UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

TAMMY IWASA ARAI

SPECIES DELIMITATION, COMPARATIVE PHYLOGEOGRAPHY AND CONNECTIVITY OF PERACARIDA (CRUSTACEA: EUMALACOSTRACA) ASSOCIATED WITH SARGASSUM IN BRAZIL WITH EMPHASIS ON ISLANDS POPULATIONS

DELIMITAÇÃO DE ESPÉCIES, FILOGEOGRAFIA COMPARATIVA E CONECTIVIDADE DE PERACARIDA (CRUSTACEA: EUMALACOSTRACA) ASSOCIADOS A SARGASSUM NO BRASIL COM ÊNFASE EM POPULAÇÕES INSULARES

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Orientadora: FOSCA PEDINI PEREIRA LEITE

Co-Orientadora: SÓNIA CRISTINA DA SILVA ANDRADE

ESTE ARQUIVO DIGITAL CORRESPONDE À VERSÃO FINAL DA TESE DEFENDIDA PELA ALUNA TAMMY IWASA ARAI E ORIENTADA PELA PROFA. DRA. FOSCA PEDINI PEREIRA LEITE.

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Os membros da Comissão Examinadora acima assinaram a Ata de defesa, que se encontra no processo de vida acadêmica do aluno.

A Ata da defesa com as respectivas assinaturas dos membros encontra-se no SIGA/Sistema de Fluxo de Tese e na Secretaria do Programa de Pós-Graduação em Biologia Animal da Unidade Instituto de Biologia.

Para Sil,
Pela parceria de aventuras nas
mais belas praias desse Brasilzão

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“Quando se for esse fim de som
Doida canção
Que não fui eu que fiz
Verde luz verde cor de arrebentação
Sargaço mar, sargaço ar”
- Dorival Caymmi

"...Que é necessário sair da ilha para ver a ilha, que não nos vemos se não saímos de nós…"
- José Saramago

RESUMO

A superordem de crustáceos Peracarida tem como característica a ausência de fase larval e consequente baixa dispersão, levando a altas taxas de endemismo. Dentre os Peracarida mais diversos estão as ordens Amphipoda, Isopoda e Tanaidacea, que também são os principais grupos de crustáceos associados aos bancos de macrófitas. Apesar da baixa taxa dispersiva de tais grupos de crustáceos, correntes superficiais podem ter deslocado massas da alga parda do gênero *Sargassum*, possivelmente levando com elas espécies exóticas para os bancos de macrófitas. Até o momento, estudos biogeográficos e filogeográficos de Peracarida no Brasil são escassos, e praticamente inexistentes em ilhas costeiras e oceânicas. Esta tese teve como objetivo geral entender e resgatar a história evolutiva e biogeográfica de espécies de Peracarida associadas a macroalgas, utilizando diferentes níveis taxonômicos com abordagens morfológicas e moleculares. Este é o primeiro estudo filogeográfico de Peracarida em ilhas brasileiras, e visa contribuir com o conhecimento da distribuição e evolução acerca de alguns dos principais grupos de Crustacea. A partir da análise filogenética do gênero de tanaidáceos *Synapseudes*, foi observada uma origem da espécie ancestral do gênero na região do Indo-Pacífico, com posterior dispersão para o Oceano Atlântico. Tal padrão também foi encontrado para a família de anfípodes Ampithoidae, na qual o novo gênero proposto *Foscampithoe* **gen. nov.** dispersou para o Oceano Atlântico e aqui se diversificou. As histórias evolutivas específicas de *Ampithoe marcuzzii* e *Chondrochelia dubia* sugerem dois complexos de espécies, com parcial congruência entre ambos. Enquanto o complexo *A. marcuzzii* apresentou uma separação continente-ilha marcada por variações abióticas, *C. dubia* possui uma maior conectividade entre regiões.

ABSTRACT

The crustacean superorder Peracarida are characterized by the lack of larval phase and, consequently, they usually present low dispersion rates that lead to high endemicity rates. Among the most diverse peracarid crustaceans are the orders Amphipoda, Isopoda and Tanaidacea, which are also the most abundant and diverse groups associated to macroalgae. Despite their low dispersion rate, surface currents could help to them to disperse by displacing patches of floating *Sargassum*, and taking exotic species to other macrophytes beds. Biogeographic and phylogeographic studies using Peracarida in Brazil are yet scarce and mostly absent in continental and oceanic islands. This dissertation's main goal is to understand and recover the evolutive history of Peracarida species associated to macroalgae, using different taxonomic levels with morphological and molecular approaches. This is the first phylogeographic study of Peracarida in Brazilian islands, and aims to contribute to the knowledge on distribution and evolution in some of the main Crustacea groups. Based on the phylogenetic analysis of the tanaidacean genus *Synapseudes*, it was observed the origin of the ancestral species in the Indo-Pacific region, with posterior dispersion to the Atlantic Ocean. This pattern was also found in the amphipod family Ampithoidae, in which the new proposed genus *Foscampithoe* **gen. nov**. dispersed to the Atlantic and herein diversified. The specific evolutionary histories of *Ampithoe marcuzzii* and *Chondrochelia dubia* suggest two species complexes, with partial congruence between them. While the *A. marcuzzii* complex presented a continent-island separation shaped by abiotic variables, *C. dubia* showed higher connectivity among localities.

SUMÁRIO

Introdução Geral

Os bancos de algas macrófitas, um dos principais ambientes formados em áreas costeiras, são caracterizados por suas altas produtividades e complexidades estruturais que proporcionam recursos alimentares e sítios reprodutivos para uma vasta diversidade de espécies, bem como abrigo contra predadores e fatores abióticos adversos (Christie et al. 2009). Dentre as espécies mais representativas que compõem os bancos de macrófitas estão aquelas do gênero *Sargassum* C. Agardh, que apresentam ampla distribuição no Oceano Atlântico e formam densos e extensos bancos, podendo representar cerca de 80% da cobertura e biomassa de algas do infralitoral dos costões rochosos de algumas áreas (Széchy & Paula 2000). O denominado Mar dos Sargaços, um característico aglomerado de macrófitas localizado no Oceano Atlântico Noroeste (228–388N; 768–438W), é formado por massas flutuantes de *Sargassum natans* (L.) Gaillon e *S. fluitans* (Børgesen) Børgesen (Guiry & Guiry 2016), espécies pelágicas que abrigam um ecossistema único (Sissini et al. 2017).

Recentemente, mudanças nos padrões das correntes superficiais vêm se intensificando e podem ter deslocado massas de *Sargassum* para novas regiões marinhas e costeiras, ocasionando a chegada de espécies exóticas e comprometendo o equilíbrio ecossistêmico (Sissini et al. 2017). Deste modo, blooms de *Sargassum* vêm sendo registrados na costa do Caribe desde 2011 (Gower et al. 2013; Gavio et al. 2015; Wang & Hu 2016), na costa norte e nordeste brasileira, Fernando de Noronha, e próximo às ilhas oceânicas de Atol das Rocas e Arquipélago de São Pedro e São Paulo entre 2014 e 2015 (Sissini et al. 2017).

O constante aumento na incidência de massas de *Sargassum* vêm gerando impactos no turismo e em recursos pesqueiros, e recentes estudos observaram a formação de um cinturão de *Sargassum* no Atlântico Equatorial (GASB – Great Atlantic Sargassum Belt), cujo monitoramento por satélites indica ser a provável fonte de macroalgas encalhadas na costa, e não o Mar de Sargaços localizado no Atlântico noroeste (Wang et al. 2019). A formação de tal cinturão é decorrente do aumento na deposição de matéria orgânica proveniente do Rio Amazonas, criando assim um ambiente adequado à proliferação exacerbada de *Sargassum* (Wang et al. 2019).

Enquanto os bancos de *Sargassum* bentônicos são bastante comuns na plataforma continental, as ilhas oceânicas brasileiras apresentam uma diferente composição ficológica, na qual outras algas pardas são mais representativas, como *Dictyota* spp. na ilha de Trindade e no Arquipélago de São Pedro e São Paulo (Pedrini et al. 1989; Secirm 2009). Apesar da composição dos bancos de algas variar de acordo com a localidade, muitas espécies de invertebrados associados a macroalgas são generalistas, podendo ocorrer em diferentes algas hospedeiras (Machado et al 2021). Deste modo, Peres et al (2019) observaram que anfípodes da família Ampithoidae que habitam diversas espécies de macroalgas não estão sob o efeito de diferenciação genética associada ao hospedeiro, sugerindo a alta mobilidade dos indivíduos entre algas hospedeiras. Portanto, espécies de macroalgas mais suscetíveis a deriva e com ciclo de vida pelágico, como *Sargassum* spp., podem levar espécies associadas a comunidades fitais de composições diferentes a outras localidades. Portanto, a dinâmica dos bancos de *Sargassum* pelágico podem influenciar na estruturação populacional genética dos organismos associados tanto aos próprio *Sargassum* pelágico quanto às comunidades associadas a macroalgas bentônicas, isolando e conectando populações.

A fauna associada aos bancos de macrófitas é composta principalmente por crustáceos da superordem Peracarida Calman, 1904, que são caracterizados por possuírem um marsúpio formado por oostegitos, os primeiros (e, às vezes, os segundos e terceiros) segmentos torácicos fusionados à cabeça, formando um cefalotórax, presença de maxilípedes e uma estrutura chamada lacinia mobilis em suas mandíbulas (Poore 2005). As ordens Amphipoda Latreille, 1816, Isopoda Latreille, 1817 e Tanaidacea Dana, 1849 correspondem às mais diversas dentro de Peracarida, e também constituem o grupo mais representativo da fauna associada a bancos de macrófitas (Tanaka & Leite 2003). Devido ao seu desenvolvimento direto, é esperado que tais crustáceos possuam uma baixa capacidade de dispersão, assumindo, assim, um alto nível de endemismo (Hurtado et al. 2016). Contudo, de acordo com Thiel

(2003), crustáceos peracáridos são extremamente apropriados a colonizações por rafting a partir de organismos flutuantes, uma vez que estas espécies de crustáceos podem persistir durante longas viagens em substratos à deriva, especialmente macroalgas, já que sua prole pode ser recrutada diretamente no flutuador parental, levando a mudanças sucessivas de gerações durante o percurso de viagem.

A fauna de anfípodes associada às espécies do gênero *Sargassum* bentônico pode ser representada por até 30 espécies (Tanaka & Leite 2003). Contudo, diversas espécies de anfípodes comuns nesta associação vêm despertando discussões entre os taxonomistas em virtude de variações morfológicas intrapopulacionais importantes (Peart 2004). Desta forma, é possível que uma subestimativa da riqueza da fauna de anfípodes esteja ocorrendo, podendo cada uma desses nomes de espécies representar, na verdade, complexos de espécies crípticas (Peart 2004).

A espécie herbívora *Ampithoe marcuzzii* Ruffo, 1954 (Fig. 1A) é bastante abundante em bancos de macrófitas, e sua distribuição estende-se da Flórida (Estados Unidos) até o litoral do estado de São Paulo (Serejo & Siqueira 2018). Nas recentes filogenias, tanto uma proposta com base em dados moleculares por Sotka et al. (2016) quanto a proposta por Peart & Ahyong (2016) com caracteres morfológicos, o gênero *Ampithoe* mostrou-se parafilético, sugerindo uma evolução complexa do grupo e futuras revisões taxonômicas (Figs. 2 e 3).

Por fim, estudos sobre a ordem Tanaidacea no Brasil vêm crescendo recentemente, especialmente com a descrição de novas espécies (Araújo-Silva & Larsen 2012), e problemas antigos sujeitos a revisões taxonômicas e delimitação de espécies permanecem escassos. A espécie *Leptochelia dubia* Krøyer, 1842 (Fig. 1B), descrita originalmente para o Brasil e abundante em bancos de macrófitas, possui ampla distribuição e pelo menos 20 táxons já foram atribuídos ao ‘grupo *Leptochelia dubia*’, que merece maior atenção, uma vez que recentes estudos revelaram a necessidade de maior detalhamento das populações brasileiras (Bamber 2010). Atualmente, a espécie está incluída no gênero *Chondrochelia* e é considerada cosmopolita (Gutu 2016).

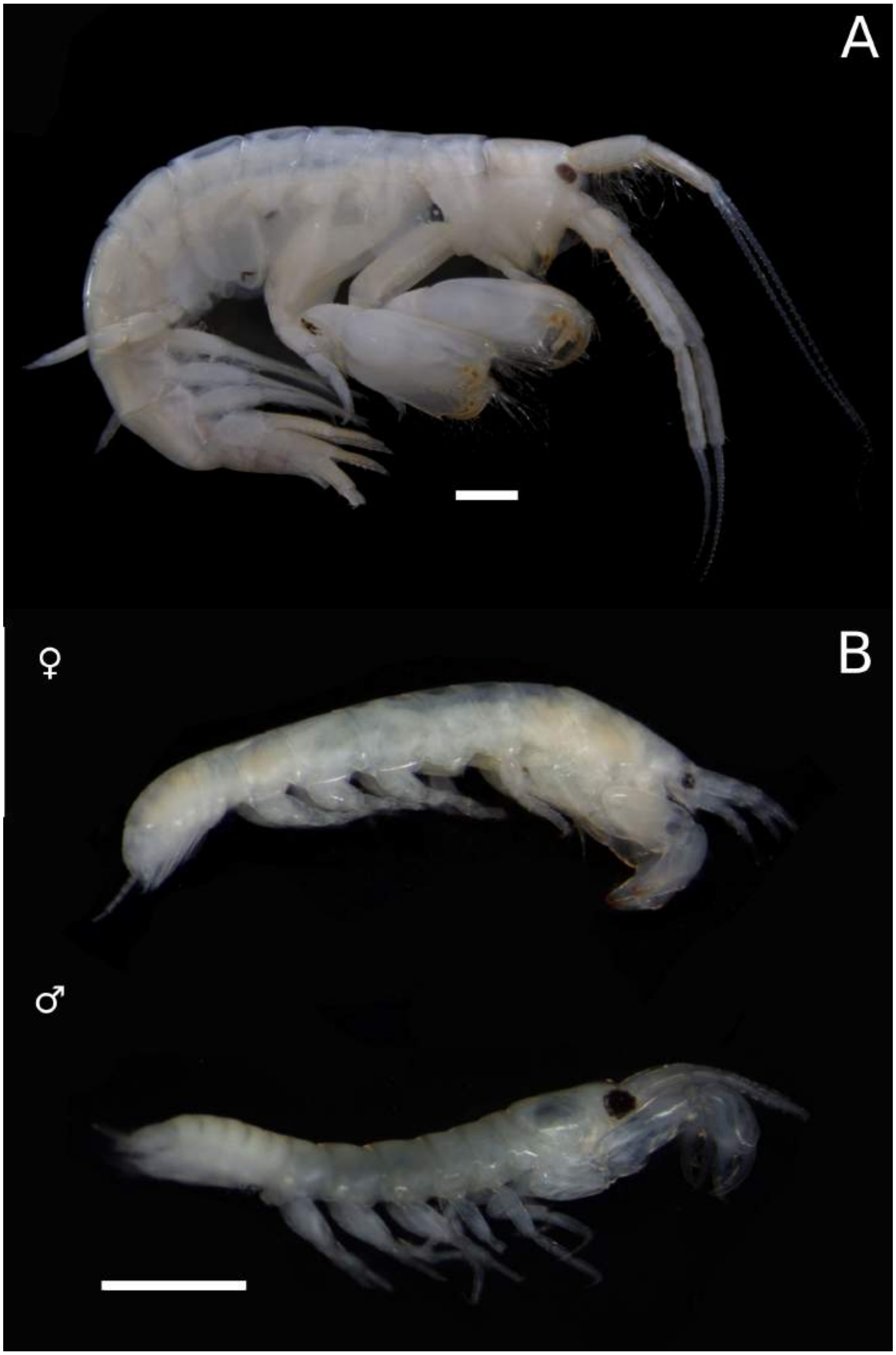

Figura 1. A. *Ampithoe marcuzzii,* Ilha da Trindade, ES. **B.** Chondrochelia dubia, Praia do Forte, BA. Escala: 1 mm.

A utilização de marcadores moleculares, como marcadores de sequência e polimorfismos de nucleotídeo único (SNPs), são muito importantes para estudos de delimitação de espécies, sistemática filogenética e filogeografia (Segatto et al. 2017). Marcadores de sequência de DNA são tradicionalmente utilizados para fins filogenéticos e filogeográficos desde a década de 1980 (Felsenstein 1988, Cavalli-Sforza 1998, Avise 1987), enquanto estudos com marcadores SNPs vêm aumentando ao longo da última década. Até pouco tempo, o uso dos marcadores SNPs era restrito a organismos modelo com genomas sequenciados, contudo, atualmente é possível utilizar SNPs em estudos com espécies não modelo, devido ao avanço das ferramentas de bioinformática e o barateamento no sequenciamento (Turchetto-Zolet et al. 2017). Ainda mais recentemente, uma nova vertente vem ganhando espaço nos estudos integrativos de genética de populações e suas interações com o ambiente, a genética/genômica da paisagem. A genômica da paisagem oferece ferramentas robustas para avaliar a influência das modificações da paisagem sobre a diversidade genética e conectividade, além de identificar adaptações às condições ambientais locais que podem moldar a distribuição de determinadas populações (Lozier & Zayed, 2017).

Atualmente, um único trabalho foi publicado a respeito da filogeografia de Peracarida no Brasil, referindo-se à espécie de isópode *Excirolana braziliensis* Richardson, 1912, abundante em praias arenosas, que revelou uma alta diversidade críptica e padrões biogeográficos que moldaram a evolução e distribuição da espécie (Hurtado et al. 2016). Deste modo, qualquer propriedade que forneça evidências de separação de linhagens é relevante para inferir os limites e números de espécies, desde propriedades específicas como monofilia e coalescência exclusiva até eventos como incompatibilidade reprodutiva e especiação ecológica (De Queiroz 2007). Com relação ao que se sabe da ecologia e conectividade de crustáceos nas ilhas brasileiras, apenas estudos referentes a algumas espécies da ordem Decapoda foram realizados, cujo desenvolvimento é indireto com fase larval planctônica, permitindo uma grande dispersão por correntes marinhas (Rodríguez-Rey et al. 2016; Teschima et al. 2016), diferenciando-se assim da estruturação populacional esperada para espécies de Peracarida, que não possuem fase larval.

Através do uso de marcadores genéticos, inferências das taxas de dispersão e fluxo gênico podem prever o tamanho, a persistência e a estrutura das populações, bem como ser subsídio para identificar populações em declínio, impedir a extinção local e promover iniciativas para programas de manutenção de variação genética (Waser & Strobeck 1998). Uma vez que a distribuição geográfica da variação genética dentro e entre os táxons fornece informações sobre os processos demográficos e evolutivos históricos e contemporâneos (Costello et al. 2003), esta contribui também para os esforços de manejo e conservação (Moritz 1994). Ilhas separadas por centenas de quilômetros podem trocar apenas um pequeno número de recrutas ou nenhum recruta, levando a um baixo fluxo gênico entre populações que, portanto, devem ser consideradas como populações ecologicamente separadas (Palumbi 2003).

Modelos de Nicho Ecológico (ENMs) têm sido utilizados para prever a distribuição geográfica potencial das espécies no tempo através de algoritmos que geram previsões de ocorrências em condições ambientais adequadas para uma espécie (Elith & Leathwick 2009). Deste modo, a distribuição prevista para um complexo de espécies pode ser modelada abrangendo a gama de condições ambientais de todas as espécies crípticas nele incluído e, consequentemente, a ampla distribuição prevista de uma única espécie com baixa capacidade de dispersão pode ser, na verdade, um indicativo de espécies crípticas. Recentemente, a utilização de métodos que englobam ENMs, simulação de coalescência e reconstrução de linhagens espaço-temporais corroboradas por dados filogeográficos vêm crescendo (Alvarado-Serrano & Knowles 2014; Menezes et al. 2020), permitindo assim definir possíveis cenários passados para serem testados com dados genéticos.

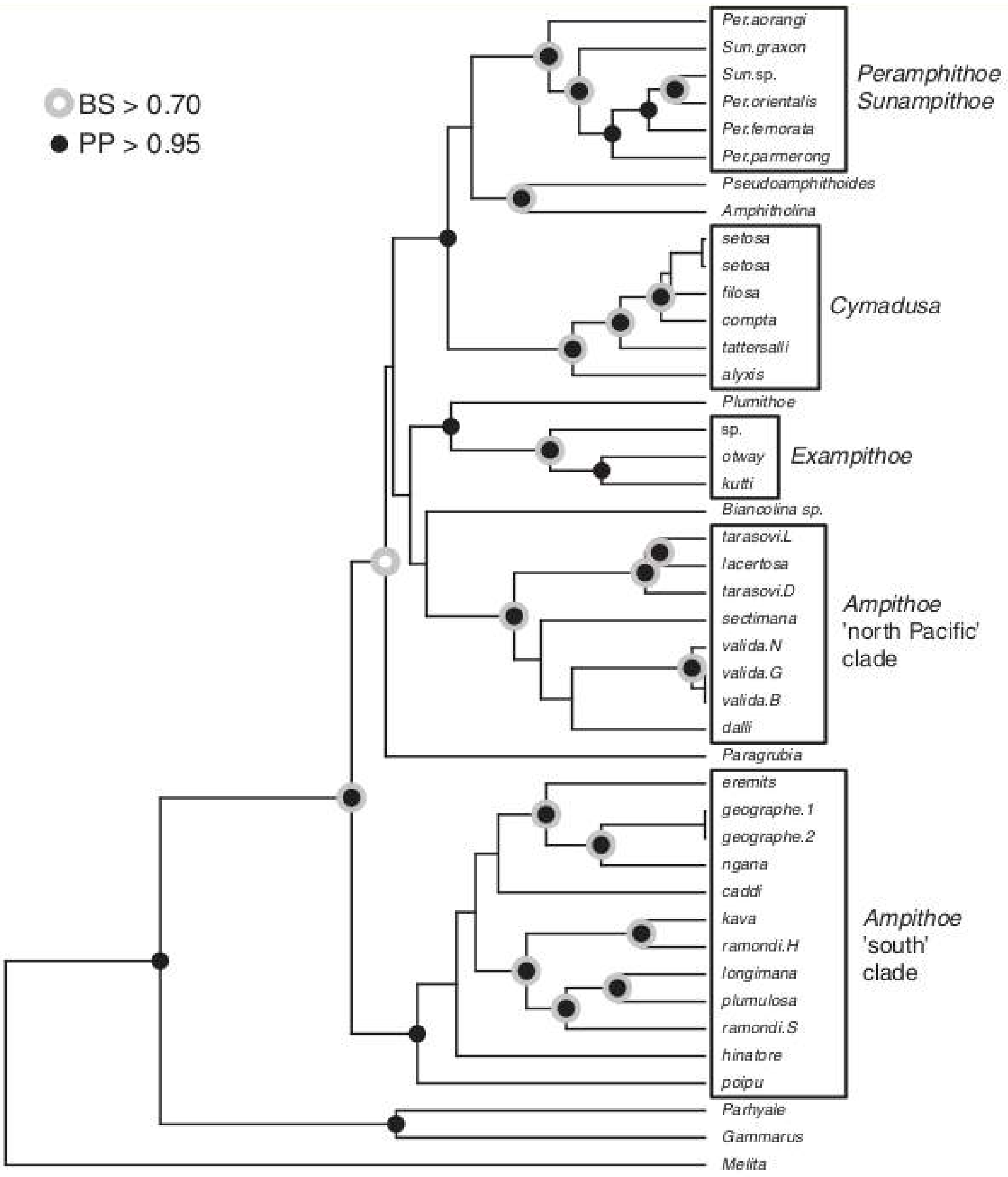

Figura 2. Árvore filogenética de Ampithoidae proposta por Sotka et al. (2017) baseada nos marcadores moleculares COI, 16SrRNA, EF1-a e NAK

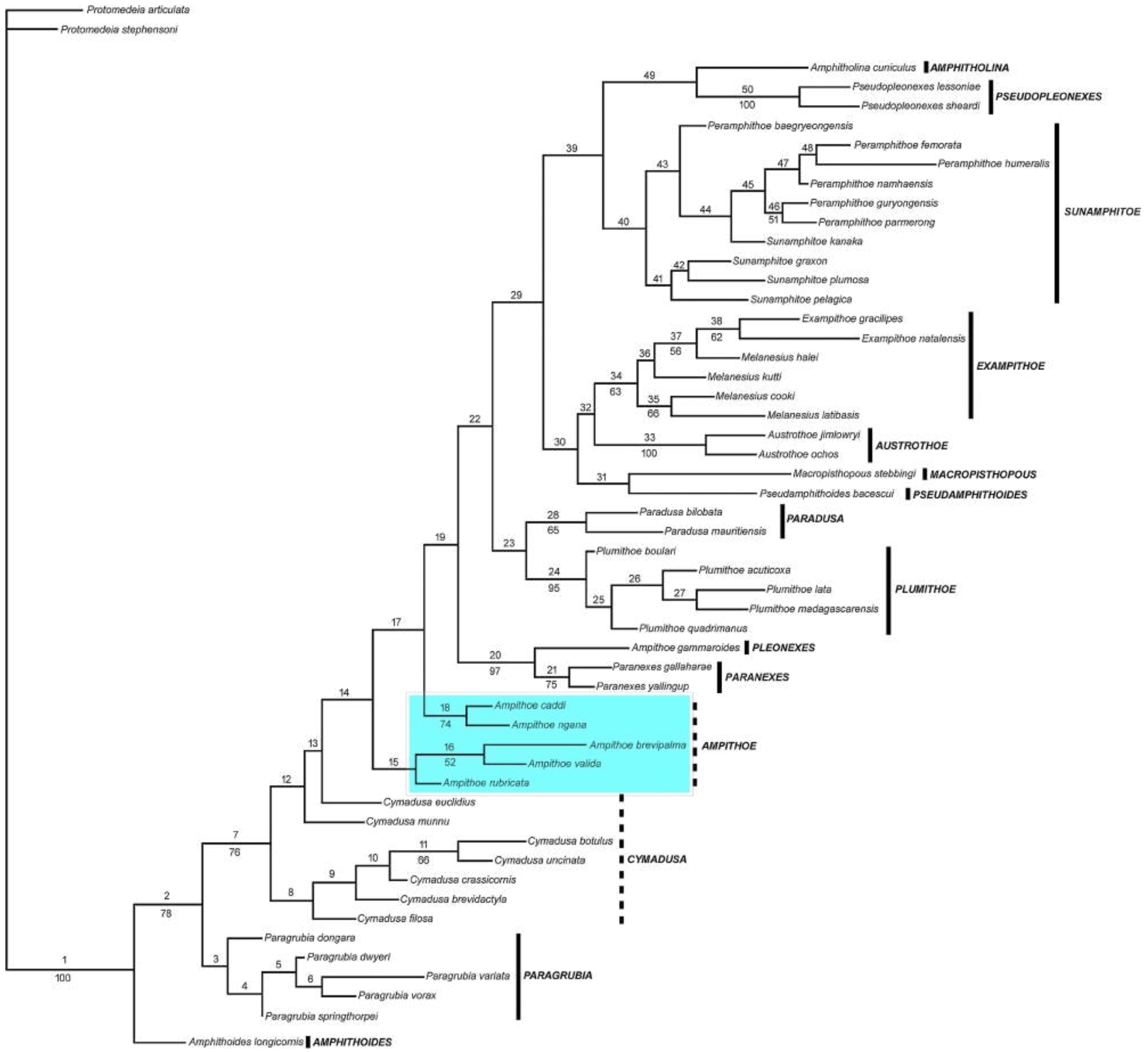

Figura 3. Árvore filogenética de Ampithoidae proposta por Peart & Ahyong (2016) baseada em 77 caracteres morfológicos. Quadro em azul evidencia a parafilia do gênero *Ampithoe*.

Em vista disso, espécies de diferentes ordens de Peracarida com ampla distribuição podem ser utilizadas como modelos a serem generalizados numa discussão sobre a evolução dos Peracarida marinhos associados a macroalgas ao longo da costa e sobre a dinâmica de colonização de ilhas isoladas.

Esta tese teve como objetivo geral entender e resgatar a história evolutiva e biogeográfica de espécies de Peracarida associadas a macroalgas, utilizando diferentes níveis taxonômicos. Assim, o presente trabalho está organizada em quatro capítulos independentes, e seus resultados mostram diferentes camadas da evolução e biogeografia de peracáridos associados a macroalgas no Oceano Atlântico Sudoeste. No primeiro capítulo, foi feito um levantamento das espécies de Peracarida associadas a algas pardas do gênero *Dictyota* na ilha da Trindade, uma comparação do número de espécies totais, compartilhadas e endêmicas de Trindade e do Arquipélago de Abrolhos, e um estudo biogeográfico e da diversificação do gênero *Synapseudes* (Tanaidacea: Metapseudidae) com base em caracteres morfológicos, com o propósito de entender a composição da comunidade de peracáridos em ilhas oceânicas remotas, bem como compreender os processos que moldaram a distribuição destas espécies. No segundo capítulo, um estudo filogenético e biogeográfico da família Ampithoidae for realizado a partir de marcadores moleculares, para comparação com propostas filogenéticas anteriores, resolvendo a monofilia de *Ampithoe*, e para compreensão dos eventos que levaram à diversificação de Ampithoidae em águas rasas de todo o mundo. No terceiro capítulo, realizamos um estudo sobre a genômica populacional de duas espécies irmãs identificadas previamente como *Ampithoe marcuzzii,* onde discutimos a diversificação das espécies e populações através de uma abordagem de genômica de paisagem. Por fim, o quarto e último capítulo propõe resolver o complexo *Chondrochelia dubia* na costa brasileira e Pequenas Antilhas, e compara as barreiras identificadas para o complexo com o observado previamente para outros artrópodes marinhos de baixa capacidade de dispersão.

Os nomes propostos para novas espécies e gênero aqui designados e ainda não publicados não devem ser considerados válidos.

Capítulo 1

THE UNIQUE AMPHIPODA AND TANAIDACEA (CRUSTACEA: PERACARIDA) ASSOCIATED WITH THE BROWN ALGAE *Dictyota* sp. FROM THE OCEANIC TRINDADE ISLAND, SOUTHWESTERN ATLANTIC, WITH BIOGEOGRAPHIC AND PHYLOGENETIC INSIGHTS

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The unique Amphipoda and Tanaidacea (Crustacea: Peracarida) associated with the brown algae *Dictyota* sp. from the oceanic Trindade Island, southwestern Atlantic, with biogeographic and phylogenetic insights

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Zoobank: http://zoobank.org/2D51BA8C-04C1-4C80-90E6-503142F3FA0D

Abstract

Oceanic islands are known by their unique evolutionary histories and high endemicity caused by isolation. This is the first survey on the biodiversity of Peracarida from Trindade Island, a volcanic island located about 1160 km off the Brazilian coast, with the first reports of Tanaidacea from the island and the description of *Synapseudes isis* **sp. nov.**, and three new species of Amphipoda (*Ampithoe thaix* **sp. nov.**, *Elasmopus gabrieli* **sp. nov.** and *Eusiroides lucai* **sp. nov.**). The results of the phylogenetic analysis of *Synapseudes* based on morphological characters and its biogeography, through the Bayesian Binary MCMC analysis (BBM) suggested an Indo-Pacific origin for the genus. Finally, the biodiversity of Trindade Island is compared to the Abrolhos Archipelago, the closest islands from the coast on the continental shelf, suggesting a high endemicity of Peracarida, corresponding to 44% of Amphipoda and 50% of Tanaidacea species in the island of Trindade.

Keywords: cladistics; dispersal; event-based biogeography; morphology; taxonomy.

Introduction

Oceanic islands are of great interest because of their isolation, high endemicity and evolutionary history (Pinheiro et al. 2017). The Trindade and Martin Vaz Archipelago, located southeastern off Brazil, is a unique place with high endemism rate compared to other Atlantic Ocean localities, and the seamounts that connect Trindade and Martin Vaz to the South American continent, known as Vitória-Trindade Seamount Chain (VTC). These areas are considered a biodiversity hotspot for fishes and invertebrates (Pinheiro et al. 2015), with the number of new species described for VTC, and especially to the Trindade Island (TR), still rapidly increasing (Lima et al. 2019; Cunha et al. 2020; Pachelle & Tavares 2020; Simone & Cavallari 2020).

Among the environments found in TR, the rocky shores comprise a large amount of the coastal area, with tidepools being found all over the island (Macieira et al. 2015), providing a stressful and changing habitat based on tide dynamics coupled with environmental characteristics and ecological processes that drive the community (Gibson 1986). Such intertidal environment can harbor macrophytal beds that allow the increase of biodiversity by providing substrata to epiphytic algae and bryozoans, food resources and shelter to several vertebrates and invertebrates (Duffy & Hay 1991; Christie et al., 2009). In the island of Trindade, 36 species of macroalgae were previously reported, including nine species of brown algae (Pereira-Filho et al. 2011).

These marine macrophytes form habitat patches to the epifaunal assemblages dominated by crustaceans of the order Peracarida (Tanaka & Leite 2003), such as amphipods, isopods and tanaidaceans, that have direct development and consequently low dispersion, favoring the establishment of endemic species (Hurtado et al. 2016; Pinheiro et al. 2017). However, data on

Peracarida biodiversity from TR remain scarce, with only two amphipod species reported from the archipelago so far, and one endemic to TR (Oliveira 1951; Barnard 1965; Andrade & Senna 2017). Records of isopods from TR are still restricted to terrestrial fauna and ectoparasites (Barth 1958; Moreira 1977; Souza et al. 2013), while tanaidaceans are unknown.

Although benthic Peracarida are considered to present high levels of endemicity, they show good ability to disperse long distances, especially on macroalgae, which provide both high food value and floating potential, once organisms with direct development may reproduce and their offspring recruit within the parental raft (Thiel 2003). Therefore, according to Błażewicz-Paszkowycz et al. (2012), transport in floating algae (rafting) and vicariance are likely to create new habitats and to provide dispersion as well as to isolate populations allowing them to diversify and speciate. However, the lack of studies on the events that have driven to the current distribution of Peracarida associated with macroalgae hinders a better understanding of the evolutionary biogeographic processes involved.

Therefore, we aim to report on the Peracarida fauna associated with the brown algae of the genus *Dictyota* sp. from TR, with the first report of tanaidaceans and the description of one new species of *Synapseudes* (Tanaidacea: Apseudomorpha) and three new species of Amphipoda. We also comment on the phylogenetic position of the new species *Synapseudes isis* **sp. nov.** based on morphological characters and perform an event-based biogeographic analysis of the genus to further understand the processes underlying the faunal diversity associated to macroalgae worldwide. Finally, we provide a discussion on the biogeographical patterns inferred for Peracarida comparing the taxa from TR with those from the Abrolhos Archipelago, the closest islands from the coast on the continental shelf.

Material and Methods

Study area

Specimens were collected from the brown algae of the genus *Dictyota* sp. under permission SISBIO 60924-3. Sampling was carried out on Trindade Island in September, 2018 and April, 2019 at Piscinas do Parcel (20°31'10.812"S, 20°31'10.812"W), Ilha do Sul (20°31'27.5"S, 29°19'25.2"W) and Piscina da Praia do Lixo (20°31'27.624"S, 29°19'22.188"W) (Fig. 1).

The island of Trindade is located at the eastern limit of the VTC (20°30'S 29°20'W) together with Martin Vaz, in southeastern Brazil, the easternmost group of islands off Brazil, about 1160 km from the coast (Fig. 1). Trindade and Martin Vaz hold the most isolated intertidal habitats within the Brazilian Province and are surrounded by calcareous algal reefs throughout the littoral zone (Gasparini & Floeter 2001).

Sampling method

Algal fronds were collected underwater by freediving, from 1 m to 10 m, stored in fabric bags (0.2 mm mesh size) within seawater and washed off for fauna separation. The associated fauna was fixed and preserved in ethanol 90% for later identification. Appendages and mouthparts of dissected specimens were mounted on glass slides and sealed with glycerol. Drawings were made with a camera lucida at a Zeiss Axioscope stereomicroscope, and digitally drawn with Inkscape. Types are deposited at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

Phylogenetic analysis

We inferred the phylogenetic position of *Synapseudes isis* **sp. nov.** by analyzing published characters from the revision of Synapseudinae Guțu, 1972 (Heard et al. 2018). A character matrix was developed with 26 terminal taxa and 22 morphological characters , including 13 characters from the cephalothorax (including antennae, mouthparts and cheliped), three from the pereon (including pereopods and gills) and six from the pleon (Suppl. Mat. 1 and 2). Characters were combined into multistate groupings to avoid overly dependent characters, resulting in nine binary characters, 11 multistate characters and two continuous characters. Polarization of the characters was conducted through outgroup comparison.

Metapseudes wilsoni Błażewicz-Paszkowycz & Bamber, 2007 and *Ronabus idios* (Gardiner, 1973) were chosen as outgroups based on Heard et al. (2018).

Data matrix of discrete characters was constructed using MorphoBank 3.0 (O'Leary & Kaufman 2012) and continuous characters were subsequently added at the data file. We adopted the parsimony criterion and performed phylogenetic reconstructions in TNT version 1.1 (Goloboff et al. 2008). A heuristic analysis was conducted using the traditional search algorithm, with 8000 replications and 500 trees held per replicate. Polymorphic characters were considered unordered. The branch-swapping algorithm used was 'tree bisection and reconnection' (TBR). Branch support was calculated using the relative Bremer support (subtrees up to ten extra steps; relative fit difference of 0.9; Bremer 1994) implemented in TNT. Character polarization was conducted *a posteriori* according to Nixon and Carpenter (1993), and character optimization was made with Winclada (Nixon 2002). For character discussion, the abbreviation used [SX(Y)] means the "state Y of character X" (Iwasa-Arai & Serejo 2018; Iwasa-Arai et al. 2019). Synapomorphic characters whose secondary homology (sensu De Pinna, 1991) was rejected are herein referred as 'homoplastic synapomorphy' synapomorphies (e.g., Wheeler et al. 1993; Gomes-da-Silva & Souza-Chies 2018; Iwasa-Arai & Serejo 2018).

The abbreviations used are as follows: A, antenna; Che, cheliped; CI, consistency index; Ep, pleonal epimera; f, female; Gn, gnathopod; Hd, head; l, left; L, length; LL, lower lip; m, male; Md, mandible; Mx, maxilla; Mxp, Maxilliped; P, pereopod; Per, pereonite; Pl, pleon; r, right; RI, retention index; S, state; T, telson; and U, uropod; UL, upper lip.

Biogeographical analysis

The distribution range of *Synapseudes* was divided into 12 areas, based on the presence of one or more endemic species according to the marine realms proposed by Costello et al. (2017) (Suppl. Mat. 3). These areas are: Mediterranean (A), North Pacific (B), Mid-Tropical North Pacific (C), Caribbean and

Gulf of Mexico (D), Gulf of California (E), Indo-Pacific and Indian Ocean (F), Coral Sea (G), Offshore Western Pacific (H), Offshore South Atlantic (I) and Rio de la Plata (J).

To examine the possible ancestral ranges of *Synapseudes*, we used the Bayesian Binary MCMC analysis (BBM) implemented in the program Reconstruct Ancestral State in Phylogenies (RASP; Yu et al., 2015) by using the morphological phylogeny described above (see Material & Methods, Phylogenetic analysis) as input topology. BBM was primarily designed for reconstructing ancestral state of given nodes by calculating the probabilities of ancestral ranges using the probabilities of each area unit generated by MrBayes (Ronquist & Huelsenbeck 2003), and it was chosen because of the ability to deal with phylogenetic uncertainty. The MCMC chains of BBM analysis were run simultaneously for two million generations, with a sampling frequency of every 100 generations and a 10% burn-in. The maximum number of areas for this analysis was kept as four.

Results

Eleven species of Peracarida are reported herein associated with *Dictyota* sp. from TR. Since records of peracarid crustaceans for this location are scarce, all observations but one are new records for the island. Of the two amphipod species previously reported, *Elasmopus besnardi* Oliveira, 1951 is currently considered a synonym of *Elasmopus brasiliensis* (Dana, 1853) (Horton et al. 2020), and *Cymadusa trindadensis* Andrade & Senna, 2017, endemic to TR, was the only previously reported species (Fig. 2). Herein we give the first records of Tanaidacea for TR, comprising two species, one new species of Apseudomorpha and one new record of Tanaidomorpha.

Taxonomy

Order Amphipoda Latreille, 1816

Suborder Senticaudata Lowry & Myers, 2013

Family Ampithoidae Boeck, 1871

Genus *Ampithoe* Leach, 1814

Ampithoe marcuzzii Ruffo, 1954

(Fig. 2A and B)

Ampithoe marcuzzii Ruffo, 1954: 120, figs I–II.—Barnard, 1958: 25.—Ortiz et al., 2007: 484.—Siqueira, 2012: 28, Anexo 1B.—Martín et al., 2013: 1705.—Paz-Ríos et al., 2013b: 9, fig. 9.—Campos et al., 2020: 2, figs. 1-3.

Ampithoe cf. *marcuzzii*.—LeCroy, 2002: 245, fig. 262.

Material examined: Three individuals (not sexed), Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4354); 3 individuals (not sexed), Ilha do Sul (20°31'27.5"S, 29°19'25.2"W), from *Dictyota* sp., April 2019, I. Batistela col. (ZUEC-CRU-4354).

Remarks: *Ampithoe marcuzzii* was described from Los Roques, Venezuela and its current distribution ranges the western Atlantic Ocean, from Florida to state of São Paulo (SP), southeastern Brazil (Serejo & Siqueira 2018; Campos et al. 2020). Specimens from TR are larger (up to 14 mm) than in the original description by Ruffo (1954), as observed by Siqueira (2012) in SP.

Ampithoe suapensis Correia, Guedes-Silva & Souza-Filho, 2016

Ampithoe suapensis Correia et al., 2016: 196, figs 1–4.

Material examined: Five individuals (not sexed), Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4356).

Remarks: *Ampithoe suapensis* was previously known only from its type locality in Suape Beach, state of Pernambuco, Brazil. The TR specimens agree well with the original description of *A. suapensis*.

Ampithoe thaix **Siqueira & Iwasa-Arai sp. nov.**

http://zoobank.org/F4432581-ECA0-49EE-90C0-3DE39566F7E1

(Figs. 3–5)

Material examined: Holotype: male, Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4357).

Paratype: one female, same as holotype. (ZUEC-CRU-4358).

Diagnosis: A2 heavily setose. Md palp article 2 2x longer than article 3, with 1 or 2 setae on margin. Mx1, inner plate with 1 seta. Gn1 slightly shorter than Gn2, Gn1 coxa produced anteriorly; propodus subrectangular and setose, palm transverse. Gn2, coxa oval; carpus with long setae on anterior margin, propodus subrectangular, palm transverse with 1 robust seta. P5–7 propodus with 3–5 robust setae posteriorly. U1 with round spur apical margin of peduncle, inner and outer rami lacking anterior robust setae. T subtriangular.

Etymology: This species is named after the marine biologist Thais Peixoto Macedo.

Description: Male (ZUEC-CRU-4357). Body (Fig. 3). Length 4.7 mm.

Eyes rounded and well developed. A1 moderately setose; flagellum 13-articulate. A2 heavily setose; flagellum 8-articulate. UL rounded. LL notched, inner and outer lobes setose apically. rMd, incisor and *lacinia mobilis* 7 and 4-toothed, respectively; accessory setal row with 3 serrated setae; palp 3-articulate, article 1 3.2x shorter than article 2; article 2 2x longer than article 3; article 3 1.5x longer than article 1; article 3 with 4 long plumose setae apically. lMd, molar with 1 long plumose seta and 1 short seta; incisor and *lacinia mobilis* 4 and 5-toothed, respectively; accessory setal row with 4 serrated setae; palp 3-articulate, article 3 with 4 long plumose setae apically, similar to right palp. Mx1, inner plate small and rounded, inner margin with 1 single short seta; outer plate with 7 stout serrated setae apically; palp 2-articulate with 3 stout setae and 1 long seta. Mx2, inner plate as long as outer plate, with marginal row of short setae, 7 long plumose setae on inner margin and 6 long plumose apical setae; outer plate, row of short setae on the inner and outer margin, long plumose setae on the apical and inner margin. Mxp, inner plate about 3x longer than wide, inner margin and apex with long setae and plumose long setae, apical margin with 2 robust setae; outer plate, 1.8x longer than wide, inner margin with 3 long plumose setae and 5 serrate robust setae, outer and apical margins with row of long plumose setae; palp 4-articulate, article 1, subtriangular, outer margin with 1 long setae, article 2 subrectangular, inner margin with row of long plumose setae, article 3 subrectangular inner margin with 6 long setae, outer margin with 5 long setae, article 4 with 2 long setae and 1 plumose seta (Fig. 4).

Gn1, slightly smaller than Gn2; coxa subtriangular, enlarged anteriorly, ventral margin bearing row of short setae; basis 2.3x longer than wide, anterodistal margin with 1 short seta, posterior margin with 2 setae; ischium subrectangular, 1.1x longer than wide, posterior margin with 1 long seta; merus 1.5x longer than wide, posterior margin with 5 long setae; carpus 1.1x longer than wide, anterodistal margin with 2 setae, posterior margin setose; propodus subrectangular, 1.8x longer than wide, anterior margin with 2 setae, anterodistal angle with 4 setae, posterior margin setose, posterodistal margin with one robust seta, palm transverse; dactylus 1.5x longer than palm, serrated, with 2 setae. Gn2, coxa oval, ventral margin bearing row of short setae; basis 1.8x longer than wide, anterior margin with 3 setae, posterior margin with 3 setae, inner face with 2 long setae; ischium small and subquadrate, as long as wide, posterior margin with 1 short seta; merus, 1.8x longer than wide, posterior margin setose; carpus, 1.3x longer than wide, anterior margin with 1 short and 4 long setae, posterior margin setose; propodus subrectangular, 1.8x longer than wide, anterior and posterior margins setose; palm transverse, with 1 robust seta delimiting palm; dactylus 1.5x longer than palm, with 2 setae (Fig. 3).

P3 not recovered (described from female). P4, coxa not recovered, basis subrectangular, 1.8x longer than wide, anterior margin with 2 setae, posterior margin with 3 setae; ischium small and subrectangular, 1.2x longer than wide, posterior margin with 2 long setae; merus subrectangular, 1.4x longer than wide, anterior margin with 2 setae, posterior margin with 2 setae; carpus subrectangular, 1.5x longer than wide, posterior margin with 3 setae; propodus subrectangular, 2.5x longer than wide, anterior margin with 5 setae, posterior margin with 5 setae; dactylus slightly curved, with one short seta. P5 not recovered (described from female). P6 not recovered (described from female). P7, coxa not recovered, basis 1.5x longer than wide, anterior margin with 3 setae, posterior margin with 2 setae; ischium small and subrectangular, 1.2x longer than wide, posterior margin with 1 seta; merus subrectangular, 2.2x longer than wide, anterior and posterior margins with setae; carpus subrectangular, 2.1x longer than wide, anterior margin with 2 setae, posterior margin with 6 setae; propodus elongate, 3.8x longer than wide, anterior margin with 8 long setae, posterior margin with 3 robust setae and 6 setae; dactylus slightly curved, with 2 short setae (Fig. 3).

U1, peduncle 3.5x longer than wide, with distoventral rounded spur, inner margin with 3 robust setae, outer margin with 2 robust setae and a row of long setae; inner ramus 1.2x longer than outer ramus, apical margin with 4 robust setae; outer ramus, apical margin with 4 robust setae. U2, peduncle 2.1x longer than wide, inner and outer margin with 1 robust setae each; inner ramus 1.2x longer than outer ramus, inner margin with 1 robust seta, apical margin with 5 robust setae; outer ramus, outer margin with 1 robust seta, apical margin with 4 robust setae. U3, peduncle slightly elongate, about 1.6x longer than wide, with 3 long setae and 4 robust setae; inner ramus slightly longer than outer ramus, apical margin with 2 long setae and 3 robust setae; outer ramus, apical margin with 2 curved robust setae. T subtriangular, lateral margins with 1 long plumose and 2 short setae, distolateral angles with 1 cusp and 1 short seta each (Fig. 4).

Female (ZUEC-CRU-4758). Body (Fig. 5). Length 4.8 mm.

Gn1, slightly smaller than Gn2; coxa subtriangular, enlarged anteriorly; basis 2.6x longer than wide, anterior and posterior margin with 1 long and 1 short setae each; ischium small and subrectangular, 1.3x longer than wide, posterodistal margin with 2 setae; merus 1.8x longer than wide, posterior margin setose; carpus 1.8x longer than wide, anterior margin with 3 setae, posterior margin setose; propodus subrectangular, 1.6x longer than wide, anterodistal and posterior margin setose, palm slightly convex, lacking robust seta; dactylus 3x longer than palm, serrated, with 1 plumose seta. Gn2, coxa oval, ventral margin with row of short setae; basis 2.4x longer than wide, anterior margin with 2 short setae, posterior margin with 1 short seta; ischium small and subrectangular, 1.4x longer than wide; merus 1.7x longer than wide, posterodistal margin setose; carpus triangular, 1.3x wider than long, anterior margin with few setae, posterior margin setose; propodus 1.7x longer than wide, anterior and posterior margins setose; palm slightly convex, with 1 robust seta delimiting palm; dactylus 2.2x longer than palm, with 1 plumose seta (Fig. 5).

P3, coxa oval, with 1 short seta; basis 2.2x longer than wide, anterior margin with 2 setae, posterior margin with 1 long and 3 short setae; ischium subrectangular, 1.2x longer than wide, posterior margin with 2 setae; merus subrectangular, 1.3x longer than wide, anterior margin with 2 setae, posterior margin with 3 setae; carpus subrectangular, 1.8x longer than wide, posterior margin with 5 setae; propodus subrectangular, 1.5x longer than wide, anterior margin with 6 setae, posterior margin with 5 setae; dactylus slightly curved, with 1 short seta. P5, coxa, ventral margin rounded with 3 short setae, lobe with 2 short setae; basis 1.2x longer than wide, anterior margin with 7 setae, posterior margin with 3 short setae; ischium subrectangular, 1.3x wider than long, anterior margin with 2 short setae; merus subrectangular, 1.7x longer than wide, anterior and posterior margins with 2 setae each; carpus subrectangular, 1.6x longer than wide, anterior margin with a tuft of apical setae, posterior margin with 4 setae; propodus elongate, 3x longer than wide, anterior margin with 3 setae and a tuft of apical setae, posterior margin with 5 robust and 5 simple setae; dactylus slightly curved, with 2 short setae. P6, coxa, ventral margin rounded and naked, lobe with 1 short setae; basis 1.5x longer than wide, anterior margin with 4 short setae, posterior margin with 2 short setae; ischium subrectangular, as wide as long, anterior margin with 1 short seta; merus subrectangular, 2x longer than wide, anterior and posterior margins with 3 setae each; carpus subrectangular, 1.8x longer than wide, anterior margin with a tuft of apical setae, posterior margin with 4 setae; propodus elongate, 3.4x longer than wide, anterior margin with 2 long setae and a tuft of apical setae, posterior margin with 4 robust and 7 setae; dactylus slightly curved, with 2 short setae (Fig. 5).

Type locality: Trindade Island, Espírito Santo state, Brazil.

Distribution: Currently known only from the type locality.

Remarks: The genus *Ampithoe* is the most speciose among Ampithoidae (Sotka et al. 2016), with 78 species described worldwide (Horton et al. 2020). Six species of *Ampithoe* were previously reported from the Brazilian coast: *Ampithoe divisura* Shoemaker, 1938, *Ampithoe marcuzzii* Ruffo, 1954; *Ampithoe ramondi* Audouin, 1826; *Ampithoe robustimana* Andrade & Senna, 2017; *Ampithoe seticoxae* Serejo & Licínio, 2002 e *Ampithoe suapensis* Correia and Guedes-Silva & Souza-Filho, 2016 (Serejo & Siqueira 2018). Among these species, *Ampithoe thaix* **sp. nov.** is morphologically closer to *A. divisura* and *A. suapensis* by presenting a round projection on the distal margin of uropod 1 peduncle. Although the validity of *A. divisura* was previously questioned (LeCroy et al. 2009), *Ampithoe thaix* **sp. nov.** can be easily differentiated from the *A. divisura* specimens from the Brazilian coast identified by Serejo & Licíno (2002) by lacking a digitiform process on gnathopod 2 palm and an anterodistal propodus projection, as well as by presenting robust setae on propodus of pereopods 5–7 (vs striated in *A. divisura*). *Ampithoe thaix* **sp. nov.** can also be differentiated from *A. suapensis* based on characters from mandible, gnathopods, uropods and telson. The mandible palp of *Ampithoe thaix* **sp. nov.** is large and robust, with 4 plumose setae on article 3, while *A. suapensis* presents a short and slender mandible palp with 3 setae on the apex. The propodus of gnathopod in *A. thaix* **sp. nov.** is subrectangular and setose on both dorsal and ventral margins, and the palm is defined by a robust seta, while the propodus of gnathopod 1 is oval and setose only on the palmar margin, which is not defined by a robust seta. The uropods of *A. thaix* **sp. nov** have asymmetric rami without setae on the inner margins, different from *A. suapensis*, where asymmetry is only observed on uropod 2, and both uropods

1 and 2 of *A. suapensis* have setae on the inner margins of the rami. Finally, *A. thaix* **sp. nov.** and *A. suapensis* can be distinguished by the telson shape, which is subtriangular in *A. thaix* **sp. nov.** and trapezoidal in *A. suapensis. Ampithoe thaix* **sp. nov.** is the third *Ampithoe* species reported from Brazilian oceanic islands.

Genus *Cymadusa* Savigny, 1816

Cymadusa trindadensis Andrade & Senna, 2017b

(Fig. 2C)

Cymadusa trindadensis Andrade & Senna, 2017b: 378, figs 12–15.

Material examined: Four females, Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4359).

Remarks: *Cymadusa trindadensis* is so far endemic to TR. Type specimens were collected over 40 years ago and lacked complete antenna. Specimens found herein differ from the original description in the number of articles in the antenna 1 flagellum, which is bi-articulate in *C. trindadensis* types and uni-articulate in the examined specimens. The number of robust and short setae on uropod 1 and 3 also varies, with the present specimens presenting uropod 1 with marginal robust setae on both rami, while in types it is present only on the inner margin of outer ramus, and uropod 3 bearing 4 robust setae and 9 long setae on the apical margin of the inner ramus whereas types have only 4 setae, as well as 1 short robust seta on the distolateral margin which is not present in the original description. The outer margin has 4 marginal setae instead of 1, as described by Andrade and Senna (2017).

Family Hyalidae Bulyčeva, 1957

Genus *Hyale* Rathke, 1836

Hyale niger (Haswell, 1879)

(Fig. 2D)

Allorchestes niger Haswell, 1879: 319.—1885: 95, pl. 11 figs 1–3.

Hyale nigra.—Stebbing, 1906: 571.—Schellenberg, 1928: 659, fig. 204.—Ledoyer, 1972: 273.—1979: 137, fig. 89.—1986: 1002, fig. 397.—J.L. Barnard, 1974: 66.—Serejo, 1999: 600, figs 5–7.—Leite, 2011: 176, fig. 3.14B.—Leite et al. 2011: 328.

Hyale niger.—Lowry & Stoddart, 2003: 129.

Material examined: Sixteen individuals (not sexed), Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4360). One individual (not sexed), Ilha do Sul (20°31'27.5" S, 29°19'25.2" W), from *Dictyota* sp., April 2019, I. Batistela col. (ZUEC-CRU-4361).

Remarks: *Hyale niger* is a species with disjunct distribution, described for southeastern Australia and later found in Brazil and Madagascar (Serejo 1999). Future works encompassing its broad distribution, detailed morphology and molecular data may elucidate the species status. The specimens from TR agree well with the specimens found in the southeastern Brazilian continental coast, where the species is usually observed especially in *Sargassum* spp. from São Paulo state (Leite 2011; Leite et al. 2011).

Protohyale Bousfield & Hendrycks, 2002

Protohyale macrodactyla Stebbing, 1899

(Fig. 2E)

Hyale macrodactylus Stebbing, 1899: 404, pl. 31d.

Hyale macrodactyla.—Stebbing, 1906: 565, fig. 96.—Oliveira, 1953: 339. Ledoyer, 1972: 273, pl. 77A.—1986: 1001, fig. 396.—Serejo, 1999: 592, figs 1, 2.—Leite, 2011.—Leite, et al. 2011.

Protohyale (Protohyale) macrodactyla.—Bousfield & Hendrycks, 2002: 79.

Protohyale macrodactyla.—LeCroy et al., 2009: 959.—Paz-Ríos et al., 2013a: 4, fig. 3.

Material examined: Seven individuals (not sexed), Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4362); 18 individuals (not sexed), Ilha do Sul (20°31'27.5"S, 29°19'25.2"W), from *Dictyota* sp., April 2019, I. Batistela col. (ZUEC-CRU-4363).

Remarks: *Protohyale macrodactyla* is a common species found in the Atlantic Ocean. The species was originally described from the Caribbean and later found along the Brazilian coast (Stebbing 1899, Serejo 1999, Leite 2011, Leite et al. 2011). The TR material agrees well with the specimens found on the Brazilian continental coast.

Family Maeridae Krapp-Schickel, 2008

Genus *Elasmopus* Costa, 1853

Elasmopus gabrieli Siqueira & Iwasa-Arai sp. nov.

http://zoobank.org/9AA8C7EB-56BD-4071-82E3-49045225BF82

(Figs 2F, 6–8)

Material examined: Holotype: male, Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-5364).

Paratypes: one male, two females, two juveniles, same as holotype (ZUEC-CRU-5365). Two females, one juvenile, same as holotype (ZUEC-CRU-5366).

Diagnosis: A1 1/2 of body length, with accessory flagellum 3-articulate. A2 short, 1/3 the length of A1. Md palp article 3 falcate, with plumose setae along margin, margin concave with 3 long setae on apex. Mxp palp with 4-articulate with terminal unguis. Gn1 propodus palm serrated. Gn2 propodus oval, with triangular process delimiting palm, with 1 subquadrate and 1 subrectangular processes close to dactylus articulation. Pereopods 37 propodus with row of robust setae on posterior margin and 1 locking seta distally. Pereopods 5–7 basis slightly serrated and convex. Epimeral plate 3 with posterior margin slightly serrate with 4 notches. U3 with several long plumose robust setae. T cleft (approximately 1/2 on its length), lobes apex slightly concave with 1 long robust plumose seta and 1 short robust seta.

Etymology: This species is named after the son of SGLS, Gabriel Siqueira.

Description: Male (ZUEC-CRU-5364). Body (Fig. 6). Legth 8.5 mm.

