013, 2014; Soledade *et al*., 2019). In addition, it is clearly demonstrated that these lineages do not form a monophyletic group, being a sister group by *A. buckupi* and *A. inopinatus* specimens. The non-monophyletic status of *A. lobidens sensu lato* have been suggested by Cunha *et al.* (2020) analyses with smaller number of samples. Those *Alpheus lobidens* lineages may be considered as cryptic species with little or no morphological differentiation but being clearly separated geographically as well as genetically distinct.

Cases like this are not uncommon in Alpheidae. In the review of the complex of cryptic species *Alpheus cylindricus* Kingsley, 1878, no morphological differences were found between *A. cylindricus* and *A. vanderbilti* Boone, 1930, however, genetic and biogeographical data supported the distinction between them (Anker *et al*., 2008). Another example of this is *Synalpheus pinkfloydi* Anker, Hultgren & De Grave, 2017. This species was considered cryptic species of *Synalpheus antillensis* Coutière, 1909 because no morphological differences and color patterns were found between them. However, the distinction between those species was supported by molecular and biogeographical data (Anker *et al*., 2017).

Many marine invertebrate taxa with Indo-West Pacific distribution do not exhibit significant population structure across this range (Keyse *et al*., 2014). This is due to the high potential for gene flow through dispersive larval that drift for weeks or months in the plankton, traveling long distances in a single generation (Udekem d'Acoz, 2000; Wirtz, 2004). However, this genetic homogeneity was not found in *A. lobidens*, evidencing that these populations are being subjected to genetic isolation, which can be the result of barriers for larvae dispersion (Avise *et al*., 1987; Thorpe *et al*., 2000; Carpenter *et al*., 2011; Keyse *et al*., 2014).

The marked genetic diversification between the Indian and Pacific for the populations of *A. lobidens* are similar to those found in studies on fish species (McMillan & Palumbi, 1995; Lacson & Clark, 1995; Gaither *et al*., 2010), starfish (Williams & Benzie, 1998; Benzie, 1999) and other crustaceans (Williams *et al*., 1999; Barber *et al*., 2000; Benzie *et al*., 2002). The most usual explanation for this fact is related to the geological and climatic history of those oceans, marked by the movement of tectonic plates, volcanism and periodic changes in sea level, associated with the presence of many islands, bays and seas (Springer, 1982; Hocutt, 1987; McMillan & Palumbi, 1995). These factors would provide a high subdivision of populations and diversity of habitats, being responsible for the formation of new species (Gaither *et al*., 2010).

Alternatively, it is suggested that the divergence of *A. lobidens* lineages may be very recent. As result, their geographic distribution would be subject to complex large-scale seasonal ocean currents, present in the Indian and Pacific oceans, such as the Monsoon, Agulhas, Kuroshio and Humboldt currents (Lavery *et al*., 2014). These currents would act forming true hydrological barriers that hinder the supply of larvae to other locations, producing low levels of gene flow in populations (Barkley, 1970; Harris *et al*., 1988; Bae *et al*. 2014; Zhang *et al*., 2015) and, over time, it can lead to speciation.

In the Pacific clade, the lineage from Japan, which refers to *A. lobidens sensu stricto* (Cunha *et al*., 2020), may have been isolated by the hot Kuroshio current. This current, for millions of years, has played a fundamental role in distribution of heat from the tropics to the middle latitudes, in addition being important in the climate control of Northeast Asia (Gallagher *et al*., 2015). Thus, geographic distribution patterns influenced by this current, have also been found for coral reefs (Tsuchiya *et al*., 2004; Iryu *et al*., 2006) and gastropods (Tomida & Kitao, 2002; Kitamura & Ubukata, 2003; Tomida *et al*., 2013).