Head with eyes rounded and well developed (Fig. 6), lateral cephalic lobes rounded, with anteroventral notch. A1 longer than A2, about 0.5x body length, peduncular article 1 with 1 robust seta and 3 setae on distolateral margin and row of short setae laterally; peduncular articles 2 and 3 with tufts of setae on lateral and distal margins; accessory flagellum 3-articulate, shorter than first proximal article of flagellum, with 3 long setae on apex; flagellum 23-articulate and 1.1x longer than peduncular articles 1–3 combined, with aesthetascs present from articles 3 to 19. A2 stout, 3x shorter than A1; peduncular articles setose; flagellum 8-articulate, 2.3x shorter than peduncular articles 3–5 combined, proximal article longest, setae present in all articles. UL rounded, setose apically. LL notched, inner and outer lobes setose apically, outer lobe with 1 small projection on inner margin. rMd, molar with 1 long plumose seta; incisor with 3 teeth and medial part of plate without evident teeth, *lacinia mobilis* 7-toothed; accessory setal row with 3 serrated setae. lMd, molar with 1 long plumose seta; incisor and *lacinia mobilis* 2 and 5-toothed, respectively; accessory setal row with 4 serrated setae; palp 3-articulate, article 1 short, 1.5x longer than wide, article 2 elongate, 2x longer than wide, article 3 falcate, similar in size to article 2, with 3 long setae apically and a row of plumose setae on inner margin, with 21 setae in total, 18 of them plumose and 3 simple setae. Mx1, inner plate small and subtriangular, inner margin with row of thin setae, apex with 2 long plumose setae; outer plate with 7 stout serrated setae apically; palp 2-articulate, article 2 with long setae apically and on inner margin. Mx2, inner plate as long as outer plate, with marginal row of short setae on inner margin, 3 long plumose setae on inner margin and several long apical setae; outer plate, row of long setae apically, with 2 long plumose setae on the inner margin. Mxp, inner plate about 2.4x longer than wide, inner margin and apex with plumose long setae; outer plate, 1.8x longer than wide, inner margin with 4 long plumose setae and 7 serrate robust setae; palp 4-articulate, article 1, subtriangular, naked, article 2 subrectangular, inner margin with row of long setae, article 3 subrectangular inner margin with long setae, outer margin with 5 long setae, thin setae apically, article 4 with 3 setae, unguis with 1 short seta, falcate (Fig. 7).

Gn1 subchelate, smaller than Gn2; coxa subtriangular, enlarged anteriorly, ventral margin bearing row of short and long setae; basis 2.5x longer than wide, anterior margin with 2 short setae, posterior margin with 2 long setae, posterodistal margin with 1 seta; ischium subtriangular, as long as wide, posterior margin with a tuft of setae; merus subrectangular, about 1.5x longer than wide, distal margin setose; carpus 1.6x longer than wide, anterodistal margin with 2 seta, posterior margin heavily setose; propodus subrectangular, 1.8x longer than wide, anterior margin with 3 pairs of short setae and 1 long seta each, anterodistal angle with a tuft of setae, posterior margin setose with a row of setae, palm transverse, serrated, with long and short setae along its margin and delimited by a robust seta; dactylus falcate, with 2 short setae. Gn2 subchelate, coxa oval, ventral margin bearing row of short setae and 3 long setae; basis 2.1x longer than wide, anterior margin with row of setae, posterior margin with 3 long and 2 short seta; ischium small and subquadrate, 1.2x longer than wide, posterodistal margin with 1 seta; merus subrectangular, 1.6x longer than wide, posterodistal margin setose; carpus subtriangular, 1.3x wider than long, anterodistal margin with 1 robust and 5 long setae, posterior margin setose with a row plumose setae and 1 long seta distally; propodus elongate, 2.1x longer than wide, anterior margin with row of short setae, anterodistal angle with a tuft of setae, posterior margin setose, with 1 triangular process delimiting palm and 1 distal subquadrate and 1 proximal subrectangular processes with 4 robust setae distally, palm slightly concave; dactylus falcate, fitting palm, posterior margin with tiny setae, with 1 single short seta on anterior margin, and apically blunt (Fig. 6).

P3, coxa oval, 1.8x longer than wide, anterior margin 2 long setae; basis subrectangular, 3.5x longer than wide, anterodistal margin with 2 short setae, posterior margin with 3 short setae; ischium small and subrectangular, as long as wide, posterior margin with 1 short seta; merus subrectangular, 2.6x longer than wide, anterior margin with 3 setae, posterior margin with 5 setae; carpus subrectangular, 2.1x longer than wide, anterior margin with 2 setae, posterior margin with 5 setae; propodus subrectangular, 3.4x longer than wide, anterior margin with 1 seta, posterior margin with 5 and 1 posterodistal locking seta; dactylus stout, with 1 distal short setae. P4, coxa oval, ventrally produced, 1.3x longer than wide, anterior margin with row of short setae and 1 long seta, ventral margin with long seta; basis subrectangular, 3.5x longer than wide, anterior margin with sparse short setae, anterodistal margin with 2 short setae, posterior margin with 4 setae; ischium small and subrectangular, 1.1x longer than wide, with 1 short setae posteriorly; merus subrectangular, 2.4x longer than wide, anterior margin with 5 setae, posterior margin with 3 setae; carpus subrectangular, 2.5x longer than wide, anterior margin with 3 setae, posterior margin with 6 setae; propodus subrectangular, 3.7x longer than wide, anterior margin with 2 setae, posterior margin with 5 and 1 robust setae, and 1 posterodistal locking seta; dactylus stout, with 2 short setae. P5, coxa bilobed, posterior lobe narrower, with 3 short robust setae; basis oval, 1.3x longer than wide, anterior margin with a row of short setae, posterior margin convex and slightly serrated; ischium subquadrate, as wide as long, posterodistal margin with tuft of setae; merus subrectangular, 1.3x longer than wide, anterior margin with 5 setae and 1 short robust seta, posterior margin with 2 tufts of setae, posterodistal margin produced with 3 setae;

carpus subrectangular, 1.5x longer than wide, anterior margin with long setae, anterodistal margin with 1 short robust seta, posterior margin with 7 setae; propodus subrectangular, 3.5x longer than wide, anterior margin with 2 setae, anterodistal margin with 3 setae and 1 short robust seta, posterior margin with 2 single and 3 paired setae; dactylus stout, with 1 short seta. P6, coxa bilobed, posterior lobe narrower, with 3 short robust setae and 2 short setae ; basis oval, 1.3x longer than wide, anterior and posterior margins with a row of short setae, posterior margin convex and casteloserrated; ischium small and subquadrate, 1.1x wider than long, anterodistal margin with 2 setae; merus subtriangular, 1.6x longer than wide, anterior margin with tufts of setae, anterodistal margin produced, with 2 setae, posterior margin with 2 long and 2 short setae, posterodistal margin with 4 short setae; carpus subtriangular, 1.9x longer than wide, anterior and posterior margins with tufts of setae; propodus subrectangular, 4.2x longer than wide, anterior margin with 4 setae, posterior margin with 4 paired robust setae, and 1 posterodistal locking seta; dactylus stout, with 1 short seta. P7, coxa naked; basis oval, 1.1x longer than wide, anterior and posterior margins with a row of short setae, posterior margin convex and slightly casteloserrated; ischium small and subrectangular, 1.1x longer than wide, posterodistal margin with 3 long setae; merus subrectangular, 1.7x longer than wide, anterior margin with pairs of setae, anterodistal margin with tuft of setae, posterior margin with 3 pairs of setae, posterodistal margin produced; carpus subrectangular, 1.8x longer than wide, anterior margin with 3 tufts of 3 setae each, anterodistal margin with 4 setae, posterior margin with 10 setae; propodus subrectangular, 3.5x longer than wide, anterior margin with tufts of long setae, posterior margin with 7 setae and 1 locking setae distally; dactylus stout, with 1 seta (Fig. 8).

Ep, epimeron 1 with 1 oblique ledge on surface, with 2 setae on ventral margin, with 1 small posterior projection; epimeron 2 flattened ventrally, with 3 pairs of setae on ventral margin, posterior margin with 2 small projections; epimeron 3 largest, slightly serrated, flattened ventrally, with 5 pairs of setae on ventral margin, posterior margin with 4 projections, 3 of them with one seta (Fig. 6).

U1, peduncle 2.7x longer than wide, inner margin with 4 short pinnate robust setae and 1 long robust seta apically, outer margin with 4 robust setae and 3 long setae, 1 robust seta posteriorly; inner ramus 1.4x longer than outer ramus, inner margin with 2 robust setae, outer margin with 3 robust setae, apical margin with 5 robust setae; outer ramus, inner margin with 3 robust seta, outer margin with 2 robust setae, apical margin with 4 robust setae. U2, peduncle 2x longer than wide, inner margin with 2 robust setae, outer margin with one robust seta; inner ramus 1.3x longer than outer ramus, inner margin with 3 robust setae, outer margin with 2 robust setae, apical margin with 5 robust setae; outer ramus, inner margin with 2 robust setae, outer margin with 3 robust setae, apical margin with 4 robust setae, 1 of them pinnate. U3, peduncle subrectangular, about 1.5x longer than wide, inner margin with 1 robust seta, outer margin with 2 setae, distal margin with 7 robust setae; outer ramus longer than inner ramus, outer margin with 9 robust setae, 4 of them pinnated, inner margin with 2 robust setae, apical margin with 2 setae and 8 robust setae, 3 of them pinnated; inner ramus, outer margin with 1 robust seta, apical margin with 5 robust setae, 2 of them pinnated. T cleft (about 1/2 length), lateral margins with 1 pappose seta, posterolateral margins with 2 robust setae (1 long and plumose, 1 short) and 1 pappose seta (Fig. 8).

Female (ZUEC-CRU-4365). Length 7.9 mm.

Gn1 similar to male, subchelate, smaller than Gn2. Gn2 subchelate, coxa oval, ventral margin bearing row of short setae and 2 long setae; basis 3.1x longer than wide, anterior margin with row of setae, posterior margin with 2 medium and 2 short seta; ischium small and subquadrate, 1.4x longer than wide, posterodistal margin with 1 long and 2 short seta; merus subrectangular, 1.4x longer than wide, posterodistal margin setose; carpus subtriangular, 1.3x wider than long, anterodistal margin with 2 setae, posterior margin heavily setose, with a row of plumose and a row of simple long setae; propodus elongate, 2.2x longer than wide, anterior margin with row of short seta, anterodistal angle with a tuft of setae, posterior margin setose, lacking processes, palm slightly concave, delimited by 2 robust setae; dactylus falcate, length similar to palm, with 4 short setae and apically blunt (Fig. 6).

U3, peduncle subrectangular, about 1.5x longer than wide, inner margin with 1 robust seta, outer margin with 3 setae, distal margin with 6 robust setae; outer ramus longer than inner ramus, inner margin with 8 robust setae, 3 of them pinnated, outer margin with 1 robust setae, apical margin with 6 robust setae, 1 of them pinnated; inner ramus, margins smooth, apical margin with 3 robust setae. T cleft (about ½ length), lateral margins with 2 pappose setae, posterolateral margins with 2 robust setae (Fig. 8).

Type locality: Trindade Island, Espírito Santo, Brazil.

Distribution: Currently known only from the type locality.

Remarks: *Elasmopus besnardi* was firstly described from TR based on a female specimen, and it was reported as *nomen dubium* by Ruffo (1959). It is currently considered a synonym of *Elasmopus brasiliensis* (Dana, 1853) (Horton et al. 2020), with types of the *E. besnardi* being lost (Souza-Filho & Serejo 2012) and the species never reported after its description. *Elasmopus gabrieli* **sp. nov.** female differs from the former *E. besnardi* in several characters, including accessory flagellum 3-articulate, shorter than first proximal article of flagellum (vs accessory flagellum 2-articulate, larger than first proximal article of flagellum), articles 2 and 3 of mandibular palp similar in length (vs article 3 lager than 2), palm of gnatopods delimited by robust setae and length dactylus similar to palm (vs not delimited palm and length dactylus shorter to palm); inner ramus of uropod 3 without robust setae on inner margins (vs inner margins with robust setae) and telson cleft about ½ length (vs telson totally cleft). Alves et al. (2016) observed that species of *Elasmopus* have some morphological patterns and therefore suggested the species separation into four groups, in which *Elasmopus gabrieli* **sp. nov.** can be placed in the group 3, together with *E. longipropodus* Senna & Souza-Filho, 2011, *E. rapax* Costa, 1853, *E. thalyae* Gouillieux & Sorbe, 2015, *E. thomasi* Ortiz & Lalana, 1994 and *E. yupanquii* Alves, Johnsson & Senna, 2016, by having 3 palmar processes on gnathopod 1 of male. Within the group, *E. gabrieli* **sp. nov.** is more related to *E. longipropodus* from Brazil and *E. thalyae* from France by sharing the following characters: antenna 1 accessory flagellum with 3 articles, pereopod 5 basis with convex posterior margin, epimeral plate 3 serrated and uropod 3 inner ramus slightly shorter than outer ramus. *Elasmopus gabrieli* **sp. nov.** differs from *E. thalyae* by having gnathopod1 palm serrated (vs smooth), 3 processes on gnathopod 2 palm, 1 proximal triangular, and 1 subquadrate and 1 subrectangular processes distally (vs triangular, triangular and subquadrate, respectively), epimeron 1–3 with short setae on ventral margin (vs long and short setae), telson cleft 0.5x length (vs 0.84x length), lobes apical margin slightly concave with undeveloped cusps (vs lobes apical margins concave with well developed cusps). *Elasmopus gabrieli* **sp. nov.** also differs from *E. longipropodus* by having a accessory flagellum shorter than first proximal article of flagellum of antenna 1 (vs larger than first proximal article of flagellum), mandible palp articles 2 and 3 with same length (vs article 2 shorter than article 3), article 3 falcate with plumose setae along its concave margin and with 3 long setae on apex (vs 4 apical setae), gnathopod 2 propodus 2x longer than wide (vs 2.5x longer than wide), palm defined by a triangular process, palm margin with a subquadrate and a subrectangular process distally (vs a subacute process and a palmar corner defined by a strong acute triagular process), length dactylus similar to palm (vs length dactylus shorter to palm), pereopods 3–7 propodus with 1 locking seta distally (without locking seta), uropod 3 with 2 setae on inner margin of outer ramus (vs one seta), and telson with undeveloped cusps, with 2 robust seta, 1 long and plumose, and 1 short in each lobe (vs with apicolateral cusps well developed, with 3 robust setae).

Krapp-Schikel and Ruffo (1990) grouped the species *Elasmopus canarius* Krapp-Schickel & Ruffo 1990, *E. pectenicrus* (Bate, 1862), *E. serricatus* J.L. Barnard, 1969, *E. spinibasus* Sivaprakasam, 1970, *E. crenulatus* Berents, 1983, *E. laufolii* Myers, 1986 based on the presence of a very dense fringe of long setae on the posterior margin of gnathopod 2 of the male and by a casteloserrate posterior margin of the basis of pereopods 6 and 7. The herein described species, *E. gabrieli* **sp. nov.** shares the casteloserrate pattern on basis of pereopods 6 and 7, however, it lacks a very dense fringe of long setae on gnathopod 2 of male. Most of these species have an intertropical distribution in the Indo-Pacific region, and future cladistic biogeographic analysis may elucidate the evolution of these characters across the ocean basins.

***Elasmopus viracochai* Alves, Johnsson & Senna, 2016**

(Fig. 2G)

Elasmopus viracochai Alves et al., 2016: 21, figs 17–22.

Material examined: One male, Ilha do Sul (20°31'27.5"S, 29°19'25.2"W), from *Dictyota* sp., April 2019, I. Batistela col. (ZUEC-CRU-4367).

Remarks: *Elasmopus viracochai* was so far known only from its type locality, in Ceará state, northeastern Brazil. Only one male specimen was found in TR samples, and it agrees well with the original description.

Family Pontogeneiidae Stebbing, 1906

Genus *Eusiroides* Stebbing, 1888

***Eusiroides lucai* Siqueira & Iwasa-Arai sp. nov.**

http://zoobank.org/B1EE8F0A-A0DB-43DB-846B-66122E836110

(Figs 2H, 9–10)

Material examined: Holotype: female, Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4368).

Diagnosis: Antennae with stout peduncular articles, with calceoli on flagellum; accessory flagellum of A1 uni-articulate, shorter than first proximal article of flagellum. rMd molar without seta, incisor with

2 teeth, 1 wide and the other weakly developed, *lacinia mobilis* serrated. lMd incisor with 3 teeth, *lacinia mobilis* 6-toothed; palp article 3 with 3 long plumose setae apically. Mx1 outer plate with 10 stout serrated setae apically, palp 2-articulate. Mx2, inner plate longer than outer plate. Mxp palp with 5 articles, article 5 falcate. Gnathopods similar to each other, dactylus falcate, with proximal plumose seta. P3–7 propodus with row of robust setae on posterior margin and 1 locking seta distally. Pleonal epimera each with 2 marginal setae ventrally; epimera 2 and 3 with oblique edge on surface; epimeron 3 with 1 process posteriorly. U1 peduncle with row of robust setae. U2 shorter than U1, inner ramus 2x shorter than outer ramus. U3 inner ramus with a row of plumose setae. T deeply cleft (approximately 1/2 on its length).

Etymology: This species is named after the son of SGLS, Luca Siqueira.

Description: Female (ZUEC-CRU-4368). Body (Fig. 9). Length 8.3 mm.

Head with eyes reniform and well developed. A1 2.1x shorter than body length; peduncular article 1 with 2 plumose setae distolateral margin and 1 plumose seta laterally, with a few setae on lateral and distal margins; peduncular articles 2 and 3 with setae on lateral and distal margins; accessory flagellum uni-articulate, shorter than first proximal article of flagellum, with 4 setae on apex; flagellum 26-articulate and 2.1x longer than peduncular articles 1–3 combined, with calceoli present from articles 2 to 10, and aesthetascs present from articles 2 to 25 discontinuously. A2 stout, 1.7x shorter than A1; peduncular articles setose; flagellum 23-articulate, slightly longer than peduncular articles 3–5 combined, proximal article longest, with calceoli present from articles 1 to 20. UL rounded, setose in medial region. LL notched, inner lobe setose on outer margin; outer lobes setose apically and on inner margin. rMd, molar without setae; incisor with 2 teeth, 1 wide and the other weakly developed, *lacinia mobilis* serrated; accessory setal row with 3 serrated setae; palp 3-articulate, article 3 with 3 long plumose setae apically. lMd, molar with 2 short setae; incisor and lacinia mobilis 3 and 6-toothed, respectively; accessory setal row with 3 serrated setae and 1 seta; palp 3-articulate, article 3 with 3 long plumose setae apically. Mx1, inner plate small and rounded, inner margin with 2 short setae; outer plate with 10 stout serrated setae apically; palp 2-articulate with 7 long setae. Mx2, inner plate longer than outer plate; inner plate, marginal row of short setae, robust setae on inner margin and short setae apically; outer plate, long plumose setae on the apical and inner margin. Mxp, inner plate small, 1.3x shorter than outer plate, inner plate, inner margin and apex with 4 plumose long setae, apical margin with 5 robust setae; outer plate, 3.2x longer than wide, inner margin and apex with row of long plumose setae; palp 5-articulate, article 1, subtriangular, apex with 2 long setae, article 2 subrectangular, inner margin with row of long setae, article 3 subrectangular inner margin with long setae, outer margin with 6 serrated long setae, 3 long plumose setae and short seta, article 4 with 3 short setae; article 5 naked, falcate (Fig. 10).

Gn1, as long as Gn2; coxa subtriangular, enlarged anteriorly, ventral margin bearing row of short setae; basis 3x longer than wide, anterior margin with 3 setae, posterior margin with 1 long and 1 short seta, anterodistal margin with a tuft of setae and 2 robust setae, posterodistal margin with 1 seta; ischium subquadrate, as long as wide, posterior margin with a tuft of setae; merus subrectangular, about 1.2x longer than wide, posterior margin heavily setose; carpus 1.1x wider than long, anterodistal margin with 1 long seta, posterior margin heavily setose; propodus oval, 1.4x longer than wide, anterior margin with 1 short seta, anterodistal angle with a tuft of setae, posterior margin setose with a row of and robust setae, palm slightly convex, serrated; dactylus falcate, with a proximal plumose setae and a row of short setae. Gn2, coxa subrectangular, ventral margin bearing row of short setae; basis 3x longer than wide, anterodistal margin with 3 setae, posterior margin with 1 seta; ischium small and subquadrate, as long as wide, posterodistal margin with 1 long seta; merus, 1.4x longer than wide, with a setose posterodistal projection, distal margin with a row of setae; carpus, 1.2x wider than long, anterodistal margin with 1 short seta, posterior margin setose; propodus oval, 1.6x longer than wide, anterior margin with 1 short seta, anterodistal angle with a tuft of setae, posterior margin setose with a row of robust setae, palm slightly convex, serrated; dactylus falcate, with a proximal plumose setae and a row of short setae (Fig. 9).

P3, coxa subrectangular, 1.7x longer than wide, anterior margin with a row of short setae; basis subrectangular, 3.6x longer than wide, with proximal long seta and anterodistal margin with 3 setae; ischium small and subrectangular, 1.5x longer than wide, posterior margin with 1 short seta; merus subrectangular, 2.5x longer than wide, anterior margin with 3 setae, posterior margin with 3 setae; carpus subrectangular, 2.2x longer than wide, anterior margin with 2 setae, posterior margin with 5 setae; propodus subrectangular, 3.8x longer than wide, anterior margin with 4 setae, posterior margin with 4 simple and 4 robust setae, and 1 posterodistal locking seta; dactylus falcate, bi-articulated, with 1 plumose seta and 2 short setae. P4, coxa acutely produced backwards posteriorly, 1.1x longer than wide, anterior margin with 2 short setae; basis subrectangular, 3.6x longer than wide, anterodistal margin with 3 setae and posterodistal margin with 2 setae; ischium small and subrectangular, 1.1x longer than wide, naked; merus subrectangular, 2.3x longer than wide, anterior margin with 4 setae, posterior margin with 4 setae; carpus subrectangular, 2.1x longer than wide, anterior margin with 3 setae, posterior margin with 4 setae; propodus subrectangular, 3.7x longer than wide, anterior margin with 4 setae, posterior margin with 4 slender and 4 robust setae, and 1 posterodistal locking seta; dactylus falcate, bi-articulated, with 1 plumose seta and 1 short setae. P5, coxa bilobed, posterior lobe narrower and more ventrally produced than anterior lobe, naked; basis oval, 1.3x longer than wide, anterior and posterior margins with a row of short setae; ischium small and subrectangular, 1.3x wider than long, posterodistal margin with 2 setae; merus subrectangular, 1.5x longer than wide, anterior margin with 4 setae, posterior margin with 2 robust setae and posterodistal margin with 2 setae; carpus subrectangular, 1.6x longer than wide, anterior margin with 3 setae, posterior margin with 5 setae; propodus subrectangular, 4x longer than wide, anterior margin with tufts of setae, posterior margin with 3 paired setae, and one posterodistal locking seta; dactylus falcate, bi-articulated, with 2 short setae (Fig. 13). P6, coxa bilobed, posterior lobe narrower and more ventrally produced than anterior lobe, naked; basis oval, 1.2x longer than wide, anterior and posterior margins with a row of short setae; ischium small and subrectangular, 1.1x wider than long, posterodistal margin with 2 setae; merus subrectangular, 2.4x longer than wide, anterior margin with 3 setae, anterodistal margin with 2 robust setae, posterior margin with 2 setae and posterodistal margin with 2 robust setae; carpus subrectangular, 2.5x longer than wide, anterior margin with 2 setae and 3 robust setae, posterior margin with 7 setae; propodus subrectangular, 4.7x longer than wide, anterior margin with tufts of setae, posterior margin with 3 paired robust setae, and 1 posterodistal locking seta; dactylus falcate, bi-articulated, with 1 short seta and 1 plumose seta. P7, coxa oval, naked; basis oval, 1.3x longer than wide, anterior and posterior margins with a row of short setae; ischium small and subrectangular, 1.1x wider than long, posterodistal margin with 2 setae; merus subrectangular, 2.3x longer than wide, anterior margin with 3 setae, anterodistal margin with 2 robust setae, posterior margin with 3 pairs of setae; carpus subrectangular, 2.5x longer than wide, anterior margin with 3 setae and 3 robust setae, posterior margin with 6 slender setae and 1 robust seta; propodus subrectangular, 4.7x longer than wide, anterior margin with tufts of setae, posterior margin with paired robust setae; dactylus falcate (Fig. 91).

Ep, epimeron 1 with 1 oblique ledge on surface, with 2 setae on ventral margin anteriorly; epimeron 2 with 2 setae on ventral margin anteriorly; epimeron 3 largest, flattened ventrally, with 2 setae on anterior half of ventral margin, posterior margin with 1 tooth (Fig. 9).

U1, margins with tiny setae, peduncle 4.7x longer than wide, inner margin with 6 robust setae, outer margin with 4 robust setae, margins with tiny setae; inner ramus 1.2x longer than outer ramus, inner margin with 2 robust setae, apical margin with 3 robust setae; outer ramus, inner margin with 1 robust seta, outer margin with 2 robust setae, apical margin with 6 robust setae. U2, peduncle 2.3x longer than wide, inner margin with 2 robust setae, outer margin with 1 robust seta; inner ramus 2x shorter than outer ramus, inner and outer margin with 3 robust setae each, apical margin with 4 robust setae; outer ramus, apical margin with 3 robust setae, margins with tiny setae. U3, lanceolate and foliaceous, peduncle subrectangular, about 1.7x longer than wide, inner margin with 2 robust setae, outer margin with 1 robust seta; inner ramus as long as outer ramus, inner margin with 5 robust setae and 4 long plumose setae, outer margin with 2 robust setae, apex with 1 seta; outer ramus, inner margin with 3 robust setae and 1 plumose seta, outer margin with 3 robust setae, apex with 1 seta, margins with tiny setae. T cleft (about 1/2 length), lateral margins with row of setae, margins with tiny setae, lobes with round apex (Fig. 91).

ype locality: Trindade Island, Espírito Santo state, Brazil.

Distribution: Currently known only from the type locality.

Remarks: The genus *Eusiroides* currently has 16 described species (Horton et al. 2020), which are very similar according to the morphology of antennae, eyes, gnathopods and uropod 3 (Barnard & Karaman, 1991). Species of *Eusiroides* can be distinguished from each other by the presence or absence of teeth and serrated posterior margin of epimeron 3, and by telson shape (cleft, moderate or deeply cleft) (Barnard, 1932; Ledoyer 1982; Thomas 1993). Based on these characters, *Eusiroides lucai* **sp. nov.** is more similar to *E. georgiana* K.H. Barnard, 1932, by having a tooth on posterior margin of epimeron 3, however, *E. lucai* **sp. nov.** can be distinguished from its congeneric by presenting gnathopods 1 and 2 palm serrated, pereopods 3–4 with 1 distal locking seta on propodus, uropods 1–3 with tiny setae on margins, inner ramus of uropod 2 2x shorter than outer ramus (vs 1.5), telson ½ cleft (vs 2/3), lateral margin of lobes with row of setae and apex round with 1 seta (vs 1 seta on lateral margins and acute apex). Although the species was described based on a single specimen, its isolated geographical distribution and its conspicuous morphological characters suggest *E. lucai* **sp. nov.** to be a new species, and further samplings on TR are likely to report more individuals. This is the third record of Pontogeniidae for Brazil, where *Eusiroides* sp. was reported from Pernambuco state (Santos & Soares 1999) and *Tethygeneia longleyi* (Shoemaker, 1933) was previously reported from São Paulo and Paraná states (southeastern Brazil).

Order Tanaidacea Dana, 1849

Suborder Apseudomorpha Sieg, 1980

Superfamily Apseudoidea Leach, 1814

Family Metapseudidae Lang, 1970

Subfamily Synapseudinae Guțu, 1972

Genus *Synapseudes* Miller, 1940

Synapseudes isis Segadilha, Siqueira & Iwasa-Arai sp. nov.

http://zoobank.org/733CEA04-27C6-42D5-AE0F-3D048DF66F6E

(Figs 11–12)

Material examined: Holotype: female, Ilha do Sul (20°31'27.5"S, 29°19'25.2"W), from *Dictyota* sp., April 2019, I. Batistela col. (ZUEC-CRU-4369).

Paratypes: one male, same as holotype (ZUEC-CRU-4370).

Diagnosis: Female. Body 4x longer than wide. Cephalothorax shorter than Per 1–3 lengths combined. Rostrum appearing undifferentiated, truncated. Pleon with 3 segments appearing functionally fused; but with 2 pleonites remnants delineated by sutures, at least dorsally. Antennule article 2 without tubercles or spiniform apophysis. Antenna article 1 with inner margin strongly serrated; flagellum bi-articulate terminating in 1 long and 1 short setae. Mxp palp article 1 with distolateral seta strongly developed; palp article 2 distolateral stout seta 1.5x longer than that on palp article 1. Cheliped merus, carpus and propodus with plumose setae ventrally; fixed finger with row of 10 setae on incisive margin. Pereopod 1 propodus with 4 stout spiniform setae on ventral margin. P1–3 basis with 3, 2 and 1 spiniform apophyses on ventral margin, respectively. Uropod endopod composed of 3 articles and exopod of 2 articles.

Male. Cheliped basis dorsal margin with strong crenulation; merus ventral margin with medial seta and large pointed apophyses distally; carpus more trapezoidal shaped than in female, ventral margin with 2 setae and small acute subdistal apophyses; propodus with 2 setae near articulation of dactylus; fixed finger with 1 rounded tubercle, 3 sub-marginal and 3 minute marginal setae on outer incisive margin. Dactylus with 2 rounded tubercles and 6 setae on ventral margin.

Etymology: "The specific epithet is a noun in apposition after the oceanographer Isis Batistela".

Description: Female (ZUEC-CRU-4369). Body (Fig. 12). Length 1.1 mm, almost 4x longer than longer wide.

Cephalothorax 27% of TBL, shorter than Per 1–3 lengths combined, longer than longer than wide; rostrum truncated with broad base, smooth; eyelobes well defined, pigment and ommatidia present. Carapace with finely plumose setae on lateral margin and near each ocular lobe (Fig. 11).

A1 shorter than cephalothorax. Peduncle with 4 articles. Article 1 robust, 2.2x longer than wide; inner margin with row of 7 irregularly shaped blunt teeth or tubercles and 2 setae distally; outer margin with 2 medial penicillate and 1 and 3 subdistal setae. Article 2 as long as wide; with 6 setae distally. Article 3 slightly longer than wide; with distal seta. Article 4 0.7x longer than wide; with distal seta. Outer flagellum with 3 articles. Article 1 wider than long, with distal aesthetasc. Article 2 0.8x longer than wide; with aesthetasc and seta distally. Article 3 short, with 3 terminal setae. Inner flagellum with 2 articles. Article 1 twice longer than wide, naked. Article 2 minute, distally with 6 setae. A2 peduncle with 4 articles: Article 1 robust with bulge, with serrate inner margin. Article 2 inner margin with seta; squama absent. Article 3 about as long as article 2; outer margin with seta. Article 4 1.8x longer than wide, inner margin with 2 medial and 1 distal setae; with 7 setae along outer margin. Flagellum with 2 articles. Article 1 with very long seta and article 2 with 2 terminal setae of different widths. rMd incisor smooth; setiferous lobe with reduced bifurcate *lacinia mobilis* and 3 serrated setae, *pars molaris* with 1 acute and 2 blunt lobes and plumose seta distally. Palp with 3 articles; article 1 longest, 1.3x longer than article 2, naked; article 2 1.5x longer than wide, naked; article 3 with 3 serrated setae. lMd serrate *pars incisiva*, *lacinia mobilis* smooth; setiferous lobe with 3 serrated setae, *pars molaris* robust, blunt, with plumose seta distally; mandibular palp broken during dissection. Mx1 outer endite with apparently 6 terminal strong serrated spines; inner endite bearing 6 finely plumose setae. Palp bi-articulate with 2 long subdistal setae. Mx2 with long seta on outer margin. Moveable endite outer lobe with distal margin bearing 4 long setae; inner lobe of moveable endite with 4 setae. Fixed endite outer lobe with 6 setae; inner be of fixed endite with 7 setae. Mxp basis naked, narrow. Palp article 1 trapezoidal, with long seta (reaching article 3) on inner distal margin and robust spine on outer distal margin; article 2 longest, inner margin finely serrate proximally, with 10 setae, outer margin with 2 small apophyses and distal long seta; article 3 with 6 setae along inner margin and 1 plumose setae distally; article 4 with 6 plumose inner setae and 3 subdistal setae. Endite inner margin with 3 sub-cylindrical tubercles proximally and 5 subdistal setae; 5 setae apically; outer margin with 5 thin setae (Fig. 12).

Che basis, 1.2x longer than wide; ventral margin with medial and distal setae; dorsal margin with strong crenulation. Merus triangular; ventral margin with plumose seta subdistally. Carpus 2.7x longer than wide, longer than basis, widest distally; ventral margin with medial plumose and distal setae; dorsal margin with minute distodorsal seta. Propodus 1.4x longer than wide; with 2 setae near articulation of dactylus; fixed finger with 3 ventral plumose setae, with 5 sub-marginal and 3 marginal setae on outer incisive margin. Dactylus and unguis slightly longer than fixed finger; with 4 setae on ventral margin (Fig. 11).

Pereon about 60% of TBL, all pereonites wider than long, all with 2 finely plumose setae on subdistal dorsal margin and one seta on each anterolateral margin; Per 1−3 wider than others; Per2−3 longer than Per1; Per6 shortest. P1 coxa lacking apophysis, with seta. Basis 2.9x longer than wide; ventral margin with sub-proximal and distal setae; 3 setae and 2 smaller and 1 larger triangular apophyses along dorsal margin. Ischium wider than long, with ventral seta. Merus 1.9x longer than wide, widest distally; ventral margin with small medial spine and subdistal long plumose seta and spine; dorsal margin with proximal seta and distal seta and large spine. Carpus about as long as wide, widest distally, ventral margin with 2 subdistal spines; distodorsal margin with 2 plumose setae (1 longer than other) and 1 spine. Propodus twice longer than wide, with 4 spines along ventral margin; dorsal margin with subdistal long plumose seta and spine. Dactylus together with unguis shorter than propodus, dactylus longer than unguis; dactylus with 2 minute ventral setae and small subdistal denticle. Unguis curved. P2 coxa lacking apophysis, naked. Basis 3.1x longer than wide; ventral margin with minute medial seta; 3 setae and 1 rounded and 2 triangular apophyses along dorsal margin. Ischium wider than long, with 3 ventral setae. Merus 1.9x longer than wide, widest distally; ventral margin with minute medial seta; distodorsal margin with large spine. Carpus 0.8x longer than wide; ventral margin with subdistal spines and 2 distal apophyses; distodorsal margin with plumose seta and small spine. Propodus 1.8x longer than wide; with 4 spines along ventral margin; dorsal margin with medial seta, distal long plumose seta, spine and triangular apophyses. Dactylus together with unguis shorter than propodus, dactylus longer than unguis; dactylus with 2 minute ventral setae and small subdistal denticle. Unguis curved. P3 basis 2.7x longer than wide; ventral margin with 2 medial and 1 distal setae; dorsal margin with 2 penicillate setae and rounded apophysis. Ischium with ventral setae. Merus 1.9x longer than wide, widest distally; ventral margin subdistal seta; distodorsal margin with seta and spine. Carpus 0.8x longer than wide; ventral margin with 2 subdistal spines; distodorsal margin with 1 plumose seta and 2 spines. Propodus twice longer than wide; with 3 spines along ventral margin; dorsal margin with medial seta, distal long plumose seta and spine. Dactylus together with unguis shorter than propodus, dactylus longer than unguis; dactylus with 2 minute ventral setae and small subdistal denticle. Unguis curved. P4 basis 3.4x longer than wide; ventral margin with proximal and distal setae; dorsal margin with 2 setae. Ischium wider than long, with ventral plumose setae. Merus 1.5x longer than wide; widest distally; distoventral margin with 2 setae and 2 spines. Carpus 1.4x longer than wide; ventral margin with spine; distodorsal margin with 2 setae (1 longer than other) and 1 spine. Propodus 2.7x longer than wide; ventral margin with 3 spines; distodorsal margin with 2 plumose and 1 setae. Dactylus curved, together with unguis shorter than propodus, dactylus longer than unguis, with 2 (1 medial and 1 subdistal) ventral setae and small subdistal denticle. Unguis curved. P5 basis 3x longer than wide; with 6 setae along ventral margin; dorsal margin subproximal seta. Ischium with 2 ventral setae. Merus about as long as wide; distoventral margin with seta; distodorsal margin with 4 setae. Carpus 0.8x longer than wide; ventral margin with seta; distodorsal margin with seta. Propodus 3.7x longer than wide; ventral margin with medial seta and subdistal spine; dorsal margin with subdistal and distal setae. Dactylus together with unguis shorter than propodus, dactylus longer than unguis, with 1 mid-dorsal and 2 subdistal ventral setae and small subdistal denticle ventrally. Unguis curved. P6 basis 3.3x longer than wide; with 3 setae along dorsal margin. Ischium with ventral setae. Merus 1.5x longer than wide; ventral margin with subdistal seta; distodorsal margin with spine. Carpus 1.2x longer than wide; ventral margin with subdistal seta; distodorsal margin with seta and spine. Propodus 3.7x longer than wide; ventral margin with sub-proximal seta and subdistal spine; dorsal margin with subdistal seta. Dactylus together with unguis shorter than propodus, dactylus longer than unguis; dactylus with 1 subdistal ventral seta. Unguis curved (Fig. 12).

Pleon about 13% of TBL, shorter than Per 1–2 lengths combined, slightly longer than wide; last 3 pleonites fused to pleotelson, all indications of pleonites similar in length, without pleopods; pleonite 1 with 3 pairs of finely plumose dorsal setae and 1 seta on each lateral margin; pleonite 3 with 2 finely plumose setae dorsally. Pleotelson length 0.2x that of all pleonites combined, apex large and rounded tip. Pleopods absent.

U biramous. Basal article longer than wide; inner margin with distal seta. Exopod with 2 articles, shorter than endopod articles 1−2 combined; article 1 with penicillate seta; article 2 with 2 distal setae. Endopod with 3 articles; article 1 with distal seta; article 2 longest, with distal seta; article 3 with 2 long and 2 short terminal setae (Fig. 12).

Male (ZUEC-CRU-4370)**.** Body (Fig. 12). Length 1.1 mm.

Che, chela symmetrical. Similar but more robust and distinctly larger than those of the female. Basis ventral margin with medial and distal setae; dorsal margin with strong crenulation. Merus triangular, ventral margin with medial seta and large pointed apophyses distally. Carpus broad and short, more trapezoidal shaped than in female, ventral margin with 2 setae and small acute subdistal apophyses. Propodus with 2 setae near articulation of dactylus; fixed finger with 1 medial and 3 subdistal plumose setae on ventral margin; with 1 rounded tubercle, 3 submarginal and 3 minute marginal setae on outer incisive margin. Dactylus and unguis slightly longer than fixed finger; with 2 rounded tubercles and 6 setae on ventral margin.

Type locality: Trindade Island, Espírito Santo state, Brazil.

Distribution: Currently known only from the type locality.

Remarks: *Synapseudes isis* **sp. nov.**, *Synapseudes menziesi* Băcescu, 1976, *S. pinosensis* (Guțu & Ortiz, 2009) and *S. rectifrons* Guțu, 1996 are distinguished from the other 23 members of the genus as follows: bi-articulate antennal flagellum terminating in a long seta, remnants of 2 pleonites present, and uropod endopod composed of 3 articles. The new species from Brazil can be separated from *S. pinosensis* by having ventral margin of P1 propodus with four stout spiniform setae (3 spiniform setae in *S. pinosensis*), and antennule article 2 without distal spiniform apophysis (peduncular article 2 innerdistally with a dentiform expansion in *S. pinosensis*). *Synapseudes isis* **sp. nov.** is different from *S. menziesi* by rostrum appearing undifferentiated, truncated (rostrum with irregularly bilobed anterior margin in *S. menziesi*) and Mxp palp article 2 distolateral stout seta 1.5x longer than that on palp article 1 (as long as in *S. menziesi*).

Synapseudes isis **sp. nov.** closely resembles the other Brazilian species *S. rectifrons*, but can be distinguished from it by antennule article 2 without tubercles or spines (with a spine on inner margin and a small tubercle on outer margin in *S. rectifrons*), antenna article 1 with inner margin strongly serrated (smooth in *S. rectifrons*), and maxilliped palp article 1 with distolateral seta strongly developed (thin and weakly-developed in *S. rectifrons*). Also, *S. isis* **sp. nov.** appears unique by having cheliped merus, carpus and propodus with plumose setae ventrally, cheliped fixed finger with row of 10 setae on incisive margin, and P1–3 with 3, 2 and 1 spiniform apophyses on ventral margin of the basis, respectively.

Suborder Tanaidomorpha Sieg, 1980
Family Leptocheliidae Lang, 1973
Genus *Chondrochelia* Guțu, 2016

***Chondrochelia dubia* (Krøyer, 1842)**

Material examined: Nine females, Piscinas do Parcel (20°31'10.812"S, 29°19'25.8"W), from *Dictyota* sp., September 2018, T. P. Macedo col. (ZUEC-CRU-4371); 3 females, Ilha do Sul (20°31'27.5"S, 29°19'25.2"W), from *Dictyota* sp., April 2019, I. Batistela col. (ZUEC-CRU-4372).

Remarks: *Chondrochelia* is a shallow water genus with dimorphic males and females, and *C. dubia* was firstly described as *Tanais dubius* from Brazil, and currently shows a worldwide distribution. Differences in morphological characters among *Chondrochelia* species are subtle, and further molecular studies may elucidate species delimitation within the genus. The new record agrees with the overall diagnosis of *C. dubia*, and extends its distribution to the island of Trindade.

Phylogenetic analysis

Heuristic searches resulted in four most parsimonious trees (L=65 steps; CI = 50 and RI = 61), which were combined into a strict consensus tree and this topology was used for the following data interpretation (Fig. 13). Clade letters are represented below branches for the clades discussed ahead.

Clade A encompasses the genus *Synapseudes,* supported by four synapomorphies, including three non-homoplastic synapomorphies: presence of three terminal setae on mandibular palp [S6(0)], presence of setae on palp article-2 of Md [S7(1)] and two coupling hooks (retinacula) on endite of Mxp [S19(0)]; and one homoplastic synapomorphy: four articles on the uropodal endopod [S16(1)].

Clade B includes two clades of *Synapseudes* (clades C and D), and it is supported by two pleonites [S17(0)]. Clade C is composed of *S. heterocheles* (Vanhöffen, 1914), *S. setoensis* Shiino, 1951, *S. dispina* Menzies, 1953, *S. minutus* Miller, 1940, *S. isis* **sp. nov.**, *S. mediterraneus* Băcescu, 1977, *S. aflagellatus* Sieg, 1986 and *S. shiinoi* Riggio, 1973*,* grouped by one non-homoplastic synapomorphy, the presence of three spiniform setae on ventral margin of propodus of pereopod 2 [S10(0)], and one homoplastic synapomorphy, one article on antennal flagellum [S12(0)]. Clade D is comprised by *S. rectifrons*, *S. rudis* Menzies, 1953, *S. australianus* Băcescu, 1981, *S. caleyi* Stępień & Błażewicz, 2018, *S. hansmuelleri* Guţu, 2006, *S. minimus* Guţu, 2006, *S. tomescui* Guţu, 2006, *S. violaceus* Băcescu, 1976, *S. pinosensis*, *S. cystoseirae* Amar & Cazaubon, 1978 and *S. erici* Błażewicz-Paszkowycz, Heard & Bamber, 2011. This clade is clustered by the absence of distal spiniform apophyses on antennular peduncle article-2 [S13(0)].

Finally, clade E comprises by *S. isis* **sp. nov.** as the sister clade of *S. mediterraneus*, *S. aflagellatus* and *S. shiinoi,* supported by the homoplastic synapomorphy of three pleonites [S17(1)] and symmetrical chelipeds in male [S18(2)].

Biogeographical analysis

The results of BBM analysis indicated that dispersal played a key role in shaping the current distribution patterns of *Synapseudes* (Fig. 14), totaling 15 dispersals between areas within the genus. According to the analysis, the neighbor realms (G) Coral Sea and (F) Indo-Pacific and Indian Ocean are the two most likely ancestral areas of *Synapseudes* (node 46), with 50.50% and 22.48% marginal probability, respectively. The analysis suggests an early dispersal to the North Pacific (B) and the Caribbean and Gulf of Mexico (D), followed by sympatric speciation events along the Indo-Pacific and Indian Oceans.

A transoceanic dispersion is proposed for ancestors on node 42, with a single dispersion from the Pacific to the Atlantic Ocean before the separation into two main *Synapseudes* clades. The first main clade (clade C, Fig. 15) shares a strict evolutionary relationship with the Atlantic followed by a late dispersal to the Mediterranean (A). On the other hand, the second main clade (clade D, Fig. 15) mostly remains in the Indo-Pacific and Coral Sea realms, with a second dispersal to the Caribbean and Gulf of Mexico.

Concerning the new species from TR, *Synapseudes isis* **sp. nov.**, its ancestor's area of distribution (node 31) suggests the last Atlantic speciation before the dispersal to the Mediterranean, with 73.26% and 15.25% marginal probabilities, respectively.

Discussion

According to the classical Theory of Island Biogeography (IBT) proposed by MacArthur and Wilson (1967), species richness is positively correlated with island area and negatively correlated with isolation. Additionally, Rosenzweig (1995) also commented on the importance of island age for predicting species richness. The General Dynamic Theory of Oceanic Island Biogeography (GDM, Whittaker et al. 2008), also takes into account island age as an important factor for predicting islands species richness on islands, together with island area and isolation, but relies not only on the island birth, but the death processes that leads to erosion and consequent habitat loss (Hachich et al. 2019). Although these factors are known to influence species richness, species richness is highly determined by the taxon studied, as observed for reef fishes, seaweed and marine gastropods in shallow waters (Hachich et al. 2015). Therefore, the results presented herein aim to contribute to the knowledge of Peracarida biogeography in shallow water habitats from oceanic islands.

The fauna of Peracarida from TR indeed agrees with the isolation of the island, in which only eleven species were sampled associated to *Dictyota* sp., whereas 30 species were found in the same algae at the Abrolhos Bank (Cunha et al. 2013), a 46,000 km^2 projection of the Brazilian continental shelf (Dutra et al. 2005), including two orders (Cumacea and Isopoda) not observed in TR (Figs. 1 and 15). The Abrolhos Bank harbors the largest and most diverse reef complex of the South Atlantic (Leão 1982; Dutra et al. 2005) presenting high levels of coral endemism (Leão and Dominguez 2000), however, benthic invertebrates such as crustaceans and polychaetes showed low levels of endemicity for the area (Paiva 2005; Young and Serejo 2005; Cunha et al. 2013).

Regarding its endemicity, Peracarida is one of the most endemic taxon among the marine invertebrate fauna (Costello et al. 2017; Arfianti & Costello 2020), and TR shows a high endemicity rate of 45%, higher than that observed for other Crustacea taxa previously reported for the island, such as Anomura, Axiidea and Caridea, with 28%, 25% and 4%, respectively (Anker 2016; Tavares et al. 2017; Lima et al. 2019; Pachelle & Tavares 2020). Other Decapoda taxa such as Achelata, Brachyura and Stenopodidea lacked any species endemic to TR (Tavares et al. 2017). Nonetheless, we believe that the actual number of Peracarida species from TR is still underestimated, once only Peracarida associated with *Dictyota* up to 10 m deep were sampled herein. Therefore, considering the broad range of Peracarida lifestyles, from planktonic to benthic and parasitic, further samplings are recommended to better assess TR biodiversity.

The cladistic analysis of *Synapseudes* supported the monophyly of the genus, and agreed with the erection of the genus *Ronabus* by Heard et al. (2018). *Ronabus* is separated from *Synapseudes* based on the number of antennal flagella [S2(2)], the number of antennal terminal setae [S4(3)], the number of articles in inner and outer antennular flagellum [S5(0) and S6(1)], the number terminal setae on mandibular palp [S7(3)], number of articles on uropodal exopod [S15(2)], and telson with bulgae [S20(1)]. The analysis also showed two main clades within *Synapseudes* (clades C and D), which are discussed according to its distribution (Fig. 13).

The BBM analysis of the genus *Synapseudes* is the first event-based biogeographic attempt to understand the dynamics of fauna associated with macroalgae over long periods of time. Even though its is well known that macroalgae are the best drifters substrata particularly for Peracarida because of lack of larval phase (Thiel 2003), providing shelter and nutrition even in harsh environments, knowledge on the evolutionary processes that have driven the current distribution are scarce.

We recovered the Indo-Pacific + Coral Sea realms as the ancestral distribution area of *Synapseudes* (Fig. 16)*,* supporting the proposal of an Indo-Pacific 'center of origin', where species originated in the biodiversity center colonize marginal areas and speciate (Bowen et al. 2013). Six species presented the current distribution within the realm of Indo-Pacific and Indian Ocean (realm F), followed by three species distributed in the Mediterranean (realm A), the Caribbean and Gulf of Mexico (realm D), and Offshore South Atlantic (realm I). Therefore, the BBM analysis suggests an Indo-Pacific + Coral Sea origin followed by multiple dispersals to other ocean realms. From the Indo-Pacific + Coral Sea origin, the first dispersal of *Synapseudes* ancestors was to the North Pacific (realm B) and to the Caribbean and Gulf of Mexico (realm D), while consecutive sympatric speciations continued to raise species number in the Indo-Pacific (Fig. 14).

The separation of *Synapseudes* into two main clades correspond to the first dispersal to the Offshore South Atlantic (realm I), where most of the ancestors speciated, suggesting a niche suitability for the genus. A possible return to the Pacific Ocean is suggested on node 33, where three dispersals to new realms within the Pacific are observed (nodes 28, 32 and 33), while the ancestors that remained in the Atlantic later dispersed to the neighboring realms of the Mediterranean (realm A) and Rio de La Plata (realm J). The second main clade remained in the Indo-Pacific region, with a second dispersal to the Atlantic, whereas successive sympatric speciations in the Indo-Pacific and Coral Sea continued to happen. Lastly, another dispersal to the Caribbean and Gulf of Mexico (realm D) followed by sympatric speciation were observed for *Synapseudes* (Fig. 14).

This first attempt to understand the evolution of Peracarida associated with macroalgae suggests multiple dispersions from an Indo-Pacific center of origin, and better understanding of the paleocurrents dynamics, other Peracarida taxa phylogenetics and molecular data will certainly help unpuzzling the historical biogeography of fauna-macroalgae association.

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Figures and Tables

Figures

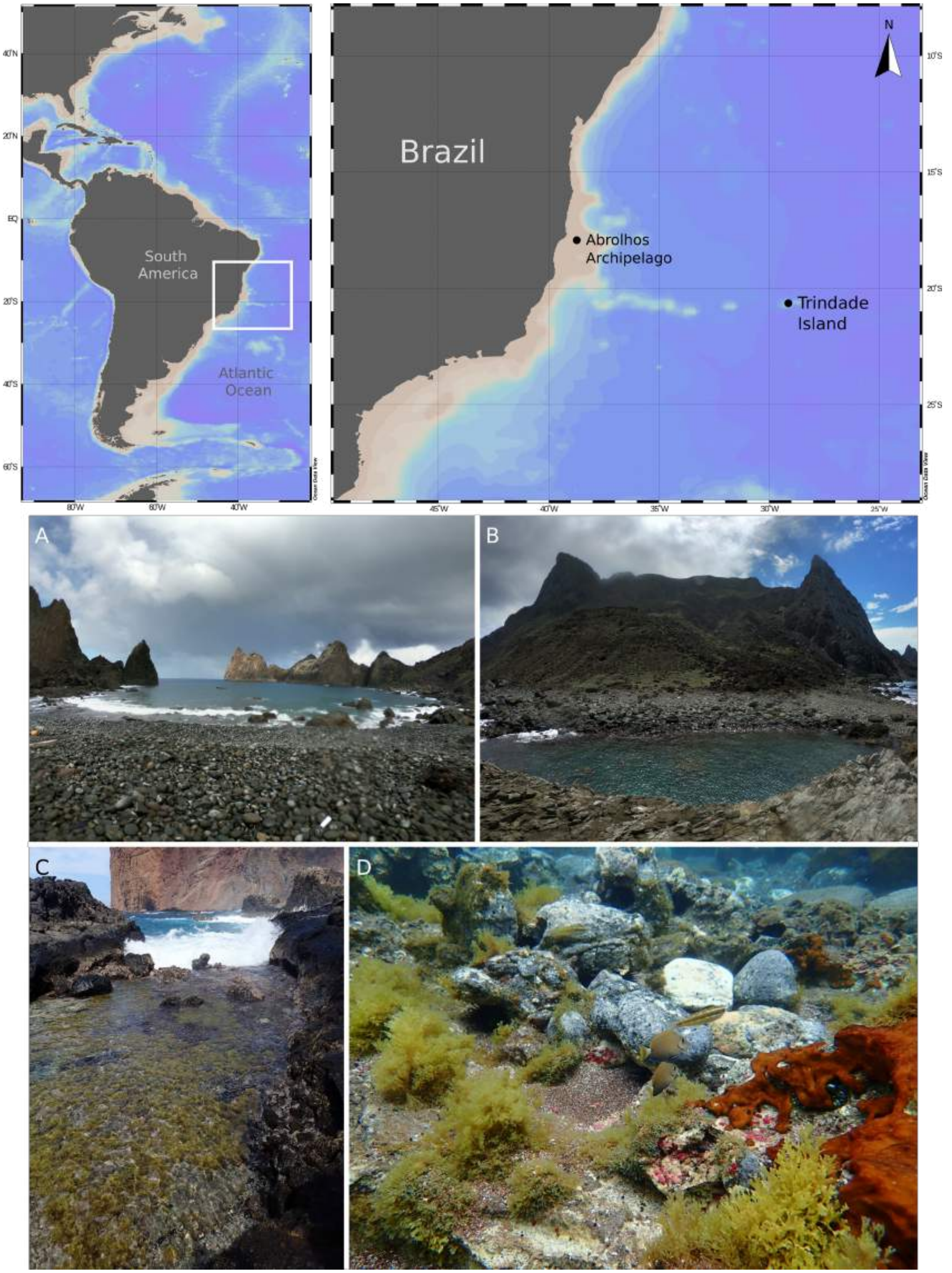

Figure 1. Location of Trindade Island and Abrolhos Archipelago and sampling localities of *Dictyota* sp. at Trindade Island. **A.** Ilha do Sul; **B.** Piscina da Praia do Lixo; **C and D**. Piscina do Parcel.

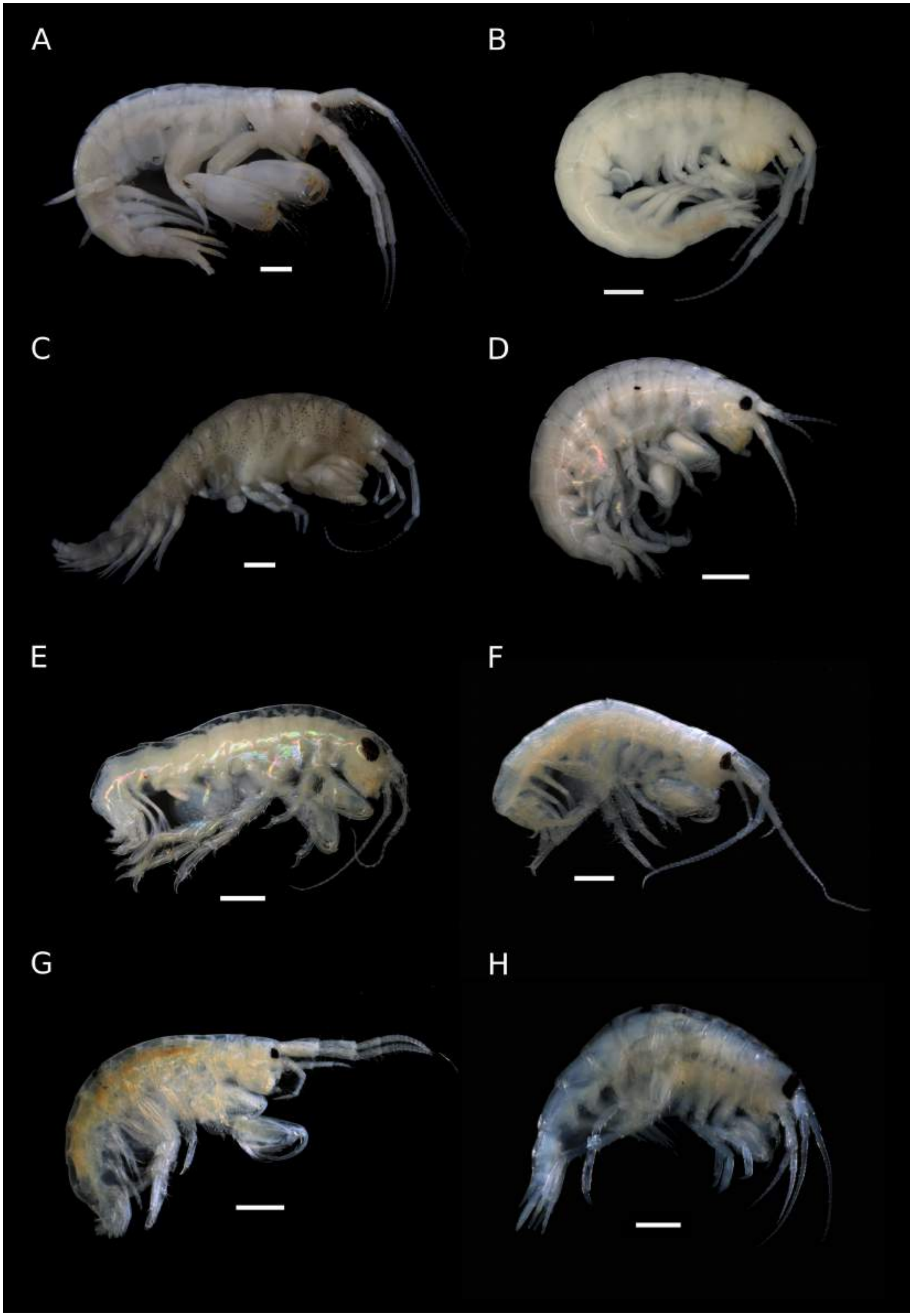

Figure 2. Amphipoda from Trindade Island. **A.** *Ampithoe marcuzzii* male (ZUEC-CRU-4354); **B.** *Ampithoe marcuzzii* female (ZUEC-CRU-4355); **C.** *Cymadusa trindadensis* (ZUEC-CRU-4359); **D.** *Hyale niger* (ZUEC-CRU-4360); **E.** *Protohyale macrodactyla* (ZUEC-CRU-4362); **F.** *Elasmopus gabrieli* **sp. nov., G.** *Elasmopus viracochai* (ZUEC-CRU-4367); **H.** *Eusiroides lucai* **sp. nov.** (ZUEC-CRU-4368). Scale bar: 1mm.

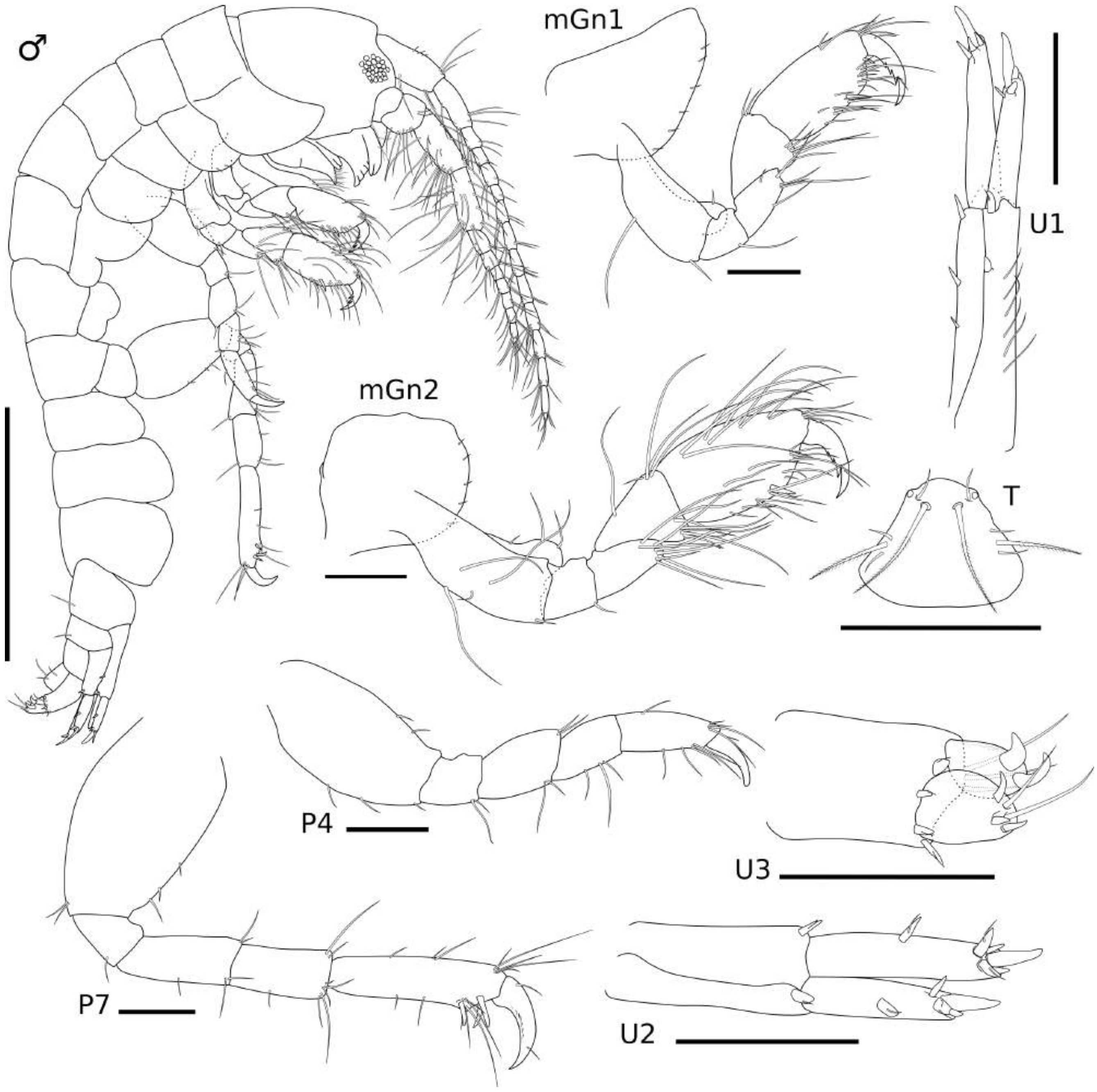

Figure 3. *Ampithoe thaix* Siqueira & Iwasa-Arai **sp. nov.** Male (ZUEC-CRU- 4357). Scale bar: 1mm. Gnathopods, pereopods, uropods and telson. Scale bar: 100 µm.

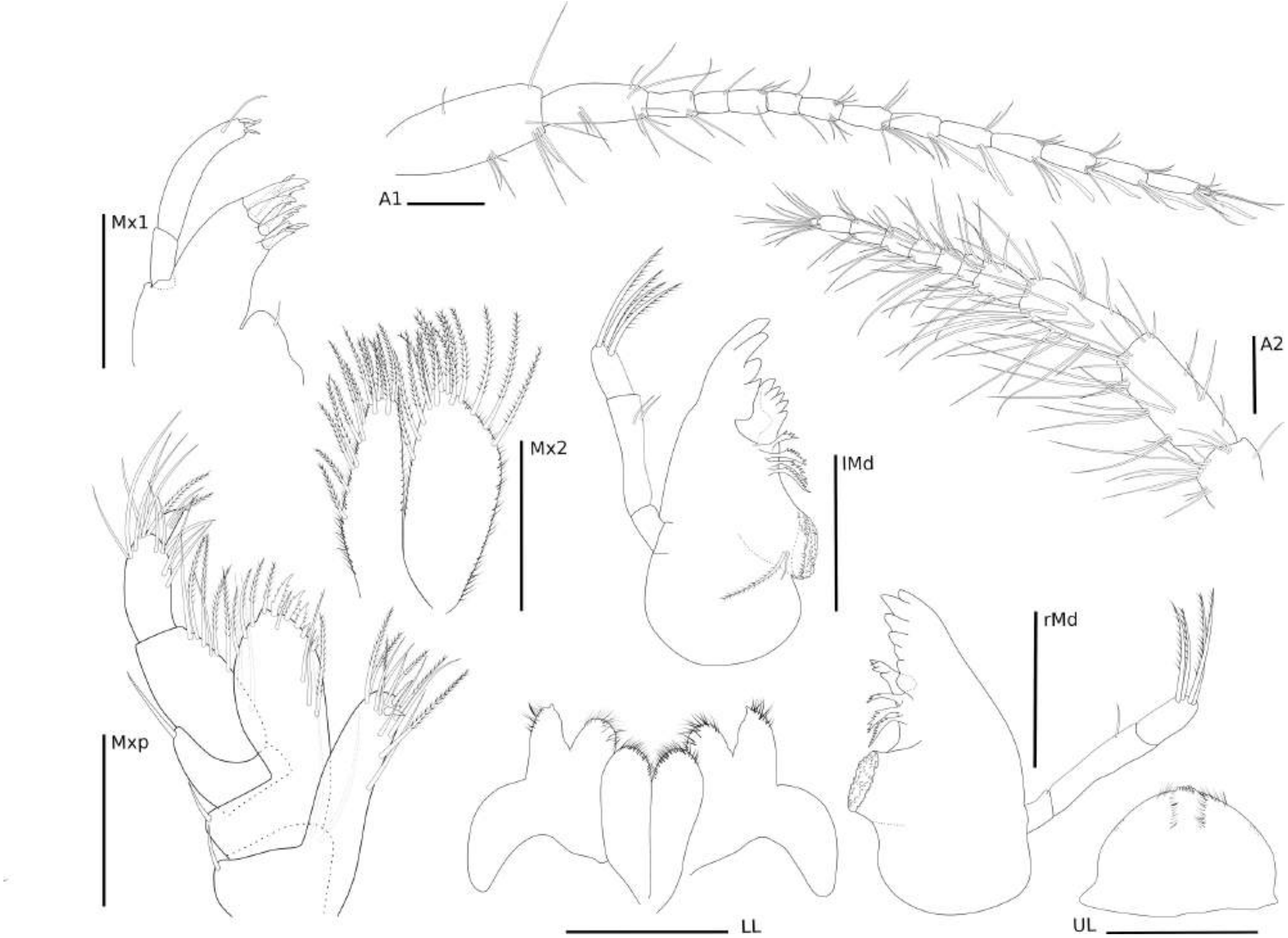

Figure 4. *Ampithoe thaix* Siqueira & Iwasa-Arai **sp. nov.** Antennae and mouthparts. Scale bar: 100 µm.

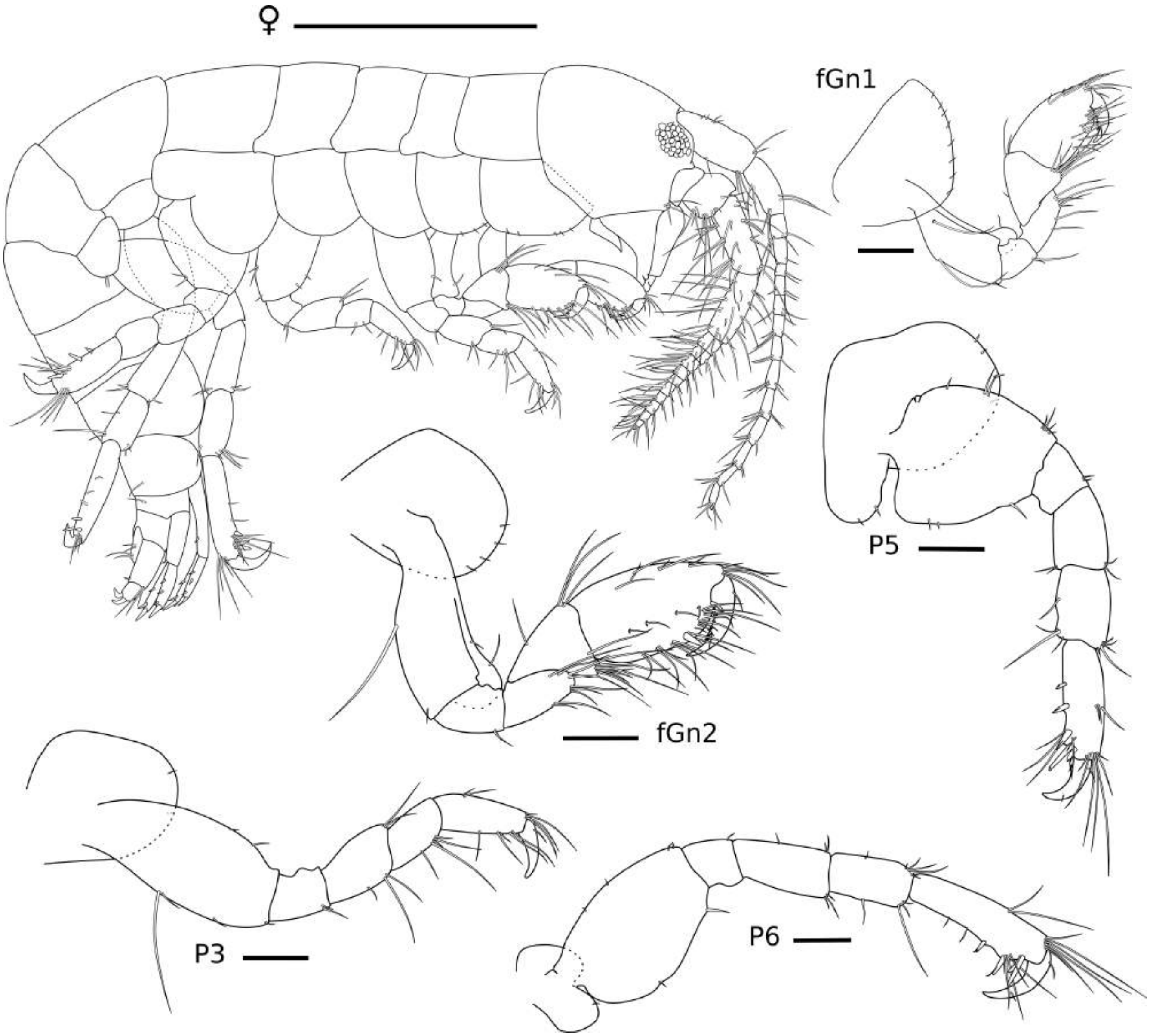

Figure 5. *Ampithoe thaix* Siqueira & Iwasa-Arai **sp. nov.** Female (ZUEC-CRU-4358). Scale bar: 1mm. Gnathopods and pereopods. Scale bar: 100 µm.

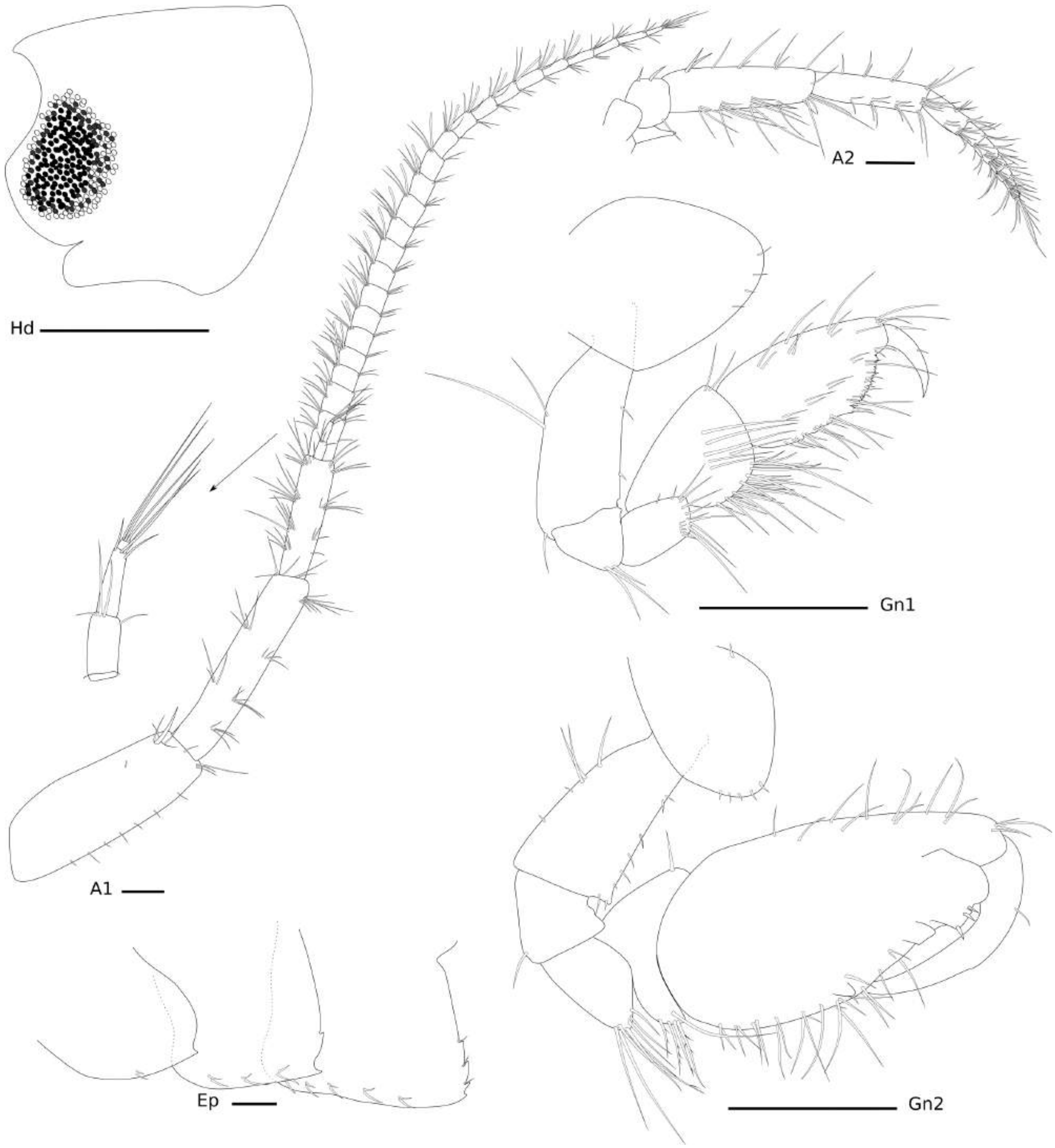

Figure 6. *Elasmopus gabrieli* Siqueira & Iwasa-Arai **sp. nov.** Male (ZUEC-CRU-5364). Head and gnathopods. Scale bar: 0.5mm. Antennae and epimeral plates. Scale bar: 100 µm.

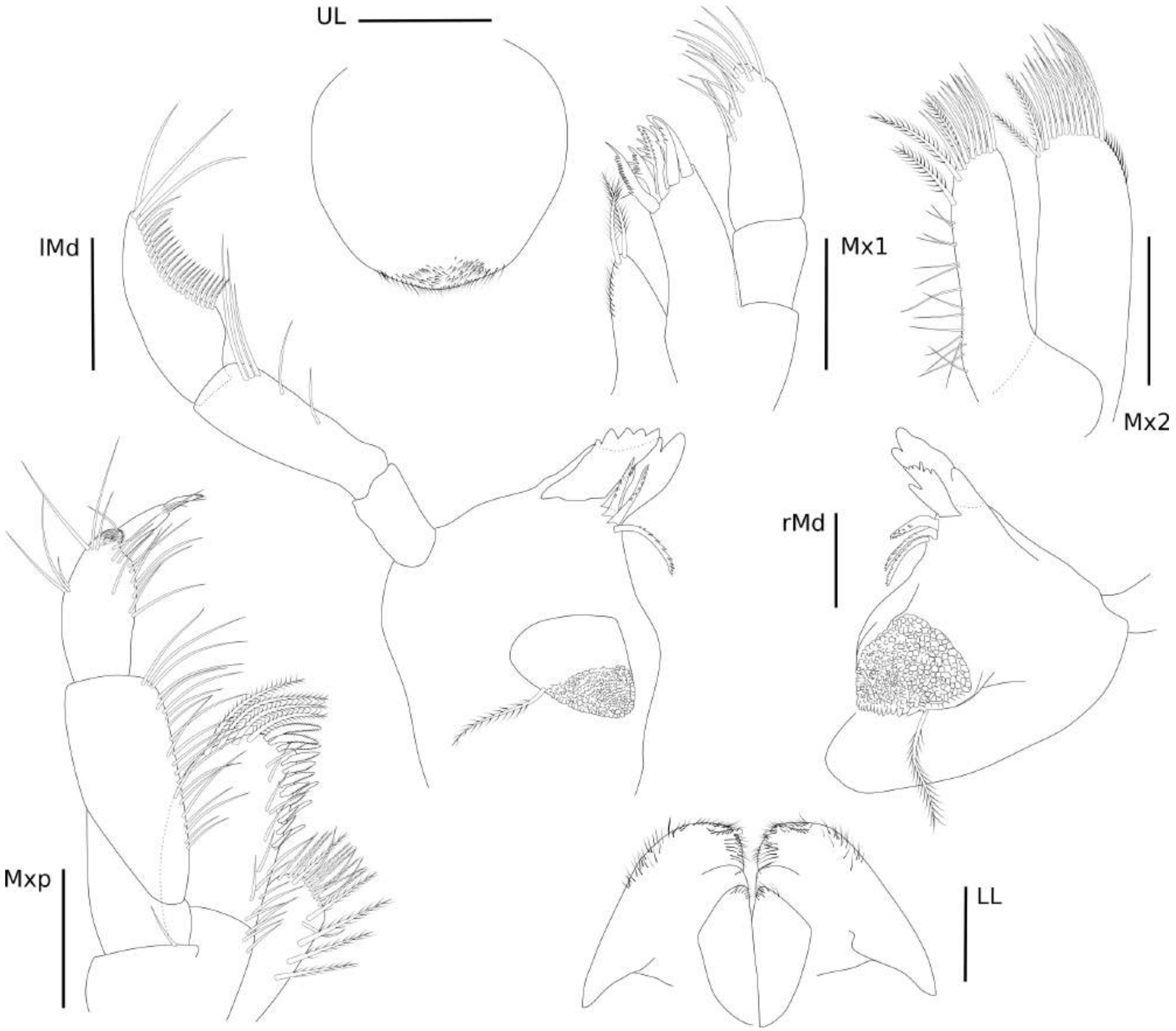

Figure 7. *Elasmopus gabrieli* Siqueira & Iwasa-Arai **sp. nov.** Mouthparts. Scale bar: 100 µm.

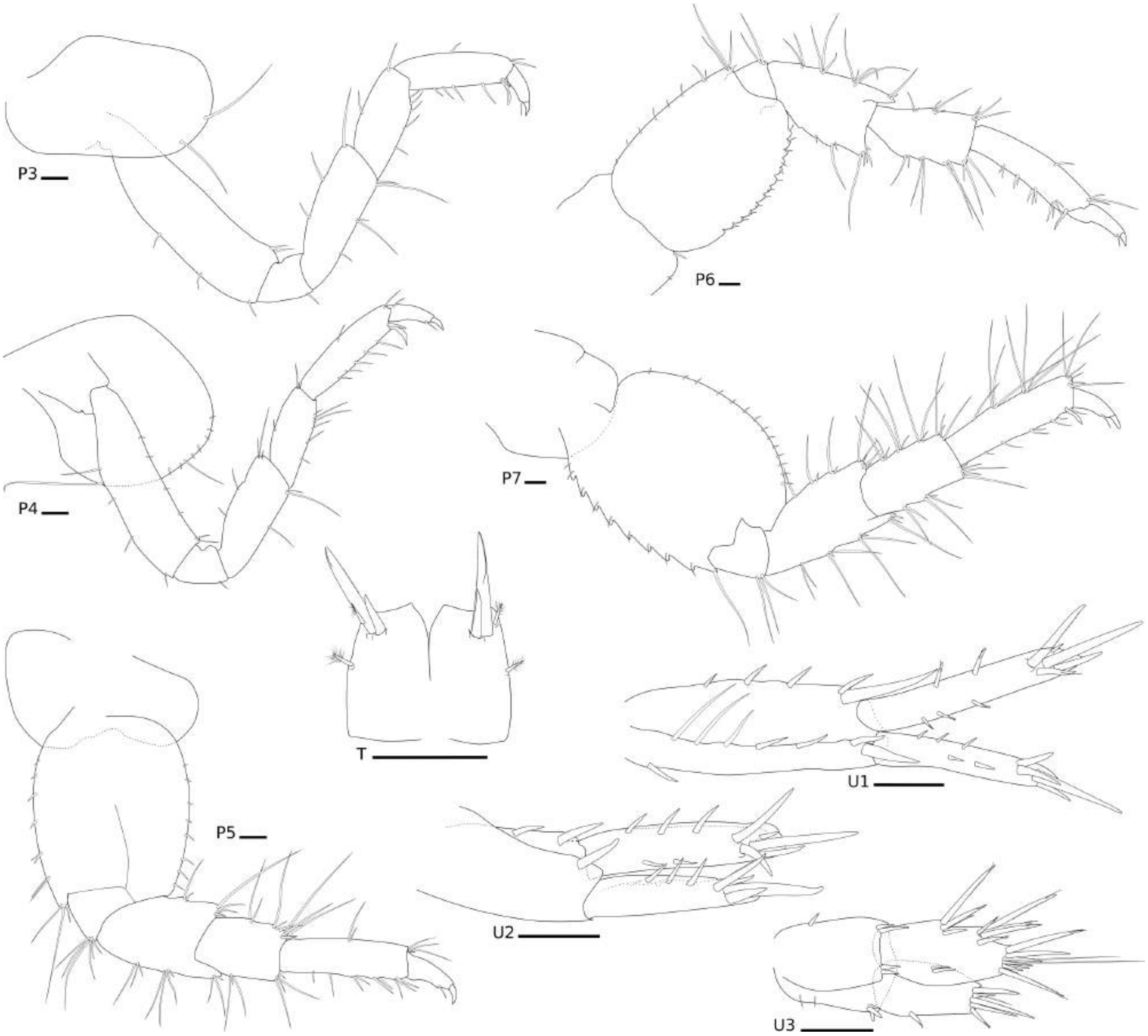

Figure 8. *Elasmopus gabrieli* Siqueira & Iwasa-Arai **sp. nov.** Pereopods, uropods and telson. Scale bar: 100 µm.

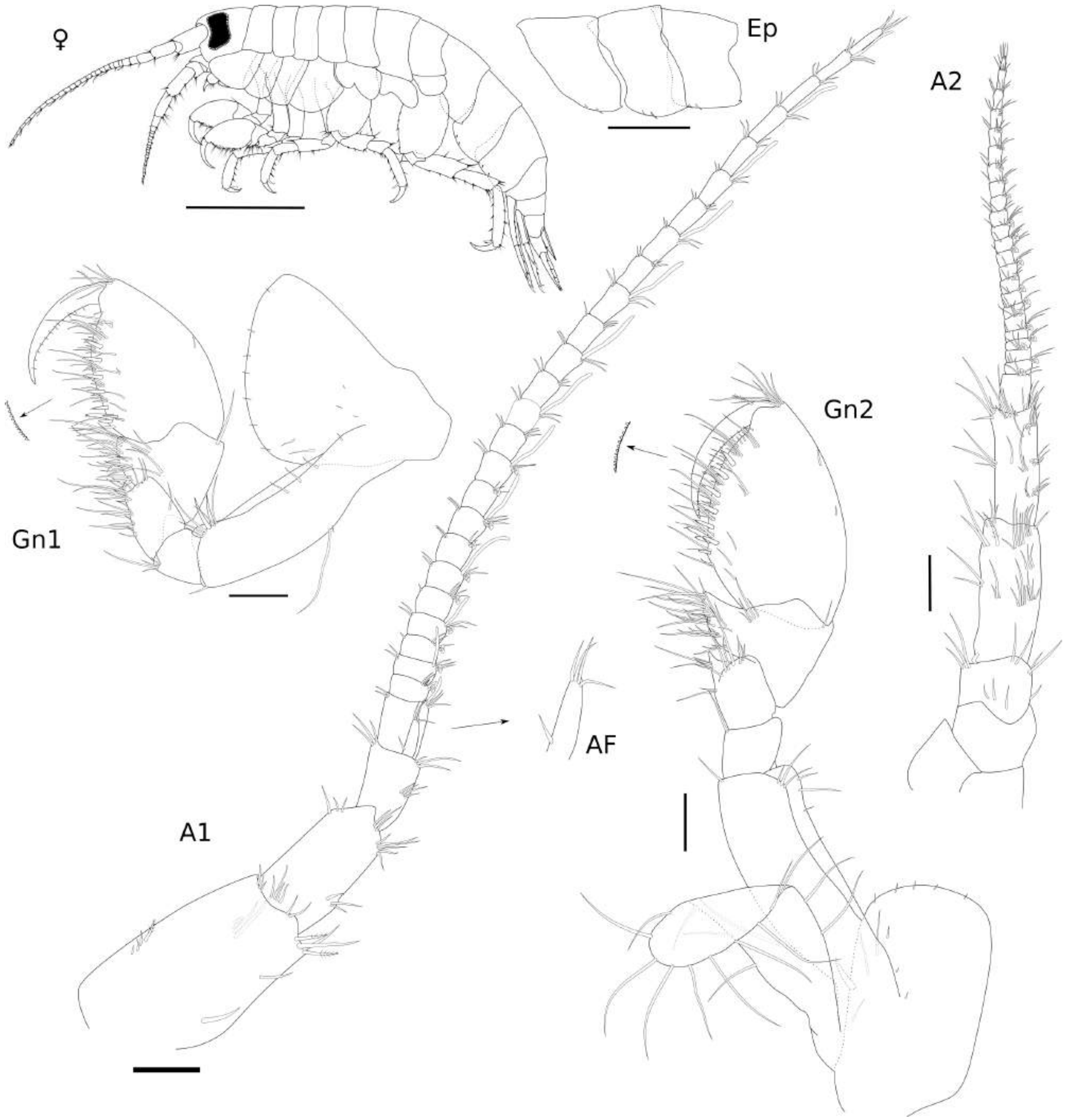

Figure 9. *Eusiroides lucai* Siqueira & Iwasa-Arai **sp. nov.** Female (ZUEC-CRU-4368). Scale bar: 1mm. Antennae, gnathopods and epimeral plates. Scale bar: 100 µm.

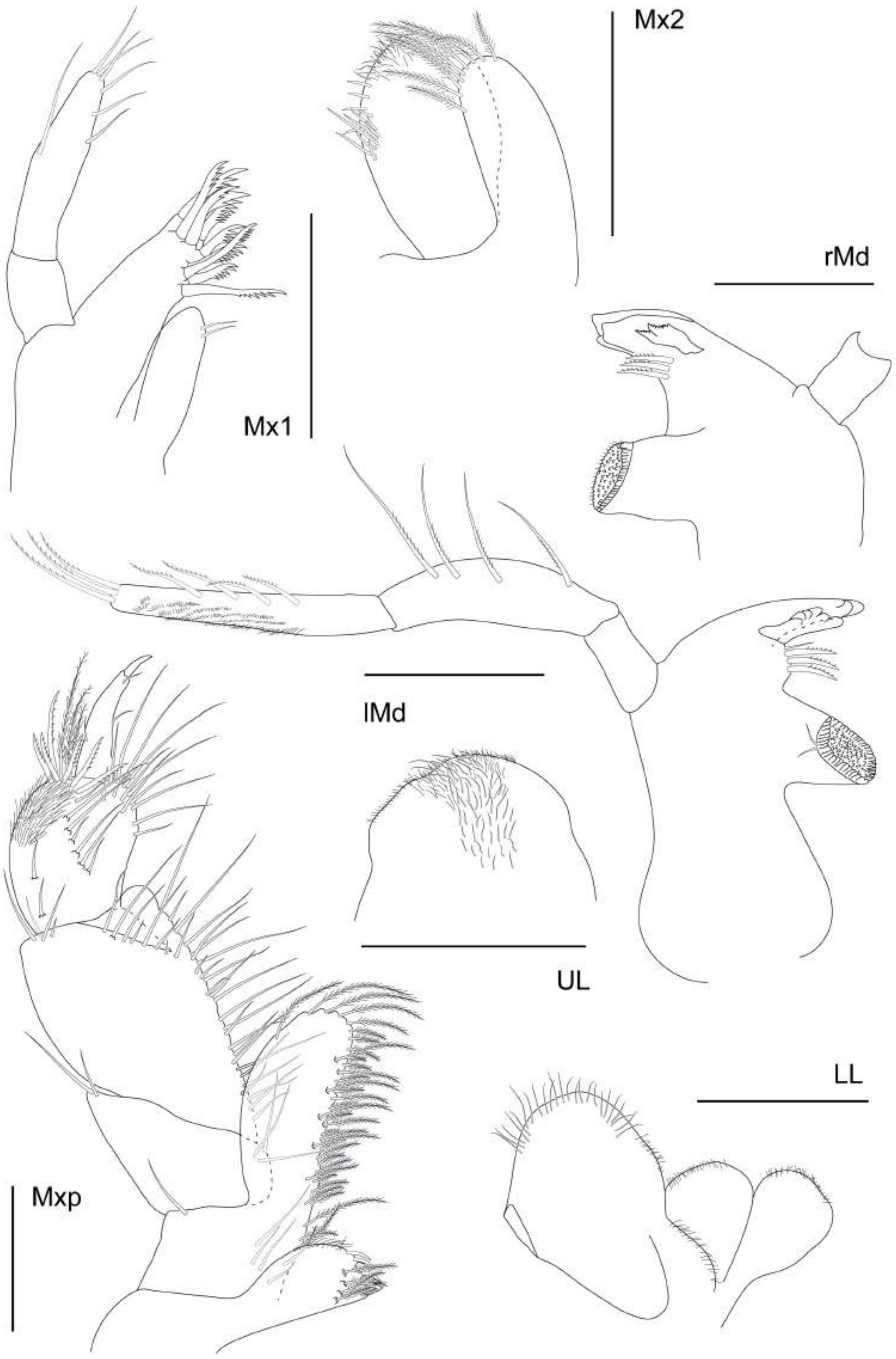

Figure 10. *Eusiroides lucai* Siqueira & Iwasa-Arai **sp. nov.** Mouthparts. Scale bar: 100 µm.

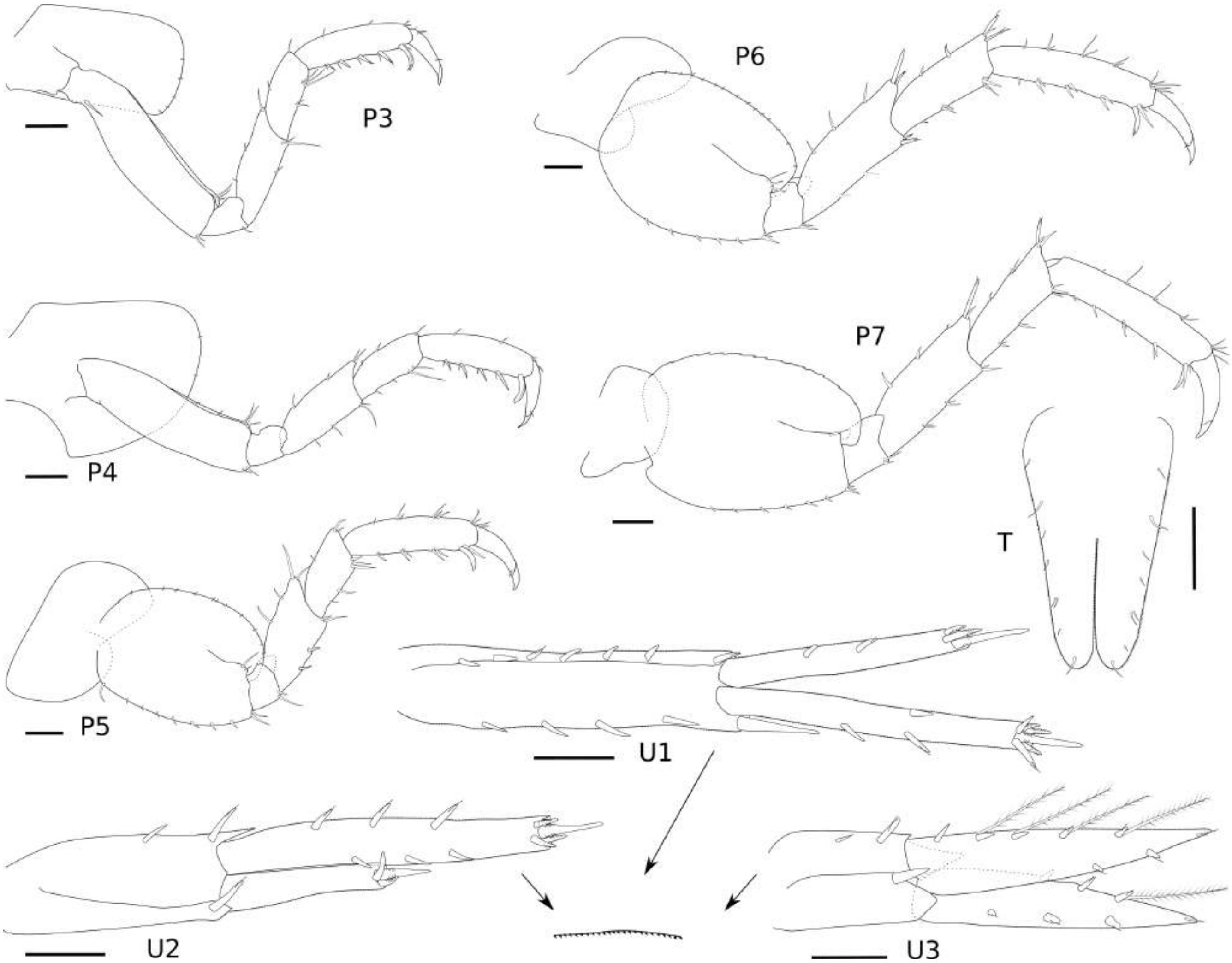

Figure 11. *Eusiroides lucai* Siqueira & Iwasa-Arai **sp. nov.** Pereopods, uropods and telson. Scale bar: 100 µm.

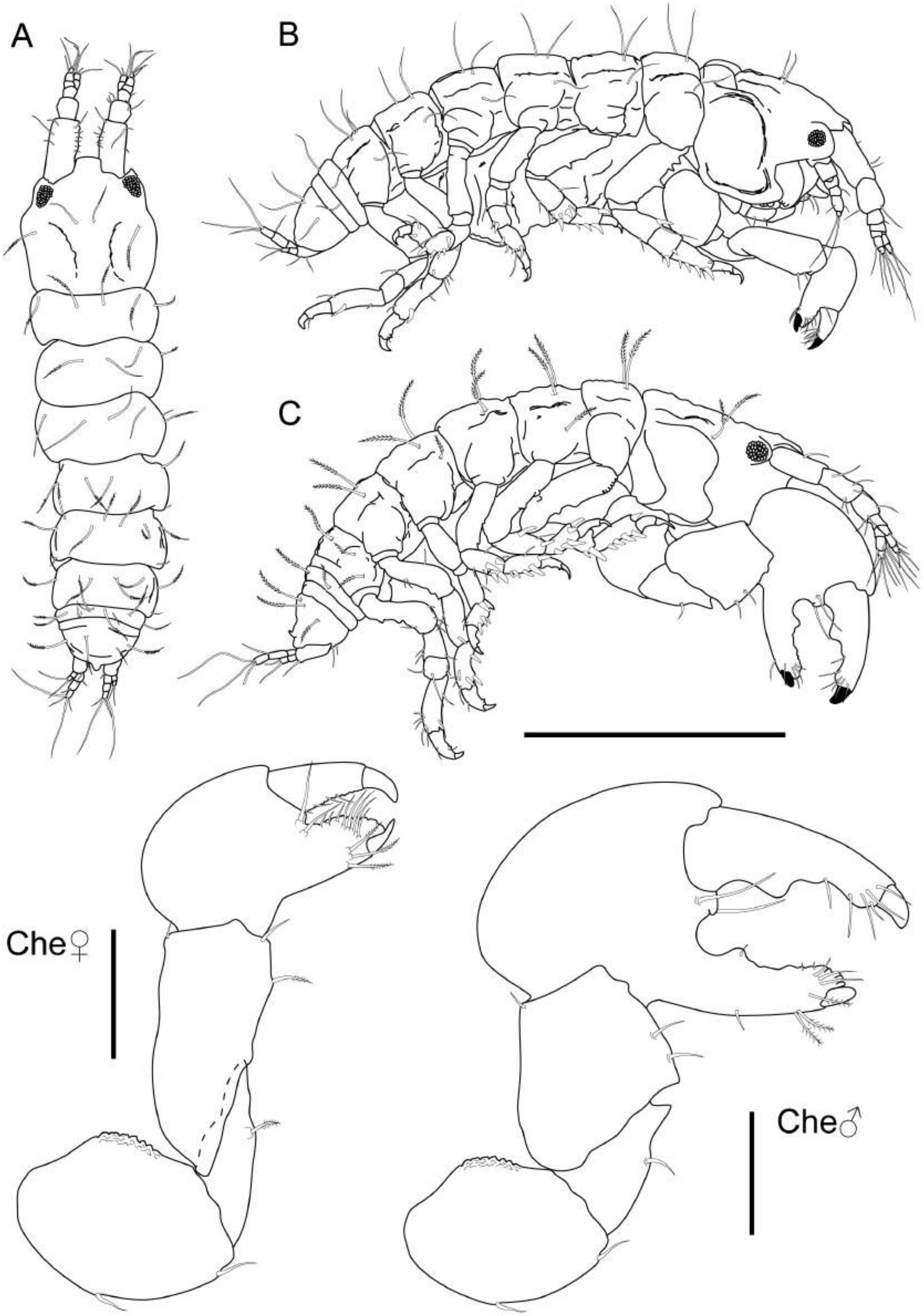

Figure 12. *Synapseudes isis* Segadilha, Siqueira & Iwasa-Arai **sp. nov.** Female (ZUEC-CRU-4369). Male (ZUEC-CRU-4370). Scale bar: 0.5mm. Gnathopods. Scale bar: 100 µm.

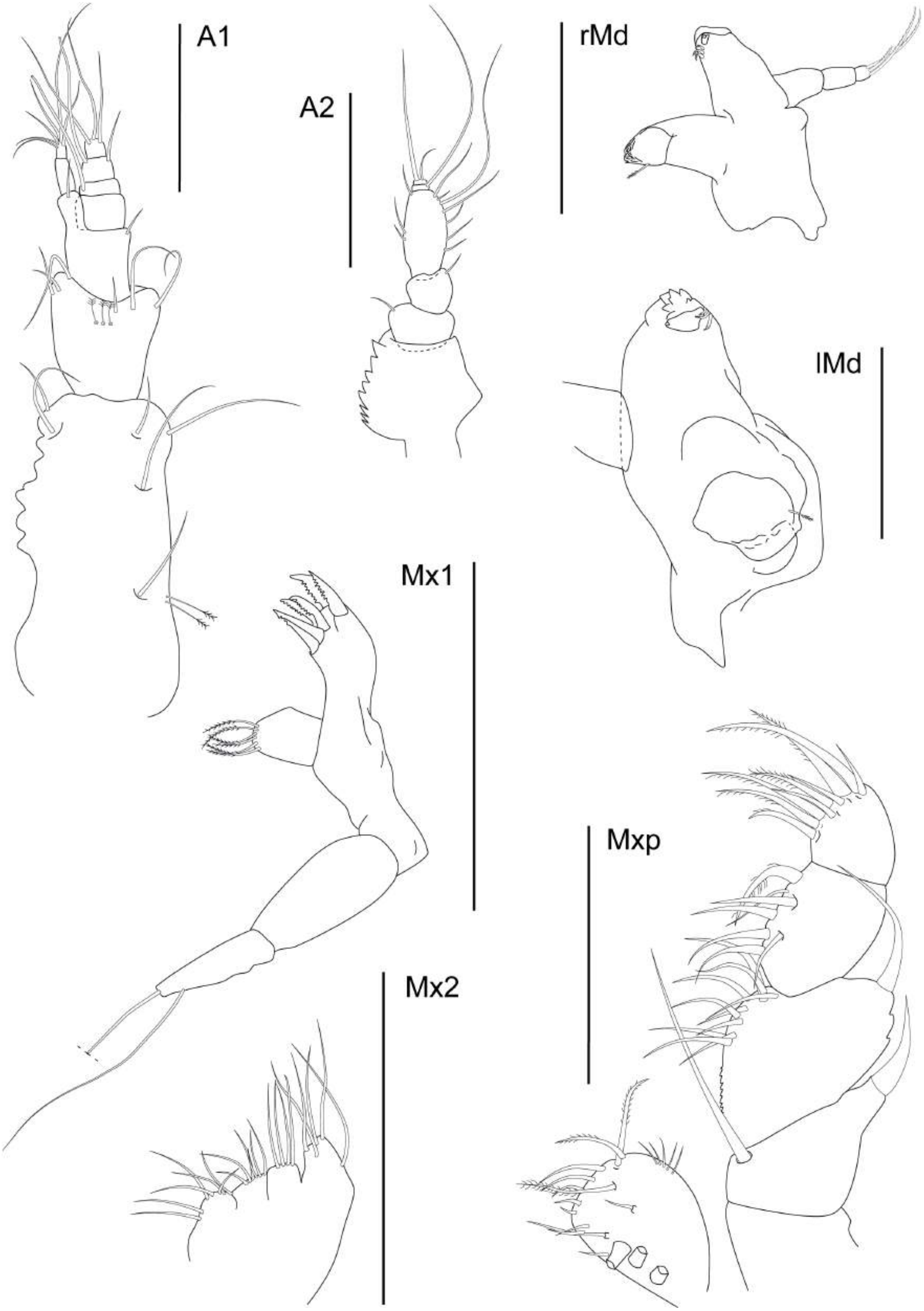

Figure 13. *Synapseudes isis* Segadilha, Siqueira & Iwasa-Arai **sp. nov.** Mouthparts. Scale bar: 100 µm.

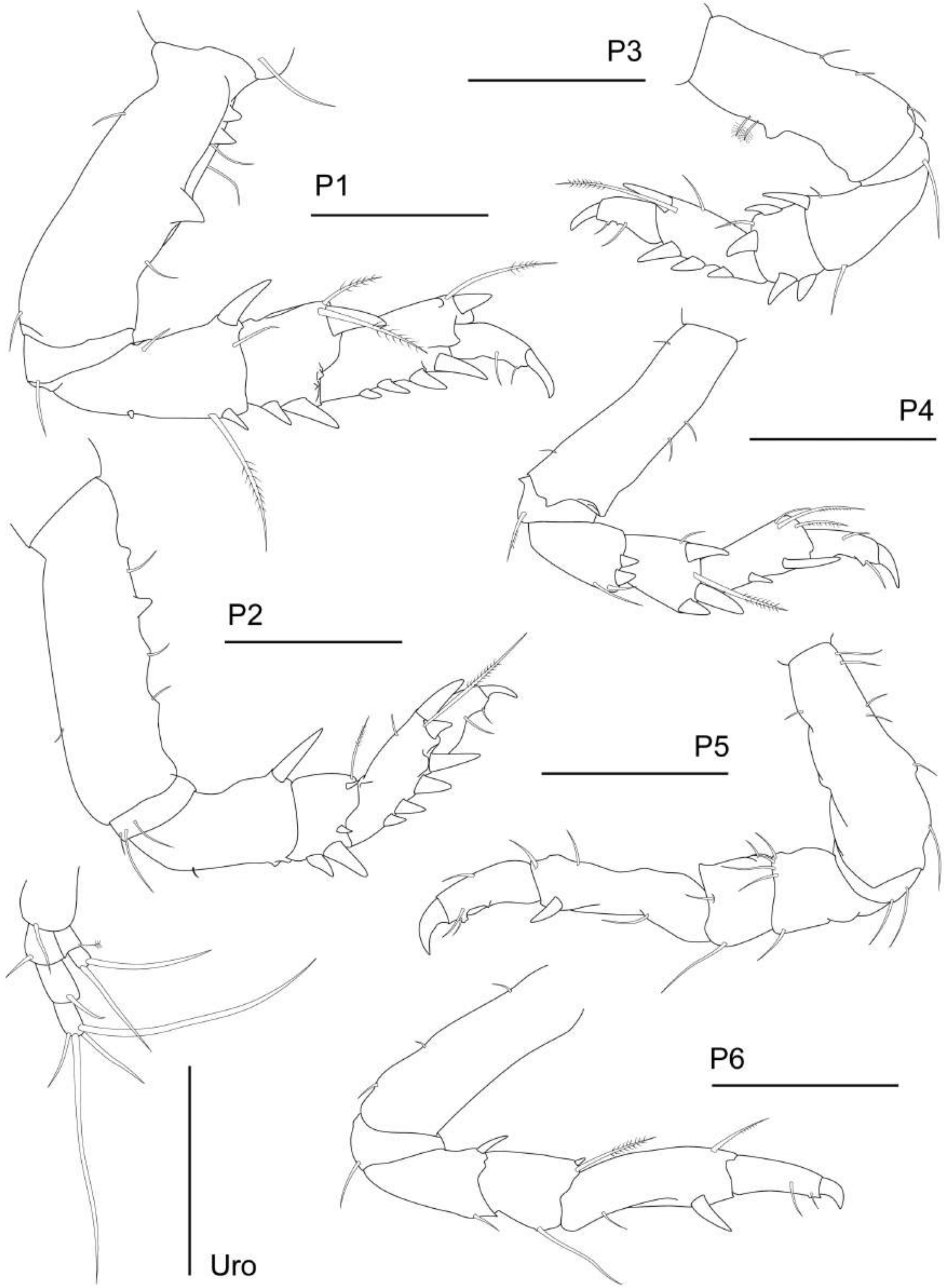

Figure 14. *Synapseudes isis* Segadilha, Siqueira & Iwasa-Arai **sp. nov.** Pereopods and uropod. Scale bar: 100 µm.

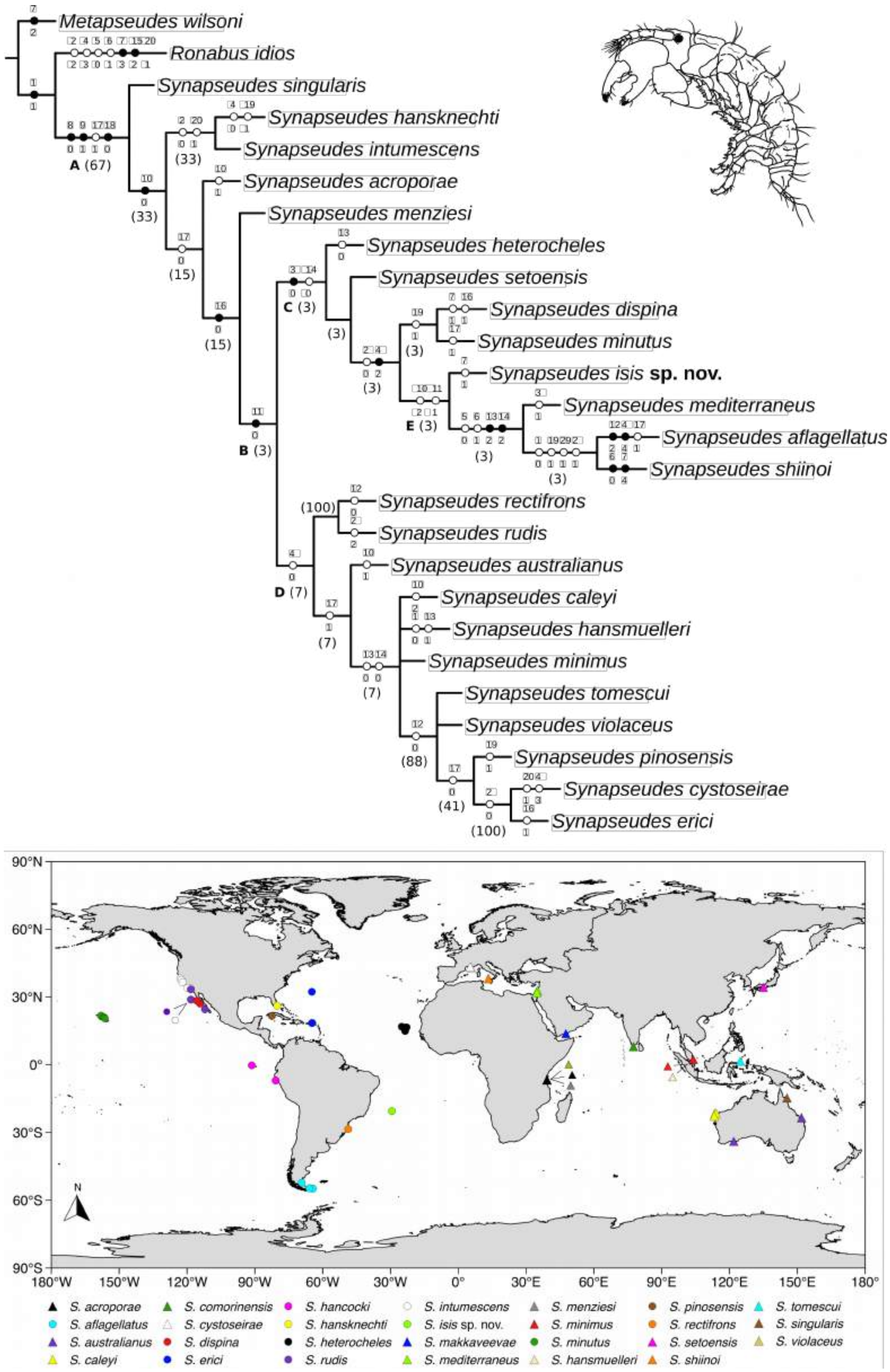

Figure 15. Details of the *Synapseudes* Miller, 1940 consensus cladogram. Letters below branches represent clades mentioned in the discussion, numbers in parenthesis correspond to Bremmer relative support. Black circles represent non-homoplastic synapomorphies; white circles represent homoplastic synapomorphies. Numbers above branches represent the characters, and states are represented below.

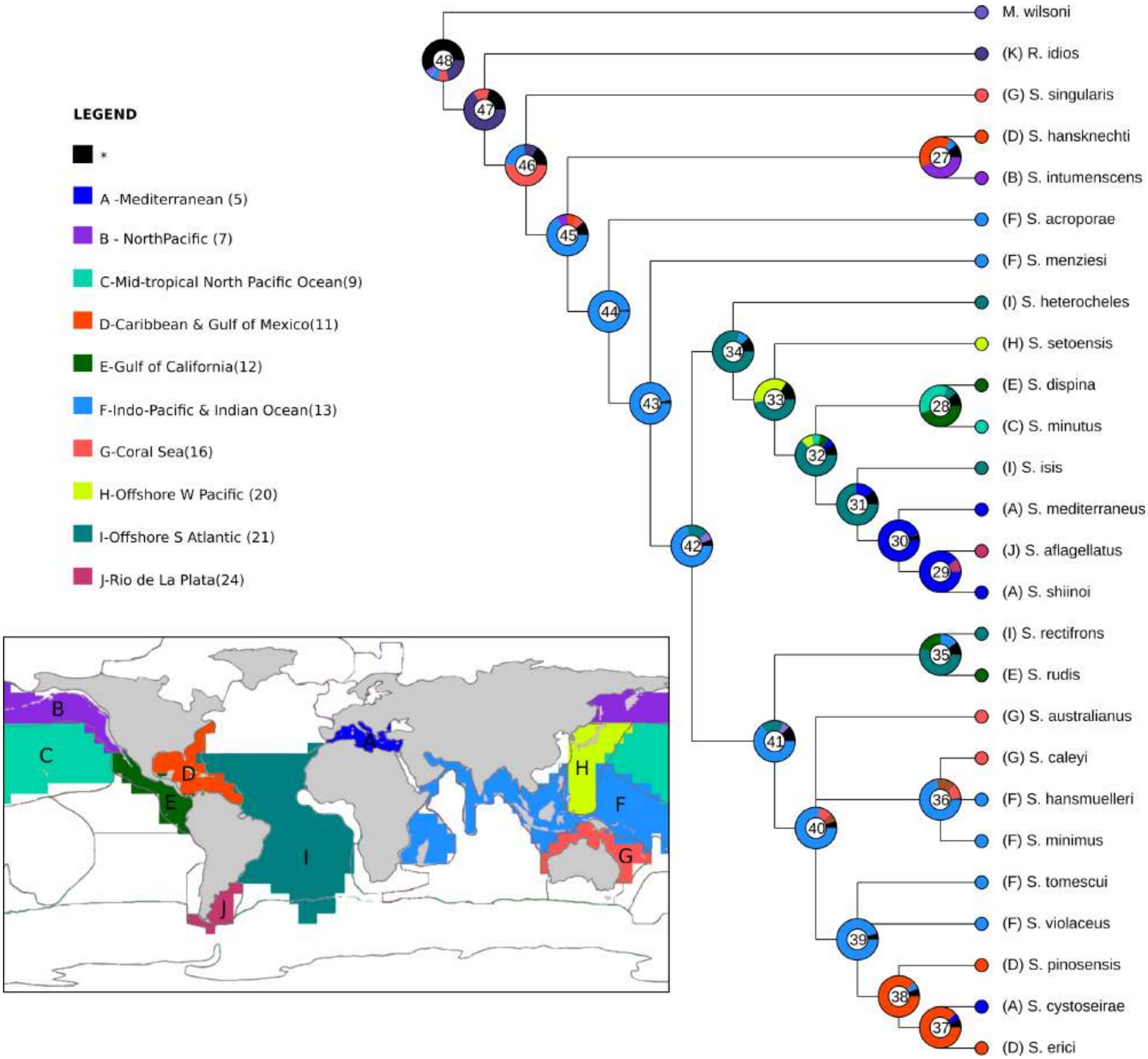

Figure 16. Bayesian Binary MCMC (BBM) analysis of *Synapseudes* Miller, 1940. Map shows realms proposed by Costello et al. (2017), and letters in map correspond to realms with *Synapseudes* Miller, 1940 distribution records. Numbers in legend correspond to realms numbers by Costello et al. (2017). Colors on terminals correspond to current distribution and colors on nodes represent potential distribution of ancestors.

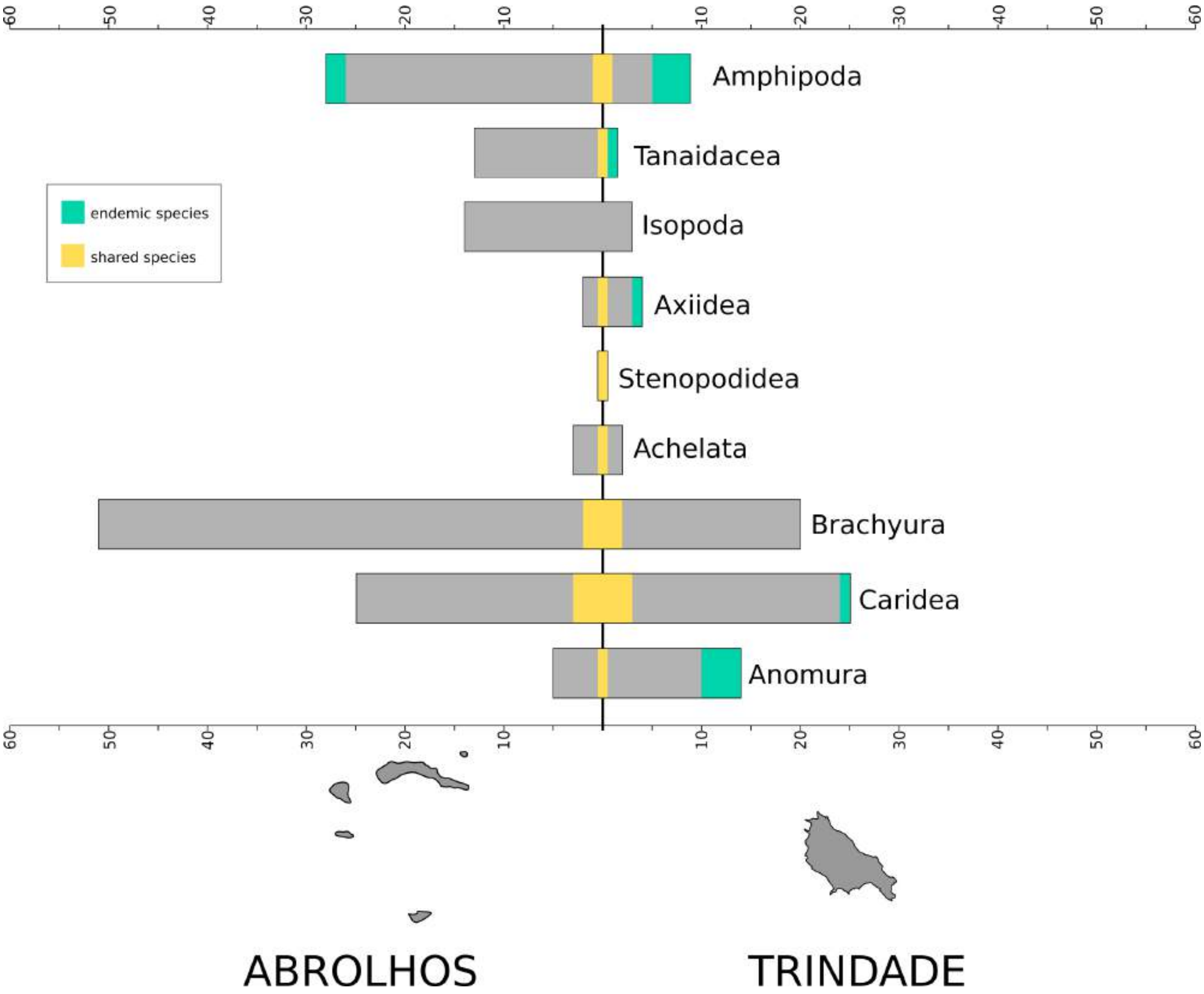

Figure 17. Crustacea species richness reported from Abrolhos Archipelago (left) and Trindade Island (right). Gray bars correspond to species not shared by both islands, yellow bars correspond to shared species, and seafoam green bars correspond to endemic species. References: Amphipoda: Cunha et al. (2013), Andrade and Senna (2017), Serejo and Siqueira (2018); Tanaidacea: Brum (1973); Gutu (1996), Cunha et al. (2013); Isopoda: Barth (1958), Moreira (1977), Cunha et al. (2013), Souza et al. (2013), Campos-Filho et al. (2017); Axiidea: Pachell and Tavares (2020); Stenopodidea: Soledade et al. (2015), Tavares et al. (2017); Achelata: Faria-Junior et al. (2013), Tavares et al. (2017); Brachyura: Almeida and Coelho (2008), Tavares et al. (2017); Caridea: Soledade et al. (2017), Soledade et al. (2017), Tavares et al. (2017), Lima et al. (2019).