The Marshall Islands and French Polynesia lineages were possibly isolated by the warm equatorial current of the South Pacific. This current and its affluents have acted in isolating marine populations, contributing to the high degree of endemism presented in this area, particularly in fish, mollusks, and crustaceans (Springer, 1982). The separation of the southeastern lineage of Australia may have been caused by the warm flow of the eastern Australian stream. This current generates numerous eddies and affluents, including the Tasmanian Front, the Eastern Auckland Current, and the Eastern Cape Current, and has been responsible for determining the distribution of tropical fish (Booth *et al*., 2007).

Three lineages of *A. lobidens sensu lato* were recovered in the Indian Ocean. The lineage formed by Mayotte and Madagascar is probably affected by the warm currents of Agulhas, Madagascar and the eddies of the Mozambique Channel. The water movements of these currents can act by minimizing the larval movement and have determined a similar geographic distribution pattern in the spiny lobsters *Panulirus homarus* (Linnaeus, 1758) (Lavery *et al*., 2014) and *Panulirus delagoae* Barnard, 1926 (Gopal *et al*., 2006).

The Pakistan and Saudi Arabia lineage can be influenced by the warm currents of Monsoon and Somalia. These currents have a strong influence on primary productivity and the geographical distribution of crustaceans (Romanov *et al*., 2009; Tsang *et al*., 2012) and reef fish (Burt *et al*., 2011). The northern Australian lineage appears to be affected by the Western Australian current. Similar results, from a genetic structure in the northern Australia, have been reported for other crustaceans such as *Penaeus esculentus* Haswell, 1879 and *Scylla serrata* (Forskål, 1775) (Gopurenko & Hughes, 2002; Ward *et al*., 2006).

Thus, the high morphological variability observed in the populations of *A. lobidens sensu lato* and the high rates of intraspecific molecular divergence, associated with ocean currents, suggest limited gene flow between those lineages, leaving no doubt that these should be treated as new species. However, the absence of consistent morphological characters (synapomorphies) prevents the description of the six new taxa of the complex recognized in this study.

It is possible that such morphological differences exist, but they were not observed by traditional taxonomic methods. New studies that aim to apply more sensitive methods for detecting structural differences, such as geometric morphometry and scanning electron microscopy (Fleischer *et al*., 1992; Giri & Collins, 2004; Marchiori *et al*., 2014; Karanovic *et al*., 2016) could help in the morphological definition of the new species of this complex, uncovered in the present study.

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4 CONCLUSÃO

A abordagem integrativa de dados moleculares e morfológicos permite-nos afirmar que *Alpheus lobidens sensu* De Haan, 1849, *Alpheus inopinatus* Holthuis & Gottlieb, 1958 e *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013 são espécies taxonomicamente válidas, que apresentam um conjunto de caracteres distintivos. *Alpheus lobidens polynesica* Banner & Banner, 1974 foi incluída em *A. lobidens sensu lato*, pois não foram encontrados caracteres diferenciais entre as mesmas. Além disso, *Alpheus lobidens sensu* De Haan, 1849, até o momento tem sua distribuição geográfica restrita à localidade-tipo no Japão e todas as outras amostras morfologicamente diferentes do topótipo foram tratadas como *A. lobidens sensu lato*.

A presença de linhagens de *A. buckupi* e *A. inopinatus* como espécies irmãs de *A. lobidens sensu lato*, demonstraram que *A. lobidens sensu lato* não forma um grupo monofilético. A elevada variabilidade morfológica e as altas taxas de distância genética observadas entre as seis linhagens de *A. lobidens sensu lato*, associadas às correntes oceânicas, sugerem um fluxo gênico inexistente entre elas, sem deixar dúvidas quanto à sua validade. Contudo, a dificuldade em observar caracteres morfológiocos consistentes (sinapomorfias) impede momentaneamente a descrição dos seis novos táxons presentes em *A. lobidens sensu lato*.

Ainda que não observadas pelos métodos taxonômicos tradicionais, é possível que diferenças morfológicas existam. Estudos com aplicação de métodos mais sensíveis para detectar diferenças estruturais são necessários para ajudar na definição morfológica das novas espécies deste complexo, sugeridas no presente estudo.

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