Supplementary Material

List S1. Morphological characters used on *Synapseudes* phylogenetic analysis.

Discrete characters
1. Carapace with lateral setae at mid length: absent (0); present (1).
2. Number of antennal flagella articles: 1 (0); 2 (1); 3 (2).
3. Distal spiniform apophyses on antennular peduncle article 2: absent (0); present (1).
4. Number of antennal terminal setae: 1 (0); 2 (1); 3 (2); 4 (3); 5 (4).
5. Number of articles in inner antennular flagellum: 1 (0); 2 (1).
6. Number of articles in outer antennular flagellum: 1 (0); 2 (1); 3 (2).
7. Number of terminal setae on mandibular palp: 2 (0); 3 (1); 4 (2); 5 or 6 (3); 10 (4).
8. Setae on palp article 2 of mandible: absent (0); present (1).
9. Number of setae on palp article 3 of mandible: 1 (0); 2 (1); many (2).
10. Number of coupling hooks (retinacula) on endite of maxilliped: 2 (0); 3 (1); 4 (2).
11. Symmetry of male chelipeds: asymmetrical (0); symmetrical (1).
12. Number of spiniform setae on ventral margin of propodus of pereopod 1: 3 (0); 4 (1); 5 (2).
13. Number of spiniform setae on ventral margin of propodus of pereopod 2: 3 (0); 4 (1); 5 (2).
14. Number of spiniform setae on ventral margin of propodus of pereopod 3: 3 (0); 4 (1); 5 (2).
15. Number of articles in uropodal exopod: 1 (0); 2 (1); 3 (2).
16. Number of articles in uropodal endopod: 3 (0); 4 (1).
17. Number of pleonites: 2 (0); 3 (1); 5 (2).
18. Pleopods absent (0); present (1).
19. First pleonite, width relative to other pleonites: all the same width (0); wider than the others (1).
20. Telson with bulgae (protrusions): absent (0); present (1).

Continuous characters
1. Carapace length/width ratio
2. Carapace length/antennule basis length ratio

Table S2. Taxa and characters matrix.

```
                          00000000011111111112
                          12345678901234567890
Metapseudes_wilsoni       01111221221111112100
Ronabus_idios             121301312?1111212101
Synapseudes_acroporae     11?112001111??110000
Synapseudes_aflagellatus  0104010012?222101011
Synapseudes_australianus  111012001l?111101000
Synapseudes_caleyi        1110[01]200120100101000
Synapseudes_cystoseirae   10?31200100000100001
Synapseudes_dispina       10021210??011?110010
Synapseudes_erici         101012001?0000110000
Synapseudes_hansknechti   1[01]101200101111111011
Synapseudes_hansmuelleri  01101200100110101000
Synapseudes_heterocheles  101012001001001100?0
Synapseudes_intumescens   10111200?0111?111001
Synapseudes_mediterraneus 101201001?11??100000
Synapseudes_menziesi      ?11[01]1200?011??1000??
Synapseudes_minimus       ?1101200???1[01]01010??
Synapseudes_pinosensis    111012001?0?00100010
Synapseudes_rectifrons    111012001??011100000
Synapseudes_rudis         12101200??011?100000
Synapseudes_setoensis     110112001?0110100000
Synapseudes_shiinoi       ?1?20040???1??1000??
Synapseudes_singularis    1111120012?111111000
Synapseudes_tomescui      ??1?1200??00001010??
Synapseudes_violaceus     111012001?00??101000
Synapseudes_minutus       1?0212001001[01]0101010
Synapseudes_isis          10021210??1110100000

Metapseudes_wilsoni       1.000 0.000
Ronabus_idios             0.326 0.179
Synapseudes_acroporae     0.567 0.179
Synapseudes_aflagellatus  0.277 0.508
Synapseudes_australianus  0.662 0.179
Synapseudes_caleyi        0.468 0.179
Synapseudes_cystoseirae   0.325 0.343
Synapseudes_dispina       0.229 0.525
Synapseudes_erici         0.257 0.589
Synapseudes_hansknechti   0.362 0.069
Synapseudes_hansmuelleri  0.300 0.250
Synapseudes_heterocheles  0.277 0.179
Synapseudes_intumescens   0.310 0.404
Synapseudes_mediterraneus 0.437 1.000
Synapseudes_menziesi      ?     ?
Synapseudes_minimus       ?     ?
Synapseudes_pinosensis    0.277 0.179
Synapseudes_rectifrons    0.241 0.302
Synapseudes_rudis         0.352 0.427
Synapseudes_setoensis     0.494 0.836
Synapseudes_shiinoi       ?     ?
Synapseudes_singularis    0.628 0.220
Synapseudes_tomescui      ?     ?
Synapseudes_violaceus     0.300 0.250
Synapseudes_minutus       0.213 0.179
Synapseudes_isis          0.000 0.543
```

Capítulo 2

EVOLUTIONARY BIOGEOGRAPHY OF AMPITHOIDAE (CRUSTACEA: AMPHIPODA) AND THE DIVERSIFICATION OF *Foscampithoe* GEN. NOV. IN THE SOUTHWESTERN ATLANTIC

Evolutionary biogeography of Ampithoidae (Crustacea: Amphipoda) and the diversification of *Foscampithoe* gen. nov. in the southwestern Atlantic

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Abstract

The family Ampithoidae is one of the most abundant associated to macroalgae in shallow marine waters. *Ampithoe*, the largest genus, was previously recovered as non-monophylethic by phylogenetic analyses based on morphological and molecular characters. Here, we reconstructed a multi-gene phylogeny of Ampithoidae and we propose a new genus, *Foscampithoe* **gen. nov.**, mostly distributed in the southern hemisphere. We performed the first biogeographic analyses for the family, which indicated the its origin in the Indo-West Pacific, with posterior dispersion to the Atlantic Ocean around the Eocene. Divergence times suggest that the diversification of Ampithoidae is congruent with the brown algae crown radiation (BACR), which allowed the colonization of new environments.

Keywords: dispersal-extinction-cladogenesis, molecular systematics, Peracarida, taxonomy

INTRODUCTION

The importance of evolutionary history on the associations between marine herbivores and their hosts is poorly understood and host choice seems to play a fundamental role in the differentiation and speciation of many small marine invertebrates (Sotka et al. 2003, Sotka 2005, Poore et al. 2008). One of the main taxa among the invertebrate assemblages associated with shallow-water macroalgae and seagrasses worldwide are represented by amphipod crustaceans of the family Ampithoidae Boeck 1871 (Conlan 1982, Poore et al. 2008, Sotka et al. 2017). Ampithoids are characterized by the outer ramus of uropod 3 having 1-2 recurved, robust apical setae (Barnard and Karaman 1991; Myers and Lowry 2003), however, intrageneric features are not well established, including several synonimies and ressurrections over the recent years (Peart and Ahyong 2016). Regarding their morphology, two comprehensive phylogenies were proposed: 1) Conlan (1982) generated a phylogeny for 12 genera based on 27 morphological characters, resulted from a numerical phenetic analysis (Fig. 1); 2) Peart and Ahyong (2016) Peart and Ahyong (2016) proposed a phylogeny based on 53 terminals and 77 characters from a cladistic analysis. Nonetheless, Sotka et al. (2017) presented the first molecular phylogeny for the family, including 35 species across 10 genera (Fig. 1). Considering the incongruences among the three phylogenies, neither species nor genera relationships are yet well understood.

One concordant result revealed by both morphology and molecules was the polyphyletic status of the genus *Ampithoe* Leach, 1814. Both phylogenetic analyses by Peart and Ahyong (2016) and Sotka et al. (2017) suggested two lineages within *Ampithoe*, which Sotka et al. (2017) named as ‘south clade’ and ‘north Pacific clade’ according to their taxa distribution. They also predicted that species not sampled but with a distribution localized to the north Pacific would likely belong to the *Ampithoe*-‘north Pacific’ clade and that other species with Atlantic, Mediterranean, Indian or south Pacific distributions would be part of the *Ampithoe*-‘south’ clade (Sotka et al. 2017). While the former proposed phylogenies embraced a rich number of Pacific distributed species, the evolution of Ampithoidae along the southwestern Atlantic remained unknown. The Brazilian coast covers the majority of the southwestern Atlantic shallow waters, where sixteen species of Ampithoidae have been reported so far (Serejo and Siqueira 2018, Iwasa-Arai et al. 2021), mostly associated with brown algae (Jacobucci and Leite 2014, Peres et al. 2019, Machado et al. 2019).

The Brown Algae Crown Radiation (BACR) is represented by the most ecologically and economically important orders, including the Fucales and Laminariales (Bringloe et al. 2020), and it forms a conspicuous clade that radiated throughout the Cretaceous period (145-66 Ma). Considering the importance of host radiation for the associated fauna diversity, we expected that BACR divergence times would anticipate the Ampithoidae's diversification. Therefore, we provide the first dated phylogeny and event-based biogeographic analyses for Ampithoidae and discuss the evolution of the family in light of its hosts and distribution, aiming to test Sotka et al. (2017) hypothesis of *Ampithoe* clades with geographical concordance and diversification thoughout the western Atlantic.

2. MATERIAL AND METHODS

2.1. Sampling and identification

Species of *Ampithoe* were collected from different localities along the western Atlantic associated to brown algae of the genera *Sargassum* sp., *Dictyopteris* sp. and *Dictyota* sp. and the green algae *Caulerpa racemosa* under the Brazilian SISBIO licence no. 60924 and national authorization by Dominica's Fisheries Division. Algal fronds were collected underwater by freediving from 1 to 10 m (except from Saint Peter and Saint Paul Archipelago, where they were manually collected at the low tide), stored in fabric bags (0.2 mm mesh size) within seawater and washed off for fauna separation, followed by fixation and preservation in ethanol 90%. Species identification followed previous works on *Ampithoe* taxonomy for Brazil (Serejo and Licinio 2002, Andrade and Senna 2017, Campos et al.

2020), Florida (LeCroy 2002) and Australia (Peart 2007), as well as comparative material from the National Museum, Universidade Federal do Rio de Janeiro (MNRJ). Appendages and mouthparts of dissected specimens were mounted on glass slides and sealed with agarose mounting media. Drawings were made with a camera lucida at a Zeiss Axioscope stereomicroscope and digitally drawn with Inkscape. Specimens and vouchers are deposited at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

2.2. Molecular methods

Genomic DNA was extracted according to the CTAB protocol of Doyle and Doyle (1987). DNA integrity was checked by 1.5% agarose gel electrophoresis and quantified using Nanodrop spectrophotometer. Partial sequences of the mitochondrial gene cytochrome oxidase subunit 1 (COI) and 16SrRNA, as well as the nuclear genes 28SrRNA were obtained for subsequent analyses. Sequences of sodium-potassium ATPase (NAK) and elongation factor 1-alpha (EF1-α) from Sotka et al. (2017) were also added to the dataset. Fragments were amplified using the universal primers HCO2198 and LCO1490 (Folmer et al. 1994) for COI, 16STf (Macdonald et al. 2005) and 16Sbr (Palumbi et al. 1991) for 16SrRNA and rd1 and rd4b (Edgecombe and Giribet 2006) for 28SrRNA.

Polymerase chain reactions (PCRs) were carried out in a total volume of 15 µL containing 1 × PCR buffer, 2.5 U Taq DNA Polymerase, 1.5 mM $MgCl_2$, 200 µM of each dNTP, 0.35 µM of each oligonucleotide and ultrapure water to achieve the reaction volume (Taq PCR Master Mix, Qiagen). The cycling profile on the thermal cycler involved a denaturation step at 94°C for 1 min, 35 cycles of denaturation at 94°C for 1 min; annealing temperature for 1 min, extension at 72°C for 1 min; and extension at 72°C for 10 min. Annealing temperatures were 48°C for COI and 28SrRNA and 52°C for 16SrRNA. PCR products were purified with polyethylene glycol solution 15% (PEG) and then amplified for sequencing using a BigDye Terminator Cycle Sequencing Kit v.3.1 (Applied Biosystems) at the Human Genome and Stem Cell Research Center, Universidade de São Paulo.

Chromatograms were analysed using Genestudio 2.2 (Genestudio Inc.), which was used to perform BLAST searches (http://blast.ncbi.nlm.nih.gov) to check for contamination or sequencing errors. Individual consensus sequences were aligned using T-Coffee server that combine multiple alingment methods (Notredame et al. 2000).

2.3. Phylogenetic and species delimitation analyses

Sequences of Ampithoidae were obtained from GenBank (National Center for Biotechnology Information, NCBI, Supplementary Material). The best partition schemes and models were determined in ModelFinder (Kalyaanamoorthy et al. 2017) based on the modified Akaike Information Criterion (AICc) available on IQ-TREE web server (Nguyen et al. 2015). The optimal partitioning strategy and evolutionary models consisted of TNe+G4 for the three codon partitions, TVM+F+I+G4 for 16SrRNA, TIM+F+I+G4 for 28SrRNA, TNe+I+G4 for EF1-α and TIM2e+I+G4 for NAK. The phylogenetic analyses of maximum likelihood (ML) were also held at the IQ-TREE web server, and the support of the nodes was evaluated with 1.000 ultrafast bootstrap replications (Hoang et al. 2018). Bayesian Inference analyses were conducted in BEAST 1.10.4 (Drummond et al. 2012) on the CIPRES server (Miller et al. 2010) using 10^8 generations, sampling every 1.000 generations.

Species delimitation analyses were used on the *Ampithoe* ‘south’ clade. The ABGD is a remote method that uses the gap observed between intraspecific diversity and interspecific (barcode gap) to partition the data (Puillandre et al., 2012). Distances were calculated using the K2P nucleotide substitution model with a cut-off value of 2.0. The mPTP is a method that fits the branching events of each delimited species to a distinct exponential distribution and does not require any similarity threshold as input (Kapli et al. 2017). We performed an analysis based on the obtained ML phylogenetic tree after removing the outgroups and using two independent MCMC chains at 100.000.000 generations each with a sampling frequency of 1.000. Both analyses were performed for mitochondrial genes separately. The morphological identification was used for specimens herein observed and putative names were used as originally identified on GenBank database and references.

2.4. Divergence time analyses

Divergence times were calculated with BEAST 1.10.4 (Drummond et al. 2012) with the same evolutionary models and partitions from the phylogenetic analysis. A thinned dataset of one individual per lineage was used to improve accuracy and computational time. We employed an uncorrelated relaxed clock with a lognormal distribution (Drummond et al. 2006). For the tree model, we used a random starting tree, and speciation was modeled using the Birth-Death Process. The MCMC chain was run for 10^8 iterations, with a thinning of 1000. Effective sample sizes of parameters and convergence were checked with Tracer 1.7.1 (Rambaut et al. 2018) after discarding 20% of the trees as burn-in. Three independent runs were performed and gave the same result. The resulting files were combined using LogCombiner 1.8 (Drummond et al. 2012), and the maximum clade credibility tree was produced using TreeAnnotator 1.8 (Drummond et al. 2012). For divergence times estimation we employed the fossil calibration scheme described in detail by Copilaş-Ciocianu et al. (2019, 2020) with two calibration points on fossil Gammaridae and Talitridae.

2.5. Biogeographic analyses

Ampithoidae ancestral areas were inferred using the calibrated phylogeny with a model-based approach in the R package BioGeoBEARS 1.1.2 (Matzke, 2014, 2013). We defined five geographic ranges based on the current distribution of the family and on delimited marine biogeographical areas (Costello et al., 2017): Eastern Pacific (EP), Central Pacific (CP), Indo-West Pacific (WP), Western

Atlantic (WA) and Eastern Atlantic (EA). Ancestral areas could then be estimated as combinations of these five areas by BioGeoBEARS.

The maximum range size was set to 4, which to our knowledge is more than the maximum number of areas in which any extant ampithoids in our analyses is present. The distribution for identified species was taken from sampling data, sequence localities available on GenBank, original descriptions and checked with global distribution records from GBIF (Global Biodiversity Information Database, http://gbif.org) and OBIS (Ocean Biogeographic Information System, http://www.iobis.org). Records from species complex that could not be confirmed were disregarded. Six biogeographic models implemented in Bio-GeoBEARS were compared: dispersal-extinction-cladogenesis (DEC) model (Ree and Smith, 2008), a maximum likelihood version of the dispersal-vicariance (DIVAlike) model (Ronquist, 1997) and a likelihood version of the Bayesian biogeographic inference with no-cladogenesis (BAYAREAlike) model (Landis et al., 2013) and jump dispersal/founder-event speciation with the additional parameter j for the three previously mentioned methods (DEC + j, DIVAlike + j, BAYAREAlike + j, Matzke, 2014). The discussed model was selected according to the lowest AICc value.

3. RESULTS

3.1. Phylogenetic and species delimitation analyses

Multilocus phylogeny resulted in monophyletic genera, except for *Pleonexes* and *Ampithoe. Ampithoe s.l.* consisted in two different clades, therefore, a new genus is herein described as *Foscampithoe* **gen. nov.** (Fig. 2A, B). ML and BI analyses resulted in congruent topologies for most of the clades, however, they differed on some relationships for genera with a single sampled species and a few intrageneric relationships. Here, we discussed only the relationships supported by both phylogenies.

Two main clades are present within Ampithoidae and correspond to the majority of the genera. The first clade encompasses the genera *Ampithoe s.s*., *Plumithoe quadrimana* (Haswell, 1879), *Biancolina japonica* Ishimaru, 1996 and *Exampithoe* (Fig. 2B)*,* while the second clade includes *Sunamphitoe*, *Cymadusa*, *Pseudopleonexes lessoniae* (Hurley, 1954) and the monotypic genus *Amphitholina* (Fig. 2B). *Ampithoe s.s.* is the sister clade of *P. quadrimana, B. japonica* and *Exampithoe* (Fig. 2B). In the second main clade, S*unamphitoe* as the sister genera of *Cymadusa* + *Pseudopleonexes (P. lessoniae)* + *Amphitholina.* Lastly, *Cymadusa* appears as the sister clade of *Pseudopleonexes (P. lessoniae)* + *Amphitholina* (Fig. 2B).

The monophyly of *Ampithoe s.s.* is supported by high bootstrap (BS) and posterior probability (PP) values. *Ampithoe s.s.* is mostly composed of north Pacific species (Sotka et al. 2017), and species with wide distribution, such as *A. valida* S.I. Smith, 1873, *A. lacertosa* Spence Bate, 1858 and *A. rubricata* (Montagu, 1808). *Ampithoe rubricata* is the type species of *Ampithoe* and, although two sequences of specimens identified as *A. rubricata* were placed in *Foscampithoe* **gen. nov.**, the combination of our results with the cladistic analyses based on morphological characters by Peart and Ahyong (2016) suggest that the name *Ampithoe* should be retained by the 'north Pacific' (Sotka et al. 2017) clade. Within *Ampithoe* s.s., three species outside the north Pacific was observed: the type species *A. rubricata*, *A. helleri* **comb. nov.** from Portugal and *A. 'ASPSP'* **sp. nov.**, from the equatorial archipelago of Saint Peter and Saint Paul in the Atlantic Ocean (Fig. 2B). Other species within *Ampithoe s.s.* include *A. sectimana* Conlan and Bousfield, 1982, *A. dalli* Shoemaker, 1938 and *A. tarasovi* Bulyčeva, 1952. Both *A. dalli* and *A. tarasovi* appeared as non-monophyletic and may characterize undescribed species.

Foscampithoe **gen. nov.** is also supported by strong BS and PP values, and encompasses several species of restricted distribution. Species delimitation analyses were performed on *Foscampithoe* **gen. nov.** and different methods resulted in different putative species. Here, we accept the congruence of molecular species delimitation, mostly in agreement with ABGD COI clusters and morphology, resulting in 21 species. Clade letters are represented below branches for the clades discussed ahead.

Foscampithoe hinatore (Barnard, 1972) **comb. nov.** is the sister clade of all remaining *Foscampithoe* spp., followed by a clade composed of. *F. poipu* **comb. nov.** and *F. 'suapensis'* (Correia, Guedes-Silva and Souza-Filho, 2016) **comb. nov.** (Clade A, Fig. 3). Clade B includes the *F. marcuzzii*'s Ruffo, 1954 **comb. nov.** species complex (Clade C, Fig. 3), a new species complex from the Brazilian coast, and the Australian species *F. ngana* (Poore and Lowry, 1997) **comb. nov.**, *F. geographe* (Peart, 2007) **comb. nov.** and *F. eremitis* (Peart, 2007) **comb. nov.** (Clade D, Fig. 3). The species of the *F. marcuzzii* **comb. nov.** complex are geographically separated into *F. 'marcuzzii'* CON **sp. nov.**, found on the Brazilian mainland, and *F. 'marcuzzii'* ISL **comb. nov.**, found on the Caribbean and southwestern Atlantic islands (Fig. 3).

Clade E is composed of species of the *F. ramondi* (Audouin, 1826) **comb. nov.** species complex and *F. kava* **comb. nov.** (Fig. 3). In the southwestern Atlantic, this complex is sympatric to *F. marcuzzii*'s complex, however, species' ranges were different. *Foscampithoe 'divisura'* NE **comb. nov.** occurring on the Brazilian northeastern mainland coast, down to the Abrolhos Archipelago in the continental shelf, and its distribution includes the oceanic equatorial island of Fernando de Noronha, while *F. 'ramondi'* SE **comb. nov.** was found on Brazilian southern mainland (Clade F, Fig. 3). Two morphotypes of males were observed within clade F, one characterized by small specimens with long 'thumb' on Gn2 propodus, and other by large specimens with short 'thumb' on Gn2 propodus (Fig. 4). However, morphology was not congruent with molecular clusters. *Foscampithoe kava* **comb. nov.** from Australia is the sister species of clade F, and the individual identified as *F. 'ramondi'* **comb. nov.** from Hawaii is possibly another undescribed species within the *F. ramondi*'s complex.

Clade G comprises two well supported clades from the northern hemisphere of possible undescribed species: clade H, that includes *F. 'rubricata'* **comb. nov.** and *F. 'ramondi'* **comb. nov.**

from the northeastern Atlantic, and *F. 'longimana'* from the Atlantic coasts of United States and Canada (Fig. 3). Another species identified as *F. 'longimana'* is found on clade I, a sister species of the *F. plumulosa* **comb. nov.** from the eastern Pacific (Fig. 3).

3.2. Divergence time analyses

Divergence time estimates indicate that crown Ampithoidae originated in the Cretaceous around 127.54 Ma [95% highest posterior density intervals (HPD): 66.52-185.71 (Fig. 5, Supplementary Material X)]. Genera ages range between 97.69 Ma (95% HPD: 59.55-135.44) on *Foscampithoe* **gen. nov.**, and 28.19 ((95% HPD: 14.82-43.26) on *Cymadusa* (Fig. 5, Supplementary Material X). Divergence time estimates for the remaining genera were 40.64 Ma (95% HPD: 23.39-59.78) for *Sunamphitoe,* 50.58 Ma (95% HPD: 43.75-95.27) for *Ampithoe* and 58.50 Ma (95% HPD: 37.56-81.03) for *Exampithoe* (Fig. 5, Supplementary Material X).

In the *Foscampithoe* **gen. nov.**, clade A diverged in the late Cretaceous [ca. 79.76 Ma (95% HPD: 52.85-107.17)], clade B in the Paleocene [ca. 61.34 Ma (95% HPD: 39.81-80.21)], and clades C and D in the Eocene [ca. 47.51 Ma (95% HPD: 29.06-64.39)]. For clades E and F, divergence times were 46.68 Ma (95% HPD: 28.89-62.63) and 17.67 Ma (95% HPD: 8.95-25.43), respectively. Lastly, northern hemisphere clade G diverged in the Eocene [ca. 54.79 Ma (95% HPD: 34.23-72.23)], with clades H and I divergence times around 39.13 Ma (95% HPD: 21.25-55.05, Figs. 3, 5, Supplementary Material X).

3.3. Biogeographic analyses

Ancestral range reconstruction from BioGeoBEARS chronogram estimated DEC + j as the best model (Table 1), with inferred ancestral ranges being similar across most models. Ampithoidae was estimated to have originated in what today constitutes the Indo-West Pacific (WP) around 127.54 Ma, in the ancient Tethys Sea (Fig. 5). The analysis suggested a first sympatric speciation event along the WP, with the diversification of *Foscampithoe* **gen. nov.** Considering that main biogeographical events took place during the Tethys Sea existence, both events from WP to the nowadays Western Atlantic (WA) and return to WP occurred before the Tethys Sea extinction (Fig. 5). Later on, one dispersion event of the ancestral *A. marcuzzii*'s species complex occurred in the Eocene from the WP to WA, while an ancestral had a recent transatlantic dispersion to the northeastern Atlantic (EA) ca. 30 Ma. Recent dispersion include the ancestor of *F. poipu* **comb. nov.** to the Central Pacific (CP), *F. caddi* **comb. nov.** and *F. kava* **comb. nov.** to the WP and *P. plumulosa* **comb. nov.** to the Eastern Pacific (EP, Fig. 5).

The other Ampithoidae genera mainly diversified along the WP, and a dispersal to the EP promoted the diversification of the genus *Ampithoe* in the late Cretaceous, ca. 70 Ma. Within *Ampithoe*, multiple dispersion to the Atlantic and WP shaped the current genus distribution. Both *Cymadusa* and *Sunamphitoe* had their origin in the WP during the Paleogene, but more sampling on this genera is needed to understand their deeper biogeographical scenarios (Fig. 5).

3.4. Systematics

Order Amphipoda Latreille, 1816

Suborder Senticaudata Lowry and Myers, 2013

Family Ampithoidae Boeck, 1871

Genus *Foscampithoe* Siqueira and Iwasa-Arai **gen. nov.**

Diagnosis: Antenna 1, length, longer or similar to Antenna 2, accessory flagellum absent; antenna 2, robust, better developed than antenna 1; peduncular articles 4 and 5 elongated, article 4 slightly broader than article 5; mandible, incisors and lacinia asymmetrical, molar well developed and triturating, palp elongated, uniform breadth, 3- articulate, article 2 with marginal and/or distal setae, article 3, setose, not expanded or clavate distally; lower lip, outer plate notched, outer lobe slender, longer than inner lobe; maxilla 1, palp developed, 2- articulated, article 2 slender, slender and robust setae presented; maxilla 2 outer plate broader than inner plate, coxae 1-4, ventral margin with setules; coxa 1 expanded distally, anteroventral angle produced; gnatopods sexually dimorphic, gnatopod 1, smaller than gnathopod 2 in male, or similar in size or form to gnathopod 2 in male; peraeon, segment 7 of male with ventral keel [thorax sternal process in Barnard & Karaman (1991)], peraeopods 3-4, simple, basis moderately inflated; peraeopods 5-7, simple or prehensile, propodus subrectangular, slightly expanded distally or not; uropod 1, peduncle, medial margin with robust setae, distoventral spur weak or absent in males, absent in females, setal fringe present; uropod 2, peduncle laterodistal projection absent; uropod 3: rami broad; outer ramus with 2 large recurved robust setae; telson subtriangular, round, agude or truncated distally, cusps, small or developed to form hooks, denticles absent.

Type species: *Foscampithoe marcuzzii* (Ruffo, 1954)

Etymology: The genus is in honor of the carcinologist and marine ecologist Dr Fosca Pedini Pereira Leite for her great contribution to the knowledge on the marine associated fauna of Brazil.

Remarks: *Foscampithoe* **gen. nov.** is morphologically similar to *Ampithoe,* as they several characters related to antennae, lower lip, maxillae, gnathopods and pereopods 3 and 4. *Foscampithoe* **gen. nov.** differs from *Ampithoe* by the morphology of mandibular palp (Sotka et al. 2017), which is uniform, not clavate or expanded distally in *Foscampithoe* ***gen. nov.***. *Foscampithoe* **gen. nov.** also present a ventral keel on segment 7 of male's pereon (LeCroy 2002), not observed in *Ampithoe* species.

Species included: *Foscampithoe 'ArABR1'* **sp. nov.**, *Foscampithoe 'araça'* **sp. nov.**, *Foscampithoe caddi (Poore and Lowry, 1997)* **comb. nov.**, *Foscampithoe 'divisura' NE* **sp. nov.**, *Foscampithoe eremitis (Peart, 2007)* **comb. nov.**, *Foscampithoe geographe (Peart, 2007)* **comb. nov.**, *Foscampithoe hinatore (J.L. Barnard, 1972)* **comb. nov.**, *Foscampithoe kava* (Myers, 1985) **comb. nov.**, *Foscampithoe longimana* (Smith, 1873) **comb. nov.**, *Foscampithoe marcuzzii* (Ruffo, 1954)

comb. nov., *Foscampithoe 'marcuzzii CON'* **sp. nov.**, *Foscampithoe ngana* (Poore and Lowry, 1997) **comb. nov.**, *Foscampithoe poipu* (J. L. Barnard, 1970) **comb. nov.**, *Foscampithoe plumulosa* (Shoemaker, 1938) **comb. nov.**, *Foscampithoe ramondi* (Audouin, 1826) **comb. nov.**, *Foscampithoe 'ramondi' S* **sp. nov.**, *Foscampithoe suapensis* (Correia, Guedes-Silva and Souza-Filho, 2016) **comb. nov.**

4. DISCUSSION

Four phylogenies of Ampithoidae have been proposed so far (Conlan 1982, Peart and Ahyong 2016, Sotka et al, 2017, present study). Conlan (1982) performed the first approach on the reconstruction of Ampithoidae relationships based on 27 morphological characters and 29 terminals on a numerical phenetic analysis. Over 30 years past from Conlan's (1982) to the second proposed phylogeny by Peart and Ahyong (2016), which was performed with the largest matrix sampling of 53 terminals and 77 characters on a cladistic analysis. One year later, Sotka et al. (2017) proposed the first molecular phylogeny for the family, including 35 species across 10 genera. Among the three previous phylogenies, no genera relationships were congruent. This is the second molecular phygenetic analyses proposed for Ampithoidae, mostly focusing on the *Foscampithoe* **gen. nov.** ingroup evolution and biogeography. Our results were partially congruent to Sotka et al. (2017), with the same major clades recovered (*Sunamphitoe* + *Pseudoamphithoides* + *Amphitholina* + *Cymadusa*, and *Plumithoe* + *Exampithoe* + *Biancolina* + *Ampithoe*), however, relationships between genera varied (Figs. 1, 2 and 5).

Three genera have a complex evolution with morphological convergence, which caused previous discussion on their validity: *Ampithoe*, *Foscampithoe* **gen. nov.**, and *Pleonexes*. *Pleonexes*' status was largely discussed, which J. L. Barnard (1970) synonymised with *Ampithoe*, and Peart & Ahyong (2016) ressurected the genus. In our analyses, *Pleonexes* is not monophyletic, however, because of the lack of *Pleonexes*' type species in our analyses, we maintained the status of the genus. We therefore ressurected *Ampithoe helleri* Karaman, 1975, and the following new combinations are proposed for the new genus: *Foscampithoe poipu* (J. L. Barnard, 1970) **comb. nov.** and *F. kava* (Myers, 1985) **comb. nov.**

Both Peart and Ahyong (2016) and Sotka et al. (2017) found *Ampithoe* as non monophyletic, with Sotka et al. (2017) proposing a 'south clade' (herein proposed as *Foscampithoe* **gen. nov.**) and a 'north Pacific clade' (*Ampithoe s.s.*). In our analyses, *Ampithoe s.l.* was also recovered as non monophylethic, on the other hand, the addition of more terminal species showed that clades are not completely geographically concordant (Fig. 5). *Ampithoe* indeed appear to have more species from the north Pacific region, however, independent dispersion also happened in more recent times, such as the dispersion of *A. rubricata*, *A. helleri* **comb. nov.** and *A. 'ASPSP'* **sp. nov.** to the Atlantic Ocean (Fig. 5). The DEC+j biogeographic analysis suggested that *Ampithoe* likely emerged before the Tethys Sea final closure, and its dispersion to this new area played a key role on the genus diversification. Another difference between *Ampithoe* and *Foscampithoe* is their species' ranges, species of *Ampithoe* present wide distributions, whereas species of *Foscampithoe* **gen. nov.** have restricted distributions.

The Saint Peter and Saint Paul Archipelago, a small archipelago in the middle of the Atlantic that arose around 9 Ma., appear to have an important part of Ampithoidae dispersion, as a suitable environment that could be used as stepping stone across the Atlantic, as well a unique place for species establishment and speciation. This archipelago harbors the only *Ampithoe* species from the western Atlantic, *Ampithoe 'ASPSP'* **sp. nov.**, as well as an undescribed species of *Cymadusa* and *F. 'suapensis'* **comb. nov.**. *Foscampithoe suapensis* **comb. nov.** was described for the Brazilian northeastern mainland coast, and so far has been found on the mid-Atlantic Trindade Island and the equatorial Saint Peter and Saint Paul Archipelago, hence, this disjunct distribution might correspond to another species complex.

On the *Foscampithoe* **gen. nov.** clade, several species from the western Atlantic are herein described. *Foscampithoe 'marcuzzii'* **comb. nov.** species complex showed a geographic distribution separated into Brazilian mainland vs Brazilian oceanic islands and Lesser Antilles (Caribbean). In contrast, the western Atlantic *F. 'ramondi'* **comb. nov.** species complex showed a different distribution pattern, with *F. 'divisura' NE* **sp. nov.** being found in the Brazilian northeastern mainland coast and the oceanic equatorial island of Fernando de Noronha, while *F. 'ramondi*' SE **sp. nov.** was found on Brazilian southern mainland (Clade F, Fig. 3). Both species complexes have overlapping distributions and their disparate occurrences of cryptic species might be correlated to species ages and colonization times. While *F. 'marcuzzii' ISL* diverged from *F. 'marcuzzii' CON* in the Oligocene, about 26 Ma., where sea levels were higher and covering part of the mainland, *F. 'divisura' NE* diverged from *F. 'ramondi' S* in the Miocene, about 15 Ma. (Fig. 5), when shallow water areas were very restricted and the continental shelf was exposed. Although the difference between divergence times are short in a geological timeline, this recent changes on the sea levels and consequently suitable habitats for the species colonization might reflect their current distribution patterns.

Foscampithoe 'ramondi/divisura' complex also showed a peculiar incongruence with morphology. When sorted, specimens were identified as *'ramondi'*-like or *'divisura'*-like, where males of *'ramondi'*-like were characterized by large specimens with short 'thumb' on Gn2 propodus (Figs. 4A and 4C), whereas *'divisura'*-like were the small specimens with large 'thumb' on Gn2 propodus (Figs. 4B and 4D). *Ampithoe 'divisura'* from northeast were smaller than *A. 'divisura'* and *A. 'ramondi*' from southern localities, while both morphotypes co-occurred and were similar in length in southern localities (Fig. 4), and females were not distinguished. Hence, this could be an indication of a reproductive strategy with polymorphic males, also observed in the intertidal isopod *Paracerceis sculpta* Holmes, 1904 (Shuster 1987) and the supralittoral amphipod *Chelorchestia darwinii* (Müller, 1864) (Serejo 2004).

We recovered the WP realm as the ancestral distribution area of Ampithoidae (Figure 5), supporting the proposal of an Indo-West Pacific "center of origin" where species originated in the biodiversity center colonize marginal areas and speciate (Bowen et al., 2013). Twenty-three species presented the current distribution within the WP, followed by 13 species distributed in the WA, and 6 species in the EP (Fig. 5). From the WP origin, the first dispersal was of *Foscampithoe* **gen. nov.** ancestors to the WA, while *Ampithoe* dispersed and speciated in the EP, while consecutive sympatric speciations continued to raise species number in these three realms and other species conquered new areas such as the CP and EA. This pattern of an Indo-West Pacific origin with a posterior colonization of the Western Atlantic around the late Cretaceous was also observed for limpets of the family Fissurelidae, where a westward colonization of new oceans via the Tethys Seaway upon the breakup of Pangea was proposed (Cunha et al. 2019).

The DEC+j analysis of the family Ampithoidae is the first dated evolutionary biogeographic attempt to understand the dynamics of fauna associated with macroalgae over time. When comparing with the biogeography of *Synapseudes* Miller, 1940, a tanaidacean genus associated to macroalgae, we also observed a possible origin in the WP, a clade dispersion to the WA followed by speciation and an independent late dispersion of a single species (Iwasa-Arai et al. 2021). It is impossible to predict that these were the same events that shaped the Ampithoidae's biogeography, once there was no time estimates for *Synapseudes* biogeographic analyses. However, we believe the shared areas for ancestral species in both Ampithodae and *Synapseudes* could reflect that dispersion through macroalgae was essential to the success of both taxa.

The BACR contains the most ecologically and economically important orders of brown algae, that radiated throughout the Cretaceous period (145-66 Ma, Bringloe et al. 2020). Considering the importance of host diversification for associated fauna, the BACR was essential for the success of Ampithoidae, providing a new suitable habitat for colonization. The earliest branching orders within

BACR radiated around 125 Ma, with hypothesized evolution in cold waters of the Southern Hemisphere (Bringloe et al. 2020), In more recent times, brown algae genera diversification mostly suggest that ancestors were distributed in the Indo-West Pacific Ocean during the Miocene, as for *Sargassum* (Yip et al. 2019) and for species *Colpomenia sinuosa* (Lee et al. 2013) and *Dictyota ciliata* (Tronholm et al. 2012), corroborating the hypothesis of the Indo-West Pacific as a center of origin and providing a resourceful substrata for Ampithoidae colonization and diversification.

As example of Australia, where a large number of Ampithoidae species was predicted and later described (Peart 2007a, 2007b, Lowry and Myers 2009, Hughes and Peart 2013), six species of *Ampithoe s.l.* were known to Brazilian waters prior to this work. A detailed study on the morphology, molecular systematics and evolutionary biogeography brought a new genus and five new species of *Foscampithoe* **gen. nov.** and *Ampithoe 'ASPSP'* to light. New species are most likely to be described in recent times, as well as larger sampled phylogenies for the family. So far, we believe this is the most comprehensive attempt to understand the evolution of Ampithoidae with integrative methods in the southwestern Atlantic.

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Figures and Tables

Figures

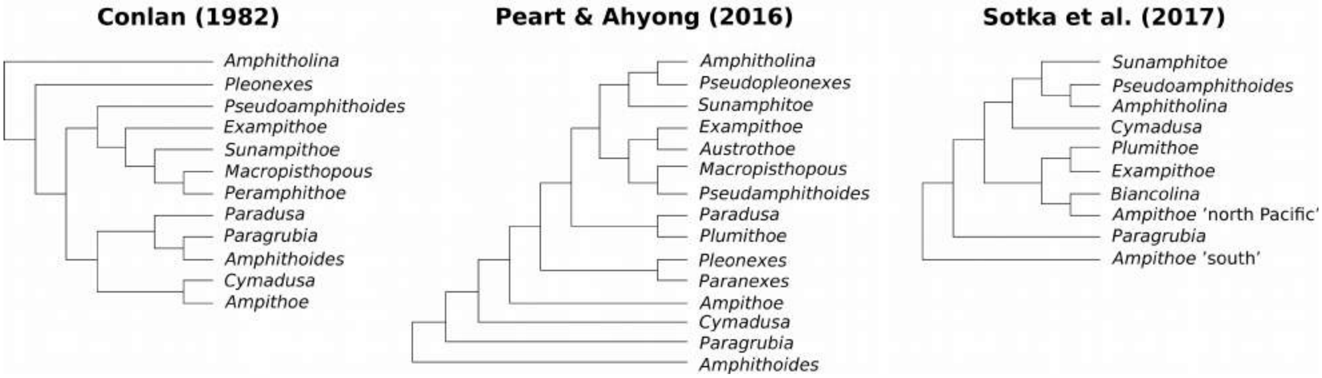

Figure 1. Phylogenies of Ampithoidae proposed by Conlan (1982), Peart and Ahyong (2016), and Sotka et al. (2017).

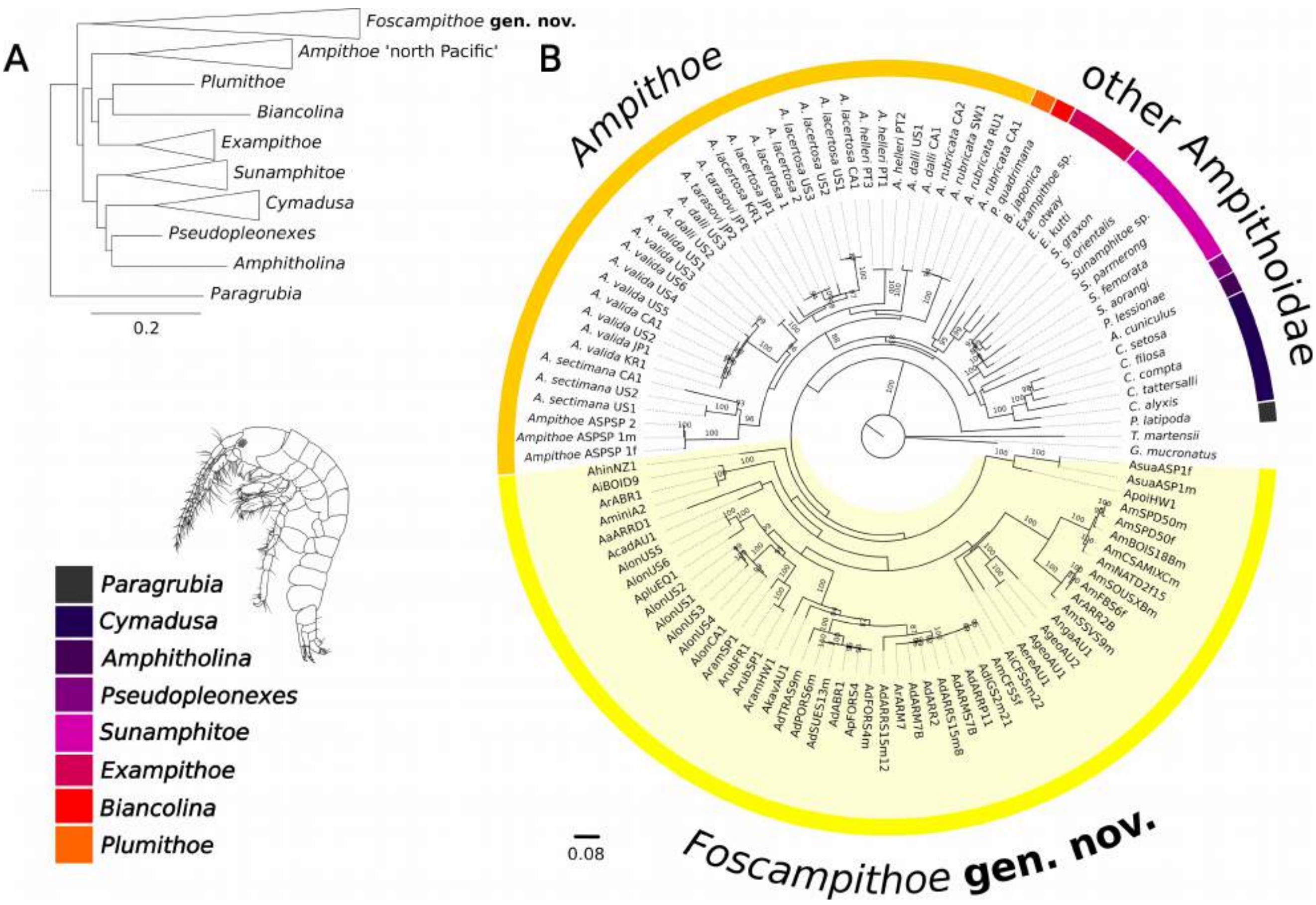

Figure 2. Maximum likelihood phylogeny of Ampithoidae recovered from the concatenated dataset of COI+16SrRNA+28SrRNA+EF1-α+NAK. **A.** Topology showing genera only. **B.** Complete topology. Numbers under branches represent bootstrap values over 80%.

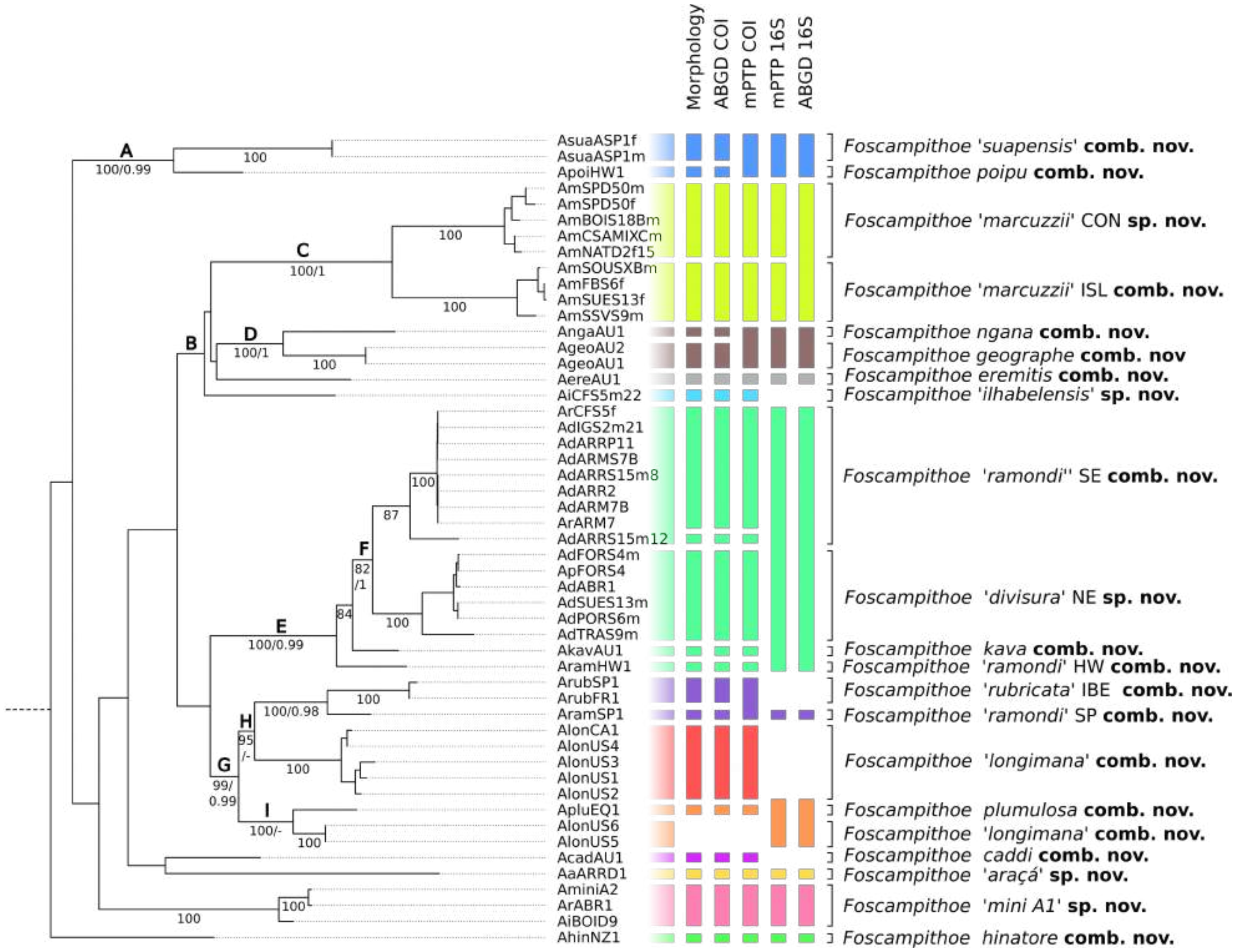

Figure 3. Maximum likelihood phylogeny of *Foscampithoe* **gen. nov.** recovered from the concatenated dataset of COI+16SrRNA+28SrRNA+EF1-α+NAK. Letters above branches represent clades mentioned in the text, numbers below branches represent bootstrap values over 80% and posterior probability values over 0.9. Color bars represent clusters from species delimitation analyses.

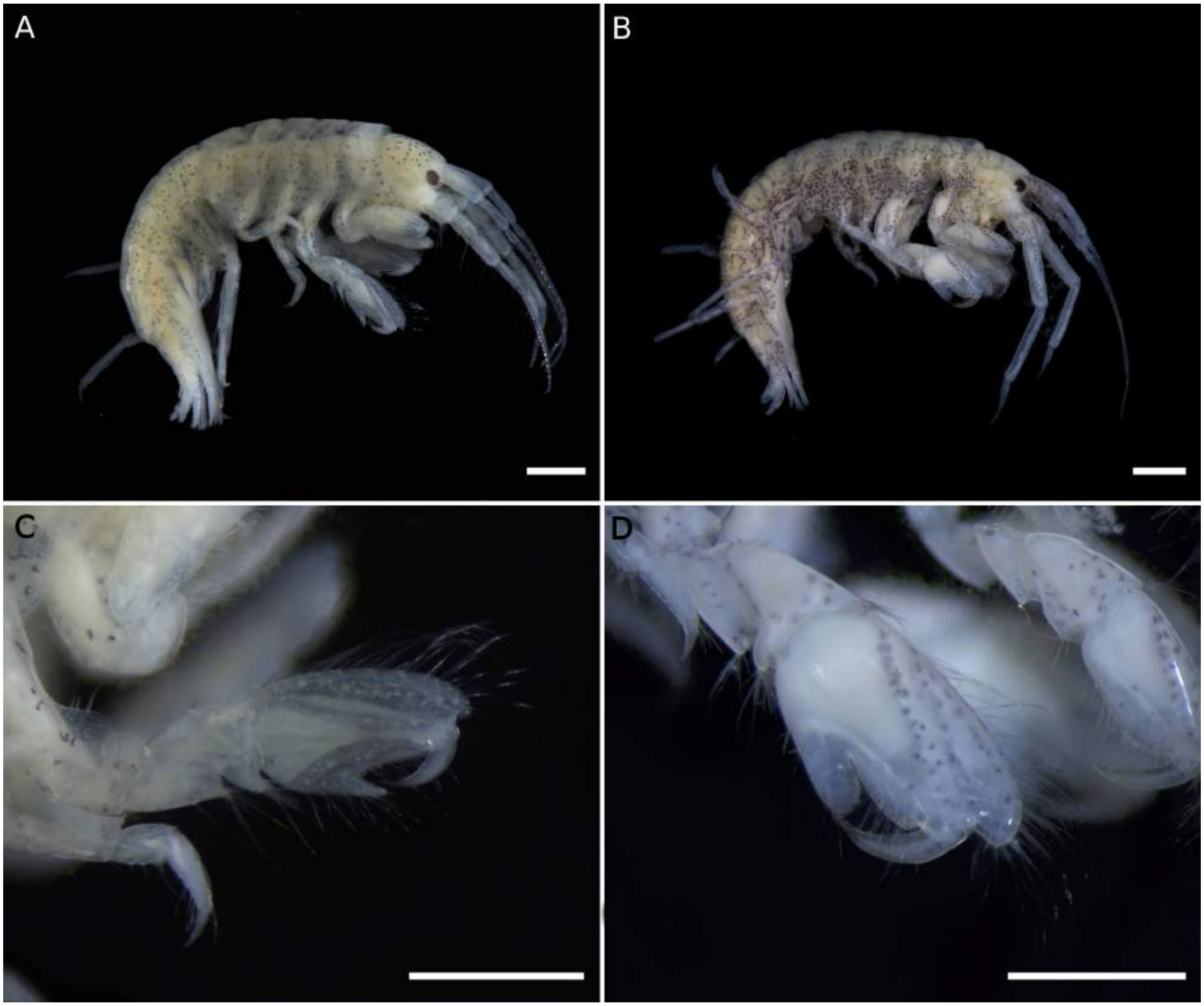

Figure 4. A. Morphological overview of *Foscampithoe 'ramondi' SE* **sp. nov. B.** Morphological overview of*Foscampithoe 'divisura' SE* **sp. nov. C.** Male Gn2 of *Foscampithoe 'ramondi' SE* **sp. nov. D.** Male Gn2 of *Foscampithoe 'divisura' SE* **sp. nov.**

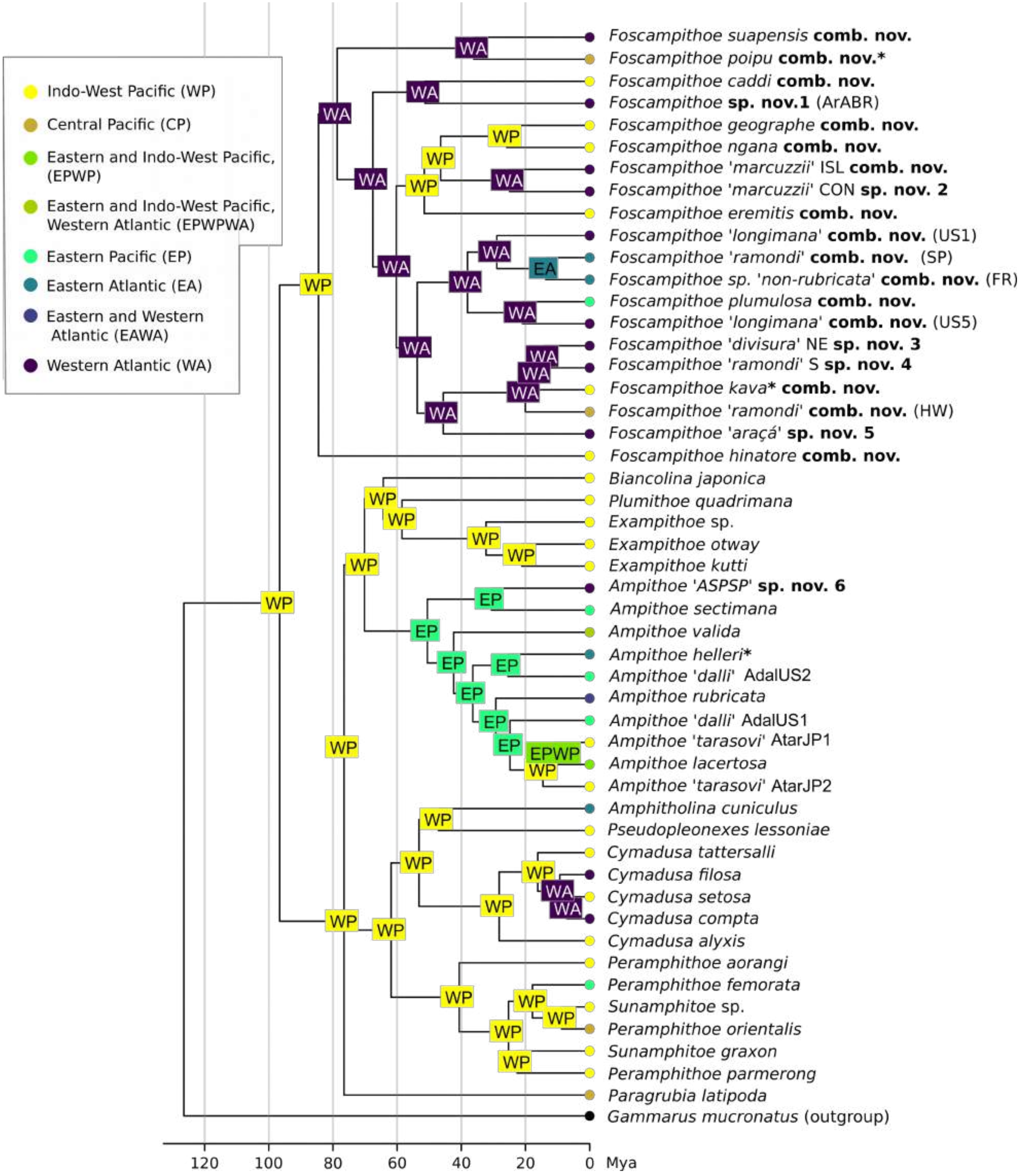

Figure 5. Ancestral range reconstruction on the calibrated tree of Ampithoidae with the best fitting DEC + j model in BioGeoBEARS. Color boxes on nodes represent most likely ancestral areas. Asterisks represent previously designated *Pleonexes.*

Table

Table 1. Model test results from BioGeoBEARS based on the Ampithoidae calibrated tree, ordered by AICc weights. LnL, log-likelihoods; params, number of parameters in the model; d, dispersal rates; e, extinction rates; j, jump dispersal rates; AICc, sample size corrected Akaike Information Criterion scores; AICc_wt, Akaike weights.

	LnL	numparams	d	e	j	AIC	AIC_wt
DEC+J	-105.6	3	0.0003	1.0e-12	0.074	217.1	0.73
DIVALIKE+J	-106.7	3	0.0003	1.0e-12	0.059	219.3	0.24
BAYAREALIKE+	-108.9	3	0.0003	1.0e-07	0.093	223.8	0.026
DIVALIKE	-134.6	2	0.0020	0.0002	0	273.2	4.7e-13
DEC	-140.4	2	0.0018	0.0037	0	284.8	1.5e-15
BAYAREALIKE	-152.1	2	0.0014	0.020	0	308.3	1.2e-20

Capítulo 3

CONTINENT-ISLANDS BOUNDARY AND ENVIRONMENT-SHAPED EVOLUTION IN THE MARINE AMPHIPOD *Ampithoe marcuzzii* COMPLEX (CRUSTACEA: EUMALACOSTRACA: AMPITHOIDAE)

Continent-islands boundary and environment-shaped evolution in the marine amphipod *Ampithoe marcuzzii* complex (Crustacea: Eumalacostraca: Ampithoidae)

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Abstract

Marine amphipods are crustaceans that lack larval phase and consequently have low dispersion rates. Despite that, these crustaceans present great ability to be transported by rafting of natural floating substrata, especially macroalgae, where they find shelter, food and mating ground. In the past years, recent changes in upwelling off West Africa during North Hemisphere winter and by Amazon River discharge are intensifying recurrent pelagic *Sargassum* blooms in the tropical Atlantic and Caribbean Sea, which could cause changes in the community associated to benthic macroalgae in coastal waters, connection of previously isolated populations, and colonization of new environments. The species *Ampithoe marcuzzii* is widely distributed throughout the western Atlantic Ocean, and it was used as a model to study the seascape genomics and phylogeography in invertebrates with low dispersion capacities. Based on mitochondrial and nuclear genes, and SNPs, we observed the presence of a species complex within *A. marcuzzii,* separating mainland and insular populations. Each species showed an independent evolutionary history, where 'continent' species was characterized by strong latitudinal population structure, with evidences of IBD and IBE. Historical expansion and environmental variables were observed associated with the southeastern population, and ecological niche modeling corroborated the region as a paleorefuge. Populations from 'islands', instead, presented complicated evolutionary histories, with closer localities genetically isolated and further localities connected. An ancient pathway across the Caribbean and southwestern Atlantic is observed, suggesting the species origin in the Caribbean and posterior diversification in the Brazilian oceanic islands.

Running title: AMPITHOE PHYLOGEOGRAPHY AND SEASCAPE GENOMICS

Keywords: Amphipoda, paleoclimate distribution, phylogeography, *Sargassum*, seascape genomics

INTRODUCTION

Macroalgal beds, one of the main environments formed in coastal areas, are characterized by their high productivity and structural complexities that provide food resources and reproductive sites for a vast diversity of species, as well as shelter from predators and adverse abiotic factors (Christie et al. 2009). Among the most representative species that make up the macroalgal beds are those of the genus *Sargassum* C. Agardh, which have a wide distribution in the Atlantic Ocean and form dense and extensive banks, representing about 80% of the cover and biomass of algae in the infralittoral rocky shores (Széchy & Paula 2000). The Sargasso Sea, a characteristic conglomerate of macrophytes located in the Northwest Atlantic Ocean, is mainly formed by pelagic floating masses of *Sargassum natans* (L.) Gaillon and *S. fluitans* (Børgesen) Børgesen (Guiry & Guiry 2016) that harbor a unique ecosystem (Sissini et al. 2017). Recently, changes driven by upwelling off West Africa during North Hemisphere winter and by Amazon River discharge are intensifying recurrent blooms in the tropical Atlantic and Caribbean Sea, denominated the 'great Atlantic *Sargassum* belt' (GASB, Wang et al. 2019). These events could be causing the arrival of exotic species and compromising ecosystem balance (Sissini et al. 2017).

The fauna associated with macrophyte beds is mainly composed of crustaceans of the superorder Peracarida Calman, 1904, which are characterized by having a marsupium formed by oostegites (Poore 2005). The order Amphipoda Latreille, 1816 corresponds to one of the most diverse within Peracarida, and also constitute the most representative group of fauna associated with macrophyte banks (Tanaka & Leite 2003). Due to their direct development, such crustaceans are expected to have a low dispersal capacity, thus assuming a high level of endemism (Hurtado et al. 2016). However, according to Thiel (2003), peracarid crustaceans are extremely suitable for colonization by rafting from floating organisms, since they can persist during long journeys on drifting substrates, as their offspring can be recruited directly on the parental float, leading to successive changes in specimen composition during the travel route. Thus, rafting may contribute to population connectivity up to >5000 km, with great effects on evolutionary processes of hitchhiker species (Thiel & Haye 2006).

The amphipod fauna associated with species of *Sargassum* can be represented by over 30 species (Tanaka & Leite 2003, Leite et al. 2007). However, several species of amphipods common in this association have aroused discussions among taxonomists due to important intrapopulation morphological variations (Peart 2004). Thus, it is possible that an underestimation of the richness of the amphipod fauna is occurring, and each of these species names may actually represent cryptic species complexes (Peart 2004, Ros et al. 2014). The herbivorous species *Ampithoe marcuzzii* Ruffo, 1954, originally described from Los Roques, Venezuela, is quite abundant in *Sargassum* banks off the Florida (LeCroy 2002) and Brazilian coasts (Serejo & Siqueira 2018, Campos et al. 2020), as well as from Atlantic oceanic islands (Iwasa-Arai et al. 2021), however, its evolutionary history remains uncertain.

The distinctive evolution on oceanic islands is recognized by the high endemicity caused by isolation (Gillespie 2013, Pinheiro et al. 2017), and the diversity of isolated places, in particular marine peracarid species, is mostly shaped by dispersion (Iwasa-Arai et al. 2021). Here, we aim to understand the evolutionary history of the amphipod *A. marcuzzii*, to then broadly discuss the evolution and biogeography of marine invertebrates with low dispersion capacities along the coast and on the dynamics of isolated islands colonization.

MATERIAL AND METHODS

Study sites, sampling and morphology

Specimens identified as *Ampithoe marcuzzii* were collected associated with brown macroalgae between 2016 and 2021 from over 5000 km in the western Atlantic Ocean, across the northeastern (NE) and southeastern (SE) regions of the Brazilian coastal zone, continental and oceanic islands, and in the islands of Dominica and Saint Martin in the Lesser Antilles, Caribbean (Fig. 1, Table 1), under the Brazilian SISBIO licence no. 60924 and national authorization by Dominica’s Fisheries Division.

Algal fronds were collected underwater by freediving (1–5 m), separated from each other in fabric bags (0.2 mm mesh size), fixed and preserved in ethanol 96–99%. After a first morphological sorting, specimens identified as *A. marcuzzii* were selected for molecular analysis. Identification was made based on the original description by Ruffo (1954), Florida's identification guides from LeCroy (2002) and comparative descriptions of the ampithoid Brazilian fauna (Andrade & Senna 2017; Campos et al. 2020). Specimens and vouchers are deposited at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

The abbreviations used for sampling sites are as follows: Brazil mainland: ABR, Abrolhos Archipelago; BA, state of Bahia; BOI, Boipeba Island; CAU, Caucaia; CF, Cabo Frio; FLE, Flecheiras; FOR, Forte Beach; NAT, Natal; PB, Coqueirinho Beach; PCR, Paracuru; SINO, Ilhabela; SPD, Ubatuba; TRA, Trancoso. Brazilian oceanic islands: CON, Conceição Beach; EI, Equatorial islands (RA+FN); FN, Fernando de Noronha (CON+POR+SUE); OI, Oceanic Islands (FN+RA+TRI); POR, Porto Beach; RA, Rocas Atoll; SUE, Sueste Beach; TRI, Trindade Island. Lesser Antilles: CDM, Caribbean Dominica (SB+SOU); LA, Lesser Antilles; SA, Southwestern Atlantic; SB, Secret Beach; SM, Saint Martin; SOU, Soufrière; SSV, San Sauveur.

DNA extractions, PCR amplification and sequencing

Genomic DNA was extracted according to the CTAB protocol of Doyle & Doyle (1987). Partial sequences of the mitochondrial genes cytochrome oxidase subunit 1 (COI) and 16SrRNA, and nuclear 28SrRNA were obtained for subsequent analyses. Fragments were amplified using the following primer pairs: HCO2198 and LCO1490 (Folmer et al. 1994) for COI, 16STf (Macdonald et al. 2005) and 16Sbr (Palumbi et al. 1991) for 16SrRNA and rd1 and rd4b (Edgecombe & Giribet 2006) for 28SrRNA.

Polymerase chain reactions (PCRs) were carried out in a total volume of 15µL containing 1 × PCR buffer, 2.5U Taq DNA Polymerase, 1.5mM MgCl2, 200µM of each dNTP, 0.35µM of each oligonucleotide and ultrapure water to achieve the reaction volume (Taq PCR Master Mix, Qiagen). The cycling profile on the thermal cycler involved a denaturation step at 94°C for 1min, 35 cycles of denaturation at 94°C for 1min; annealing temperature for 1min, extension at 72°C for 1min; and extension at 72°C for 10min. Annealing temperatures were 48°C for COI and 28SrRNA, and 52°C for 16SrRNA. PCR products were purified with polyethylene glycol solution 15% (PEG) and then amplified for sequencing using a BigDye Terminator Cycle Sequencing Kit v.3.1 (Applied Biosystems) at the Human Genome and Stem Cell Research Center, Universidade de São Paulo.

Chromatograms were analysed using Genestudio 2.2 (Genestudio Inc.), which was used to perform BLAST searches (http://blast.ncbi.nlm.nih.gov) to check for contamination or sequencing errors. Individual consensus sequences were aligned using T-Coffee server that combine multiple alignment methods (Notredame et al. 2000). Each marker was analyzed separately for most population analyses, and concatenated for phylogenetic analyses.

Library preparation, sequencing and SNP filtering

Individual libraries were generated based on the genotyping-by-sequencing (GBS) method described by Elshire et al. (2011) and modified by Nunes et al. (2017). Genomic DNA was digested with the PstI restriction enzyme (5′-CTGCAG-3′) and ligated to barcode and common adaptors with appropriate sticky ends. The products were pooled into sets up to 60 samples and then amplified by PCR using generic primers matching the common adaptors under the following conditions: 5min at 72°C, 30s at 98°C, 18 cycles of 10s at 98°C, 30s at 65°C and 30s at 72°C, and an extension step of 5min at 72°C. The presence of spare adapters and the sizes of the DNA fragments were assessed by quantification on an Agilent 2100 Bioanalyzer (Agilent Technologies) with the Agilent DNA 1000 kit and by quantitative PCR on a Light Cycler 480II (Roche) with a Kappa Biosystems kit for library quantification. Libraries were constructed by EcoMol Consultoria (Piracicaba, SP, Brazil), and sequencing was performed at the Center for Functional Genomics Applied to Agriculture and Agroenergy (LZT/ESALQ/USP, Brazil) on a HiSeq 2500 platform (Illumina Inc.).

Firstly, SeqyClean pipeline (Zhbannikov et al. 2017) was used to filter out sequences smaller than 50 bp and to remove sequences with an average Phred quality score ≤ 20, adapters and contaminants from the UniVec database (NCBI, ftp://ftp.ncbi.nlm.nih.gov/pub/UniVec/), followed by the reads assignment to individual samples and consensus sequence edition at iPyrad v.0.7.28 (Eaton 2014). In iPyrad, we discarted reads with more than five Ns or shorter than 35 bp. Minimum read depth was set to six. The clustering threshold was set to 90% and the maximum number of single-nucleotide polymorphisms (SNPs) per locus was set to 30. A locus had to be present in at least 50% of the samples to be retained in the final dataset. All the remaining parameters were set as default. The density of missing data per locus was observed through matrix occupancy (de Medeiros & Farrell 2018) and PLINK (Purcell et al. 2007) was used to remove SNPs with minimum allele frequency lower than 1%, missing genotypes higher than 50% and linkage disequilibrium ($r^2 = 0.50$).

Phylogenetic analyses and divergence time estimate

mtDNA and 28SrRNA

For comparative phylogenetic analyses, fragments of COI, 16SrRNA and 28SrRNA from *Ampithoe marcuzzii s.l.* were concatenated for phylogenetic analyses. Sequences of *Cymadusa filosa* Savigny, 1816 were obtained from GenBank (National Center for Biotechnology

Information, NCBI) for rooting. The optimal partitioning strategy and evolutionary models consisted of subdividing the COI data set by codon positions with the model JC for the three codon partitions, HKY+F+G4 for 16SrRNA, and TIM2+F+G4 for 28SrRNA. The phylogenetic analyses of maximum likelihood (ML) were held at the W-IQ-TREE web server (Trifinopoulos et al. 2016), and the support of the nodes was evaluated with 1.000 ultrafast bootstrap replicates (Hoang et al. 2018). For the species confirmation, we performed the Automatic Barcode Gap Discovery (ABGD, Puillandre et al., 2012) and the multi-rate Poisson Tree Process (mPTP, Kapli et al. 2017) on COI dataset. The species were inferred on trees of ML in the web interface of the program (http://mptp.h-its.org).

Divergence times were calculated with BEAST 1.8.4 (Drummond et al. 2012) with the same evolutionary models and partitions from the phylogenetic analysis. We employed an uncorrelated relaxed clock with a lognormal distribution (Drummond et al. 2006). For the tree model, we used a random starting tree, and speciation was modeled using the Birth-Death Process. Estimated divergence times were based substitution rates of 1.773% Ma $^{-1}$ for COI (herein also used for 16SRNA) and 0.161% Ma^{-1} for 28SrRNA previously inferred for Amphipoda (Copilaș-Ciocianu et al. 2019). The MCMC chain was run for 10^{8} iterations, with a thinning of 1000. Effective sample sizes of parameters and convergence were checked with Tracer 1.7.1 (Rambaut et al. 2018) after discarding 20% of the trees as burn-in. Two independent runs were performed and gave the same result. The resulting files were combined using LogCombiner 1.8 (Drummond et al. 2012), and the maximum clade credibility tree was produced using TreeAnnotator 1.8 (Drummond et al. 2012).

SNPs

The prospected SNPs from *A. marcuzzii s.l.* were used for the phylogenomic analysis using IQ-TREE v.1.5.6 (Nguyen et al. 2015), under the GTR+ASC model, with 1000 bootstrap replicates.

Genetic diversity and population structure

mtDNA and 28SrRNA

Two datasets ('continent' and 'islands') were build for population analyses according to phylogenetic and species delimitation results. Number of haplotypes (N) and their frequencies, as well as haplotype (h) and nucleotide (π) diversities were estimated using DNAsp v5 (Librado and Rozas 2009), and θ_S and θ_π were measured in Arlequin v.3.5 (Excoffier et al. 2005) for COI, 16SrRNA and 28SrRNA.

Pairwise genetic divergences between localities were estimated using unbiased *F*ST estimator θ (Weir & Cockerham 1984) using Arlequin, and the population structure was examined through hierarchical analyses of molecular variance (AMOVA), clustering localities recovered by phylogenetic and population analyses defining as groups 'continent': E, NE and SE; 'islands': OI, CDM and SSV. The statistical significance of estimates was assessed by 10,000 permutations. Genealogical relationships among haplotypes were assessed through a haplotype network constructed using TCS algorithm as implemented in PopART v.1.7 (Leigh & Bryant 2015).

SNPs

For the following analyses, two SNPs datasets were built following previously mentioned methods, separating the species from 'continent' and 'islands'. Diversity indexes θ_S and θ_π, and fixation index F_{IS} (Weir & Cockerham, 1984) across loci were calculated using the Arlequin for SNPs. Principal components analysis (PCA) was implemented using the *adegenet* package to describe the variance among the genomic data (Jombart 2008). Pairwise *F*ST and hierarchical AMOVA were calculated as previously described for mtDNA and 28SrRNA.

Structure software (Pritchard et al. 2000) was used to analyze the complete SNP dataset for *A. marcuzzii s.l.*, and for 'continent' and 'islands' datasets separately, using values of K from one to 10 according to phylogenetic and population analyses results, as well as because of the null values of ΔK after k=4. For each analyses, lambda value was first estimated in one run with all other values fixed, and estimated values were used in the posterior 10 runs. The results from the 10 iterations were compacted and analyzed in the R package Structure Harvester (Earl 2012), for K likelihood comparison. The selected K was used to generate a bar plot showing the most likely ancestry of each individual in the R package 'PopHelper*'* (Francis 2017).

A first Mantel test (Mantel 1967) was performed to identify possible correlation between the geographical and genetic distances between populations [isolation-by-distance (IBD), Wright 1943] using the R package *vegan* (Oksanen et al. 2020). Each sampling site was considered a different population and the genetic distance was inferred using pairwise F_{ST} (Weir & Cockerham 1984). The smallest linear distance between two sites was calculated using latitude/longitude distance calculator provided by the National Oceanic and Atmospheric Administration website (https://www.nhc.noaa.gov/gccalc.shtml).

Demographic history and divergence times

mtDNA

Demographic processes over time were assessed for each lineage using Tajima's D (Tajima 1989) and Fu's FS (Fu 1997) neutrality tests performed by Arlequin with 10,000 permutations for mtDNA. Changes in effective population sizes of each lineage over evolutionary time were inferred for mtDNA using BEAST (Drummond & Rambaut 2007) with the same evolutionary models and partitions from the phylogenetic analysis. Analyses were run for 5,000,000 generations, with the first 500,000 generations discarded as burn-in. Convergence was detected based on sufficiently large effective sample sizes (>200) for each parameter using TRACER 1.5 (Rambaut & Drummond 2007), and posteriorly used to plot reconstructed Bayesian skyline plots (Drummond et al. 2005).

SNPs

A migration matrix and demographic scenarios were estimated in Fastsimcoal v.2.7 (Excoffier & Foll 2011) using SNPs datasets of 'continent' and 'islands'. The historical migration rates were estimated using each locality as a population, with 10 independent replicates, each including 40 estimation loops with 60,000 coalescence simulations and assuming current migration between all pairs of populations. For the population expansion scenarios, the three clusters identified in the Structure analyses were used as populations for each dataset (continent: NE, E and SE; islands: CDM, OI and SSV), and three expansion models were tested. For each model, 50 independent replicates, each including 40 estimation loops with 300,000 coalescence simulations, were performed. The probability of each model given the observed data was determined based on both the maximum likelihood value and AIC. In both cases the mutation rate was also estimated by Fastsimcoal, with prior ranging from 1e^{-9} to 1e^{-6}.

Climate association analyses

Suitability maps were constructed under ecological niche modelling approaches (ENMs) using climate and paleoclimate simulations layers were accessed from the MARSPEC database (Sbrocco & Barber 2013) for current and past (last glacial maximum, LGM) scenarios with 5 arc min (~ 10km resolution in the Equator region). Climatic layers were clipped to the Western Atlantic Ocean with an extent of 80° and 20° W longitude and 35° S and 20° N latitude and a factorial analysis with Varimax was performed to select variables according to Sobral-Souza et al. (2015) and Menezes et al. (2020).

ENMs were built using the occurrence points obtained from our sampling sites and selected climatic variables for the current climate scenario and predicted for the LGM, with implementation of five mathematical algorithms to increase the reliability of models based on a forecast ensemble approach (Araújo & New 2007), including three based only on the present records: (1) envelope score, Bioclim (Booth et al. 2014); (2) Mahalanobis distance (Farber & Kadmon 2003), and (3) Domain–Gower distance (Carpenter et al. 1993); and two machine-learning methods based on presence/background records: (4) support vector machines (SVMs) (Tax & Duin 2004) and (5) maximum entropy (MaxEnt) (Phillips & Dudík 2008). A consensual map was built with the frequency of each grid cell predicted from all accurate models, taking values of the true skill statistic (TSS) and the "maximum sensitivity and specificity threshold" for each model (Sobral-Souza et al. 2015; Menezes et al. 2020).

SNPs To identify possible isolation-by-environment (IBE) evidences (Wang & Bradburd 2014), SNPs datasets were used to perform Mantel and partial Mantel tests with 1,000 simulations. The partial Mantel tests were performed separately for each environmental variable, using the geographic distance and variables available from Bio-Oracle (Tyberghein et al.

2012), MARSPEC (Sbrocco & Barber 2013) and WorldClim (Fick & Hijmans 2017) (Table S1). Variable's distances were calculated as Euclidean distances using the dist function in R.

Lastly, the redundancy analysis (RDA) was applied to correlate distribution and genomic traits of individuals with changes in abiotic variables (Forester et al. 2018). We used the same environmental variables used in the IBE inferences to perform a pairwise correlation analyses and selected ten variables with the lowest correlation ($|r| < 0.3$, Table S1).

RESULTS

SNPs prospection and data analysis

Sequenced libraries ranged from 312,772 to 12,261,962 reads per sample. After filtering and clustering steps, the average consensus read number was 26,284 (Table S2). One 'merged' dataset was used for *Ampithoe marcuzzii s.l.,* in which 5,857 SNPs were recovered from 134 specimens, with 31,19% of total missing data (Fig. S3). Two posterior datasets were built, with SM specimens removal, and separation of 'continent' and 'islands' lineages for comparative population analyses, resulting in 21,126 SNPs, 72 specimens and 27.55% of total missing data, and 17,237 SNPs, 55 specimens and 16.09% of total missing data, respectively (Figs. S4 and S5).

Phylogenetic analyses and divergence time estimates

mtDNA and 28SRNA

Three distinct species were identified by the phylogenetic tree and species delimitation analysis (Fig. 2A and S6), both showing a clear distinction between *A. marcuzzii s.l.* from 'continent', 'islands', and Saint Martin. Concatenated dataset of COI+16SrRNA+28SrRNA did not recover most of the localities clades (Fig. 2A and S6). Instead, a 'continent' clade was recovered, with NE as the sister clade of E, and SE as the sister clade of E+NE, and the multilocus tree of mtDNA+28SrRNA was used to infer the divergence times within *Ampithoe marcuzzii s.l.* (Fig. 2A). Specimens not included in the phylogenomic analyses from the northeastern localities of CAU, FLE and PCR clustered within NE, while TRA, in the eastern mainland belonged to E (Fig. S6).

According to our divergence time estimatives, 'continent' and 'islands' clades has deep divergence in the Eocene, around 51.8 Mya (95% HPD: 1.13–80.95, Fig. 2A). Within 'continent', SE split from E+NE in the Miocene, around 14.3 Mya (95% HPD: 5.70–71.44), while NE split from E around 10.72 Mya (95% HPD: 0.14–18.74). Caribbean population from SM split from 'islands' clade in the Miocene, around 15.72 Mya (95% HPD: 10.13–71.36), followed by the split of SSV around 7.58 Mya (95% HPD: 1.04–18.24), and the divergence of OI from CDM in the Pliocene, around 2.06 Mya (95% HPD: 1.36–11.56, Fig. 2A).

SNPs

Unrooted phylogenomic reconstruction agreed with spatial distribution of *A. marcuzzii s.l.*, with separation of main clades into southeastern mainland (SE), northeastern mainland (NE), and one clade grouping the Brazilian oceanic islands (OI) and the Dominican sites in the Lesser Antilles (Fig. 2B). Moreover, phylogenomic findings also recovered locality clades for several sampling sites, including one clade from the estuarine island of BOI, FOR in the NE mainland, CF in the SE mainland, the oceanic islands of TR and RA, the Caribbean coast of Dominica (CDM), the Atlantic coast of Dominica (SSV), and one last clade from the island of Saint Martin (SM, Fig. 2AB).

A highly supported clade herein named 'islands' was recovered, comprising a clade from the tropical oceanic island of TR and another from the equatorial island of RA, whereas FN was recovered as paraphylethic and including TR and RA clades (Fig. 2B), clustering together the three Brazilian oceanic islands (OI) where *Ampithoe marcuzzii s.l.* was found. OI is the sister clade of CDM, which includes specimens from SOU and SB, in the Caribbean Dominica. The only locality sampled in the Atlantic Dominica, San Sauveur (SSV), is the sister clade of OI+CDM, while SM is the sister clade of all remaining 'islands' specimens.

According to the phylogenomic analyses, 'islands' is the sister clade of NE, which includes the mainland localities of NAT, CSA and FOR (Fig. 2B), and 'islands'+NE is the sister clade of SE, composed of the mainland localities of CF and SPD, as well as the continental island of Ilhabela (SINO). Finally, BOI is recovered as the sister clade of 'islands'+NE+SE, and the continental archipelago of ABR is the sister clade of all remaining *A. marcuzzii s.l.*

Genetic diversity and population structure

Because of the low sampling of Saint Martin lineage, further analyses were performed for 'continent' and 'islands' only. Genetic diversity indexes slightly differed between 'continent' and 'islands', with overall haplotype diversity (H) similar for 'continent' and 'islands', and nucleotide diversity (θ_π) between individuals being lower for 'continent' on COI (θ_π =1.50) and SNPs (θ_π =118.60), and higher on 16SrRNA (θ_π =12.33) and 28SrRNA (θ_π =0.12). Overall θ_π values for 'islands' varied from 0.00 for 28SrRNA to 260.24 for SNPs. Within 'continent', greater diversity varied among markers, with values of 8.00 in FLE (NE) for COI, 57.60 in CF (SE) for 16SrRNA, 0.536 in CSA (NE) for 28SrRNA and 194.00 and 187.48 for SNPs in FOR (NE) and ABR (E), respectively. Regarding the 'islands' clade, highest values of θ_π also varied among localities, with values of 14.55 in CDM for COI, 31.72 in FN for 16SrRNA and 409.64 in RA for SNPs, while θ_π

values were null for 28SrRNA (Table 2). F_{IS} values across the loci were only significant for two localities in the ‘island’ dataset (RA=0.093 and SSV=0.382, $p<0.05$, Table 2).

Using the genetic clusters E, NE and SE for ‘continent’, and OI, CDM and SSV for ‘islands’ to perform a hierarchical AMOVA, the ‘continent’ results of COI and 16SrRNA suggested that most of the total variance is retained within populations, while 28SrRNA and SNPs presented the majority of the variance among groups, with high significative Φ_{ST} and Φ_{CT} indices for all genes (Table 3). ‘Islands’ results recovered most of the total variance within populations for COI, 16SrRNA and SNPs, while 28SRNA showed most of the variance among groups (Table 3).

The pairwise F_{ST} suggests greater differentiation between localities from different regions (NE, E and SE) in the ‘continent’ clade for all markers (Fig. 3), and within the ‘islands’ clade, highest values of F_{ST} were observed between SSV and remaining sites for 16SrRNA, 28SrRNA and SNPs, while for COI the greater F_{ST} values were between TRI and other sites instead (Fig. 3). Mantel tests with SNPs dataset for IBD were significant for the ‘continent’ (Mantel r^2=0.71, p=0.002), whereas no sign of IBD was observed for ‘islands’ (Mantel r^2=0.06, p=0.334).

mtDNA and 28SrRNA

The haplotype networks of COI, 16SrRNA and 28SrRNA presented a clear geographic pattern with two sets of haplotypes separated by over 100 mutational steps in the 28SrRNA network (Fig. 4). These two main sets of haplotypes are consistent with the ‘continent’ and ‘island’ clusters. In all networks, specimens from NE and SE localities were separated into different haplotypes, with one shared haplotype from the NE region in all networks, one shared haplotype from SE on 16SrRNA and 28SrRNA whereas for COI multiple haplotypes from a single locality within SE were observed (Fig. 4). The population structure from E region in the mainland diverged among networks, with unique haplotypes from ABR and BOI in COI, shared haplotypes between ABR and BOI in 28SrRNA, and individuals from ABR and BOI sharing the NE haplotype as well as having unique haplotypes, separated from each other with over 50 substitutions (Fig. 4). The ‘islands’ clade, on the other hand, presented different network shapes, mostly constituted of unique haplotypes on COI and 28SrRNA, and a main shared haplotype on 16SrRNA (Fig. 4). For COI, specimens from OI localities shared haplotypes, whereas specimens from the LA presented unshared haplotypes. In turn, 16SrRNA had a main haplotype shared by seven localities, including both OI and LA sites. Lastly, 28SrRNA showed shared haplotypes for EI and SB in the CDM, and unique haplotypes for each one of the following localities: TRI, SSV and SM (Fig. 4).

SNPs

The genotypic structure attribution recovered with SNPs resulted in two genetic clusters for the whole *Ampithoe marcuzzii s.l.* dataset, in strong agreement with the two proposed clades of ‘continent’ and ‘islands’ (Fig. 5, Fig. S7), except from one single individual (SSVS5F8) from the Atlantic Dominican locality of SSV that presented 28% of ‘continent’ cluster identity (Fig. 5). A second Structure analysis with separated datasets into ‘continent’ and ‘islands’ recovered two and three genetic clusters, respectively. The ‘continent’ analyses revealed two Ks with highest ΔK values: structure analyses with K=2 suggested full separation of populations from NE+E and SE (Fig. 5), whereas K=3 separated E from NE (Figs. S8 and S9). The ‘islands’ analyses was also geographically congruent, separating individuals into three genetic clusters, corresponding to OI, CDM and SSV samples (Figs. 5 and S10).

In addition, PCA and DAPC scatter plots from SNPs agree with the Structure analyses, showing a symmetric spatial distribution of clusters NE, E and SE within 'continent' for the first two PC axes (Fig. 6 and S11), with the main separation of NE and E from SE in the first axis, and the separation of E from NE and SE on the second axis (Fig. 6 and S11). Within 'islands', PCA's first axis separated the three genetic clusters of OI, CDM and SSV, while the second axis mostly separated CDM from the two remaining genetic clusters (Fig. 6), whereas DAPC analysis suggested four clusters, including two clusters from SSV (Fig S12).

Demographic history and divergence times

mtDNA and 28SrRNA

The investigation of mtDNA demographic history was obtained from Tajima's D and Fu's Fs analyses, which not resulted in significant evidences of population expansion for most lineages, except for OI (D = -2.69, $p < 0.005$, Table S13). The estimates of variation in population size over evolutionary time based on the Bayesian skyline plots suggested that lineages' population sizes have remained constant over their recent evolutionary past (Figs. S14-S17).

SNPs

For SNPs, demographic history was assessed by Fastsimcoal with three different expansion scenarios for each dataset. As result, the most likely expansion scenario within 'continent' occurred on SE toward E and NE regions around 601.900 generations ago, and greater gene flow from SE to NE (Fig. 7). In the 'islands' clade, the most likely scenario was the expansion of the Caribbean SSV population to the CDM and OI, around 373.749 generations ago and migration rates showed a stronger gene flow from SSVto OI (Fig. 7). The historical migration between localities also inferred by Fastsimcoal resulted in highest probabilities of migrants by SINO (SE) as source and NAT (NE) as receiver in the ‘continent’, and between the equatorial islands, with RA as source and FN as receiver in the ‘islands’ (Figs. 5B, S18 and S19). Nevertheless, other most likely routes of migration were from CF (SE) to BOI (E), from CDM to FN, and from FN to TRI (Figs. 5B, S19).

Climate association analyses

ENM suitability maps were built based on ‘continent’ and ‘islands’ distribution of specimens and variables selected on factorial analysis: distance to shore (biogeo5), concavity (biogeo7), sea surface salinity (SSS) of the saltiest month (biogeo10), annual range in SSS (biogeo11), sea surface temperature (SST) of the coldest month (biogeo14), and annual range in SST (biogeo 16), as well as bathymetry because of its biological importance for benthic macroalgae distribution (Table S20).

ENM results confirmed the clade ‘continent’ distribution suitability in the South America mainland, including greater suitability on shallow waters of the continental shelf, mainly in the Brazilian SE and NE regions (Fig. 8). A small patch of adequate climate for ‘continent’ *A. marcuzzii* is also observed on the Venezuela’s coastline (Fig. 8). Suitability for ‘islands’ clade, on the other hand, is much lower, with a thin suitable line on the margin of the continental shelf and islands of the FN seamount chain (Fig. 8). In the Caribbean, adequate sites include the islands of the LA (Fig. 8). Paleodistribution models suggested a considerable geographical expansion from the LGM to the present time for the ‘continent’ clade, with a refuge in southeastern Brazil, with higher suitability in the SE region along the margin of the continental shelf. In contrast, the paleodistribution of ‘islands’ revealed higher suitability in the OI, including not only the FN seamounts as well as Vitoria-Trindade seamount chain (Fig. 8), therefore showing a pattern of distribution retraction from the LGM to contemporary days. In the Caribbean, due to the less shallow areas available in the LGM, suitability increased from the past model to the present (Fig. 8).

SNPs

The association of environmental variables with the structure values (F_{ST}) and geographic distance tested by partial Mantel's for IBE indicated that more climatic factors are related to the 'continent' clade variation, including features from seafloor structure (Mantel r=0.572–0.576), oxygen concentration (Mantel r= 0.391–0.520), nitrate concentration (Mantel r=0.636), salinity (Mantel r=0.448) and temperature (Mantel r=0.469, Table 4), whereas changes in the 'islands' clade significantly varied with sea surface temperature (Mantel r=0.620) and carbon phytoplankton biomass (Mantel r=0.702) only (Table 4).

The RDA recovered ten environmental variables with low correlation, with four variable in common to 'continent' and 'islands' (Figs. S21 and S22): bathymetric slope, concavity, north/south aspect and plan curvature, all related to seafloor structure (Table S1). Three and two statistically significant axis were found for 'continent' and 'islands', respectively. Of these, the first two first axis explain over 70% for the 'continent', as well as for the first axis for 'islands'. Variables related to dissolved oxygen concentration, temperature and sea surface salinity were also recovered by both analyses, whereas chlorophyll and nitrate concentration were only found for the 'continent', and carbon phytoplankton biomass were only recovered for 'islands', the latter two variables in agreement with IBE association results (Tables 4 and 5). Within 'continent', genomic variation in SE populations of CF, SINO and SPD are explained by changes in dissolved oxygen and nitrate concentration (Fig. 9), while E and NE populations are associated with changes in mean temperature of the wettest month, distinguished from each other on the second axis (Fig. 9). Within 'islands', individuals from SSV showed the greatest variation along the first axis (Fig. 9). Both Caribbean populations of SSV and CDM appear to be associated with mininum dissolved oxygen concentration, separated from each other on the second axis, while Brazilian populations from the OI are related to changes in maximum dissolved oxygen concentration, carbon phytoplankton biomass, sea surface salinity, temperature annual range and seafloor related variables (Fig. 9).

DISCUSSION

The 'continent' and 'islands' diversification

The genetic population structure of *Ampithoe marcuzzii s.l.* unveiled a complex evolutionary history shaped by the environment. Its direct development plays a key role in the lineages diversification, showed by the phylogenetic, phylogenomic and structure results, that characterized an ancient separation between the South America mainland ('continent'), and the clade that encompasses the Lesser Antilles and Brazilian OI ('islands'). The split was observed prior to the Brazilian OI formation, suggesting speciation of *A. marcuzzii* from 'islands' in the Caribbean region, with a posterior colonization pathway to the OI. Here, we considered *A. marcuzzii s.l.* as a species complex, and each species was treated separately for population analyses purposes.

Evidences of 'continent' and 'islands' separation were already observed in the Brazilian waters for the coral *Mussismilia hispida* (Verrill, 1901) (Peluso et al. 2018), showing that fauna associated to benthic macroalgae, especially the ones with low dispersion capacity, may reflect similar patterns to sessile invertebrates (Peluso et al. 2018). In agreement with *M. hispida* results, *A. marcuzzii s.l.* also presented high gene flow between TRI and the EI, regardless its distance of over 1800 km, whereas there was lack of gene flow between EI and their geographically closer mainland (NAT), patterns without obvious explanation in the surface currents (Peluso et al. 2018). This could be because surface currents observed nowadays do not reflect neither the lineages' ancient divergences nor the ancient currents. Instead, we observed that other environmental variables might shape the 'continent' and 'islands' distribution. While several climatic features are associated with the genomic structure in the 'continent', only two variables related to the sea surface were associated with 'islands'. Thus, a combination of abiotic and biotic plasticity capacity might had led the 'island' clade to persevere in the most harsh environments. One could hypothesizes that salinity is a key factor to clades diversification, once OI are mainly deprived of freshwater sources, however, sea surface salinity (SSS) was not recovered as a potential driver to genetic structure. This result is possibly because despite of clade 'islands' being on the OI, the same lineage is abundant in the Caribbean region, which is rich in freshwater sources and in strong seasonal rainfall.

Indeed, 'islands' species showed greater genomic diversity within most of the sites than 'continent' species, which could result in a more limited ability to adapt genetically to environmental change (Frankham 1997). The resilience capacity of 'islands' *A. marcuzzii* is distinctive, considering that it is the only species observed in all sampled islands so far (T. Iwasa-Arai and S. Siqueira, *pers. obs.*).

'Continent' population structure

After 'continent' and 'islands' separation, clades presented independent evolutionary histories, with speciation processes and environmental factors that drove each lineage to a different scenario. The population structure also reflects the direct development, observed within populantions NE, E and SE for 'continent' and OI, CDM and SSV for 'islands', whose strong population structure is congruent with IBD in the ‘continent’, as well as for the monophyly of most localities.

While NE localities presented mean low genetic diversity in all markers, as for the localities of CSA and NAT, populations from E and SE showed higher values of population diversity. This result of high diversity within SE is congruent in most analyses, from the divergence time estimates with the first split of the SE population, showing that SE is older and possibly the source population, to the migration and demographic genomic analyses that suggested migrants exchange from SE to both E and NE sites, as well as by the estimates of historical expansion of SE around 601.900 generations ago. Nevertheless, the mainland SE had a larger suitable area during the LGM, allowing geographic and genetic diversification, whereas populations from E and NE were extremely affected by the lower sea levels, pattern observed for other marine invertebrates such as the brain coral *Mussismilia braziliensis* and the marine gastropod *Littoraria flava* (Menezes et al. 2020, Cortez et al. 2021) . The congruence of higher diversity in higher latitudes is a unusual finding, once most of the marine species, from macroalgae to corals and crustaceans, presented lower levels of genetic diversity in southernmost regions when assessed by microsatellites and mitochondrial markers (Peluso et al. 2018, Mattos et al. 2019, Martins et al. 2022a). On the other hand, higher diversities found in southernmost sites were also observed for *L. flava* in a genome-wide study (Cortez et al. 2021), showing that evolution recovered by SNPs reflect more recent timescales.

Barriers to gene flow across the mainland are detailed discussed in the recent review by Martins et al. (2022b), where the bifurcation of the offshore South Equatorial Current around Cape São Roque (NE) is the most frequent barrier with phylogeographic concordance. Other representative barriers included the Vitória-Trindade seamount chain (SE), the Cabo Frio upwelling system (SE), and the main river mouths of São Francisco (NE), Paraguaçu (NE), Jequitinhonha (E), Doce (E), and Paraíba do Sul (SE, Martins et al. 2022b). Of these, two BGFs are observed as shaping the main lineages within 'continent': the first separated the SE from NE and E populations, and are concordant with the Vitória-Trindade seamount chain. Hence, our data suggests that the most likely scenario was vicariance driven, with the presence of a widespread population through the mainland, followed by the posterior barrier emergence in the Quaternary (Peterson & Stramma 1991, Stramma & England 1999, Martins et al. 2022a).

Despite the historical sea level dynamics in which the seamount chain acted as a barrier, other current environmental variables may maintain the isolation in this region. Results from IBE and RDA showed that variables related to the seafloor structure play an important role in the NE, E and SE populations structure (Table 4), whereas sea water composition shaped the separation of SE populations (Tables 4 and 5, Fig. 9). In the RDA, we observed that the SE localities of CF, SINO and SPD are directly associated to changes in dissolved oxygen and nitrate concentration (Fig. 9). Both of these variables are higher in sites with strong water dynamism, and the presence of the cold upwelling from the South Atlantic Central Water in this region could be an important feature to isolate the SE lineage (Peluso et al. 2018, Seixas et al. 2020).

The second barrier found to delimit the populations is the Paraguaçu river mouth, in the Todos os Santos Bay (BA). This barrier is much less studied by previous works, especially because samplings are usually scarse and do not overlap the barrier borderss . Our study succeeded in sampling close sites with high genetic variation: FOR, in the north of the Todos os Santos Bay, belongs to the NE population, while BOI, in the south, was characterized as the population from the E, with greater gene flow between the southern BA localities of TRA and ABR. Despite the lower sampling, Mattos et al. (2019) found several unique haplotypes from

Canasvieiras, southern BA, separated from shared haplotypes from the NE region, as well as one shared haplotype between Canasvieiras and Prainha, in the state of Espírito Santo for the sandy beach isopod *Excirolana braziliensis.* This barrier is also indicated for the marine annelid *Diopatra marinae*, where one main haplotype is found and shared between Morro de São Paulo (close to BOI), in the south of the Todos os Santos Bay, and Aracruz, in the state of Espírito Santo, while separated from the NE region (Seixas et al. 2020).

Interestingly, ABR, the furthest continental island, showed high genetic diversity and high connectivity with E populations in the mainland (BOI and TRA, Table 2, Fig. 6). The Abrolhos Archipelago is the largest and most diverse reef complex of the South Atlantic (Leão, 1982), and its species composition and abiotic characteristics suggests a unique environment, different from all other continental Brazilian marine provinces (Cord et al. 2022). Despite its singularity, the genetic connectivity among ABR and nearby localities in the mainland for other taxa, such as the coral *M. hispida* (Peluso et al. 2018) and endosymbiotic dinoflagellates associated with *Favia gravida* (Teschima et al. 2019)*,* suggests that ABR might work as a genetic diversity reservatoir in the region.

Lastly, no evidences of population isolation was observed regarding the Cape São Roque, the easternmost mainland point. Specimens from the state of Ceará (CAU, FLE and PCR) from three localities showed high genetic diversities and unique haplotypes, but also shared haplotypes with the remaining NE (Fig. 4). FLE, the northernmost locality in the Brazilian coastline, presented the highest differentiation, indicating a possible population turnover in the North region. According to the niche projections, *A. marcuzzii* from 'continent' has a medium suitability until the São José Bay, in the state of Maranhão (2.36 S, 43.94 W). Thus, specimens from the western Ceará and Maranhão could reveal one unsampled population.

Brazilian oceanic islands and Lesser Antilles connectivity

The second species is distributed throughout the Brazilian oceanic islands of RA, FN and TRI, as well as in Dominica in the Lesser Antilles, and presented a much more complex evolutionary history. While phylogenomic analyses recovered the monophyly of all localities but FN (Fig. 2B), concatenated phylogeny of mtDNA + 28SrRNA only recovered main clades, which includes one well supported clade from SSV, onde from CDM, and one from the OI (Fig. 2A). Despite the consensus separation of OI from CDM, haplotype networks of 16SrRNA and 28SrRNA showed shared haplotypes between the two localities while Structure analyses indicated a thin mix of the CDM genetic cluster into the FN population (Fig. 5). This relationship between CDM and FN is corroborated by the historical migration analyses assessed with Fastsimcoal, which suggests a migration pathway from CDM to FN (Fig. 5), which could also be a sign of the ancient colonization route from the Caribbean to the OI. Connectivity among the Caribbean and EI is also observed for the sally lightfoot crab *Grapsus grapsus*, a species restricted to the Caribbean and OI in the Atlantic Ocean (Freire et al. 2021).

The number of migrants that leave CDM to FN is smaller than the number of migrants that RA send to FN, and from FN to TRI, showing a stronger connectivity among the OI (Fig. 5). Therefore, regardless the distance between TRI and the EI, a strong gene flow is yet observed across the southwestern Atlantic, which maintain the low genetic structure of each OI. As previously mentioned, the connectivity between TRI and the EI is also observed for the coral *M. hispida* (Peluso et al. 2018), however, this results strongly differed from other insular species that co-occur in the OI, such as the crabs *G. grapsus* and *Johngarthia lagostoma*, that showed connectivity among EI but high population structure in the TR island (Rodríguez-Rey et al. 2016, Teschima et al. 2016, Freire et al. 2021). Thus, despite the closer phylogenetic relationship with crabs, the population structure of 'islands' amphipods agrees more with sessile invertebrates. However, connectivity among EI and TRI for species with short pelagic larval duration (PLD), as in *M. hispida,* whose PLD is approximately 10 days (Pires et al. 1999), and *A. marcuzzii* from 'islands', which lack a dispersive larval phase is unexpected. In contrast, *G. grapsus* and *J. lagostoma* that present a longer PLD, ranging from 30 to 60 days (Hines 1986, Cuesta et al. 2011), indicated isolation of the TR population.

Rafting by macroalgae would explain the migration rates and genetic connectivity among sites, considering that amphipods are great hitchhikers on floating substrata (Thiel 2003), however, this would not explain the connectivity for *M. hispida,* once adults are large sessile animals, and larvae would not find an adequate substrate for settlement. Nonetheless, in spite of the ability of amphipods for rafting, surface currents disagree with migration routes inferred by genomic markers. Moreover, *Ampithoe marcuzzii* was not found on samplings of pelagic *Sargassum* in the Caribbean (A. Freire, *pers. comm*.). This peculiar results shows a much more complex evolutionary history that we were unable to recover.

Dominican populations also showed an interesting pattern, once the localities of the Caribbean coast (SB and SOU) showed high connectivity, while the Atlantic coast (SSV) remained isolated. Dominica is a small island of 750 km^2, therefore, we did not expect the high differentiation between Atlantic (SSV) and Caribbean (CDM) populations, which are much closer from each other, higher than the differentiation between the Brazilian OI. Indeed, Structure analysis of 'islands' separated into three genetic clusters, OI, CDM and SSV, in which there is a light contribution of CDM into the OI population, but SSV presented a unique genomic pattern (Fig. 5). PCA also showed the separation of the same three clusters, with greater differentiation of

CDM from SSV in the second axis, while the first axis indicated a widespread distribution of SSV (Fig. 6).

SSV uniqueness was corroborated by most of the analyses, including the pairwise F_{ST}, which showed greater differentiation between SSV and its pairs for three of the four markers (Fig. 3). Additionally, demographic analyses suggested historical expansion of SSV around 373.749 generations ago (Fig. 7), with migration to OI and CDM, in agreement with the species origin in the Caribbean region and later dispersion to the southwestern Atlantic. The particularities of SSV population are better observed with the environmental association provided by the RDA, where specimens from SSV presented a wide distribution in the first axis, and association with minimum dissolved oxygen concentrations (Fig. 9). We believe the locality is subjected to more environmental changes than any other sampled locality within 'islands', because pelagic *Sargassum* patches are regularly washed to the region during boreal summer/autumn seasons (Fig. S23), and therefore there is a direct association with changes in minimum dissolved oxygen concentrations. Gases (H_2S, NH_3, CO_2, CH_4), organic matter, and high biological oxygen demand areas are formed by biological degradation of brown algae in near-shore environments, giving rise to anaerobic zones (Song et al. 2020, Robledo et al. 2021). Dissolved compounds, such as mannitol, volatile fatty acids, alcohols and polyphenols, can also be released from their tissues, as well as other nutrients released by bacteria involved in these processes could cause eutrophication (van Tussenbroek et al. 2017). In summary, SSV is a key population to understand not only historical events, but also current processes that might shape future populations.

Comparative genomics of *Ampithoe* species

A recent study by Harper et al. (2022) investigated the cryptic diversity of *Ampithoe valida*, a much more widespread species, distributed through north Pacific and Atlantic oceans. *Ampithoe* *valida* and *A. marcuzzii s.l.* presented different evolutionary histories, with *A. valida*'s divergence times being more recent, and with larger connectivity among populations. In contrast to *A. marcuzzii s.l.*, that is only observed in marine environments, *A. valida* is an estuarine species, which would imply in even more difficult dispersion across oceans. This results are explained by two native Pacific and one native north Atlantic mitochondrial lineage, with introductions to Argentina and Pacific/Atlantic human-mediated hybridization (Harper et al. 2022). Human mediated dispersion was not considered for *A. marcuzzii s.l.* due to its old divergence times, and its highly structured populations recovered by both conservative and variable genetic markers. The only results that could possibly be explained by anthropogenic ways is the connectivity among the OI. However, Brazilian OI are marine protected areas (MPAs) with low traffic between each other, and we believe other events could be associated with this unusual connectivity.

Final considerations

Finally, regardless the genome wide and large scale sampling, *A. marcuzzii s.l.* revealed a complex evolutionary and biogeographic history that remains partially explained. While 'continent' lineage presented a clear population structure into NE, E and SE, with evidences of IBD, IBE and environmental variables that are associated with SE region, 'islands' indicated a much more intriguing pattern, lacking IBD and with closer populations (CDM and SSV) highly structured, while further localities (OI) were connected without environmental explanation. Despite rafting being a powerful mechanism for fauna dispersion, especially peracarid crustaceans such as *A. marcuzzii s.l.*, neither signals of surface currents connecting mainland and EI populations nor *A. marcuzzii s.l.* was found associated with pelagic *Sargassum* patches. Therefore, results of isolation and connectivity observed nowadays suggest complex evolutionary and biogeographic events possibly associated with other traits not analysed herein. Nevertheless, each major population (‘continent’: NE, E and SE; ‘islands’: OI, CDM and SSV) presented association with different environmental traits, which indicates independent ecological and evolutionary histories.

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Figures and Tables
Figures

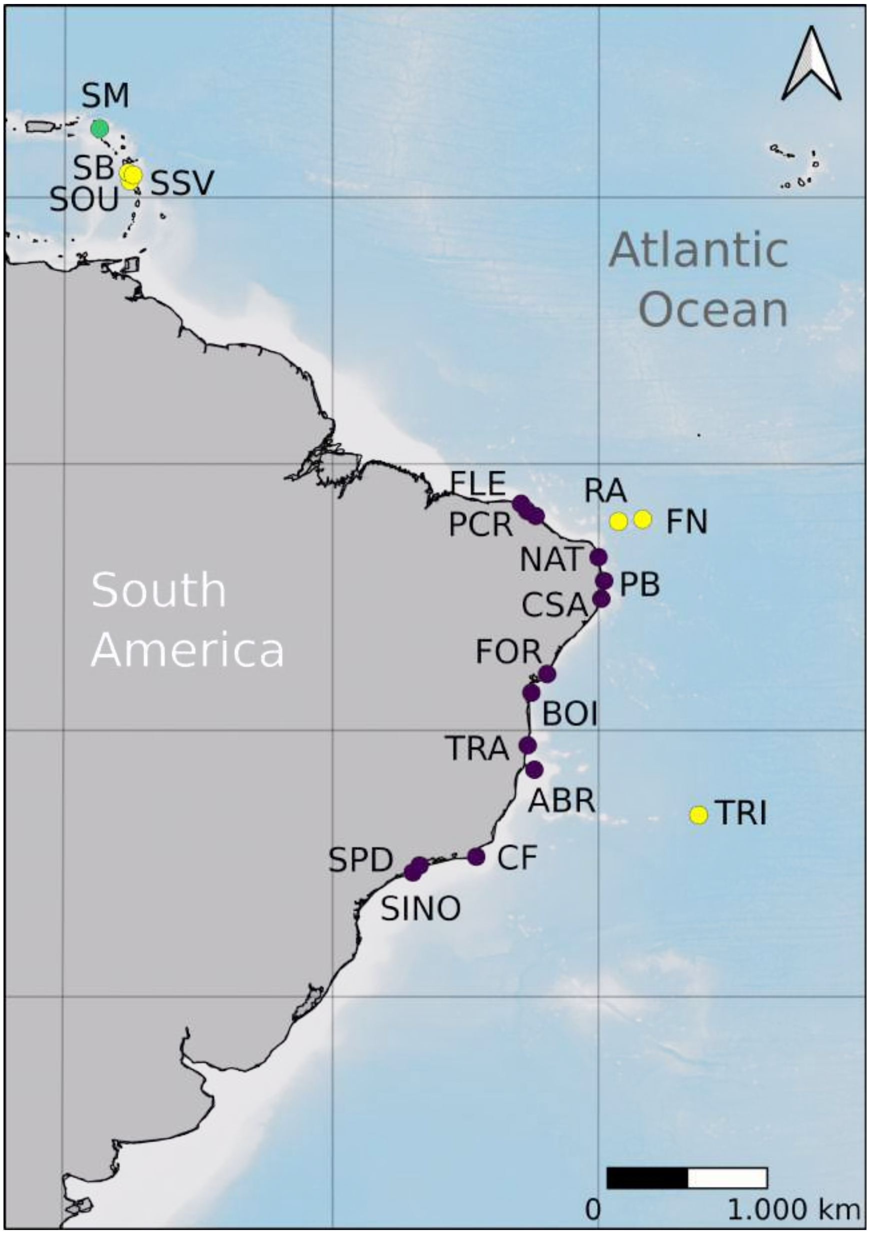


Figure 1. Map with sampling localities. Mainland: ABR, Abrolhos Archipelago; BOI, Boipeba Island; CAU, Caucaia; CF, Cabo Frio; FLE, Flecheiras; FOR, Forte Beach; NAT, Natal; PB, Coqueirinho Beach; PCR, Paracuru; SINO, Ilhabela; SPD, Ubatuba; TRA, Trancoso; Oceanic islands: FN, Fernando de Noronha; RA, Rocas Atoll; TRI, Trindade Island. Caribbean: SB, Secret Beach; SM, Saint Martin; SOU, Soufrière; SSV, San Sauveur.

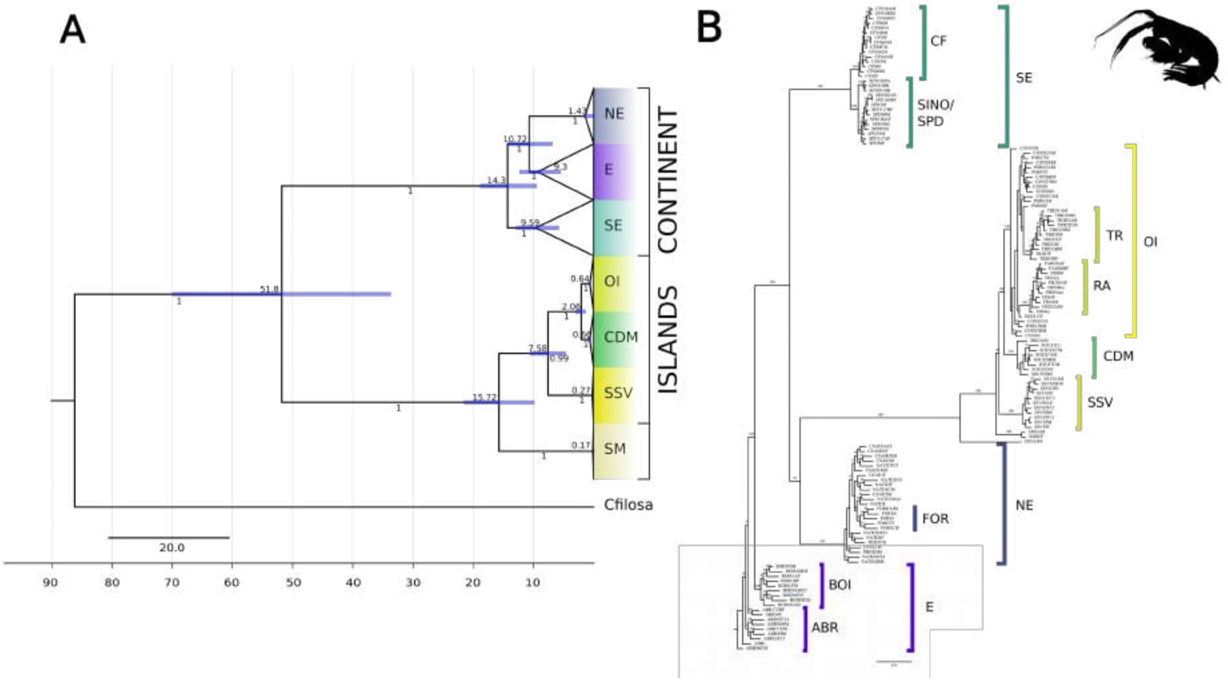


Figure 2. Phylogenetic trees of *Ampithoe marcuzzii s.l.* **A.** Maximum likelihood tree recovered from 5,857 SNPs. Bootstraps above 80% are shown above branches. **B.** Bayesian calibrated tree of *Ampithoe marcuzzii s.l.* using concatenated COI+16SrRNA+28SrRNA. Numbers below branches represent posterior probability values over 0.9. Node bars represent the 95% HPD interval. Time divergence bar is in a Mya scale.

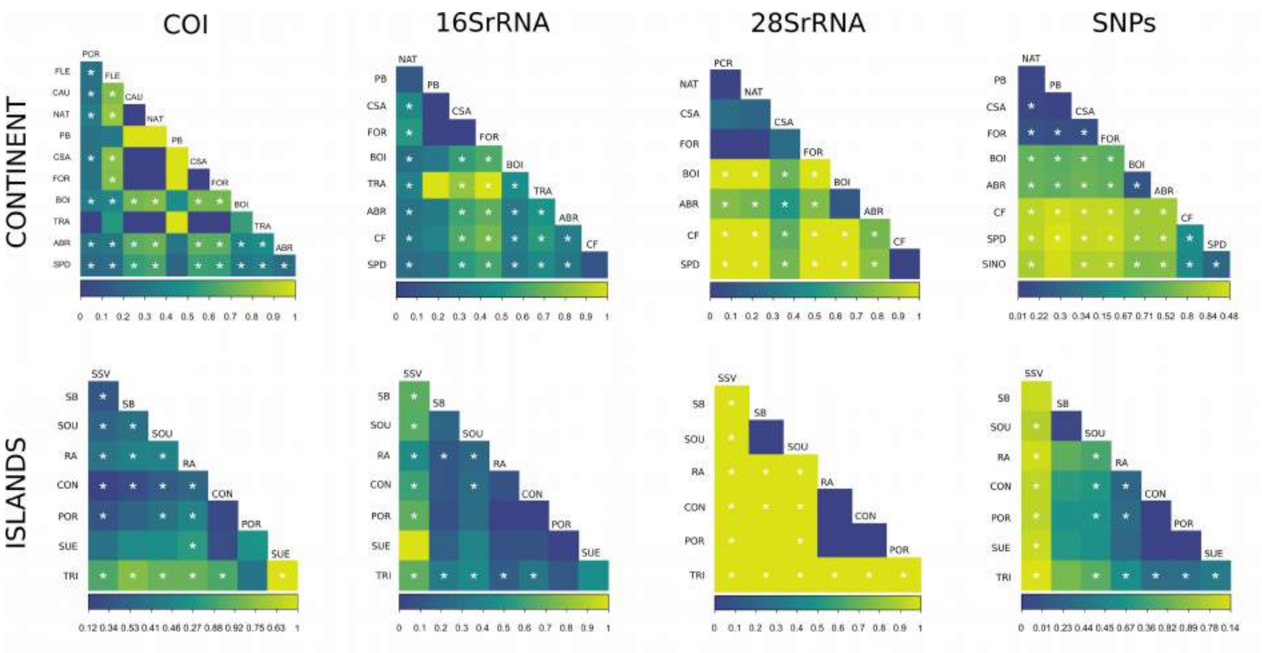


Figure 3. Pairwise F_{ST} heatmaps for each genetic marker. Colour coding illustrates the observed F_{ST} value. Asterisks correspond to significant values ($P < 0.05$).

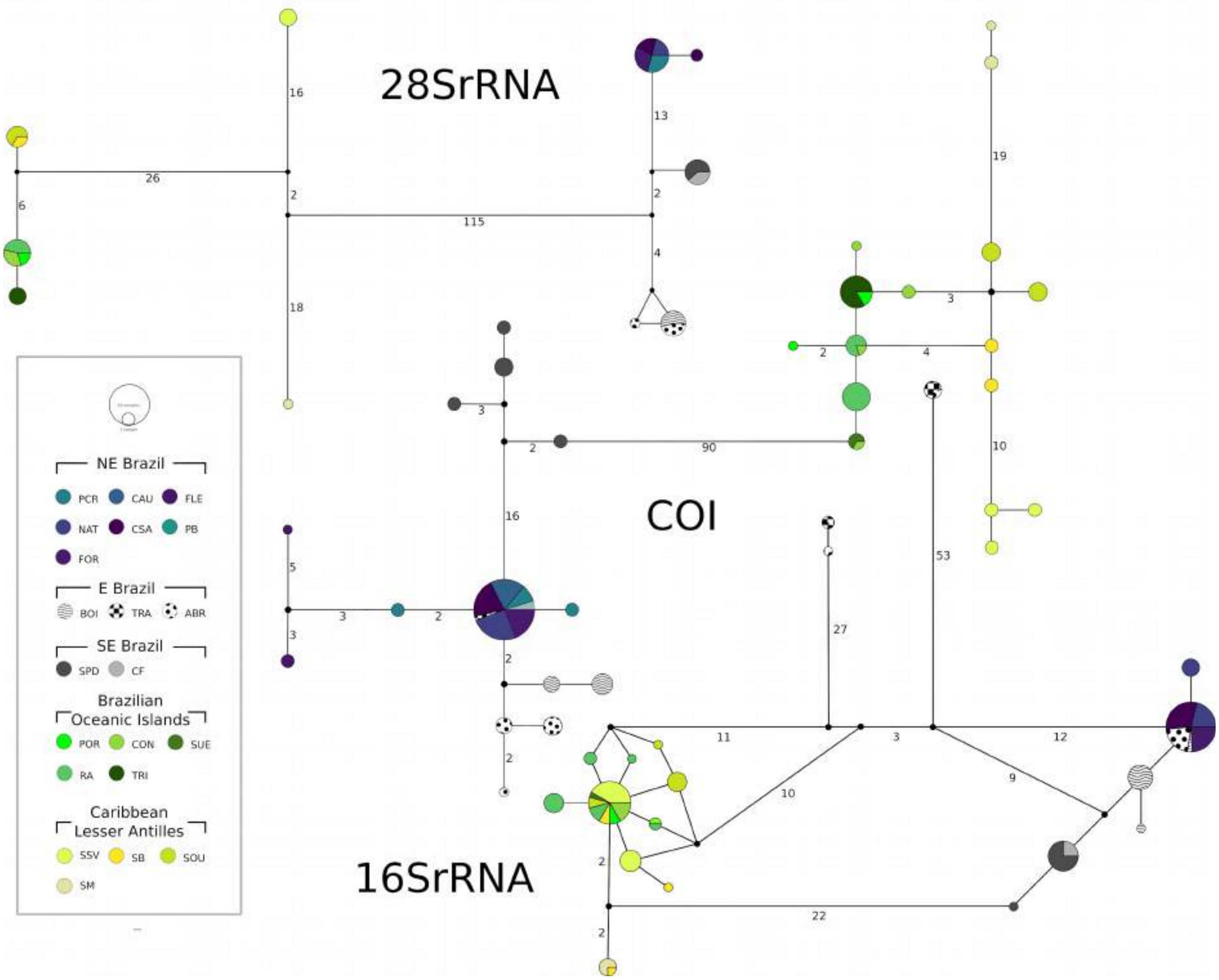


Figure 4. Minimum spanning network of 28SrRNA above, COI in the middle, and 16SrRNA below. Each node represents a haplotype, its size corresponds to the haplotype frequency and its colours indicate the locality. Black nodes represent inferred ancestral nodes. Numbers on branches represent mutational steps.

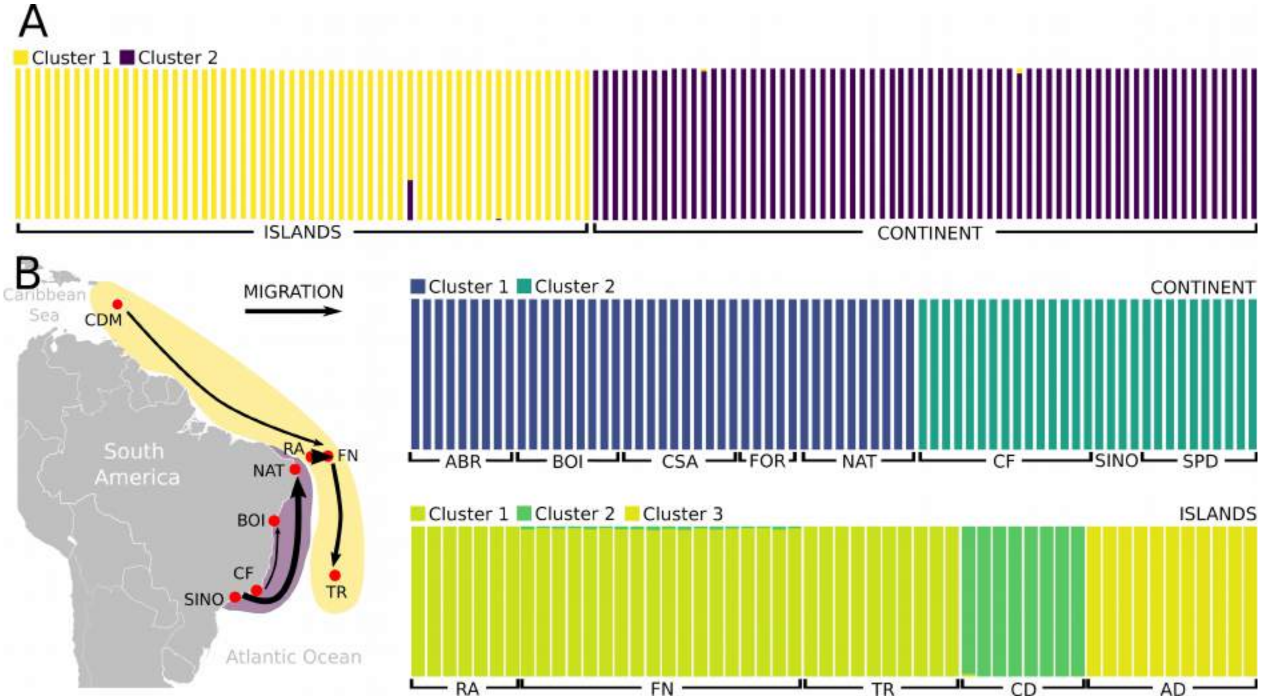


Figure 5. A. Structure results from *A. marcuzzii s.l.* dataset (k=2), 'continent' (k=2) and 'islands' (k=3). Each vertical bar corresponds to one individual, and the colour indicates the proportion of membership in each genetic cluster. **B.** Main migration routes inferred from Fastsimcoal. Arrows width correspond to comparative amount of migrants (see figures S18 and S19 for more information on migration rate).

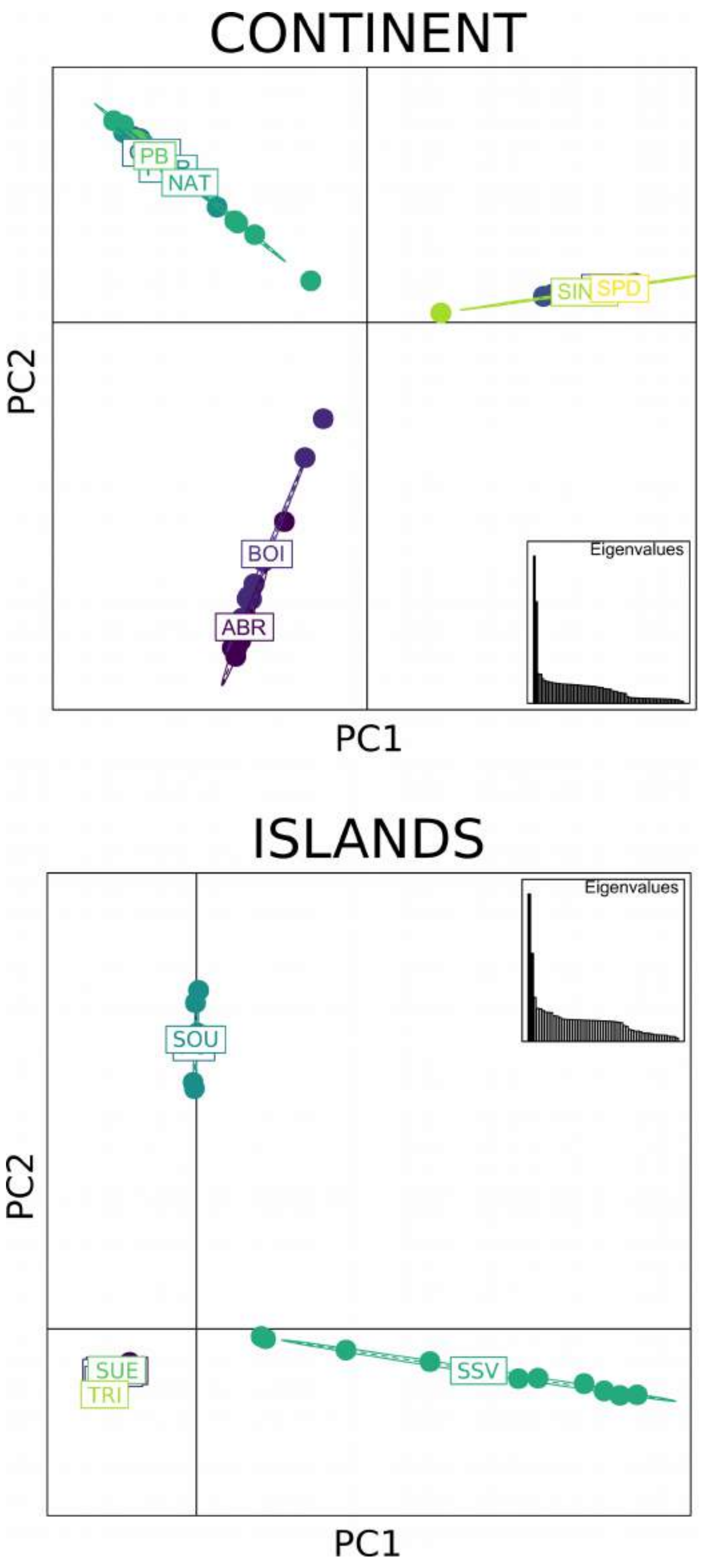
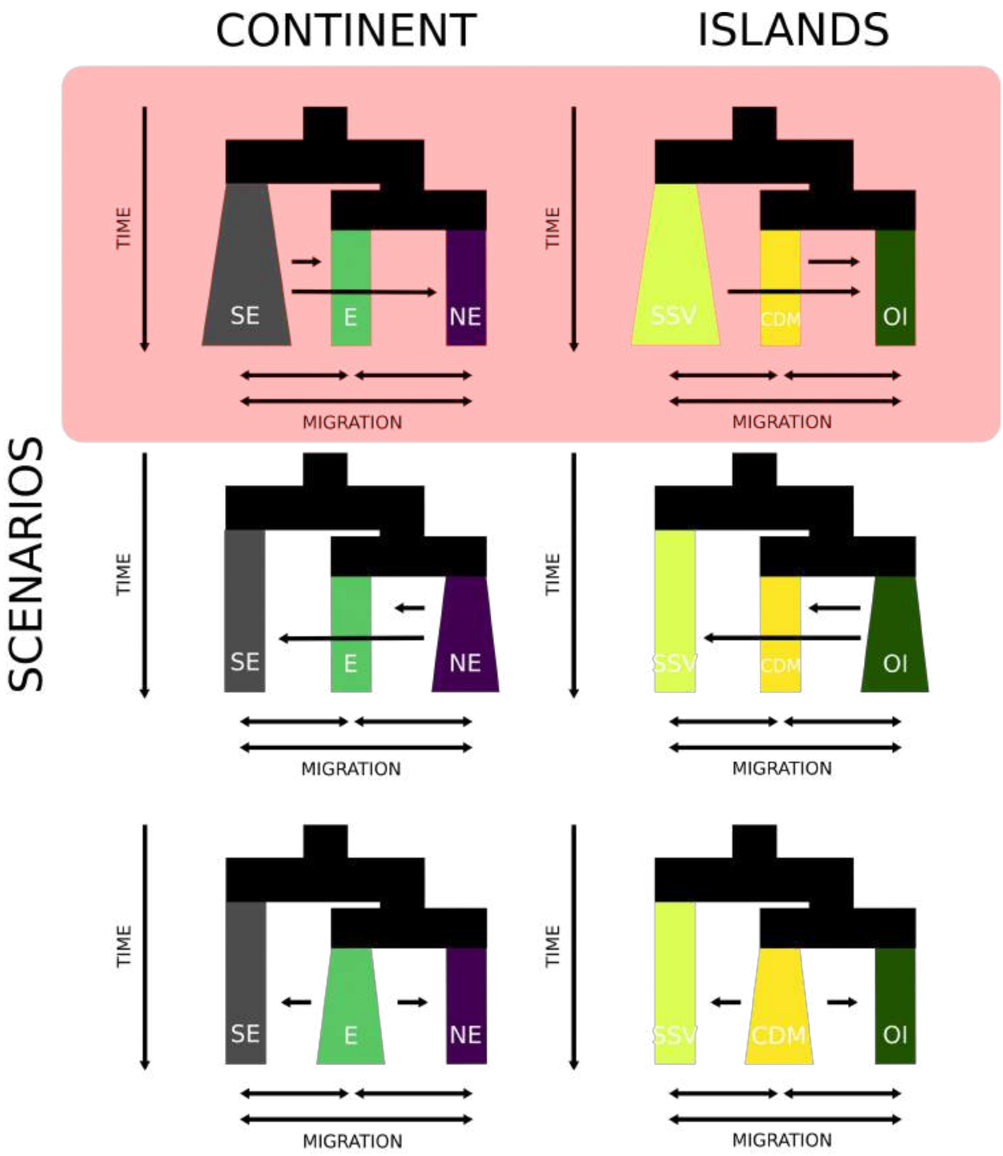


Figure 6. PCA plots for ‘continent’ and ‘islands’ showing the first two axis. Dots represent individuals, with colours denoting the localities.



	E Expansion	NE expansion	SE expansion
Divergence time (TDIV)	1262493	971775	601900
AIC	1586.589	1524.143	1515.835
Δlhood	126.877	113.317	111.513

	OI expansion	CDM expansion	SSV expansion
Divergence time (TDIV)	989217	545427	373749
AIC	3156.717	3145.660	3145.200
Δlhood	142.505	140.104	140.004

Figure 7. Comparisons among demographic models of population expansion for ‘continent’ (E, NE and SE), and ‘islands’ (OI, CDM and SSV). Scenarios with lower AIC are highlighted in red shadow.

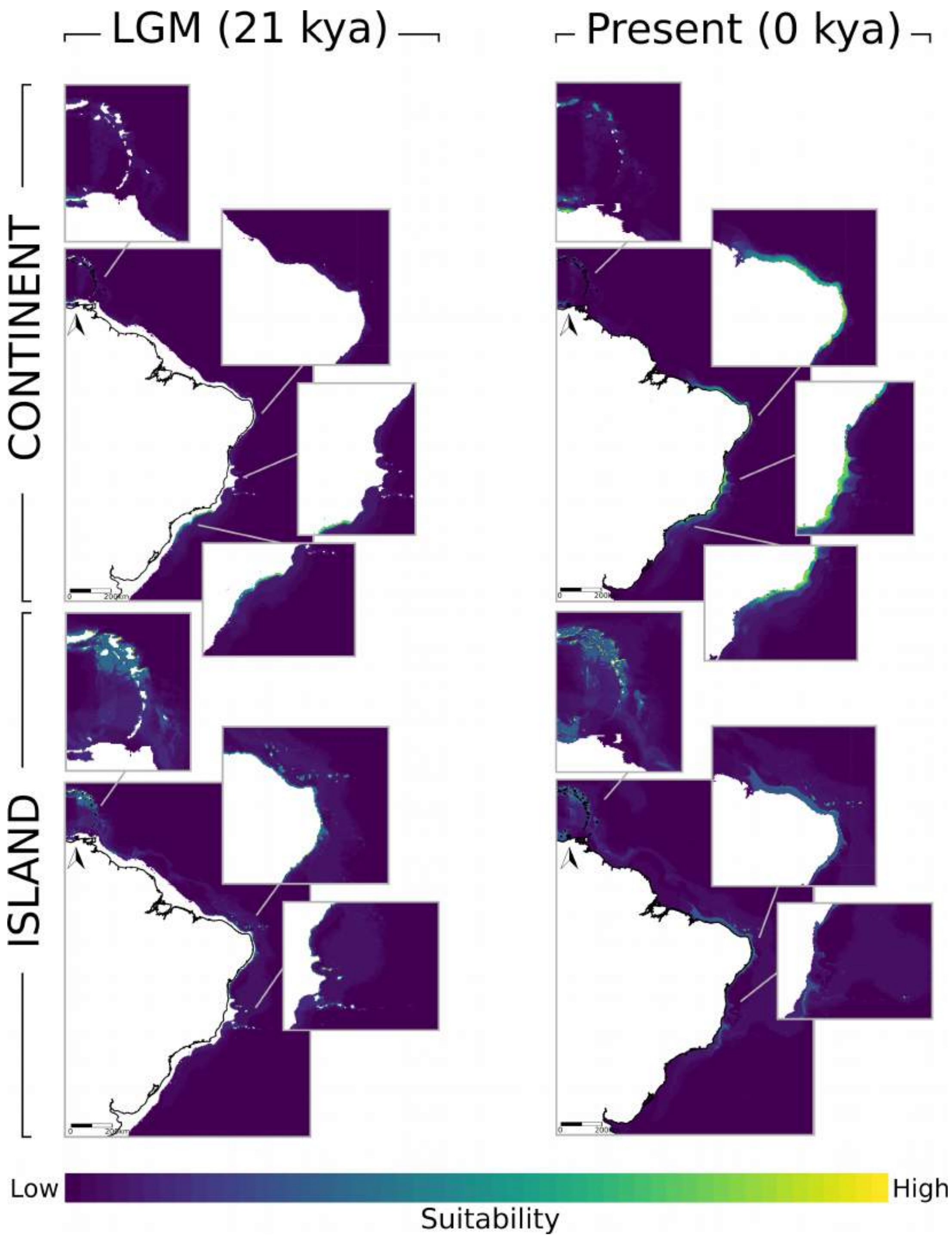


Figure 8. Modelled distributions of 'continent' and 'islands' for the Last Glacial Maximum (21 kya) and present (0 kya) scenarios. The suitability value predicts how adequate the environment is for the species occurrence.

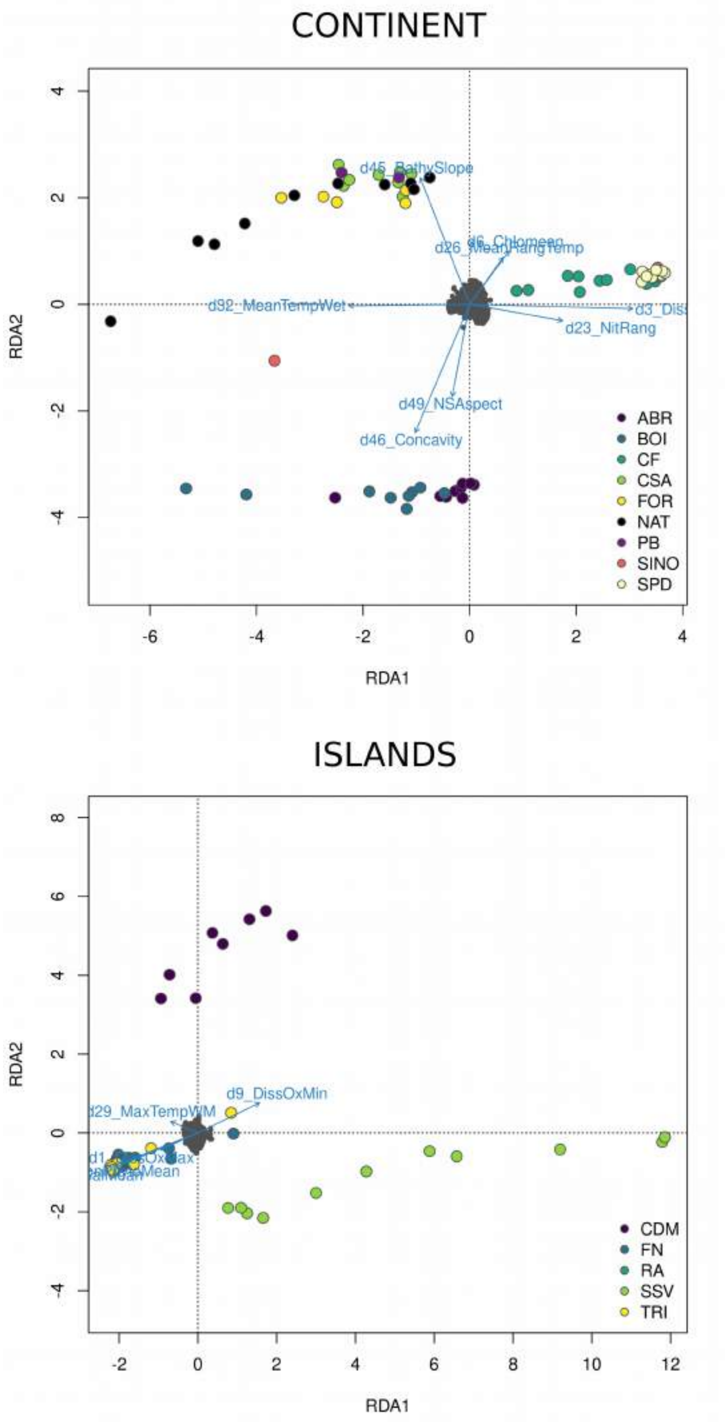


Figure 9. RDA results for ‘continent’ and ‘islands’. Arrows correspond to environmental variables, and arrows length correspond to environmental variation in axis 1 and 2. Dots represent individuals and colours represent assigned localities.

Table 1. Sampling data from *Ampithoe marcuzzii s.l.*

Acronym	Locality	Lat	Long	Domain	Date	Depth	Macroalgae
ABR	Redonda Island, Abrolhos Archipelago, BA	-17.96835	-38.709264	Continent – E	12/01/19	3m	*Sargassum* sp. and *Dictyota* sp.
BOI	Moreré Beach, Boipeba Island, BA	-13.628983	-38.88702	Continent – E	07/01/19	1m	*Sargassum* sp. and *Dictyota* sp.
CAU	Pacheco Beach, Caucaia, CE	-3.68584	-38.63456	Continent – NE	14/11/21	1m	*Hypnea* sp.
CF	Peró Beach, Cabo Frio, RJ	-22.86632	-41.97831	Continent – SE	25/01/21	1m	*Sargassum* sp.
FLE	Flecheiras Beach, Trairi, CE	-3.21691	-39.26537	Continent – NE	12/11/21	1m	*Sargassum* sp.
FOR	Forte Beach, Mata de São João, BA	-12.580166	-38.000772	Continent – NE	30/12/18	1m	*Sargassum* sp. and *Dictyota* sp.
NAT	Pirambúzios Beach, Natal, RN	-6.006086	-35.105394	Continent – NE	17/11/18	5m	*Dictyota* sp.
PB	Coqueirinho Beach, Conde, PB	-7.332474	-34.794167	Continent – NE	16/11/18	3m	*Dictyota* sp.
PCR	Pedra Rachada Beach, Paracuru, CE	-3.39661	-39.01099	Continent – NE	10/11/21	1m	*Sargassum* sp.
SINO	Pedra do Sino Beach, Ilhabela, SP	-23.75153	-45.34941	Continent – SE	2016	1m	*Sargassum* sp.
SPD	Domingas Dias Beach, Ubatuba, SP	-23.49694	-45.14718	Continent – SE	2016	1m	*Sargassum* sp.
TRA	Coqueiros Beach, Trancoso, BA	-16.596985	-39.087873	Continent – E	26/12/18	1m	*Sargassum* sp. and *Dictyota* sp.
CON	Conceição Beach, Fernando de Noronha, PE	-3.839021	-32.415273	Islands – SA	24/11/18	1m	*Sargassum* sp.
POR	Porto Beach, Fernando de Noronha, PE	-3.836277	-32.404728	Islands – SA	21/11/18	1m	*Sargassum* sp.
RA	Falsa Barreta Pool, Rocas Atoll, RN	-3.856736	-33.801844	Islands – SA	10/12/19	1m	*Sargassum* sp. and *Dictyota* sp.
SUE	Sueste Beach, Fernando de Noronha, PE	-3.868175	-32.421794	Islands – SA	20/11/18	1m	*Sargassum* sp. and *Dictyota* sp.
TRI	Parcel Pool, Trindade Island, ES	-20.50502	-29.34430	Islands – SA	05/02/19	5m	*Dictyota* sp.
SB	Secret Beach, Portsmouth, Dominica	15.546467	-61.473314	Islands – LA	08/07/19	1m	*Sargassum* sp.
SM	Baie Rouge, Saint Martin	18.071326	-63.121448	Islands – LA	19/07/19	1m	*Sargassum* sp.
SOU	Soufrière, Dominica	15.228475	-61.36082	Islands – LA	17/07/19	1m	*Sargassum* sp.
SSV	San Sauveur, Dominica	15.403329	-61.250248	Islands – LA	12/07/19	1m	*Sargassum* sp.

Table 2. Diversity indices based on mtDNA (COI and 16SrRNA), 28SrRNA, and SNPs of *Ampithoe marcuzzii s.l.* N: number of individuals; S: polymorphic sites; K: number of haplotypes; H: haplotype diversity; π: nucleotide diversity; θ_S: nucleotide differences; $\theta\pi$: nucleotide diversity; F_{IS}: fixation coefficient values; SD: standard deviation. Significant values for F_{IS} are shown in bold.

	COI							16SrRNA						
Locality	N	S	K	H (SD)	π (SD)	θS (SD)	θπ (SD)	N	S	K	H (SD)	π (SD)	θS (SD)	θπ (SD)
CONTINENT	77	36	14	0.679 (0.059)	0.012 (0.002)	1.098 (0.661)	1.499 (1.045)	65	93	9	0.710 (0.049)	0.043 (0.013)	8.888 (4.073)	12.330 (7.115)
PCR	8	3	3	0.714 (0.123)	0.002 (0.001)	1.157 (0.781)	3.857 (2.466)							
FLE	4	12	2	0.123 (0.204)	0.013 (0.004)	6.545 (3.859)	8.000 (5.631)							
CAU	8	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)							
NAT	11	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	11	2	3	0.727 (0.068)	0.003 (0.000)	1.060 (0.704)	2.178 (1.487)
CSA	9	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	10	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0.400 (0.456)
FOR	8	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	8	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)
BOI	8	1	2	0.536 (0.123)	0.001 (0.000)	0.386 (0.386)	0.536 (0.561)	10	49	3	0.378 (0.181)	0.181 (0.024)	18.381 (7.744)	18.467 (10.133)
TRA	2	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	2	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)
ABR	8	3	3	0.679 (0.122)	0.002 (0.001)	1.157 (0.781)	1.071 (0.895)	8	69	2	0.250 (0.180)	0.057 (0.041)	26.998 (11.929)	31.321 (17.476)
CF								6	74	2	0.600 (0.600)	0.134 (0.134)	32.847 (15.739)	57.600 (33.657)
SPD	10	8	4	0.800 (0.089)	0.005 (0.001)	2.828 (1.459)	3.022 (1.944)	10	1	2	0.200 (0.154)	0.001 (0.000)	0.707 (0.539)	1.000 (0.829)
ISLAND	51	24	14	0.896 (0.024)	0.011 (0.001)	0.896 (0.607)	5.615 (3.836)	49	79	12	0.735 (0.060)	0.014 (0.010)	7.746 (4.719)	10.586 (7.852)
SM	3	1	2	0.667 (0.314)	0,001 (0,001)	0.667 (0.667)	0.667 (0.832)	3	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)
SSV	6	2	3	0.800 (0.122)	0.002 (0.000)	0.876 (0.684)	1.067 (0.937)	6	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)
CDM	12	4	4	0.788 (0.070)	0.003 (0.000)	1.656 (0.932)	14.545 (7.897)	12	10	5	0.758 (0.093)	0.006 (0.002)	3.643 (1.722)	3.364 (2.087)
FN	10	7	6	0.889 (0.075)	0.004 (0.001)	2.474 (1.312)	2.444 (1.632)	9	76	3	0.417 (0.191)	0.055 (0.040)	30.171 (12.852)	31.722 (17.380)
RA	13	1	2	0.462 (0.110)	0.001 (0.001)	0.322 (0.322)	0.462 (0.485)	12	4	5	0.788 (0.090)	0.003 (0.001)	1.325 (0.794)	3.379 (2.095)
TRI	10	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	10	0	1	0 (0.000)	0 (0.000)	0 (0.000)	1.067 (0.867)

	28SrRNA							SNPs			
Locality	N	S	K	H (SD)	π (SD)	θS (SD)	θπ (SD)	N	θS (SD)	θπ (SD)	F_{IS}
CONTINENT	55	26	5	0.706 (0.036)	0.016 (0.001)	0.096 (0.096)	0.121 (0.131)	73	129.954 (46.690)	118.600 (60.615)	
PCR	7	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)				
NAT	5	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	11	59.181 (19.370)	48.594 (24.307)	0.059
CSA	8	1	2	0.536 (0.123)	0.001 (0.000)	0.386 (0.386)	0.536 (0.561)	10	202.216 (72.014)	165.858 (84.067)	-0.016
FOR	7	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	5	206.082 (83.149)	194.000 (102.859)	0.109
BOI	7	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	9	67.741 (23.672)	57.948 (29.375)	0.051
ABR	8	1	2	0.429 (0.169)	0.001 (0.000)	0.386 (0.386)	0.429 (0.488)	9	217.179 (75.080)	187.484 (94.215)	0.012
CF	5	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	15	85.065 (26.327)	90.145 (44.370)	-0.015
SPD	8	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	10	144.317 (48.753)	140.095 (70.047)	-0.025
SINO								4	57.851 (25.152)	64.679 (35.676)	0.011
ISLAND	36	58	4	0.729 (0.040)	0.024 (0.006)	0 (0.000)	0 (0.000)	55	282.099 (93.234)	260.237 (129.409)	
SM	2	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)				
SSV	6	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	11	48.481 (15.649)	41.111 (20.546)	**0.382**
CDM	9	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	8	226.325 (80.556)	232.183 (117.535)	-0.025
FN	8	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	18	401.946 (135.122)	326.863 (162.939)	0.064
RA	7	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	7	505.509 (159.685)	409.640 (201.476)	**0.093**
TRI	6	0	1	0 (0.000)	0 (0.000)	0 (0.000)	0 (0.000)	11	228.235 (75.160)	291.385 (144.547)	-0.056

ABR: Abrolhos Archipelago; BOI: Boipeba Island; CAU: Caucaia; CF: Cabo Frio; FLE: Flecheiras; FOR: Forte Beach; NAT: Natal; PB: Coqueirinho Beach; PCR: Paracuru: SINO: Ilhabela; SPD: Ubatuba; TRA: Trancoso; FN: Fernando de Noronha; RA, Rocas Atoll; TRI, Trindade Island; CDM, Caribbean Dominica; SM, Saint Martin; SSV, San Sauveur.

Table 3. Hierarchical analysis of molecular variance (AMOVA) results from all genetic markers. Localities grouped according to lineages (Continent: NE, E and SE; Islands: CDM, SSV and OI).

	Among groups					**Among populations within groups**					**Within populations**				
	%	**d.f.**	**Variance components**	**Φ_{CT}**	***p***	**%**	**d.f.**	**Variance components**	**Φ_{SC}**	***p***	**%**	**d.f.**	**Variance components**	**Φ_{ST}**	***p***
CONTINENT															
COI	30.45	2	0.13	0.30	0.02	28.43	8	0.12	0.41	0.00	41.12	66	0.17	0.59	0.00
16SrRNA	19.85	2	0.10	0.20	0.04	28.05	6	0.14	0.35	0.00	52.09	56	0.26	0.48	0.00
28SrRNA	81.82	2	0.41	0.82	0.01	3.92	5	0.02	0.22	0.02	14.26	47	0.07	0.86	0.00
SNPs	68.20	2	28.86	0.68	0.00	5.88	6	2.49	0.19	0.00	25.92	135	10.97	0.74	0.00
ISLANDS															
COI	-3.08	2	-0.02	-0.03	0.66	53.27	5	0.25	0.52	0.00	49.80	43	0.24	0.50	0.00
16SrRNA	22.38	2	0.12	0.22	0.01	15.33	5	0.08	0.20	0.00	62.30	41	0.33	0.38	0.00
28SrRNA	56.91	2	0.29	0.57	0.03	43.09	4	0.22	1.00	0.00	0.00	29	0.00	1.00	0.00
SNPs	43.90	2	29.27	0.44	0.09	7.63	2	5.09	0.14	0.00	48.47	105	32.31	0.52	0.00

Table 4. Isolation-by-environment (IBE) partial Mantel environmental variables and significative ($p<0.05$) results.

Variable	**Mantel r^2**	**p-value**
Bathymetry	0.572	0.003
Bathymetric slope	0.576	0.011
Dissolved oxygen concentration (maximum at min depth)	0.520	0.020
Dissolved oxygen concentration (mean at min depth)	0.391	0.043
Nitrate concentration (range at min depth)	0.636	0.003
Sea surface salinity (mean)	0.448	0.027
Mean Temperature of Driest Quarter	0.469	0.024
Sea surface temperature (warmest ice-free month)	0.620	0.033
Carbon phytoplankton biomass (maximum at min depth)	0.702	0.017

Table S1. Climatic variables used for IBE and RDA. Environmental variables used in RDA of *Ampithoe marcuzzii s.l.* for continent (†) and islands (‡) according to minimum correlation from Bio-Oracle, World Clim and MARSPEC databases.

Bio-Oracle Variables	**WorlClim variables**
Dissolved oxygen concentration (maximum at min depth)‡	Annual Mean Temperature
Dissolved oxygen concentration (longterm max at min depth)	Mean Diurnal Range (Mean of monthly (max temp - min temp))
Dissolved oxygen concentration (range at min depth)†	Isothermality (BIO2/BIO7) (×100)
Chlorophyll A (maximum)	Temperature Seasonality (standard deviation ×100)
Dissolved oxygen concentration (mean at min depth)	Max Temperature of Warmest Month‡
Chlorophyll A (mean)†	Min Temperature of Coldest Month
Dissolved oxygen concentration (longterm min at min depth)	Temperature Annual Range (BIO5-BIO6)‡
Chlorophyll A (range)	Mean Temperature of Wettest Quarter†
Dissolved oxygen concentration (minimum at min depth)‡	Mean Temperature of Driest Quarter
Chlorophyll A (minimum)	Mean Temperature of Warmest Quarter
Carbon phytoplankton biomass (maximum at min depth)	Mean Temperature of Coldest Quarter
pH	Annual Precipitation
Carbon phytoplankton biomass (range at min depth)	Precipitation of Wettest Month
Sea water temperature (range at min depth)	Precipitation of Driest Month
Sea water temperature (range at sea surface)	Precipitation Seasonality (Coefficient of Variation)
Sea surface temperature (range)	Precipitation of Wettest Quarter
Carbon phytoplankton biomass (longterm max at min depth)	Precipitation of Driest Quarter
Carbon phytoplankton biomass (mean at min depth)‡	Precipitation of Warmest Quarter
Chlorophyll concentration (maximum at min depth)	Precipitation of Coldest Quarter
Chlorophyll concentration (range at min depth)	
Chlorophyll concentration (longterm max at min depth)	
Nitrate	
Nitrate concentration (range at min depth)†	
Sea surface salinity (mean)‡	
MarSpec variables	
Bathymetry	Sea surface salinity (monthly minimum)
Bathymetric slope†/‡	Sea surface salinity (monthly maximum)
Concavity†/‡	Sea surface salinity (annual range)†
Distance to shore	Sea surface salinity (annual variance)
East/West aspect	Sea surface temperature (annual mean)
North/South Aspect†/‡	Sea surface temperature (coldest ice-free month)
Plan curvature†/‡	Sea surface temperature (warmest ice-free month)
Profile curvature	Sea surface temperature (range)
Sea surface salinity (annual mean)	Sea surface temperature (variance)

Table S2. Number of sequenced reads per specimen before and after iPyrad filtering steps, in the final consensus and final number of loci.

	# reads before filtering	# reads passed filters	# reads in cluster	# reads in clusters passed filter of depth	# reads in consensus	# loci in assembly
ABR1	3162442	3162343	58529	30116	23584	3140
ABR172BF	7128230	7128004	84042	38955	31531	3347
ABR172M	3913288	3913168	61343	31120	25047	3177
ABRS2F14	3180198	3616999	58562	28790	22887	2964
ABRS2F15	4021893	4573119	78121	37586	29204	3257
ABRS4F	2012097	2288223	52201	21785	16180	2138
ABRS6CM	4126578	4692151	75265	37164	30319	3294
ABRS6DM	4971249	5654075	76224	37959	30830	3295
ABRS9M	4625170	4625022	94687	36174	29618	3278
AmFBS1m	2356549	2356495	69343	29007	24992	6060
AmFBS6m	2550914	2550862	65353	29532	25217	6116
AmFBS9Am	4722849	4722731	79453	36650	31690	6408
AmFBS9Bm	2240929	2240875	60249	28625	24830	6109
BOID10M	4320946	4320844	80595	38582	28785	3129
BOID10M27	1804519	2052227	46588	23654	18934	2754
BOID9F25	1351654	1537242	41924	18438	12875	1575
BOID9F26	771985	877957	28995	12377	8955	1065
BOIS18AM	1311746	1311699	66414	22964	18529	2532
BOIS18BM	1225887	1225846	64910	22785	18570	2400
BOIS1AF	1422470	1422434	64743	25007	20261	2738
BOIS1BF	1449776	1449733	52104	23153	18730	2769
BOIS1F28	2807578	3192671	56307	28924	23039	3024
CFS10AM	1981530	2253099	75654	29575	25393	3204
CFS10BM	1546349	1757572	68537	25589	22281	2950
CFS4AM	972545	1106226	40851	17497	15245	2362
CFS4BM	1546834	1759298	67930	24937	21589	3066
CFS4DM	2636723	2998996	62854	28748	24891	3525
CFS4F	1349187	1534652	54856	21775	18836	2859
CFS5F	1592523	1811259	66890	30869	26820	2674
CFS5M	997834	1134395	43405	18168	15804	2468
CFS6F	4954151	5633888	80899	36028	31455	3774
CFS6F44	4791894	5450119	68761	33884	29026	3678
CFS6M	3932255	4472028	75467	33514	29266	3702
CFS8F36	4664162	5303411	88072	36632	30533	3626
CFS8F41	5452728	6201208	118556	44591	37068	3730
CFS8M35	3433145	3904370	71624	28947	23585	2980
CFS8M38	4753662	5405522	82674	35689	30822	3756
CONS1M	2524117	2524059	68094	30013	24870	5960
CONS2AM	2153112	2153054	82691	33915	28438	5996
CONS2BM	1736816	1736766	71027	31575	26463	5918
CONS4	1372594	1372561	49122	22058	17413	4386
CONS5AF	3977328	3977222	78034	35726	29818	6266
CONS5BF	4095103	4095003	79621	35920	29625	6271
CONS6BF	3673951	3673841	80384	35513	29528	6230
CONS7AM	1007407	1007375	56551	22241	18548	5019
CONS7BM	5675327	5675182	106743	42976	35935	6297
CONS9	7411257	7411079	110718	53060	41325	6188
CSAD14AF	1780753	1780707	48560	23974	19133	2854
CSAD14BF	3786161	3785865	65654	31850	25563	3265
CSAD1F	3014693	3014590	65405	30723	24946	3196
CSAD1M	2136215	2136150	115896	33402	27730	3050
CSAL12F	1468446	1468400	42969	20709	16614	2525
CSAMIXF	1840915	1840855	53041	25245	18841	2754
CSAMIXM	1735912	1735827	67740	28274	23132	3028
CSAS2M	1108150	1108125	45248	19983	16158	2478
FARD6AF	3657932	3657843	82562	35822	30019	6314
FARD6BF	4182262	4182170	79342	35308	30200	6384
FB2S2AM	1933995	1933942	61025	27272	23428	5990
FB2S4AF	5042102	5041975	80310	35646	30584	6400
FBS4F	2310229	2626109	56652	29783	25556	6018
FBS4M	2101068	2388367	51835	27792	23936	5867
FBS6F	4327578	4327480	84232	35215	30249	6450
FORD14M	2563955	2563878	72172	29713	24449	3125
FORD6	746750	746715	39189	16739	13107	2071
FORD7F	1205225	1205183	79365	24534	20545	2460
FORS12F	1090594	1240363	42688	20900	16861	2411

FORS4	2752082	2751990	60626	29235	23610	3133
NATD2F21	633972	721139	26181	9808	6788	793
NATD2F22	1187448	1350096	34148	16452	12402	1578
NATD2F24	2336182	2655596	43051	19847	13622	1706
NATD2M16	1242385	1411659	39430	19188	15368	2256
NATD2M23	2849380	3239072	51612	27620	22235	2955
NATD4CM	1250906	1423120	45987	22439	17605	2543
NATD4DM	805693	915332	35888	15350	12203	1823
NATD4F	5102133	5101993	80863	35443	28379	3288
NATD5F	5849134	5848962	81145	35703	28718	3359
NATD8	5873434	5873256	79147	37555	30511	3327
PBD2CM	2173411	2470706	52668	27168	21997	2980
PBD2DM	1166960	1327145	50847	25235	20574	2513
PORS1M	3036114	3036034	74201	34206	28694	6200
PORS3AM	4492177	4492052	90752	38762	32292	6319
PORS3BM	7698203	7697991	91489	45475	37732	6351
PORS6F	6279580	6279396	97227	45284	37306	6404
PORS7F	4447304	4447194	85652	39489	30173	6021
PORS7M	6168302	6168134	105264	45584	37918	6356
SBS3AM	1124213	1124184	62660	24867	21172	5059
SINO100A	4773303	4773151	68239	31488	27842	3741
SINO100B	3396042	3395917	67416	30387	27003	3743
SINOS10A	216453	216445	31624	7688	6666	994
SINOS10B	4231998	4231845	75982	36364	31785	3775
SMSAM	3220583	3220503	74463	36003	29864	5351
SMSCF	4041494	4041378	84119	38441	32758	5414
SOUS3F2	1131421	1286780	41990	22001	18459	4557
SOUS7AM	1278529	1453775	53541	25805	20726	4783
SOUS7BM	837564	952064	43000	20085	16670	4118
SOUS7CM	1168488	1329205	50134	22714	18833	4422
SOUSXBM	2530601	2878311	65527	33745	26746	5561
SOUSXCM	1981128	2252928	64447	30270	25604	5540
SOUSXM5	1798378	2044717	47603	23933	18886	4084
SPD100AF	3330914	3330810	58389	28132	23922	3678
SPD100BF	2943331	2943245	90068	30588	26924	3625
SPD117AF	3224199	3224087	80677	27740	24290	3507
SPD117BF	2227440	2227347	66275	25217	21817	3372
SPD39F	3404602	3404502	84281	31403	27473	3674
SPD39M	1923929	1923879	51163	23007	20180	3311
SPD50F	2368776	2368688	52834	24349	21195	3477
SPD50M	3101009	3100939	78989	28616	24572	3465
SPD95M	1259756	1259698	48674	22710	19900	3351
SPD96M	2091417	2091345	79878	26427	23311	3423
SSVS14M	312772	355765	26909	10262	8529	1980
SSVS1F13	1496223	1701069	41696	19936	15885	3323
SSVS3F9	355739	404783	19150	7214	5205	1021
SSVS3M10	2333752	2654201	47872	24554	19312	3931
SSVS5F11	344786	392188	18955	6824	5011	908
SSVS5F12	5328314	6058517	74797	38906	32522	5683
SSVS5F8	2649203	3012796	53641	28256	23664	2611
SSVS5M	1591213	1591181	66097	27757	23821	5095
SSVS9AF	3439983	3439901	81287	37041	30334	5639
SSVS9C	1110599	1262559	45797	22067	18772	4349
SSVS9D	2729287	3104257	61422	32080	27247	5322
SSVS9M	593843	593830	35954	14705	12486	3005
SUES13F	3275333	3275261	72196	35482	28069	6141
SUES8M	1251056	1251030	138269	33177	28858	5197
TRID1AM	5538739	5538581	92641	41402	36036	6446
TRID1BM	6047437	6047266	87474	40828	35256	6445
TRID2AM	3275418	3275341	90973	38426	32766	6655
TRID2BM	4755377	4755249	79530	37320	32336	6453
TRID2CM	1016997	1157682	41561	20200	17369	4443
TRID3BF	2670743	3037196	61373	31483	27297	5915
TRID3BM	1795987	2042079	54750	27823	24056	5507
TRID3CF	2992349	3402390	70921	36475	31536	6302
TRID3F	12261962	12466997	113410	54536	44758	6475
TRID3M	3144977	3144898	71800	33647	29025	6343
TRID5M	4095241	4095136	85876	37706	32706	6424

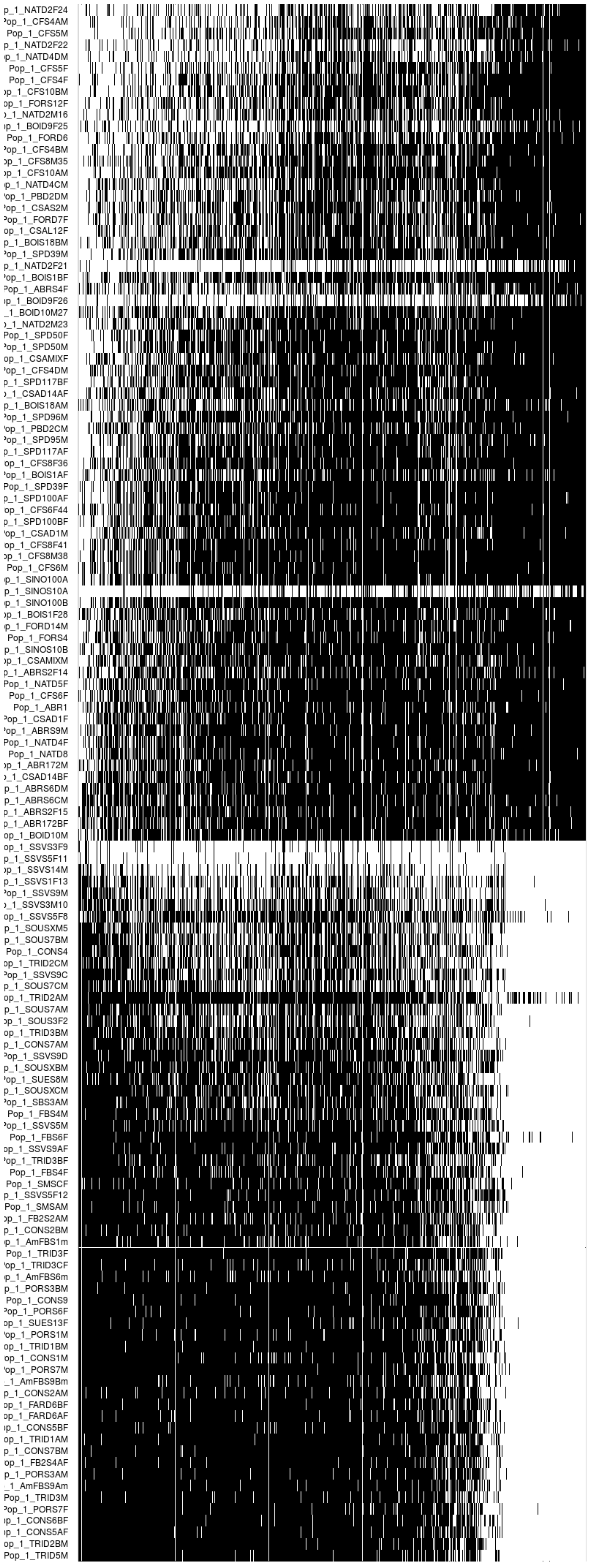


Figure S3. Matrix Condenser results showing 5,857 SNPs after PLINK filtering for ‘merged’ dataset. Each column is a SNP, where the black bars represent a SNP present in the individual, and the blank bars indicate that the SNP is missing.

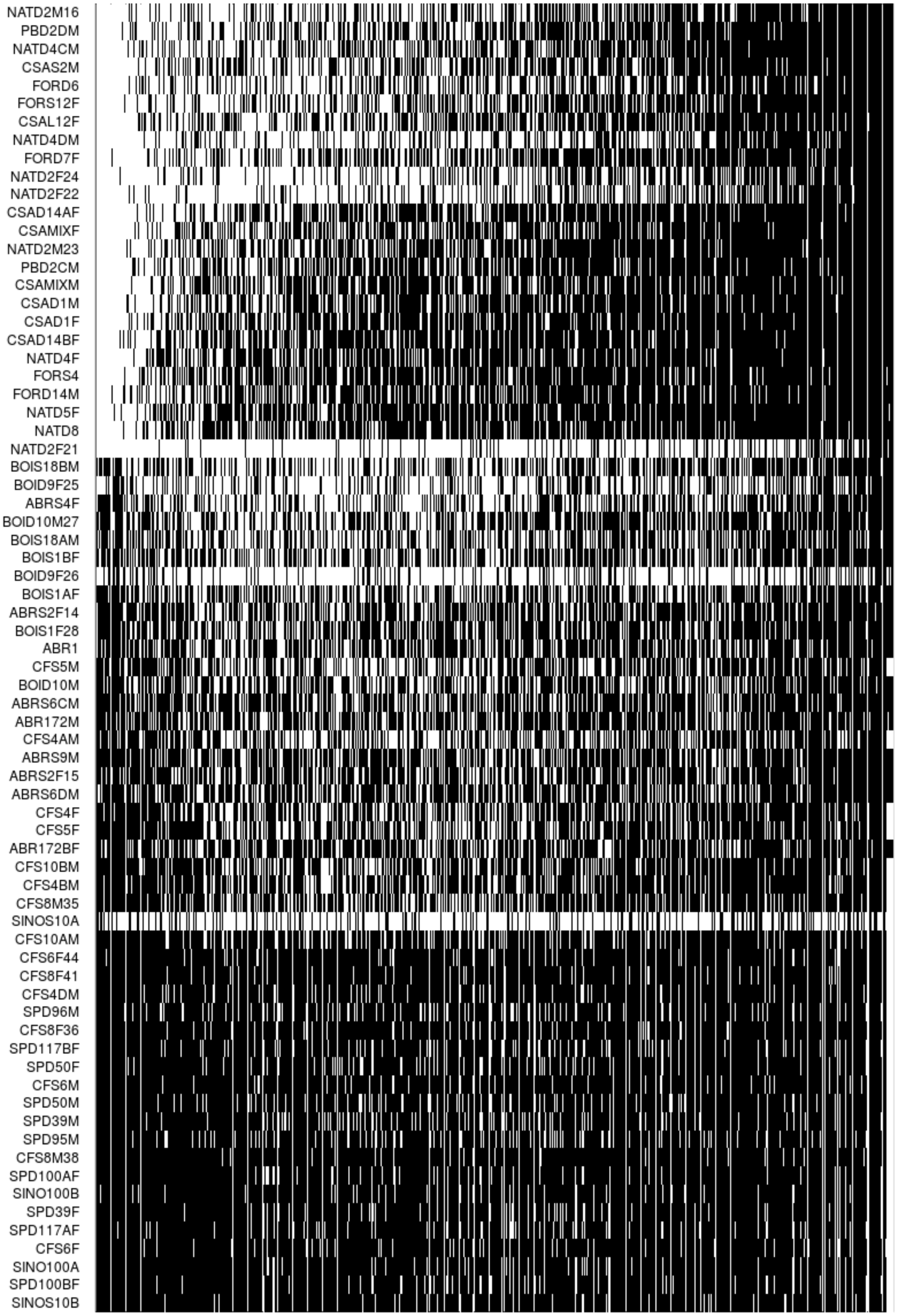


Figure S4. Matrix Condenser results showing 21,126 SNPs after PLINK filtering for ‘continent’ dataset. Each column is a SNP, where the black bars represent a SNP present in the individual, and the blank bars indicate that the SNP is missing.

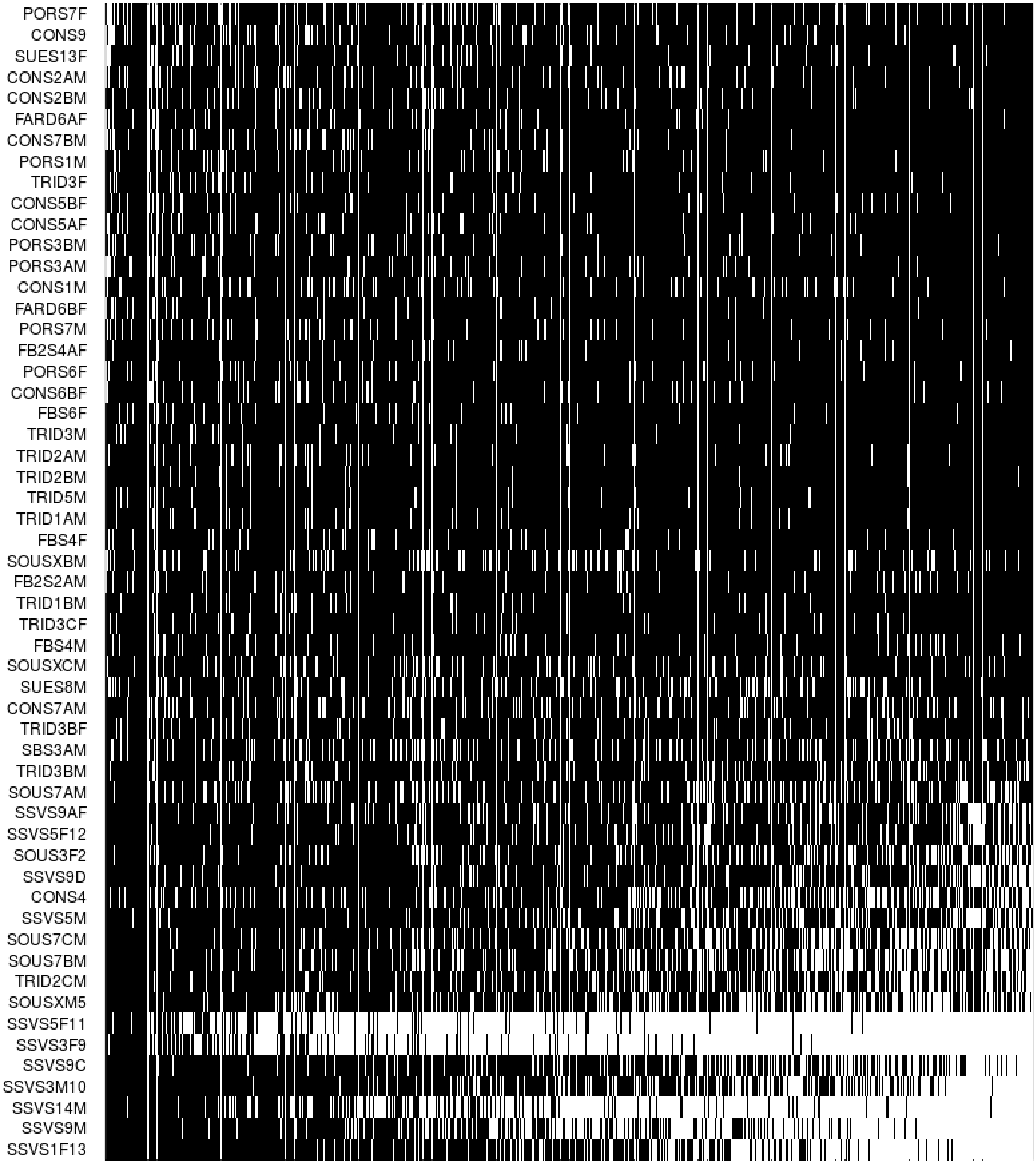


Figure S5. Matrix Condenser results showing 17,237 SNPs after PLINK filtering for ‘islands’ dataset. Each column is a SNP, where the black bars represent a SNP present in the individual, and the blank bars indicate that the SNP is missing.

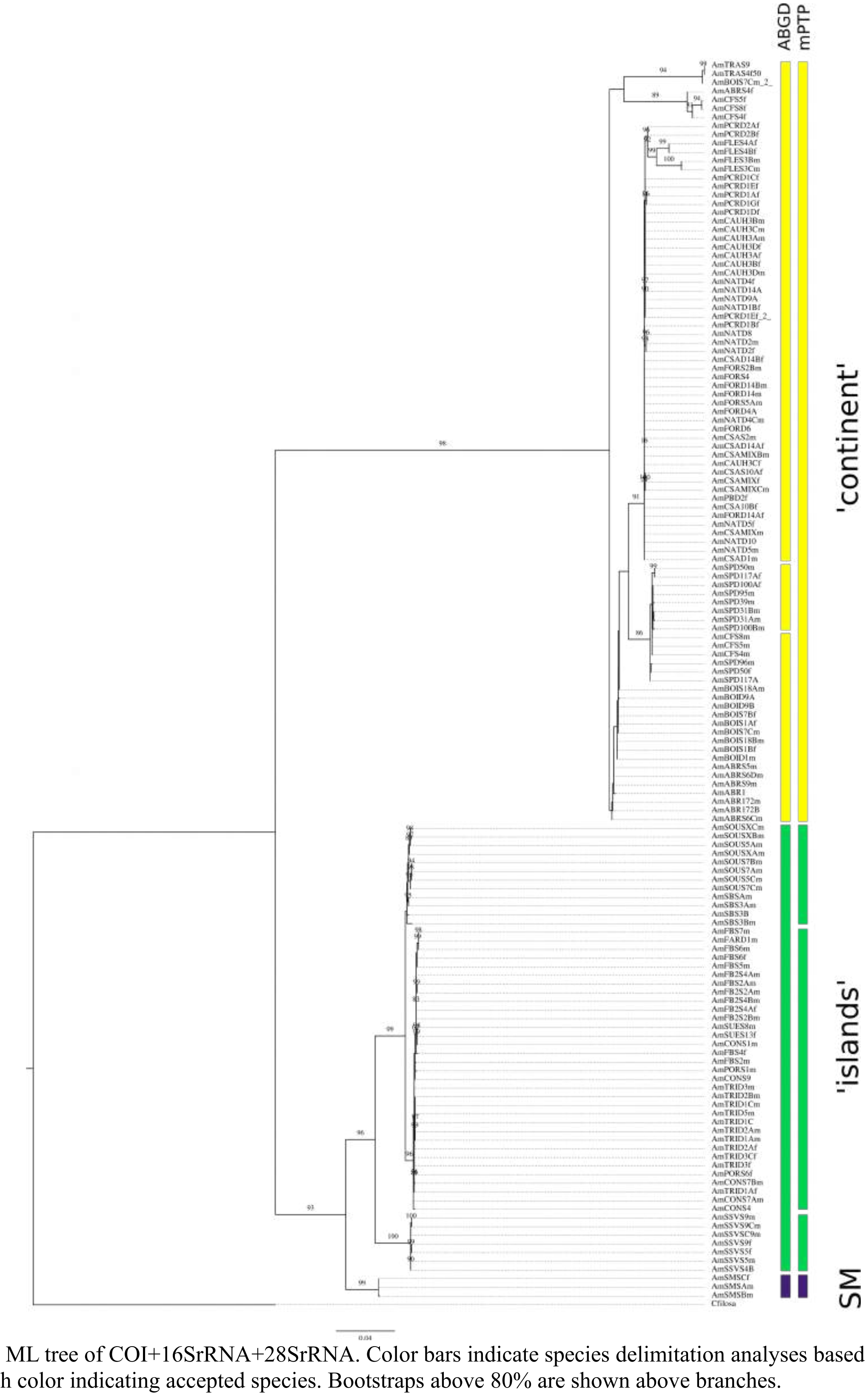


Figure S6. ML tree of COI+16SrRNA+28SrRNA. Color bars indicate species delimitation analyses based on COI results, with color indicating accepted species. Bootstraps above 80% are shown above branches.

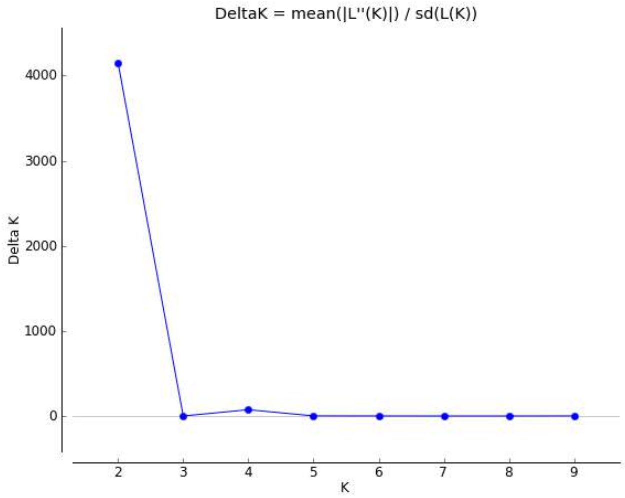


Figure S7. Structure Harverster results for each ΔK for *A. marcuzzii s.l.*

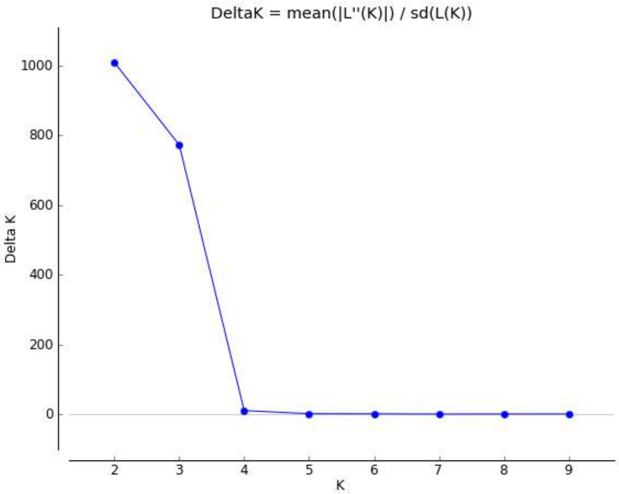


Figure S8. Structure Harverster results for each ΔK for 'continent'.

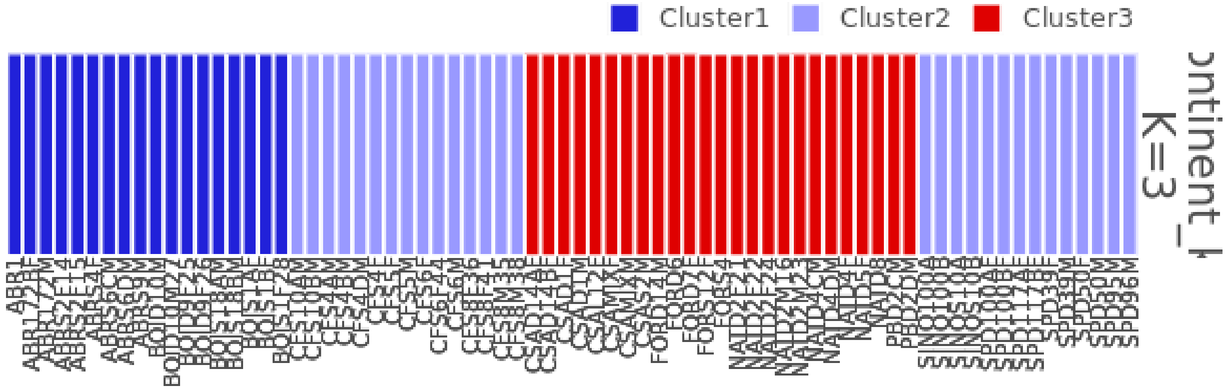
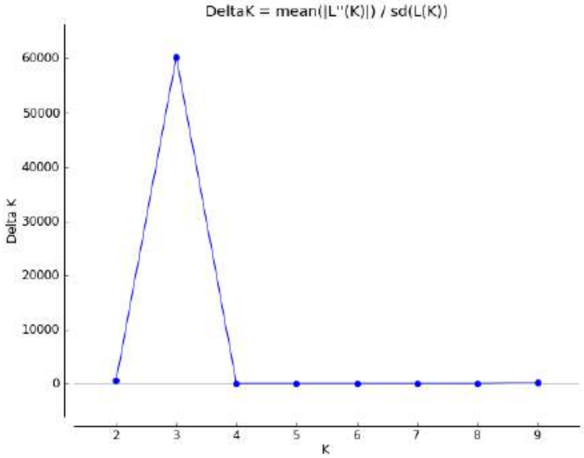


Figure S9. Strucure results for 'continent' with second highest ΔK value of k=3.



S4. Structure Harverster results for each ΔK for ‘islands’.

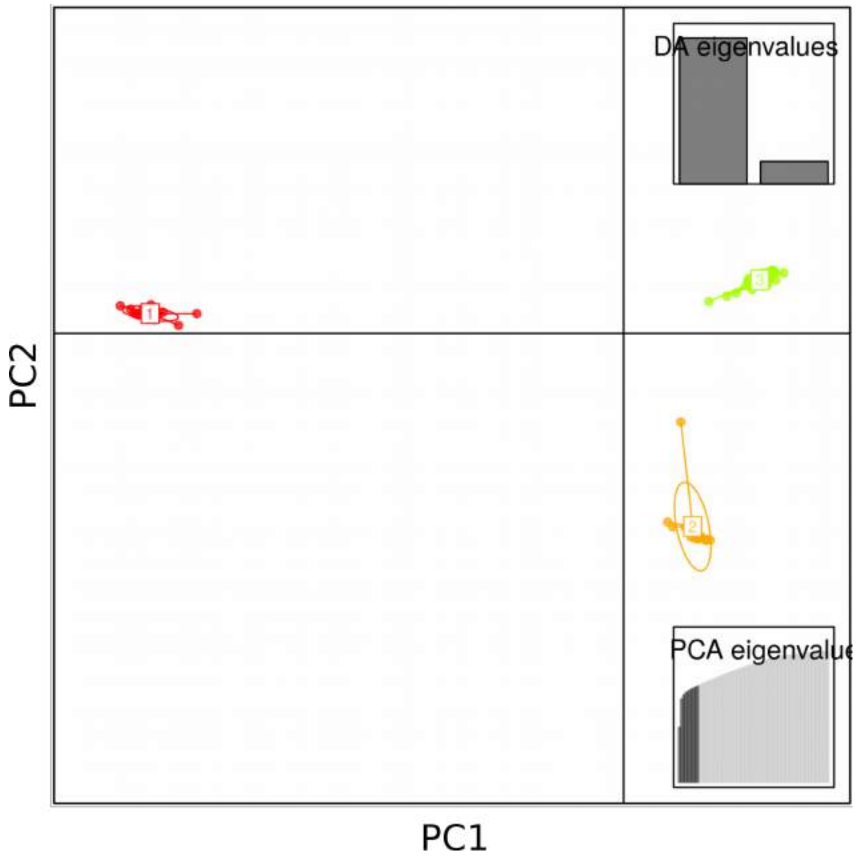


Figure S11. DAPC results for ‘continent’. Cluster 1: E; Cluster 2: NE; Cluster 3: SE.

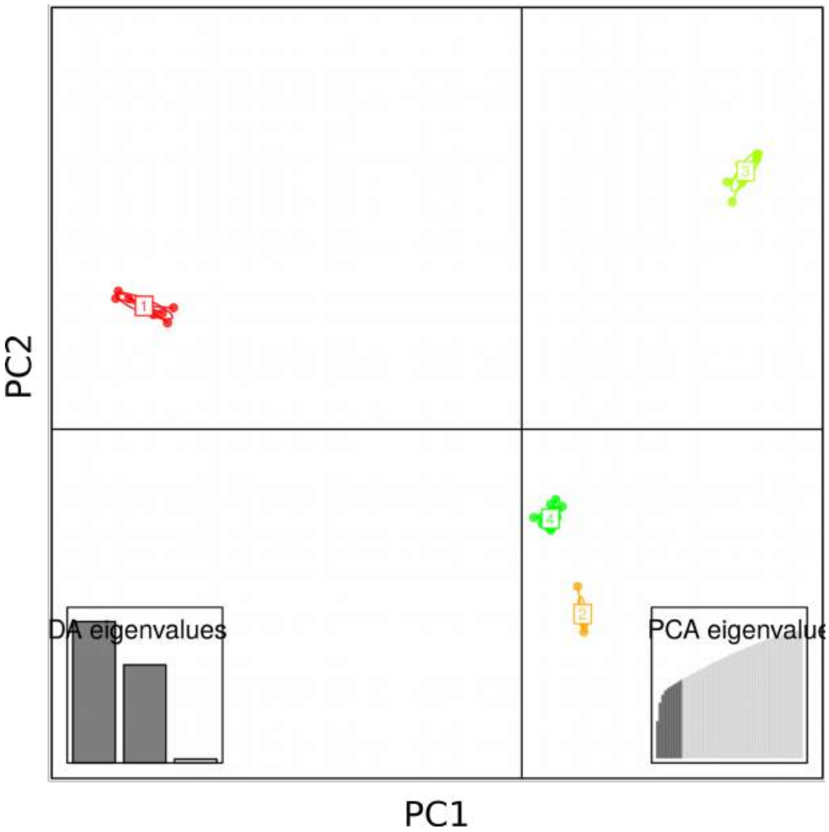


Figure S12. DAPC results for ‘islands’. Cluster 1: OI; Cluster 2: CDM; Cluster 3: SSV (1); Cluster 4: SSV (2).

Table S13. Neutrality tests results.

Lineage	Tajima's D	P-value D	Fu's Fs	P-value Fs
NE	-1.19488	0.10900	34.00000	1.00000
E	14.59037	1.00000	11.70793	0.99980
SE	0.08807	0.59080	14.47543	1.00000
CDM	-0.79866	0.22590	2.33347	0.84690
OI	-2.69152	0.00000	7.40179	0.99120
SSV	-0.27492	0.39220	10.27260	0.99930

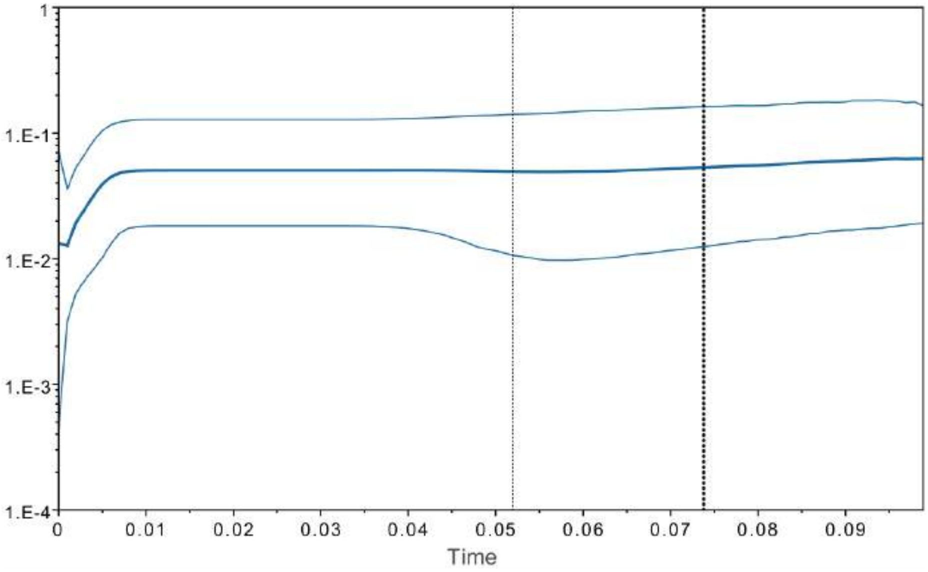


Figure S14. Bayesian Skyline Plot of E population.

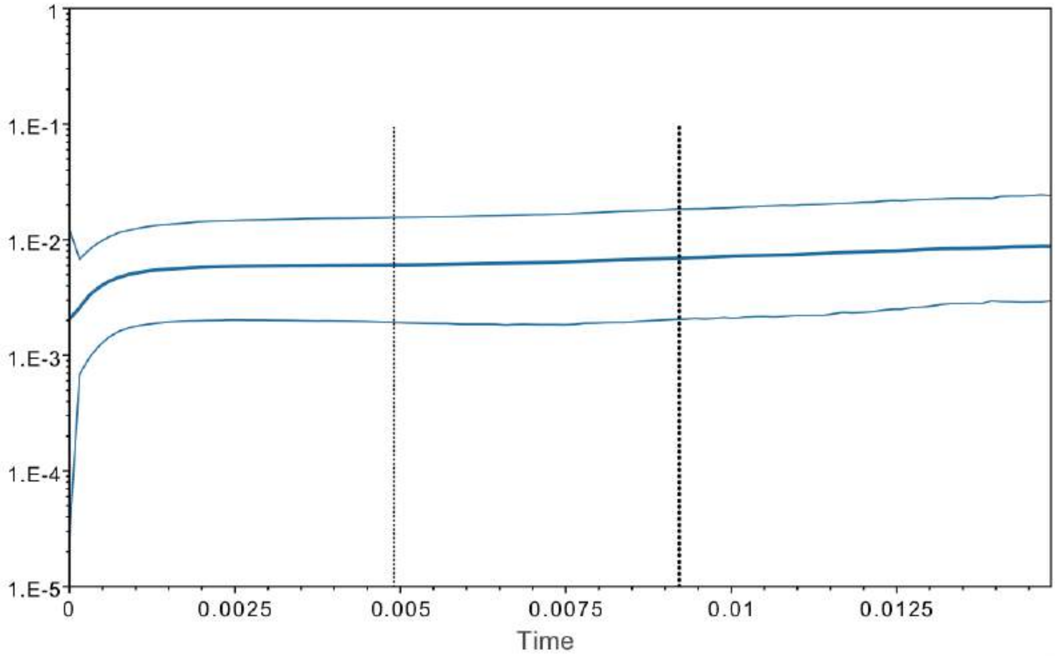


Figure S15. Bayesian Skyline Plot of NE population.

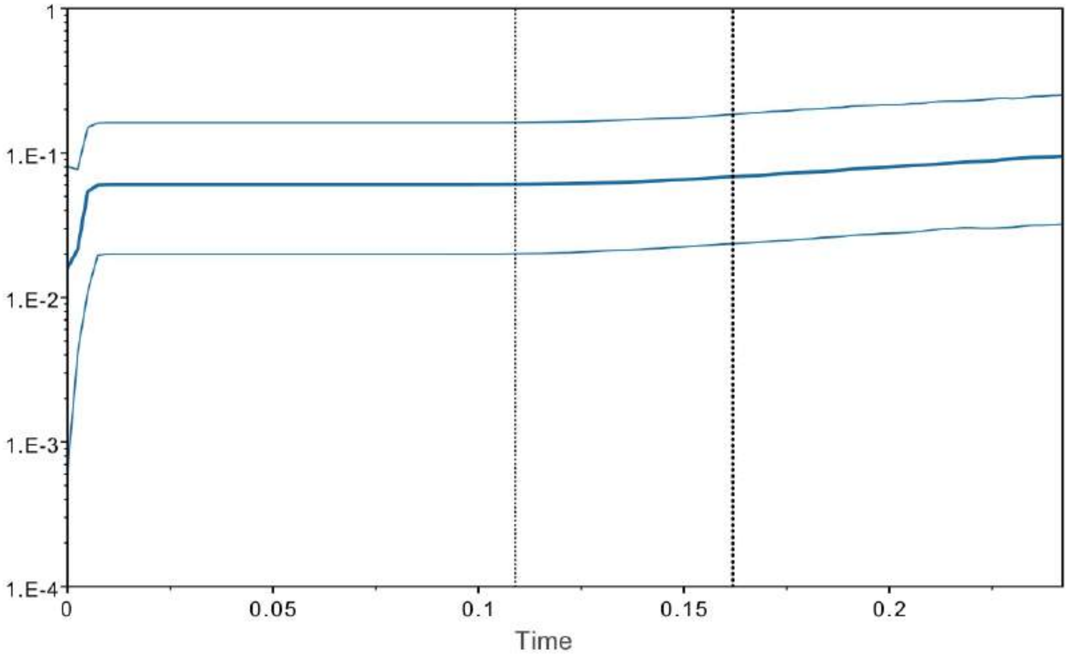


Figure S16. Bayesian Skyline Plot of SE population.

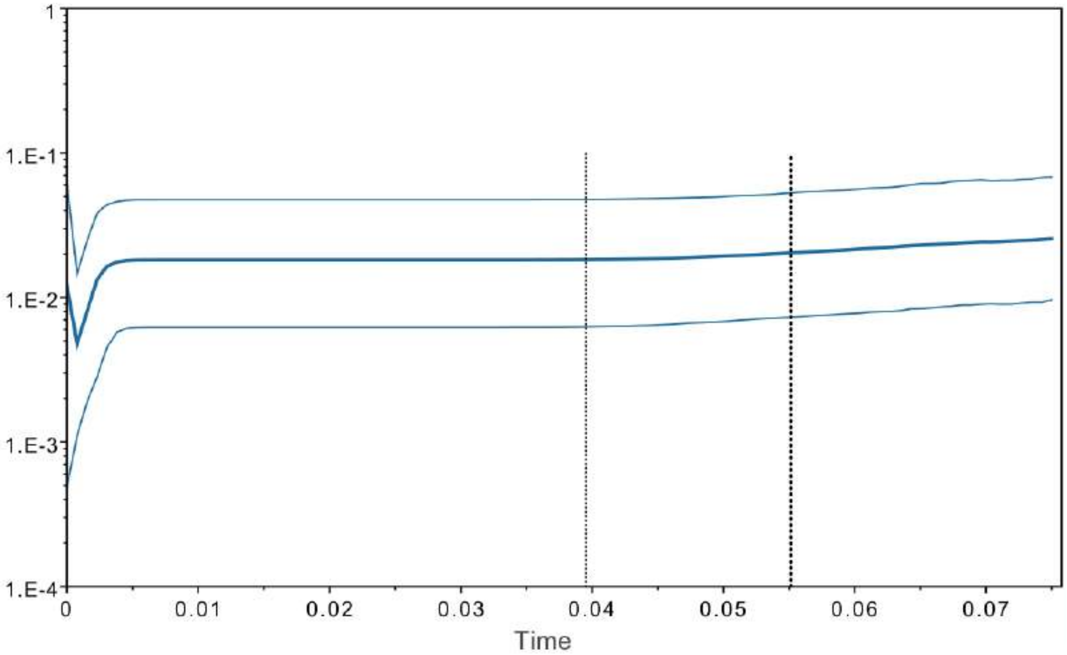


Figure S17. Bayesian Skyline Plot of OI population.

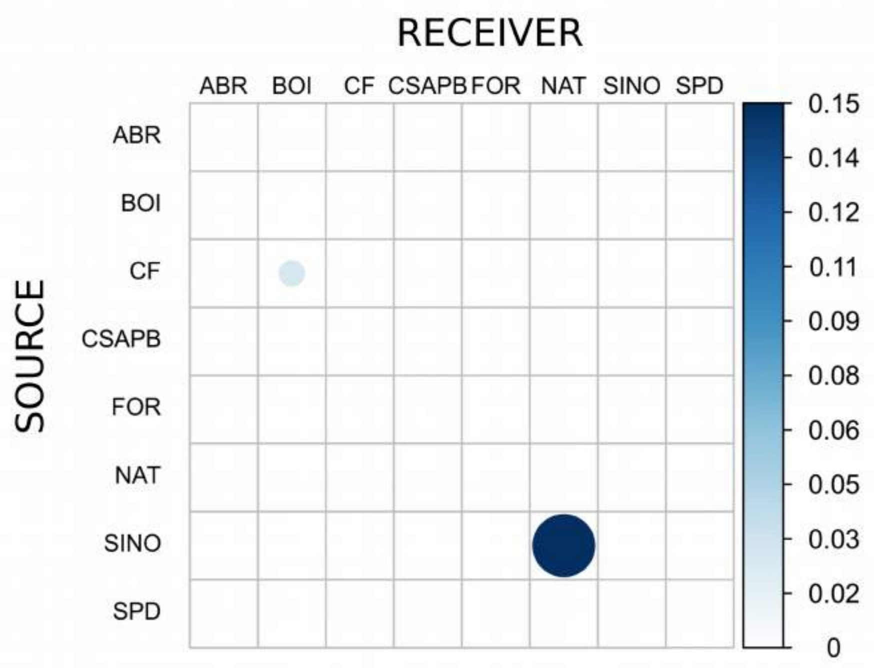


Figure S18. Fastsimcoal migration results for ‘continent’

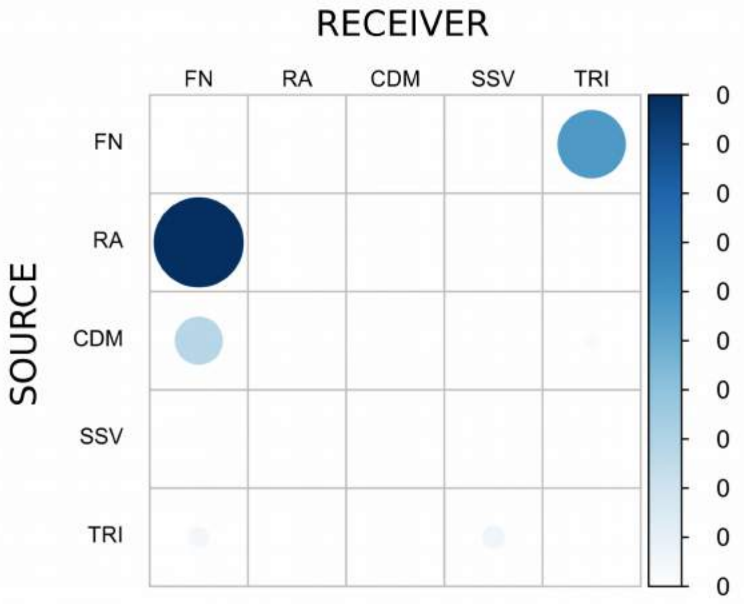


Figure S19. Fastsimcoal migration results for ‘islands’

Table S20. Variable selection results based on Factorial Analysis.

	ML1	ML2	ML3	ML4	ML5
Bathymetric slope	0.01	0.03	0	0.02	0.09
Concavity	0.17	0.06	0	0.04	0.02
Distance to shore	0.08	0.03	0.65	0	0.01
East/West aspect	0.06	0.05	0.75	0.01	0
North/South Aspect	0.23	0.18	0.01	0.09	0.48
Plan curvature	0.25	0.12	0.14	0.04	0.02
Profile curvature	0.02	0.01	1	0	0
Sea surface salinity (annual mean)	0.3	0.61	0.01	0.73	0.03
Sea surface salinity (monthly minimum)	0.1	0.88	0.01	0.44	0.14
Sea surface salinity (monthly maximum)	0.49	0.16	0	0.84	0.16
Sea surface salinity (annual range)	0.12	0.96	0.01	0.11	0.24
Sea surface salinity (annual variance)	0.04	0.84	0.01	0.09	0.12
Sea surface temperature (annual mean)	0.92	0.04	0	0.19	0.35
Sea surface temperature (coldest ice-free month)	0.95	0.04	0	0.2	0.25
Sea surface temperature (warmest ice-free month)	0.85	0.06	0	0.18	0.48
Sea surface temperature (range)	0.95	0.03	0.01	0.2	0.25
Sea surface temperature (variance)	0.84	0.04	0	0.37	0.32
Bathymetry	0.05	0.37	0.09	0.24	0.29

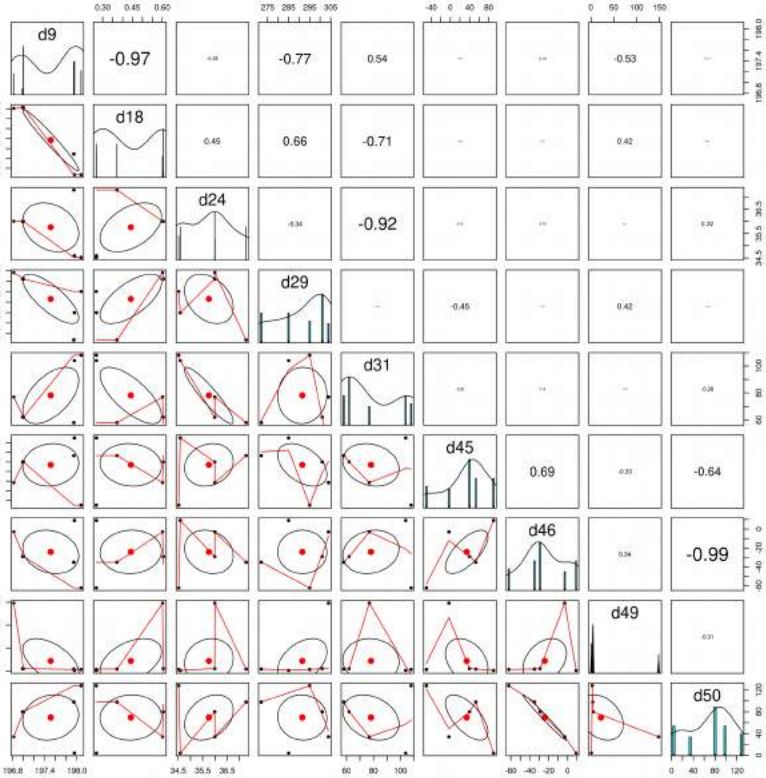


Figure S21. Pairwise correlation with ten chosen variables for ‘continent’.

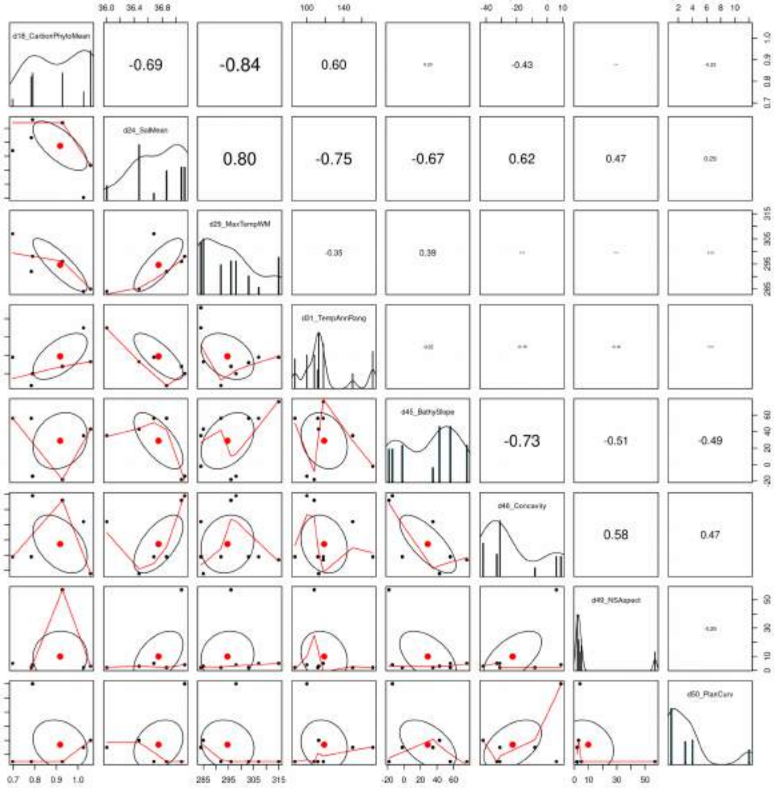


Figure S22. Pairwise correlation with ten chosen variables for ‘islands’.

Figure S23. Pelagic *Sargassum* washed ashore at San Sauveur, Dominica. July, 2019.

Capítulo 4

OCEANIC BOUNDARIES DELIMITING NOVEL LINEAGES IN THE COSMOPOLITAN TANAIDACEAN *Chondrochelia dubia* (TANAIDACEA: LEPTOCHELIIDAE) COMPLEX IN THE SOUTHWESTERN ATLANTIC

Oceanic boundaries delimiting novel lineages in the cosmopolitan tanaidacean *Chondrochelia dubia* (Tanaidacea: Leptocheliidae) complex in the southwestern Atlantic

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Abstract

Cosmopolitanism in the marine environment is the linked to specific biological traits. Although several species are considered widespread, some of them possibly hide a range of species with similar morphology lead by environmental pressures. *Chondrochelia dubia* is a cosmopolitan tanaidacean with tubicolous lifestyle that is commonly found in shallow waters. The lack of a dispersive larval stage, however, suggests that several endemic species under a species complex might be present. Here, we studied the *Chondrochelia dubia* complex on over 5000 km of its oceanic spatial distribution, including its type locality, and we confirm the species complex status in the Western Atlantic with five species: *C. dubia s.s.*, *C. brasiliensis* **comb. nov.**, *C. baronia* **sp. nov.**, *C. trindadensis* **sp. nov.** and *C. cacandocae* **sp. nov.**. Species delimitation analyses corroborate the morphological separation of species, and divergence times dated up to 12 Mya for *C. trindadensis* **sp. nov.**. The genetic diversity and structure of the widespread species *C. dubia s.s.* and *C. brasiliensis* **comb. nov.** strongly differed between each other, with a spatially geographic separation at the Paraguaçu river mouth, suggesting independent evolution of both lineages. The paleodistribution simulation suggested a considerable spatio-temporal expansion for *C. dubia s.s.* and *C. brasiliensis* comb. nov. since the LGM, where species were restricted to the submerged continental shelf. The simplified morphology observed in *Chondrochelia* species hid a great diversity within the western Atlantic, with approximately one species per ecoregion. Therefore, coupling detailed morphology with molecular and ecological data might disentangle the *Chondrochelia dubia* complex worldwide.

Keywords: Crustacea, macrofauna, phylogeography, species complex

INTRODUCTION

Marine cosmopolitan taxa are assumed as those with a wide spatial distribution, at least occurring in both major oceans basins (i.e. Pacific and Atlantic) (Hutchings & Kupriyanova 2018). However, cosmopolitanism is linked to specific biological traits such as lifespan, adaptation to new environments and dispersion capacity. For those cosmopolitan species with low dispersion ability, such as benthic invertebrates with direct development, environmental pressures might hide a range of species with similar morphology instead of true cosmopolitanism (Cerca et al. 2018).

On the other hand, the dispersion ability of an organism goes beyond its intrinsic factors such as larval dispersal, instead, the capacity of survival and population maintenance on a floating substrata may be as useful as, or more favorable to dispersal than pelagic larval dispersal itself. Rafting on biotic and abiotic substrates has been inferred as an important dispersal mechanism for several marine invertebrates (Ingólfsson 1995, Thiel 2003), and substrata suitability depends on its quality, such as food value and flotation potential, with macroalgae combining both relatively high food value and high floatation potential (Thiel 2003).

Besides the substrata suitability, hitchhicker species also have their own adaptations for rafting events, with peracarid crustaceans being one of the most favorable to rafting dispersal, once their offspring may recruit directly to the parental raft, leading to successional changes of the rafting assemblage during the voyage (Thiel 2003). Peracarid crustaceans associated to macroalgae gsó me enerally include three of the 12 extant orders: Amphipoda, Isopoda, and Tanaidacea (Jacobucci & Leite 2002; Cunha et al. 2013), and according to Blazewicz-Paszkowycz et al. (2012), transport in floating algae is one of the potential causes of passive dispersion that could explain cosmopolitan tanaidacean species.

Chondrochelia dubia (Krøyer, 1842) is a cosmopolitan tanaidacean with tubicolous lifestyle and its found associated to several substrata, including bryozoans, sponges and macroalgae. The species was described from Salvador, Bahia, in northeastern Brazil, and several records around the world were made thereafter (GBIF 2022, OBIS 2022).However, based on its morphological and ecological traits, it is believed that *C. dubia* is a species complex that may comprise several species (Gutu 2016). Jarquín-González & Carrera-Parra (2022) recently studied specimens previously identified as *Leptochelia dubia* by previous authors, and found cryptic species among *C. dubia* from the Mexican Caribbean and Gulf of Mexico. Therefore, five species of *Chondrochelia* are reported from the western Atlantic: *C. dubia*, *C. algicola* (Harger, 1878), *C. caribensis* Jarquín-González & Carrera-Parra, 2022, *C. ortizi* (Jarquín-González, 2016) and *C. winfieldi* Jarquín-González & Carrera-Parra, 2022. In Brazil, *C. dubia* is often found associated to macroalgae, and it was reported from Ceará (NE) (Araújo-Silva et al. 2022) and São Paulo (SE) coasts (Bueno et al. 2016), including records on continental (Cunha et al. 2013) and oceanic islands (Iwasa-Arai et al. 2021).

Here, we aimed to study the genetic diversity and the evolution of the complex *C. dubi*a along the Brazilian coastal zone(continental and oceanic islands) comparing with Caribbean specimens and previously described species from the western Atlantic to investigate the cosmopolitan status of *C. dubia* complex and its dispersal ability. Hence we combined morphology, molecular markers and palaeoclimatic simulations to understand the species complex evolutionary history

MATERIAL AND METHODS

Study sites, sampling and morphology

Specimens of *C. dubi*a were collected associated with brown macroalgae between December 2016 and February 2022 from over 5,000 km in the western Atlantic, across the northeastern (NE), southeastern (SE) and southern (S) regions of the Brazilian coastal zone (continental and oceanic islands) and Dominica (Fig. 1, Table 1). Our samplings were based on the Brazilian SISBIO licence no. 60924 and national authorization by Dominica's Fisheries Division.

Algal fronds were randomly collected underwater by freediving (1–5 m), stored in fabric bags (0.2 mm mesh size), fixed and preserved in ethanol 96–99%. At the laboratory, the associated fauna was sorted, and specimens identified as *C. dubia* were selected for further morphological and molecular analysis. Appendages and mouthparts of dissected specimens were mounted on glass slides and sealed with glycerol. Drawings were made with a camera lucida at a Zeiss Axioscope stereomicroscope, and digitally drawn with Inkscape. Specimens are deposited at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC). The abbreviations used for morphological characters are as follows: A, antenna; Che, cheliped; f, female; Hd, head; l, left; LL, lower lip; m, male; Md, mandible; Mx, maxilla; Mxp, Maxilliped; P, pereopod; Per, pereonite; Pl, pleon; r, right; U, uropod; UL, upper lip.

The abbreviations used for localities are as follows: ABR, Abrolhos Archipelago; ALC, Alcatrazes Archipelago; ARR, Arraial do Cabo; BOI, Boipeba Island; BOM, Bombinhas; BRT, Barretão pool, Rocas Atoll; CF, Cabo Frio; FN, Fernando de Noronha; FOR, Forte Beach; IG, Ilha Grande; NAT, Natal; PCR, Paracuru; PT, Portsmouth; SOU, Soufrière; SSV, San Sauveur; TRA, Trancoso; TRI, Trindade Island; UBA, Ubatuba.

DNA extraction , amplification and sequencing

Genomic DNA was extracted according to the CTAB protocol of Doyle & Doyle (1987). DNA integrity was checked by 1.5% agarose gel electrophoresis and quantified using Nanodrop spectrophotometer. Partial sequences of the mitochondrial gene cytochrome oxidase subunit 1 (hereafter, COI) and nuclear 28SrRNA were obtained for subsequent analyses. Fragments were amplified using the following primer pairs: COI: 18F_COX1/869R_COX1 (18F_COX1: 5′-TTCWACWAAYCATAARGATATTGG-3′, 869R_COX1: 5′-ATRTGRTGDGCYCAHACWABRAAHCCTAA-3′, Jakiel et al. 2019); 28SrRNA: rd1a/rd4b (rd1a: 5′-CCCSCGTAAYTTAGG CATAT-3′; rd4b: 5′-CCTTGGTCCGTGTTT CAAGAC-3′, Edgecombe & Giribet 2006).

Polymerase chain reactions (PCRs) were carried out in a total volume of 15 µL containing 1 × PCR buffer, 2.5 U Taq DNA Polymerase, 1.5 mM MgCl2, 200 µM of each dNTP, 0.35 µM of each oligonucleotide and ultrapure water to achieve the reaction volume (Taq PCR Master Mix, Qiagen). The cycling profile on the thermal cycler involved a denaturation step at 94 °C for 1 min, 35 cycles of denaturation at 94 °C for 1 min; annealing temperature for 1 min, extension at 72 °C for 1 min; and extension at 72 °C for 10 min. Annealing temperatures were 48°C for both genes. PCR products were purified with polyethylene glycol solution 15% (PEG) and then amplified for sequencing using a BigDye Terminator Cycle Sequencing Kit v.3.1 (Applied Biosystems) at the Human Genome and Stem Cell Research Center, Universidade de São Paulo.

Chromatograms were analysed using Genestudio 2.2 (Genestudio Inc.), which was used to perform BLAST searches (http://blast.ncbi.nlm.nih.gov) to check for contamination or sequencing errors. Individual consensus sequences were aligned using T-Coffee server that combine multiple alingment methods (Notredame et al. 2000). COI and 28SrRNA data were analyzed separately for most population and species delimitation analyses, and concatenated for phylogenetic analyses.

Phylogenetic analyses and species delimitation

Sequences of *Chondrochelia* spp., *Leptochelia forresti* (Stebbing, 1896), *L. longichelipedes* (Lang, 1973) and *Pseudoleptochelia* sp. were obtained from GenBank (National Center for Biotechnology Information, NCBI) and BOLD Systems (Table 2). The best partition schemes and models were determined in PartitionFinder v.X (Lanfear et al. 2012). The optimal partitioning strategy and evolutionary models consisted of subdividing the COI data set by codon positions with the model JC for the three codon partitions, and TIM+F+I+G4 for 28SrRNA. The phylogenetic analyses of maximum likelihood (ML) were held at the W-IQ-TREE vX web server (Trifinopoulos et al. 2016), and the support of the nodes was evaluated with 1.000 ultrafast bootstrap replicates (Hoang et al. 2018). Two species delimitation methods were used. The Assemble Species by Automatic Partitioning (ASAP) uses the implementation of a hierarchical clustering algorithm that only uses pairwise genetic distances, and it proposes species partitions ranked by a new scoring system that uses no biological prior insight of intraspecific diversity (Puillandre et al. 2020). The mPTP is a method that fits the branching events of each delimited species to a distinct exponential distribution and does not require any similarity threshold as input (Kapli et al. 2017). We performed an analysis based on the obtained ML phylogenetic tree after removing the outgroups and using two independent MCMC chains at 100,000,000 generations each with a sampling frequency of 1,000. Both analyses were performed for genes separately with COI results discussed below, and 28SrRNA delimitation analysis was only considered for populations that were not available for COI.

Genetic diversity and population structure

Number of haplotypes (N) and their frequencies, as well as haplotype (h) and nucleotide (π) diversities were estimated using Arlequin 3.5.2 (Excoffier et al. 2005). Pairwise genetic divergences between localities were estimated using unbiased FST estimator θ (Weir & Cockerham 1984) using Arlequin, and the population structure was examined through analyses of molecular variance (AMOVA) using the pairwise difference algorithm in Arlequin and the statistical significance of estimates was assessed by 10,000 permutations. Genealogical relationships among haplotypes were assessed through a haplotype network constructed using TCS algorithm as implemented in PopART v.1.7 (Leigh & Bryant 2015).

The historical migration between localities was estimated for each COI using Migrate v.4.4.3 (Beerli, 2009) by multiplying the mtDNA ploidy with the population size parameter (θ) and the average number of migrants per generation, with 2 × 106 recorded genealogies, and 200 sampling increments with a burn-in of 10% in addition to an adaptive heating scheme.

Mantel tests (Mantel, 1967) were performed to identify possible isolation-by-distance (IBD, Rousset 1997) and isolation-by-environment (IBE, Wang & Bradburd, 2014) using the R package vegan (Oksanen et al. 2020). Each collection site was considered a different population and the genetic distance was inferred using pairwise F_{ST} (Weir & Cockerham, 1984). The smallest distance between the two sites was calculated using latitude/longitude distance calculator provided by the National Oceanic and Atmospheric Administration website (https://www.nhc.noaa.gov/gccalc.shtml). The partial Mantel tests were performed separately for each environmental variable, using the geographic distance as control for variables available from Bio-Oracle (Tyberghein et al. 2012), MARSPEC (Sbrocco & Barber 2013) and WorldClim (Fick and Hijmans 2017) (Supplementary Material). Climatic distances were calculated as Euclidean distances using the *dist* function in R.

Demographic history and divergence times

Demographic processes over time were assessed using Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) neutrality tests, and mismatch distribution analyses (Harpending et al. 1993), performed by Arlequin with 10,000 permutations.

Changes in effective population sizes of each island over evolutionary time were inferred using

BEAST (Drummond & Rambaut 2007) with the same evolutionary models and partitions from the phylogenetic analysis. Analyses were run for 5,000,000 generations, with the first 500,000 generations discarded as burn-in. Convergence was detected based on sufficiently large effective sample sizes (>200) for each parameter using TRACER 1.5 (Rambaut & Drummond 2007), and posteriorly used to plot reconstructed Bayesian skyline plots (Drummond et al. 2005).

Divergence times were calculated with BEAST 1.8.4 (Drummond et al. 2012) with the same evolutionary models and partitions from the phylogenetic analysis. We employed an uncorrelated relaxed clock with a lognormal distribution (Drummond et al. 2006). For the tree model, we used a random starting tree and speciation was modeled using the Birth-Death Process. The MCMC chain was run for 108 iterations, with a thinning of 1000. Effective sample sizes of parameters and convergence were checked with Tracer 1.7.1 (Rambaut et al. 2018) after discarding 20% of the trees as burn-in. Two independent runs were performed and gave the same result. The resulting files were combined using LogCombiner 1.8 (Drummond et al. 2012), and the maximum clade credibility tree was produced using TreeAnnotator 1.8 (Drummond et al. 2012). Because of the lack of Leptocheliidae fossils, we chose to use only the estimated divergence times based on applying substitution rates of 1.773% Ma -1 for COI and 0.161% Ma-1 for 28SrRNA previously inferred for Amphipoda (Copilaș-Ciocianu et al. 2019).

Current and paleodistribution models

We used ecological niche modelling (ENM) approaches to predict current and paleodistributions of *Chondrochelia dubia*. Initially, we obtained known occurrence records of *C. dubia* from the OBIS (Ocean Biogeographic Information System, http://www.iobis.org) and GBIF (Global Biodiversity Information Database, http://gbif.org), and records of our own samples.However, because of the genetic results of cryptic diversity and the linnean shortfall on this taxa, we opted to use only our sampling data to avoid distribution superestimation.

The climate and paleoclimatic variable were accessed from the MARSPEC database (Sbrocco & Barber 2013), comprising 18 available marine environmental data items for current and past (LGM) scenarios with 5 arc min (~ 10km resolution in the Equator region). Climatic layers were clipped to the

Western Atlantic Ocean with an extent of 80° and 20° W longitude and 35° S and 20° N latitude and a factorial analysis with Varimax was performed to select variables following Sobral-Souza et al. (2015) and Menezes et al. (2020).

ENMs were built using the occurrence points and selected climatic variables for the current climate scenario and predicted for the LGM. We built the models using five mathematical algorithms to increase the reliability of models based on a forecast ensemble approach (Araújo & New 2007), including three based only on the present records: (1) envelope score, Bioclim (Booth et al. 2014); (2) Mahalanobis distance (Farber & Kadmon 2003), and (3) Domain–Gower distance (Carpenter et al. 1993); and two machine-learning methods based on presence/background records: (4) support vector machines (SVMs) (Tax & Duin 2004) and (5) maximum entropy (MaxEnt) (Phillips & Dudík 2008).

A consensual map was built with the frequency of each grid cell predicted from all accurate models, taking values of the true skill statistic (TSS) and the “maximum sensitivity and specificity threshold” for each model (Sobral-Souza et al. 2015; Menezes et al. 2020).

RESULTS

Phylogenetic analyses and species delimitation

Phylogenetic analyses of both markers separated, as well as of a concatenated dataset, suggested the existence of more than one species under the name of *C. dubia*. In addition, the species delimitation analyses of ASAP and mPTP corroborated the separation of *C. dubia* from Brazil into five different species: *C. dubia* from northeastern Brazil and Dominica, *Chondrochelia brasiliensis* (Dana, 1849) **comb. nov.** from east/southern Brazil, *Chondrochelia baronia* **sp. nov.** from Rocas Atoll (RA), *Chondrochelia trindadensis* **sp. nov.** from Trindade Island (TR) and *Chondrochelia cacandocae* **sp. nov.** from Ubatuba (UBA), southeastern Brazil (Fig. 2). For the Brazilian species, only the mPTP analysis of COI was not congruent with other analyses, suggesting that specimens from TR and RA might be one single species.

The species *C. dubia s.s.* was identified as the species distributed along the northern of the northeastern Brazilian coast, as well as in Dominica and the oceanic island of Fernando de Noronha (FN), and a detailed redescription based on topotype material and designation of a neotype is provided herein. *Chondrochelia brasiliensis*, also previously described from the Brazil, was identified as the species distributed along the south, southeast and northern part of the norteastern coast, including continental islands of Boipeba (BOI) and Abrolhos Archipelago (ABR) in the south part of the northeastern region, and Alcatrazes Archipelago (ALC) in the southeastern Brazil. *Chondrochelia brasiliensis* **comb. nov.** is also described in detail and a neotype is designed in the present study. The three new species described herein show a restrict distribution and morphological description is provided for them below.

According to the phylogenetic tree, *C. dubia* is the sister species of the clade *C. baronia* **sp. nov.**+ *C. cacandocae* **sp. nov.**, while *C. brasiliensis* **comb. nov.** is the sister species of the clade *C. savignyi* (Kroyer, 1842) + *C. winfieldi*. *Chondrochelia trindadensis* **sp. nov.** is placed as the sister clade of all other *Chondrochelia* spp. and *Leptochelia* spp., but future analyses with the remaining *Chondrochelia* and *Leptochelia* species are needed to understand the group diversification patterns. For now, *C. trindadensis* **sp. nov.** is described within *Chondrochelia* based on diagnostic morphological characters.

Genetic diversity and population structure

Overall haplotype (H) and nucleotide diversity (π) for *C. dubia* was low, in contrast, *C. brasiliensis*' genetic diversity showed higher overall and local H and π, with highest values in BOI for COI and in ABR and Alcatrazes (ALC) for 28SrRNA. The three new species that have restricted distribution presented low values of H and π for COI, while 28SrRNA diversity indexes varied between species. *Chondrochelia trindadensis* **sp. nov.** presented low values of H and π, while high values were observed for *C. baronia* **sp. nov.** and *C. cacandocae* **sp. nov.** (Table 3).

The COI minimum spanning network (MSN) presented a clear geographical separation, with *C. brasiliensis* **comb. nov. located** in the middle of the network and localities of Arraial do Cabo (ARR), ALC and Trancoso (TRA) with exclusive haplotypes, whereas BOI, ABR and Cabo Frio (CF) shared haplotypes (Fig. 3). *Chondrochelia trindadensis* **sp. nov.** presented a single haplotype, closer to *C. caribensis*, while *C. baronia* **sp. nov.** is closer to *C. winfieldi* and *C. dubi*a, and showed a single exclusive haplotype (Fig. 3). *Chondrochelia dubia* had one main haplotype shared by Natal (NAT), Paracuru (PCR) and Praia do Forte (FOR), in NE mainland, and one shared by Soufrière (SOU) in the Caribbean and the equatorial oceanic island of FN (Fig. 3). The structure of the 28SrRNA MSN is similar, with geographical concordance, where *C. brasiliensis* **comb. nov**. had two haplotypes shared with all its localities, *C. trindadensis* **sp. nov.** also presented a single exclusive haplotype, *C. baronia* **sp. nov.** and *C. cacandocae* **sp. nov.** had five and three close haplotypes, respectively. For the species *C. dubia*, a single haplotype was found (Fig. 3).

For the next analyses, only *C. dubia* and *C. brasiliensis* **comb. nov.** were considered due to low sampling and restrict distribution of the remaining species. Two scenarios were tested on a hierarchical AMOVA (scenario 1: islands vs continent; scenario 2: Dominica vs Brazil), in which scenario 1 presented the highest Φ_{CT} and lowest Φ_{SC}, though Φ_{CT} values were not significant for both scenarios. In contrast, only one scenario was tested for *C. brasiliensis*, which separated the Bahia state from the southeast/southern coast, where both Φ_{CT} and Φ_{SC} presented low values.

Chondrochelia dubia presented a high and statistically significant overall F_{ST} of 0.97 for COI, and 0.00 for 28SrRNA, once all sequences were identical. For *C. brasiliensis* **comb. nov.**, F_{ST} values were statistically significant and moderate, with 0.54 for COI and 0.38 for 28SrRNA, respectively (Table 4).

Pairwise F_{ST} indicated greater differences between NE mainland (Brazil: NAT, FOR, PCR) and Caribbean (Dominica: SOU, PT) localities for *C. dubia* COI, while the pairwise difference among mainland Brazilian localities is very low (Fig. 4A). In contrast, the two Dominican localities, both in the Caribbean Sea, presented high differentiation (Fig. 4A). Historical migration between localities suggested lower migration rates to the Dominica, and higher migrants flow to the oceanic island of FN and NAT in the mainland (Fig. 4B). In the southeastern Brazil, no latitudinal pattern was found, and the greater difference was found between Arraial do Cabo (ARR) and remaining localities for COI, and between ARR with ABR, BOI and Trancoso (TRA), BOI with CF and IG, CF with TRA, and ABR with IG and CF (Fig. 4A). Apparently, there is no marked difference among continental islands and mainland, corroborated by the historical migration analyses, that showed high migration rates among all localities except ARR (Fig. 4B). Neither IBD nor IBE were observed for *C. brasiliensis* **comb. nov.**, while a positive correlation (Mantel r2=0.6231, p=0.039) was found with the range diurnal temperature for *C. dubia*.

Demographic history

The population events investigation did not find significant evidences of population expansion for most lineages, with only negative D for the *C. brasiliensis* **comb. nov.** lineage and CF population for COI ($P < 0.05$; Supplementary Material). The estimates of variation in population size over evolutionary time based on the Bayesian skyline plots suggest that population sizes of *C. dubia* and *C. brasiliensis* have remained constant over their recent evolutionary past (Supplementary Material).

Molecular dating of nodes showed large time intervals for speciation and bayesian phylogenetic tree (BI) was not completely congruent with ML tree (Fig. 5). Divergences in clades topology between BI and ML trees are mostly concerning *C. trindadensis* **sp. nov.**, *C. caribensis* and *Leptochelia* species, while relationships among other *Chondrochelia* spp. are consistent (Fig. 5). According to our analysis, the estimated divergence time for *C. trindadensis* **sp. nov.** is 12.88 Mya (95% HPD: 1.96–20.12), older than TR age of volcanism (Mohriak 2020). The other two clades of *Chondrochelia* spp. diverged around 14.95 Mya (95% HPD: 3.90–23.54), splitting *C. brasiliensis* around 9.10 Mya (95% HPD: 0.40–14.98), with intraspecific separation of southeastern and northeastern populations about 3.53 Mya (95% HPD: 0.40–5.33). The species *C. baronia* **sp. nov.** from RA and NAT, splitted from *C. dubia* around 6.26 Mya (95% HPD: 1.19–9.74), while *C. dubia* and *C. cacandocae* **sp. nov.** diverged around 3.47 Mya (95% HPD: 0.35–5.24, Fig. 5).

Present and paleodistribution models

The chosen variables based on factorial analysis were: distance to shore (biogeo5), concavity (biogeo7), sea surface salinity (SSS) of the saltiest month (biogeo10), annual range in SSS (biogeo11), sea surface temperature (SST) of the coldest month (biogeo14), and annual range in SST (biogeo 16, Supplementary Material). Additionally, we also included bathymetry in the modeling because of its biological importance for benthic macroalgae distribution, although it has not been retained in factorial analysis.

Distribution datasets were separated into *C. dubia* and *C. brasiliensis* **comb. nov**. for ENM analyses, while suitability maps were not modelled for *C. cacandocae* **sp. nov**., *C. trindadensis* **sp. nov.** and *C. baronia* **sp. nov.** because of their restricted distribution.

Ecological Niche Modeling indicated that *C. dubia* is currently potentially distributed across the Lesser Antilles in the Caribbean, north and northeastern coast of Brazil, with decreasing suitability on Maranhão (MA) and Alagoas (AL) states. Praia do Forte (FOR), the closer sampling site to *C. dubia*'s type locality, presented a very low suitability (Fig. 6). For *C. brasiliensis* **comb. nov.**, the potential distribution is broader than for *C. dubia*, with higher suitability in southern Bahia (BA) and Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP) and Santa Catarina (SC) states (Fig. 6). Paleodistribution models suggested a considerable geographical expansion from the LGM to the present time for both species, with a refuge in southeastern Brazil, with higher suitability in the RJ region for *C. brasiliensis* **comb. nov.**, while potential distribution of *C. dubia* was restrict to a thin northeastearn continental margin (Fig. 6).

DISCUSSION

This is the first study to investigate the *Chondrochelia dubia* complex on a broad range including its type locality, using integrative approaches to ellucidate its distribution, molecular ecology and evolution. Our findings suggest that the species *C. dubia*, considered cosmopolitan until now, may indeed represent a species complex comprised by several species with restricted distributions. This misidentifications might be associated with the simple and convergent morphology observed in leptocheliid tanaidaceans (Blazewicz-Paszkowycz et al. 2012) and further integrative studies might unpuzzle the *Chondrochelia dubia* species complex.

Chondrochelia dubia s.s. is the most widespread species from this study and occurs on three ecoregions in the Tropical Atlantic (Spalding 2007): Eastern Caribbean, Fernando de Noronha and Atol das Rocas, and Northeastern Brazil. *Chondrochelia dubi*a was described from Salvador by Krøyer, northeast Brazil and therefore, based on its geographic distribution and morphology, we recognize the species from Brazil's northeast mainland, the oceanic island of FN and Dominica (Fig. 1B, 3). According to both ML and BI trees, relationships among *C. dubia* + *C. baronia* **sp. nov.** + *C. cacandocae* **sp. nov.** are consistent (Figs. 2 and 5), with clade divergence around 11 Mya (Fig. 5).

Chondrochelia brasiliensis **comb. nov.** is the second species with larger distribution, corresponding to two ecoregions in Tropical Southwestern Atlantic and Temperate South America provinces: Eastern Brazil and Southeastern Brazil, respectively. *Chondrochelia brasiliensis* **comb. nov.** was originally described by Dana (1849) as *Tanais brasiliensis* for Rio de Janeiro, southeastern Brazil, and types were lost. According to Gutu (2016): "the status of this species is in dispute, and it has being included in different genera and families. Because of this, I have adopted, without any scientifical basis, the name most often for records in Brazilian waters". We herein transferred the species for the genus *Chondrochelia* and also adopted the name of *C. brasiliensis* **comb. nov.** for the species found in Rio de Janeiro region, with a detailed redescription of the material. Another species, *Intermedichelia gracilis* Gutu, 1996, also reported for Rio de Janeiro state, was not found in our samplings. *Chondrochelia brasiliensis* represent the second main clade within the southwestern Atlantic, with closer relationships with *C. savignyi* from Spain, *C. winfieldi* from Mexico and *C.* cf. *dubia* from France, diverging around 9.1 Mya (Fig. 5).

The other three analysed species presented restricted distributions: *C. cacandocae* **sp. nov.** from UBA, *C. baronia* **sp. nov.** from RA and *C. trindadensis* **sp. nov.** from TR. *Chondrochelia cacandocae* **sp. nov**., have a sympatric distribution with *C. brasiliensis* **comb. nov.** in the sourtheastern Brazil. According to species' time estimatives, *C. cacandocae*'s clade split from *C. brasiliensis'* clade over 10 Mya (Fig. 5), with a more recent speciation around 3.5 Mya from *C. dubia* (Fig. 5). The latter two species are found in Brazilian oceanic islands, and their genetic structure might reflect the lack of connectivity by surface currents. Moreover, abiotic factors such as salinity can possibly shape the species distribution in the oceanic islands, and therefore, the presence of *C. baronia* **sp. nov.** and *C. trindadensis* **sp. nov.** on the islands without permanent freshwater sources could be associated with long term salinity tolerance of ancient lineages. Salinity was not found as a driver of isolation within species, but it could have different effects on *Chondrochelia* species. *Chondrochelia dubia* was found in FN in very low abundance, only in Sueste beach, a unique place that harbors the only oceanic mangrove system in the South Atlantic (Garla et al. 2009; Sazima et al. 2009). Hence, the occurrence of *C. dubia* in FN might be associated with freshwater, as previously observed for other peracarid species in Sueste beach (Iwasa-Arai et al. 2020).

Besides the oceanic island of RA, *C. baronia* **sp. nov.** was also found in NAT, the closest locality in the mainland to RA, and the two clades of *C. baronia* **sp. nov.** diverged around 5.4 Mya. *Chondrochelia trindadensis* **sp. nov.**, at last, has the oldest age estimative for the western Atlantic, with over 12 Mya, whereas the species' age is older than island age of volcanism, around 3,9-2,8 Mya. According to Heads (2011), using the islands' age to date the endemic taxa there will often give unreliable results with unpredictable and possibly massive errors, therefore, we chose not to use islands ages to calibrate phylogenies due to the lack of knowledge of species total distribution, such as its presence on other neighbour islands in the mid-Atlantic ocean and seamounts.

On a more recent time perspective, while estimates of variation in population size over evolutionary time suggest that population sizes of *C. dubia* and *C. brasiliensis* **comb. nov.** have remained constant over their recent evolutionary past, paleodistribution models suggested a considerable geographical expansion since the LGM, where species were restricted to the submerged continental shelf (Fig. 6). The only exception is the *C. brasiliensis*' population of Cabo Frio (CF), whose genetic demographic analyses suggested to be in expansion (D = -2.231, p = 0.000), concordant with paleodistribution models that indicated a refuge with higher suitability in the same area. Thus, Cabo Frio might indeed habour a relict population in the LGM that later recolonized the south and eastern coasts.

When comparing with other phylogeographic studies of marine arthropods without larval dispersion, we observed that cryptic species were found across the mainland coast for *C. dubia* complex (present study), *Ampithoe marcuzzii* complex (Iwasa-Arai et al. *in prep*), *Excirolana braziliensis* Richardson, 1912 (Hurtado et al. 2016; Mattos et al. 2019) and *Rhombognathus levigatoides* Pepato & da Rocha, 2007 (Pepato et al. 2019). However, distributions breaks change for each species (Fig. 7). Apparently, *C. brasiliensis*' distribution goes from southern Brazil to Bahia, with a barrier between latitudes 12-13°S, where the species is replaced by *C. dubia*. This is two degrees south from the São Francisco river mouth, that separates the marine ecoregions (MEOWs) of northwestern and eastern Brazil (Spalding et al. 2007), and it is concordant with the Todos os Santos Bay, where the Paraguaçu river mouth disembogues. For the marine mite *R. levigatoides* complex, also found in macroalgae, a species break is found at the Abrolhos Plateau (Pepato et al. 2019). In this study, we found population genetic structure for the localities in the eastern Brazil, including Abrolhos Archipelago (ABR+BOI+TRA), separated from the southwestern Brazil, but without evidence of diversification (Fig. 3). For the sandy beach isopod *E. braziliensis* complex, distribution break of mainland species are southernmost and in agreement with Cabo Frio upwelling system (Hurtado et al. 2016; Mattos et al. 2019). *Excirolana braziliensis* also showed a connectivity between FN and NE mainland, showing that despite the lack of dispersive larval stages, peracarid crustaceans can maintain gene flow through other mechanisms such as rafting (Thiel 2003). Lastly, amphipods from the *A. marcuzzii* complex had a different boundary, with species isolation into oceanic islands + Caribbean separated from the South America mainland (Fig. 7), but with mainland species separation into northeast and southeast clades with a break on the Vitória-Trindade seamount chain (Fig. 7).

Nonetheless, the *Chondrochelia* species studied herein had most of their distributions in agreement with MEOWs (Fig. 1B; Spalding et al. 2007), with a few species being present in more than one ecoregion, while other ecoregions presented more than one species. The Caribbean population of *C. dubia s.s.* is one of the incongruences on distribution, where although several endemic species are found in the region, *C. dubia* is abundant in the Lesser Antilles, showing the connectivity across the Amazon-Orinoco river mouth, as observed for the swimming crab *Callinectes danae* Smith, 1869 as result of population structure mediated by salinity tolerance (Peres & Mantelatto 2020).

Chondrochelia phylogeography

Regarding the comparative phylogeogeography of the most widespread species of *Chondrochelia* in the western Atlantic, *C. dubia* showed genetic connectivity among the Brazilian northeastern coast, with shared haplotypes and low pairwise F_{ST} values, while populations from the Lesser Antilles appear to have a stronger genetic structure, even though localities are very close (~30 km). Curiously, specimens from the Brazilian oceanic island of Fernando de Noronha are genetically identical to the population from Soufrière (SOU), Dominica, despite the distance over 3500 km. The sally lightfoot crab Grapsus grapsus (Linnaeus, 1758), distributed in the Caribbean and southwestern Atlantic oceanis islands also shared this connectivity, where individuals from FN shared haplotypes with the Caribbean localities of Belize and San Andrés (Freire et al. 2021). According to Freire et al. (2021), particle trajectories that simulated larval dispersion suggested that the crab larvae from the Brazilian equatorial islands could reach the Lesser Antilles by a dispersion route out of the Amazon plume, therefore, if *C. dubia* is prone to be dispersed by rafting, surface currents could explain the connectivity between the

Caribbean and the oceanic island of FN. And in spite of the differences into clades “islands” and “continent” in the mitochondrial COI, nuclear 28SrRNA data showed a conserved pattern, with all individuals sharing the same haplotype. The same results were observed for sandy beach crustaceans with occurrence in the mainland and FN, where the both the isopod *E. braziliensis* and the ghost crab *Ocypode quadrata* (Fabricius, 1787) presented signs of connectivity between FN and the continental coast (Mattos et al. 2019).

For *Chondrochelia brasiliensis* **comb. nov.**, the continental islands of Alcatrazes (ALC) in the southeastern coast, and Abrolhos (ABR) in the eastern coast, showed different patterns of isolation. Alcatrazes archipelago is about 35 km from the mainland, and presented unique haplotypes and moderate pairwise structuring . In turn, ABR, which is twice farther from the coast, shared haplotypes with BOI, an estuarine island in the mainland. The localities of CF and ARR, in Rio de Janeiro state, also drew our attention due to their geographic proximity besides their genetic difference. CF and ARR are only 10 km distant, but CF showed high genetic diversities and connectivity with Bahia’s populations of ABR and BOI, while ARR presented high population structure with a unique haplotype for COI and strong differentiation. Although this area is subjected to upwelling events that could isolate the population, we believe the specimens from CF would also behave equally, therefore, ARR could represent a different deme with distinct reproductive periods, or other biotic traits not analysed herein could shape the population structure of ARR. For 28SrRNA, an more conservative pattern of population structure into eastern and southern populations is seen, separating ABR+TRA+BOI from CF+ARR+ALC+BOM (Figs. 3 and 4).

Final considerations

To conclude, different species among the *C. dubia* complex presented different genetic diversities and population structure, showing that evolutive mechanisms might had worked differently amidst species. This is only the first piece to unveil the *C. dubia* complex, and further studies on the populations of other ocean basins are needed to unravel its whole evolution and biogeography. By now, we can hypothesize that there is one species from *C. dubia* complex for each ecoregion where *C. dubia s.l.* is currently known.

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Figures and Tables

Figures

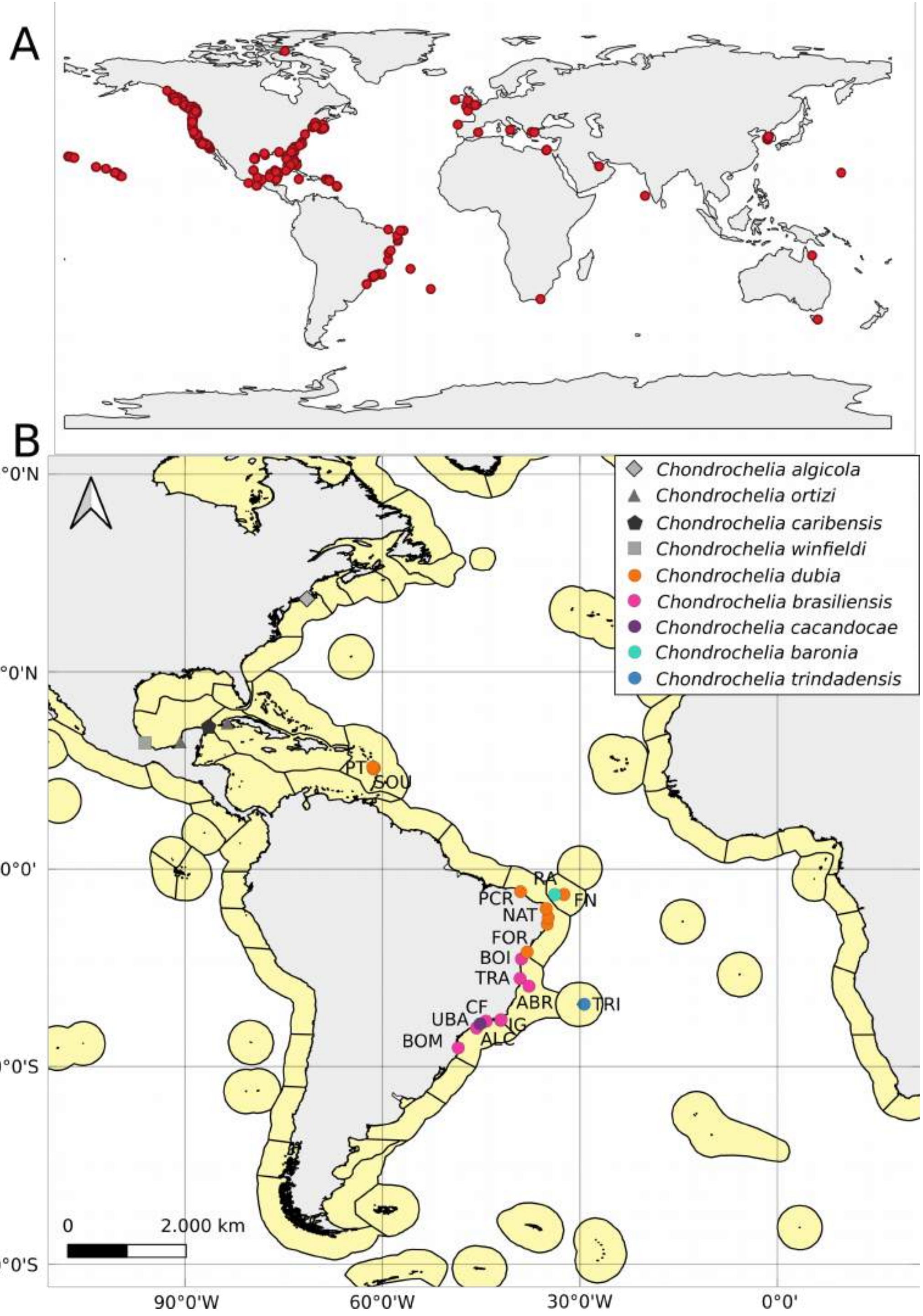


Figure 1. A. Current known world distribution of *Chondrochelia dubia s.l.* from literature, GBIF and OBIS. **B.** Occurrence of *Chodrochelia* spp. in the Western Atlantic Ocean. Light orange shape corresponds to MEOWs (Spalding et al. 2007). Acronyms according to the current sampling localities: ABR, Abrolhos Archipelago; ALC, Alcatrazes Archipelago; ARR, Arraial do Cabo; BOI, Boipeba Island; BOM, Bombinhas; BRT, Barretão pool, Rocas Atoll; CF, Cabo Frio; FN, Fernando de Noronha; FOR, Forte Beach; IG, Ilha Grande; NAT, Natal; PCR, Paracuru; PT, Portsmouth; SOU, Soufrière; SSV, San Sauveur; TRA, Trancoso; TRI, Trindade Island; UBA, Ubatuba.

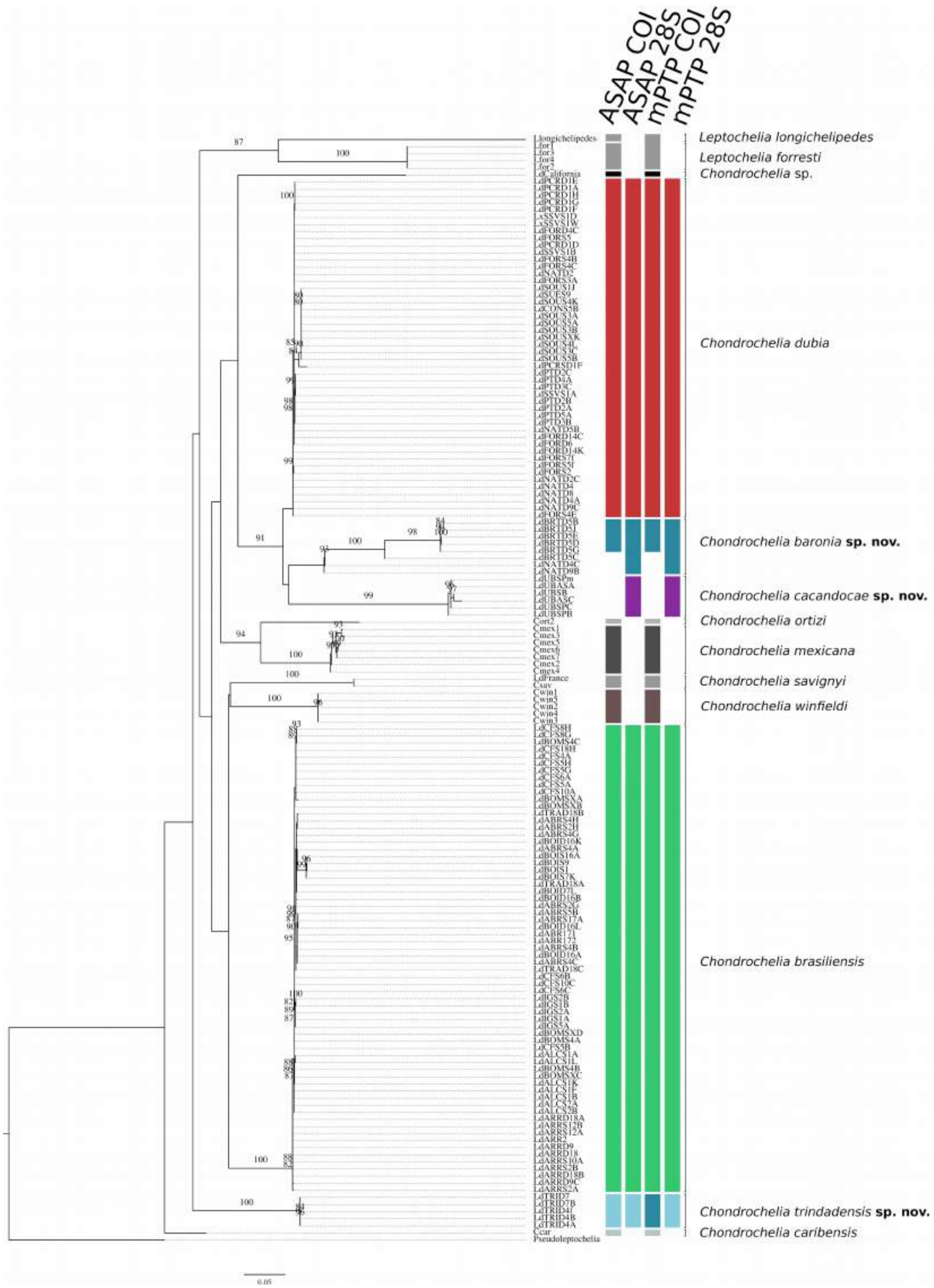


Figure 2. Maximum likelihood tree of *Chondrochelia* spp. Bootstrap values over 80% are shown on branches. Color bars correspond to species demilitation analyses of ASAP and mPTP for COI and 28SrRNA. ABR, Abrolhos Archipelago; ALC, Alcatrazes Archipelago; ARR, Arraial do Cabo; BOI, Boipeba Island; BOM, Bombinhas; BRT, Barretão pool, Rocas Atoll; CF, Cabo Frio; FN, Fernando de Noronha; FOR, Forte Beach; IG, Ilha Grande; NAT, Natal; PCR, Paracuru; PT, Portsmouth; SOU, Soufrière; SSV, San Sauveur; TRA, Trancoso; TRI, Trindade Island; UBA, Ubatuba.

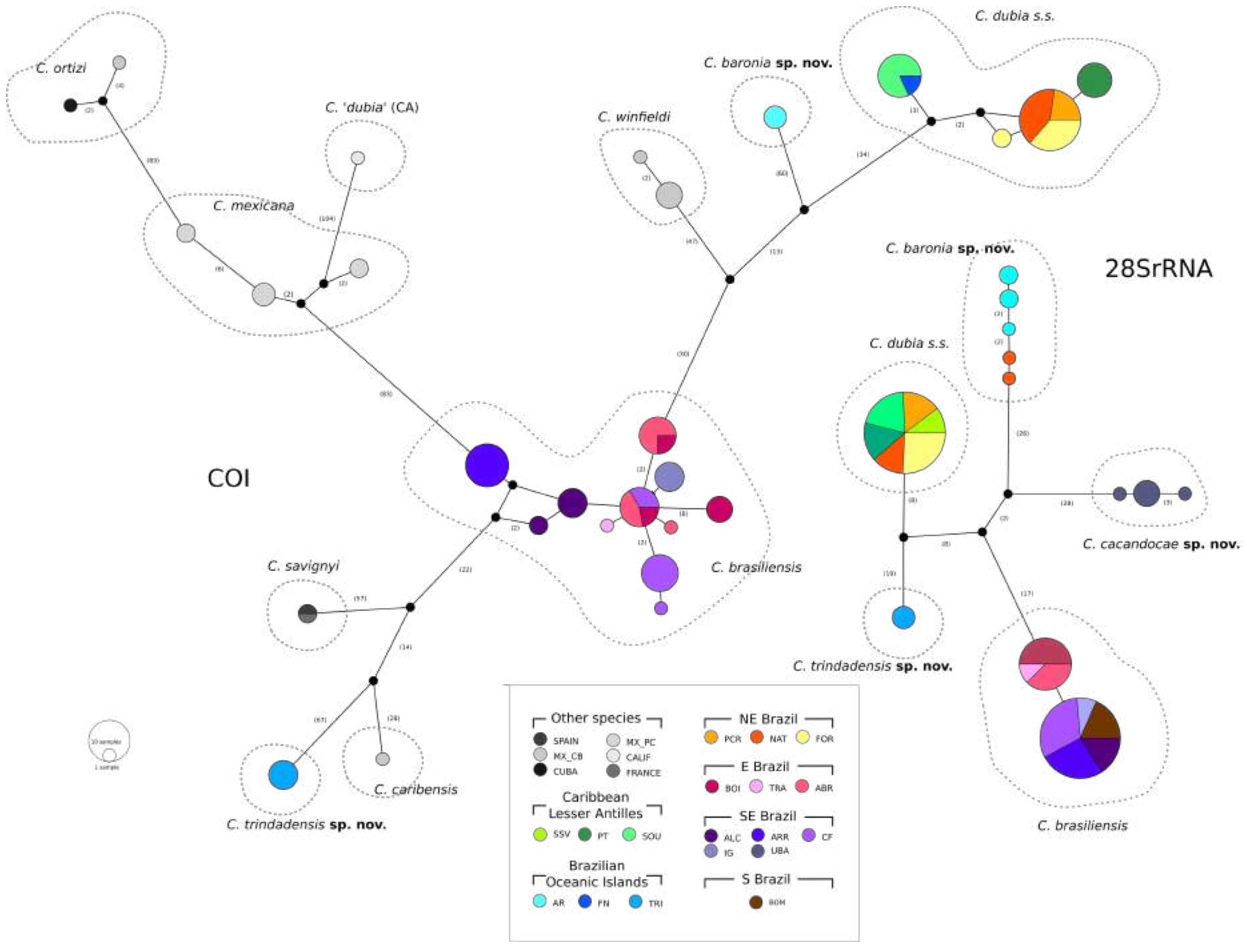


Figure 3. Minimum spanning network of COI to the left, and 28SrRNA to the right. Each node represents a haplotype, its size corresponds to the haplotype frequency and its colours indicate the locality. Black nodes represent inferred ancestral nodes. Numbers on branches represent mutational steps.

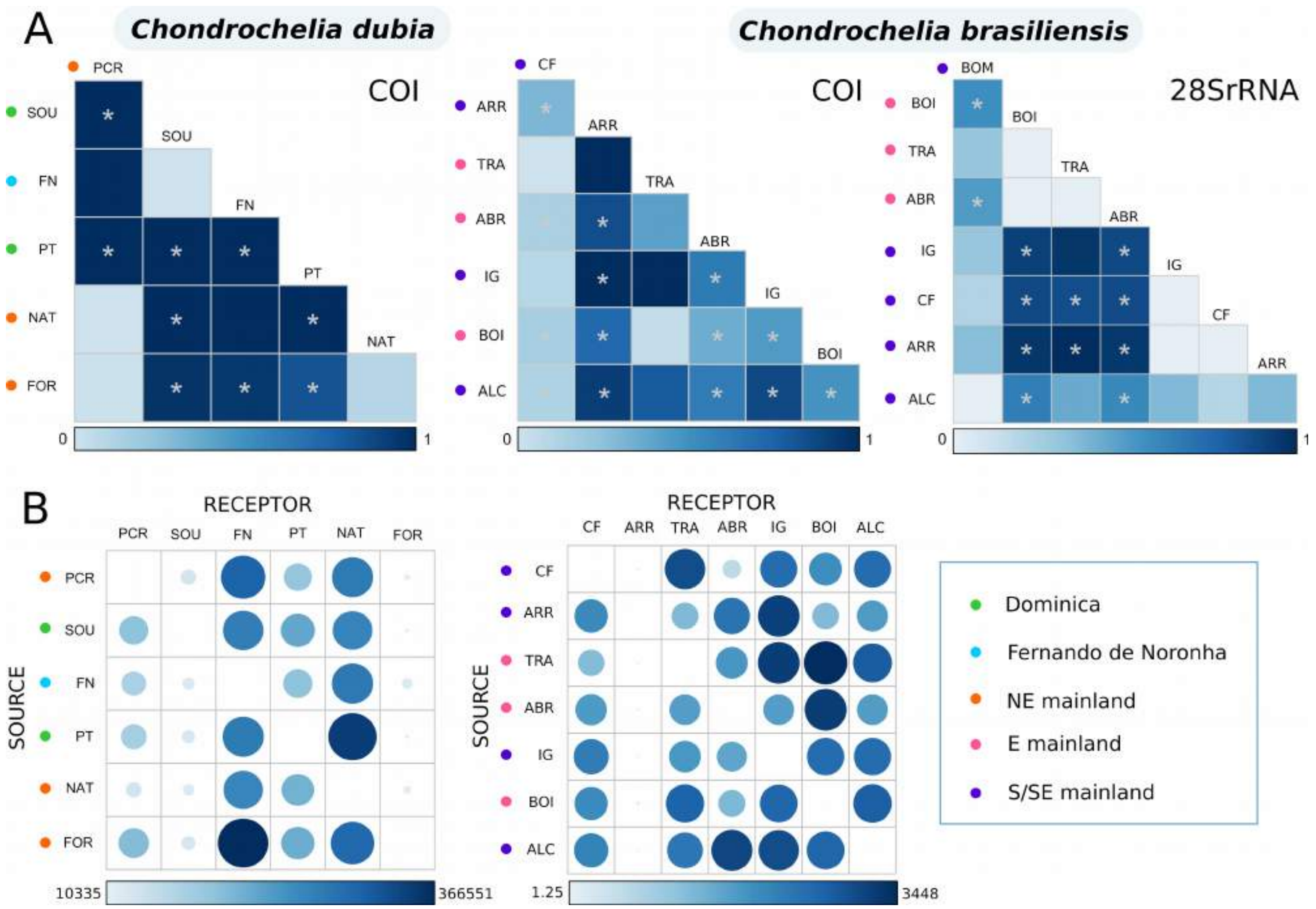


Figure 4. A. Heatmaps of the pairwise F_{ST} for COI and 28SrRNA for *C. dubia* and *C. brasiliensis*. Colour coding illustrates the observed F_{ST} value. Asterisks represent statistically significant values ($P < 0.05$). **B.** Historical migration rates for COI. Circle sizes and colours represent the rates of migrants from the source locality (rows) toward the receiver locality (columns). Map indicate the most likely migration routes according to COI data.

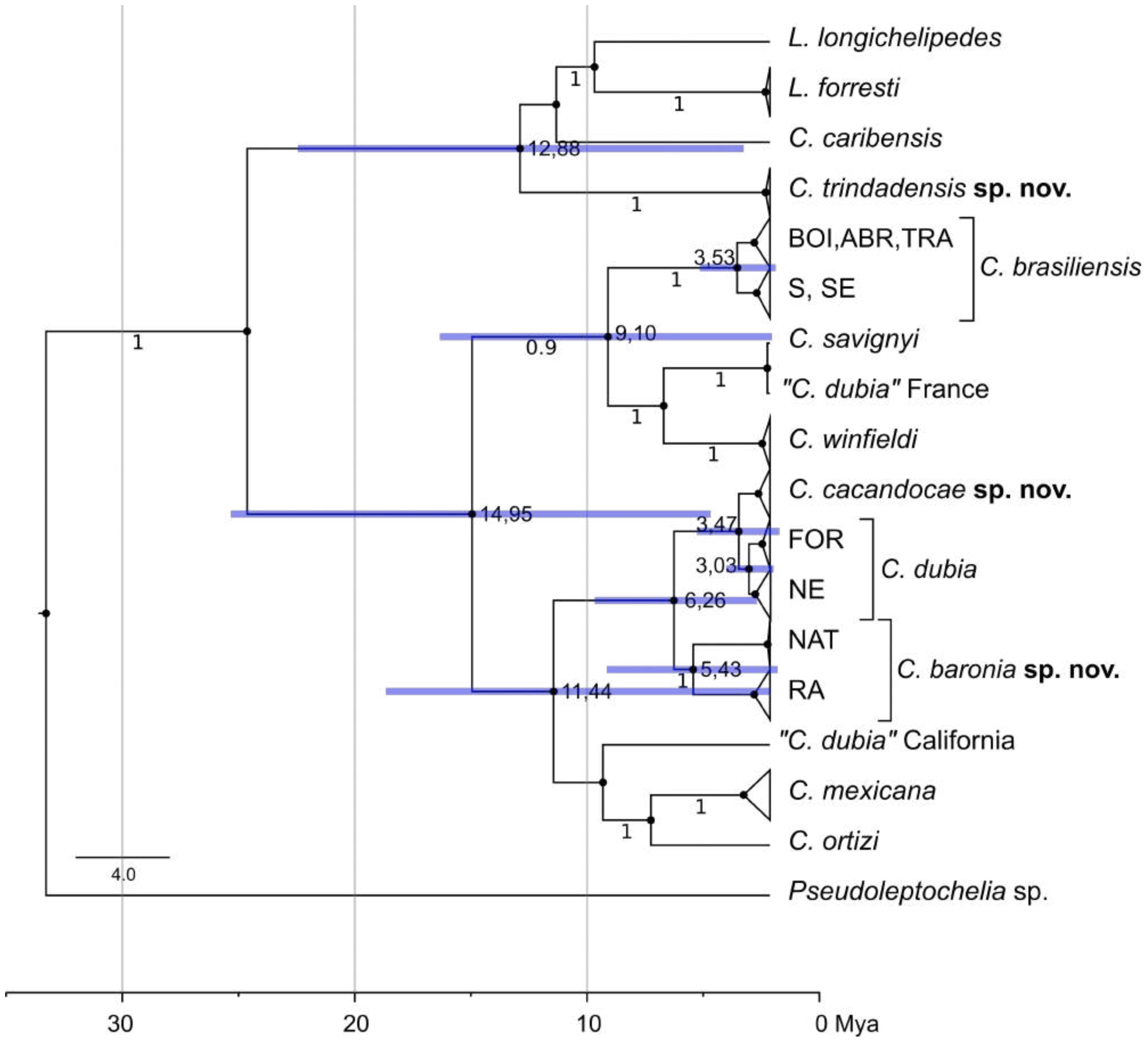


Figure 5. Bayesian calibrated tree of *Chondrochelia* spp. using concatenated COI/28SrRNA. Numbers below branches represent posterior probability values over 0.9. Node bars represent the 95% HPD interval. Time divergence bar is in a Mya scale.

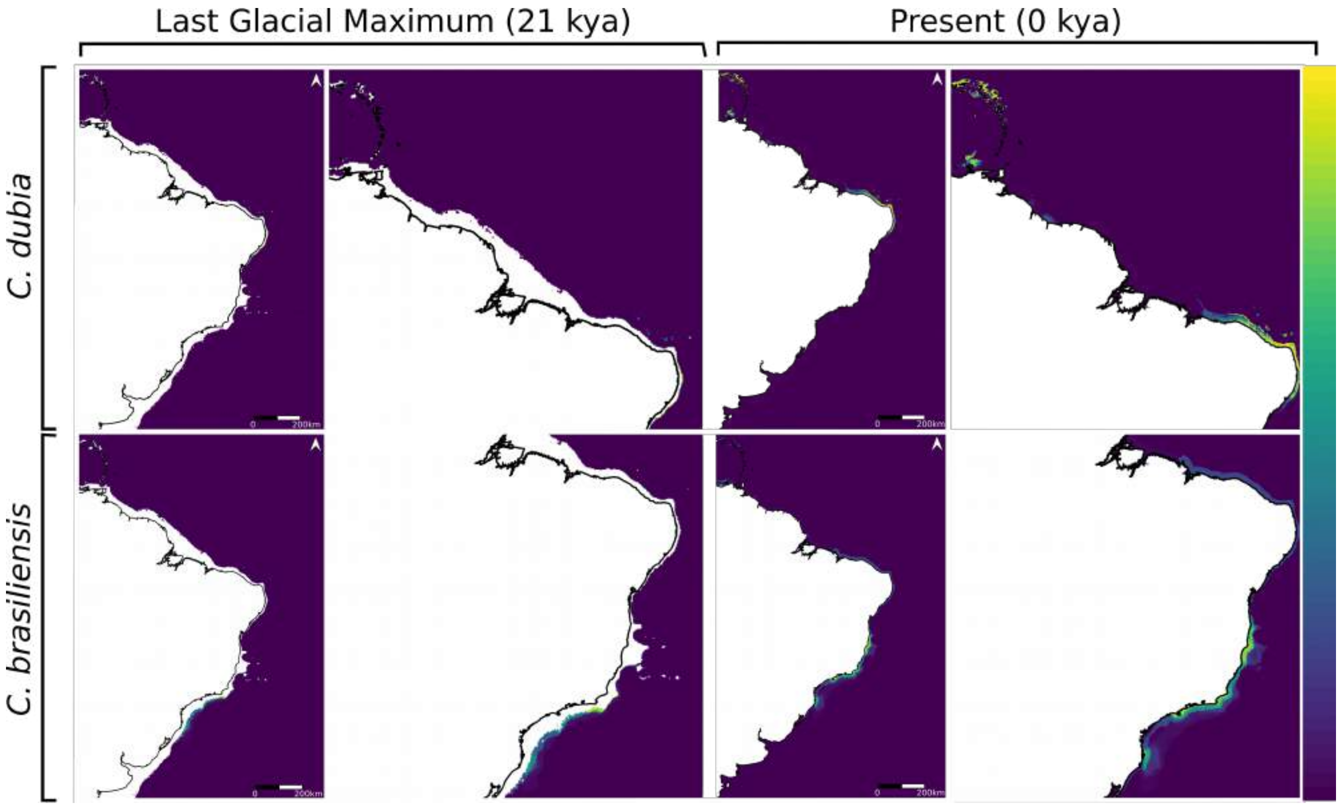


Figure 6. Modelled distributions of *C. dubia* and *C. brasiliensis* for the Last Glacial Maximum (21 kya) and present (0 kya) scenarios. The suitability value predicts how adequate the environment is for the species occurrence.

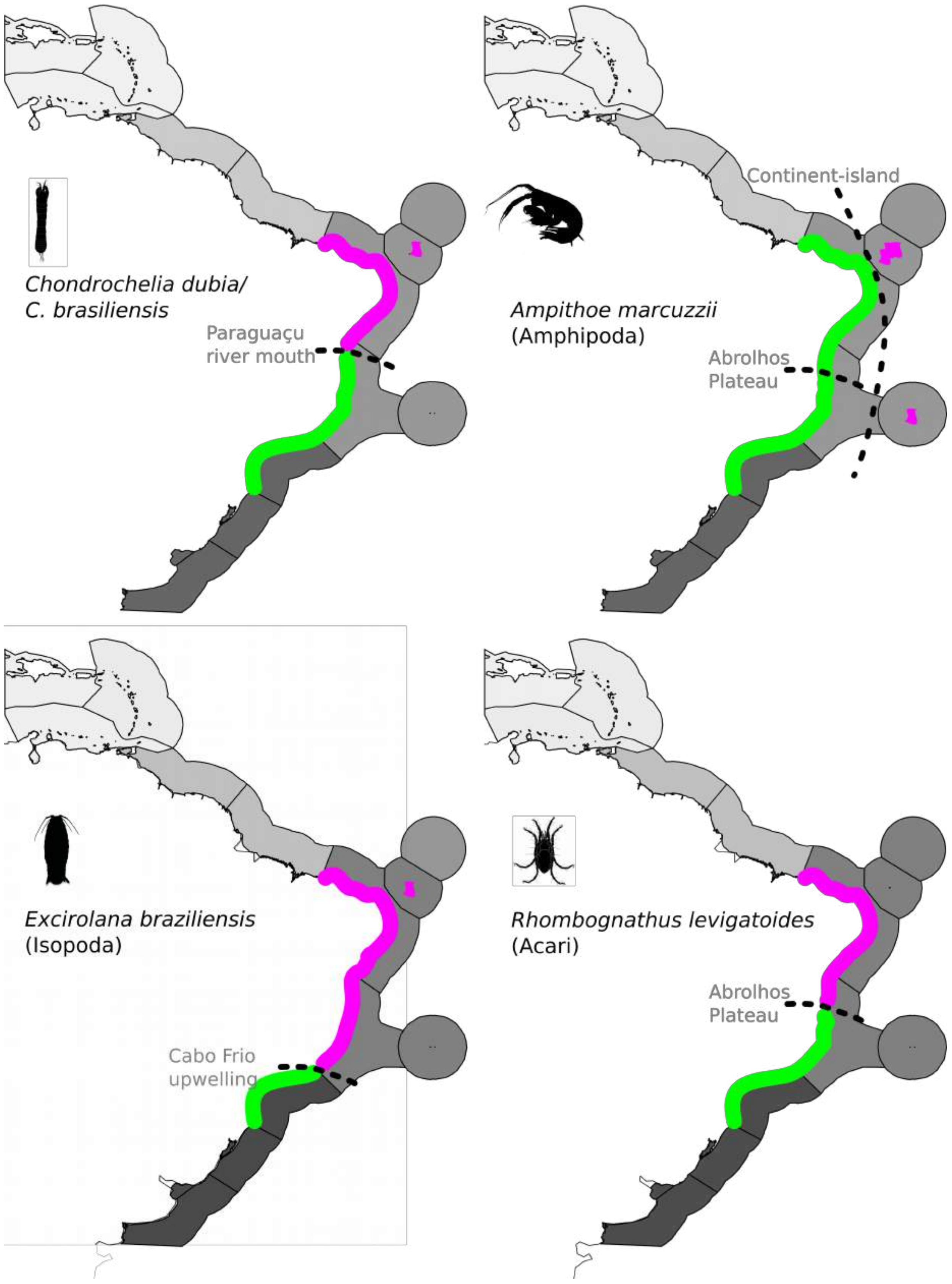


Figure 7. Distribution of marine arthropods species complex along the Brazilian mainland according to Iwasa-Arai et al. (*in prep*) for *Ampithoe marcuzzii*, Hurtado et al. (2016) and Mattos et al. (2019) for *Excirolana braziliensis*, and Pepato et al. (2019) for *Rhombognathus levigatoides*. Dashed lines correspond to species' break.

Tables

Table 1. Sampling locations of *Chondrochelia* spp.

Date	Acronym	Locality	Lat	Long	Depth	Macroalgae
Jul/2019	PT	Secret Beach, Portsmouth, Dominica	15.546467	-61.473314	1m	*Sargassum* sp.
Jul/2019	SSV	San Sauveur, Dominica	15.403329	-61.250248	1m	*Sargassum* sp.
Jul/2019	SOU	Soufrière, Dominica	15.228475	-61.36082	1m	*Sargassum* sp.
Nov/2021	PCR	Praia da Pedra Rachada, Paracuru, CE	-3.39661	-39.01099	1m	*Sargassum* sp.
Nov/2018	NAT	Praia de Pirambúzios, Natal, RN	-6.006086	-35.105394	5m	*Dictyota* sp.
Dec/2019	RA	Atol das Rocas, RN	-3.856736	-33.801844	1m	*Sargassum* sp. and *Dictyota* sp.
Nov/2018	FN	Praia do Sueste, Fernando de Noronha, PE	-3.868175	-32.421794	1m	*Sargassum* sp. and *Dictyota* sp.
Dec/2018	FOR	Praia do Forte, Mata de São João, BA	-12.580166	-38.000772	1m	*Sargassum* sp. and *Dictyota* sp.
Jan/2019	BOI	Praia de Moreré, Ilha de Boipeba, BA	-13.628983	-38.88702	1m	*Sargassum* sp. and *Dictyota* sp.
Dec/2018	TRA	Praia dos Coqueiros, Trancoso, BA	-16.596985	-39.087873	1m	*Sargassum* sp. and *Dictyota* sp.
Jan/2019	ABR	Ilha Redonda, Abrolhos, BA	-17.96835	-38.709264	3m	*Sargassum* sp. and *Dictyota* sp.
Feb/2019	TRI	Ilha da Trindade, ES	-20.50502	-29.34430	5m	*Dictyota* sp.
Jan/2021	CF	Praia do Peró, Cabo Frio, RJ	-22.86632	-41.97831	1m	*Sargassum* sp.
Dec/2018	ARR	Praia das Tartarugas, Arraial do Cabo, RJ	-22.946494	-42.025671	2m	*Sargassum* sp. and *Dictyota* sp.
Jan/2021	IG	Ilha Grande, RJ	-23.10015	-44.25154	2m	*Sargassum* sp.
Dec/2016	UBA	Praia Domingas Dias, Ubatuba, SP	-23.49694	-45.14718	1m	*Sargassum* sp.
Mar/2020	ALC	Arquipélago de Alcatrazes, SP	-24.106207	-45.697840	5m	*Sargassum* sp.
Nov/2019	BOM	Praia da Sepultura, Bombinhas, SC	-27.141232	-48.478229	1m	*Sargassum* sp.

Table 2. Comparative data of *Chondrochelia* spp. and other genera of Leptocheliidae from GenBank and BOLD.

Species	**Genbank access no.**	**BOLD access no.**	**ID**	**Locality**
Chondrochelia caribensis			Ccar	Mexico, Quintana Roo
Chondrochelia winfieldi			Cwin1	Mexico, Veracruz
Chondrochelia winfieldi			Cwin2	Mexico, Veracruz
Chondrochelia winfieldi		TANAI040-15	Cwin3	Mexico, Veracruz
Chondrochelia winfieldi		TANAI270-15	Cwin4	Mexico, Veracruz
Chondrochelia winfieldi		TANAI271-15	Cwin5	Mexico, Veracruz
Chondrochelia ortizi		TANAI272-15	Cort1	Mexico, Campeche
Chondrochelia ortizi		TANAI273-15	Cort2	Cuba, Pinar del Rio
Chondrochelia mexicana		TANAI274-15	Cmex1	Mexico, Oaxaca
Chondrochelia mexicana		TANAI019-15	Cmex2	Mexico, Oaxaca
Chondrochelia mexicana		TANAI089-15	Cmex3	Mexico, Oaxaca
Chondrochelia mexicana		TANAI223-15	Cmex4	Mexico, Oaxaca
Chondrochelia mexicana		TANAI238-15	Cmex5	Mexico, Guerrero
Chondrochelia mexicana		TANAI241-15	Cmex6	Mexico, Guerrero
Chondrochelia mexicana		TANAI243-15	Cmex7	Mexico, Guerrero
Leptochelia forresti	KP254788		Lfor1	USA, Florida, Indian River Lagoon
Leptochelia forresti	MH826261		Lfor2	USA, Florida, Fort Pierce - Indian River Lagoon
Leptochelia forresti	MH826262		Lfor3	USA, Florida, Fort Pierce - Indian River Lagoon
Leptochelia forresti	MH826263		Lfor4	USA, Florida, Fort Pierce - Indian River Lagoon
Chondrochelia savignyi		BCASB002-16	Csav	Spain, North Spain

Table 3. Genetic variability in *Chondrochelia dubia s.s., C. brasiliensis s.s., C. trindadensis* **sp. nov.**, *C. baronia* **sp. nov.** and *C. ubatubensis* **sp. nov.** Number of specimens (N), number of polymorphic sites (S), number of observed haplotypes (K), haplotype diversity (H), nucleotide diversity (π), and standard deviation (SD). * = continental island; ** = oceanic island.

	COI					28SrRNA				
Locality	N	S	K	H (SD)	π (SD)	N	S	K	H (SD)	π (SD)
Chondrochelia dubia	42	7	4	0.642 (0.053)	0.005 (0.001)	39	0	1	0.000 (0.000)	0.000 (0.000)
Paracuru, CE, Brazil (PCR)	5	0	1	0.000 (0.000)	0.000 (0.000)	6	0	1	0.000 (0.000)	0.000 (0.000)
Natal, RN, Brazil (NAT)	9	0	1	0.000 (0.000)	0.000 (0.000)	7	0	1	0.000 (0.000)	0.000 (0.000)
Praia do Forte, BA, Brazil (FOR)	10	1	2	0.356 (0.159)	0.001 (0.000)	10	0	1	0.000 (0.000)	0.000 (0.000)
Fernando de Noronha, PE, Brazil (FN)**	2	0	1	0.000 (0.000)	0.000 (0.000)	-	-	-	-	-
Soufrière, Dominica (SOU)	9	0	1	0.000 (0.000)	0.000 (0.000)	8	0	1	0.000 (0.000)	0.000 (0.000)
Portsmouth, Dominica (PT)	7	0	1	0.000 (0.000)	0.000 (0.000)	6	0	1	0.000 (0.000)	0.000 (0.000)
San Sauveur, Dominica (SSV)	-	-	-	-	-	4	0	1	0.000 (0.000)	0.000 (0.000)
Chondrochelia brasiliensis	55	102	13	0.893 (0.017)	0.012 (0.006)	48	3	5	0.614 (0.065)	0.001 (0.000)
Cabo Frio, RJ, Brazil (CF)	13	92	5	0.692 (0.119)	0.028(0.021)	12	1	2	0.303 (0.147)	0.001 (0.000)
Arraial do Cabo, RJ, Brazil (ARR)	11	0	1	0.000 (0.000)	0.000 (0.000)	10	1	2	0.200 (0.154)	0.000 (0.000)
Ilha Grande, RJ, Brazil (IG)*	5	0	1	0.000 (0.000)	0.000 (0.000)	3	0	1	0.000 (0.000)	0.000 (0.000)
Abrolhos Archipelago, BA, Brazil (ABR)*	11	3	3	0.618 (0.104)	0.002 (0.000)	6	1	2	0.600 (0.600)	0.001 (0.000)
Boipeba, BA, Brazil (BOI)*	8	8	3	0.714 (0.123)	0.008 (0.001)	8	1	2	0.536 (0.123)	0.001 (0.000)
Alcatrazes Archipelago, SP, Brazil (ALC)*	7	1	2	0.476 (0.171)	0.001 (0.000)	6	1	2	0.600 (0.129)	0.001 (0.000)
Bombinhas, SC, Brazil (BOM)	-	-	-	-	-	7	2	3	0.714 (0.127)	0.001 (0.000)
Chondrochelia trindadensis **sp. nov.**	5	0	1	0.000 (0.000)	0.000 (0.000)	3	0	1	0.000 (0.000)	0.000 (0.000)
Trindade Island, ES, Brazil (TRI)**	5	0	1	0.000 (0.000)	0.000 (0.000)	3	0	1	0.000 (0.000)	0.000 (0.000)
Chondrochelia baronia **sp. nov.**	3	0	1	0.000 (0.000)	0.000 (0.000)	7	9	5	0.905 (0.905)	0.905(0.002)
Rocas Atoll, RN, Brazil (RA)**	3	0	1	0.000 (0.000)	0.000 (0.000)	5	5	3	0.800 (0.164)	0.003 (0.001)
Natal, RN, Brazil (NAT)	-	-	-	-	-	2	1	2	1.000 (0.500)	0.002 (0.002)
Chondrochelia ubatubensis **sp. nov.**	-	-	-	-	-	6	5	3	0.800 (0.172)	0.003 (0.001)
Ubatuba, SP, Brazil (UBA)	-	-	-	-	-	6	5	3	0.800 (0.172)	0.003 (0.001)

Table 3. Analysis of molecular variance (AMOVA) results from COI and 28SrRNA markers.

		Among groups					**Among populations within groups**					**Within populations**				
		%	**d.f.**	**Variance components**	F_{CT}	*p*	**%**	**d.f.**	**Variance components**	F_{SC}	*p*	**%**	**d.f.**	**Variance components**	F_{ST}	*p*
C. dubia																
ISLANDS (SOU+PT+FN)	CONTINENT (PCR+NAT+FOR)	37.72	1	0.72	0.38	0.21	59.97	4	1.16	0.96	0.00	2.31	36	0.04	0.98	0.00
CARIBBEAN (SOU+PT)	BRAZIL (FN+PCR+NAT+FOR)	10.13	1	0.17	0.10	0.20	87.27	4	1.49	0.97	0.00	2.60	36	0.04	0.97	0.00
C. brasiliensis																
SE (ARR+CF+IG+ALC)	BA (BOI+TRA+ABR)	4.51	1	0.16	0.05	0.22	30.69	5	1.09	0.32	0.00	64.80	48	2.29	0.35	0.02

Supplementary Material

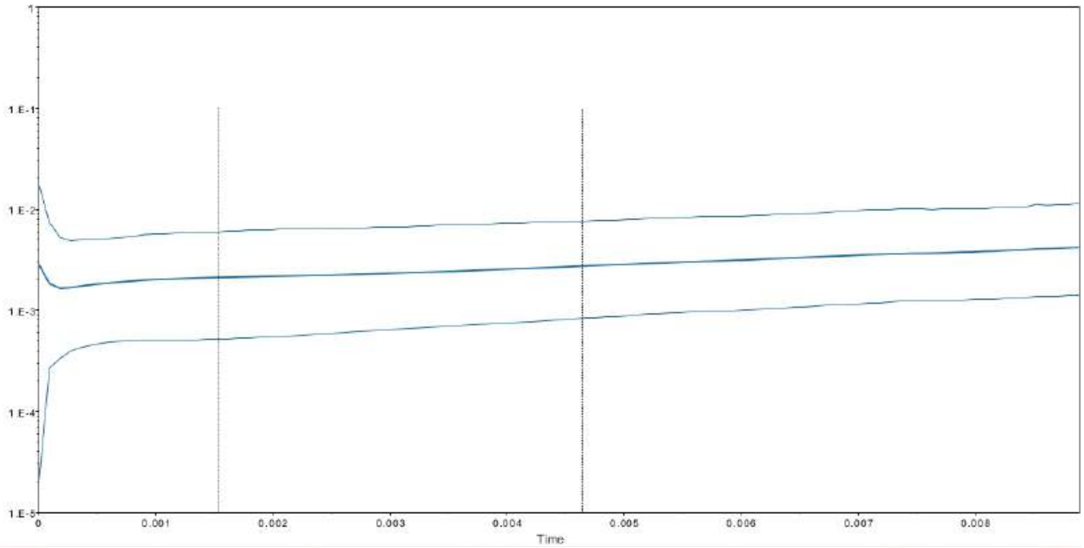
S1. List of environmental variables tested for IBE.

Bio-Oracle Variables	WorlClim variables
BO2_dissoxmax_bdmin	Annual Mean Temperature
BO2_dissoxltmax_bdmin	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BO2_dissoxrange_bdmin	Isothermality (BIO2/BIO7) (×100)
BO_chlomax	Temperature Seasonality (standard deviation ×100)
BO2_dissoxmean_bdmin	Max Temperature of Warmest Month
BO_chlomean	Min Temperature of Coldest Month
BO2_dissoxltmin_bdmin	Temperature Annual Range (BIO5-BIO6)
BO_chlorange	Mean Temperature of Wettest Quarter
BO2_dissoxmin_bdmin	Mean Temperature of Driest Quarter
BO_chlomin	Mean Temperature of Warmest Quarter
BO2_carbonphytomax_bdmin	Mean Temperature of Coldest Quarter
BO_ph	Annual Precipitation
BO2_carbonphytorange_bdmin	Precipitation of Wettest Month
BO2_temprange_bdmin	Precipitation of Driest Month
BO2_temprange_ss	Precipitation Seasonality (Coefficient of Variation)
BO_sstrange	Precipitation of Wettest Quarter
BO2_carbonphytoltmax_bdmin	Precipitation of Driest Quarter
BO2_carbonphytomean_bdmin	Precipitation of Warmest Quarter
BO2_chlomax_bdmin	Precipitation of Coldest Quarter
BO2_chlorange_bdmin	
BO2_chloltmax_bdmin	
BO_nitrate	
BO2_nitraterange_bdmin	
BO2_salinitymean_ss	
MarSpec variables	
Bathymetry	Sea surface salinity (monthly minimum)
Bathymetric slope	Sea surface salinity (monthly maximum)
Concavity	Sea surface salinity (annual range)
Distance to shore	Sea surface salinity (annual variance)
East/West aspect	Sea surface temperature (annual mean)
North/South Aspect	Sea surface temperature (coldest ice-free month)
Plan curvature	Sea surface temperature (warmest ice-free month)
Profile curvature	Sea surface temperature (range)
Sea surface salinity (annual mean)	Sea surface temperature (variance)

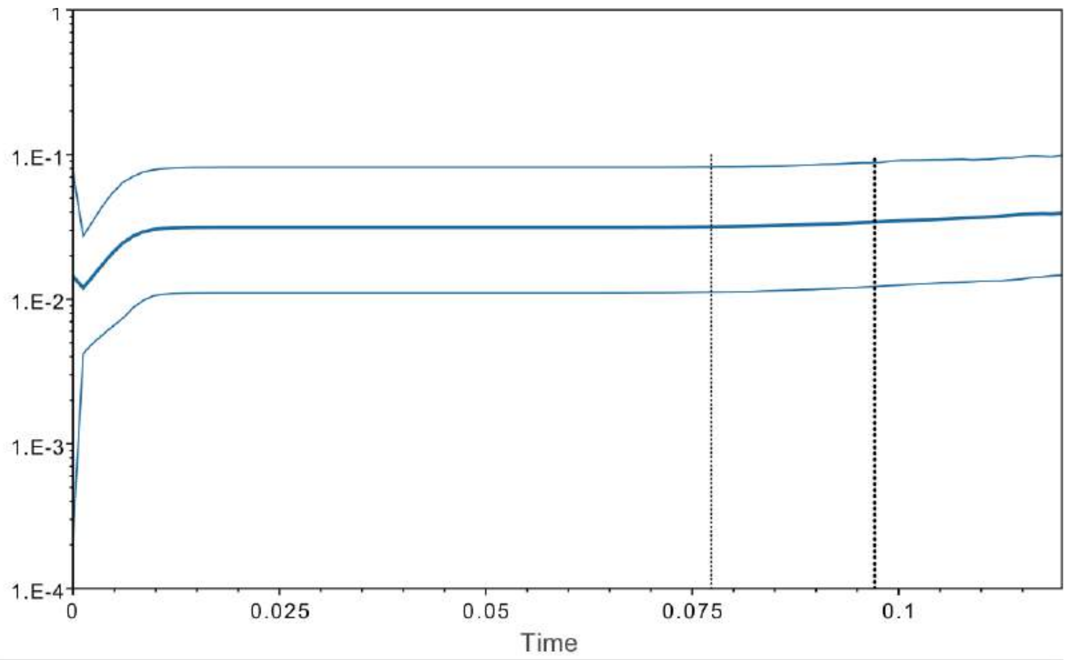
S2. Neutrality tests results.

Lineage	Tajima’s D	P-value D	Fu’s Fs	P-value Fs	Harpending's Raggedness index	P-value Harpending
C. dubia	1.85553	0.96790	4.45402	0.95410	0.21144147	0.18500000
PCR	0.0000	1.00000	0.00000	NA	*	
SOU	0.0000	1.00000	0.00000	NA	*	
FN	0.0000	1.00000	0.00000	NA	*	
PT	0.0000	1.00000	0.00000	NA	*	
NAT	0.0000	1.00000	0.00000	NA	*	
FOR	0.01499	0.73020	0.41670	0.37780	*	
C. brasiliensis	-2.48029	0.00010	1.47642	0.75130	0.02790962	0.75910000
CF	-2.23096	0.00000	6.96006	0.99300	0.08815427	0.83270000
ARR	0.00000	1.00000	0.00000	NA	*	
TRA	0.0000	1.00000	0.00000	NA	*	
ABR	0.83031	0.80500	1.08459	0.73020	0.34677686	0.42240000
IG	0.0000	1.00000	0.00000	NA	*	
BOI	1.88129	0.98600	3.53848	0.95090	0.44897959	0.05450000
ALC	0.55902	0.83560	0.58867	0.43470	0.22902494	1.00000000

*The variance of the mismatch distribution is to small,
no demographic parameters can be estimated.



S3. Bayesian Skyline Plot of *Chondrochelia dubia s.s.*



S4. Bayesian Skyline Plot of *Chondrochelia brasiliensis* **comb. nov.**

S5. Variables selected by the Factorial Analysis for ecological niche modeling

Variable	**ML1**	**ML2**	**ML3**	**ML4**	**ML5**
Bathymetric slope	0.01	0.03	0	0.02	0.09
Concavity	0.17	0.06	0	0.04	0.02
Distance to shore	0.08	0.03	0.65	0	0.01
East/West aspect	0.06	0.05	0.75	0.01	0
North/South aspect	0.23	0.18	0.01	0.09	0.48
Plan curvature	0.25	0.12	0.14	0.04	0.02
Profile	0.02	0.01	1	0	0
Sea surface salinity (annual mean)	0.3	0.61	0.01	0.73	0.03
Sea surface salinity (monthly minimum)	0.1	0.88	0.01	0.44	0.14
Sea surface salinity (monthly maximum)	0.49	0.16	0	0.84	0.16
Sea surface salinity (annual range)	0.12	0.96	0.01	0.11	0.24
Sea surface salinity (annual variance)	0.04	0.84	0.01	0.09	0.12
Sea surface temperature (annual mean)	0.92	0.04	0	0.19	0.35
Sea surface temperature (coldest ice-free month)	0.95	0.04	0	0.2	0.25
Sea surface temperature (warmest ice-free month)	0.85	0.06	0	0.18	0.48
Sea surface temperature (range)	0.95	0.03	0.01	0.2	0.25
Sea surface temperature (variance)	0.84	0.04	0	0.37	0.32
Bathymetry	0.05	0.37	0.09	0.24	0.29

Considerações Finais

Este é o primeiro trabalho focado em organismos com desenvolvimento direto associados a macroalgas, e suas implicações para a conectividade marinha e biodiversidade em áreas remotas, como as ilhas oceânicas brasileiras. Durante estes quatro anos de doutorado, as coletas ao longo da costa permitiram a descrição de várias espécies não somente de ilhas oceânicas (Iwasa-Arai et al. 2021) quanto continentais (Iwasa-Arai et al. 2019), novos registros (Iwasa-Arai et al. 2020), além da realização de estudos ecológicos experimentais com crustáceos peracáridos em ambientes de máxima preservação (Siqueira et al. 2021).

Além disso, os resultados apresentados na presente tese tiveram dois principais objetivos: 1) entender quais os padrões de estruturação populacional genética ao longo da costa continental, ilhas costeiras e ilhas oceânicas, e se tais padrões seriam idênticos para organismos que compartilham o mesmo ambiente e com distribuições semelhantes; 2) estudar os eventos biogeográficos globais que moldaram a distribuição das espécies atuais. Para tanto, utilizamos duas espécies (*Chondrochelia dubia s.l.* e *Ampithoe marcuzzii s.l.*), um gênero (*Synapseudes*), e uma família (Ampithoidae) de Peracarida para entender tais processos.

1) Filogeografia comparativa e conectividade

As duas espécies aqui analisadas mostraram resultados congruentes quanto à presença de complexos de espécies. Tanto o tanaidáceo *Chondrochelia dubia* quanto o anfípode *Ampithoe marcuzzii* são espécies encontradas associadas a macroalgas ao longo da costa brasileira e ilhas oceânicas. Tal resultado corrobora com a hipótese de que organismos com baixa capacidade de dispersão possuem um maior número de espécies endêmicas, muitas vezes formando complexos com espécies de distribuição restrita (Hurtado et al. 2016). Contudo, tanto o número de espécies, quanto as distribuições dos complexos *C. dubia* e *A. marcuzzii* foram discordantes.

O complexo *C. dubia* foi caracterizado em quatro espécies dentro da área amostrada: *C. dubia s.s.*, distribuída ao longo da costa continental nordeste, ilha de Fernando de Noronha e Dominica, *C. brasiliensis* **comb. nov.**, com ocorrência na costa continental sudeste, *C. baronia* **sp. nov.**, em Atol das Rocas e Natal, *C. cacandocae* **sp. nov.**, em Ubatuba, e *C. trindadensis* **sp. nov.**, na Ilha da Trindade. Assim, duas espécies apresentaram distribuições mais amplas na costa, três são (quase) restritas às ilhas oceânicas, e uma possui distribuição restrita co-ocorrendo na costa continental. Além das espécies amostradas, o complexo *C. dubia* inclui outras espécies presentes no Caribe, como *C. caribensis*, *C. mexicana*, *C. ortizi* e *C. winfieldi,* além da espécie *C. savignyi*, espécie bastante discutida na literatura quanto à sua validade e semelhança com *C. dubia* (Bamber 2010, Gutu 2016).

Já o complexo *A. marcuzzii* foi caracterizado em menos espécies, sendo *A. marcuzzii 'continent'* presente na costa continental brasileira, do Ceará até São Paulo, *A. marcuzzii 'islands'* com distribuição nas ilhas oceânicas brasileiras e na Dominica, e *A. marcuzzii SM*, com ocorrência na ilha de Saint Martin. Neste caso, não houve sobreposição na distribuição das espécie do complexo.

A linhagem de *A. marcuzzii* 'continent' apresentou estruturação populacional em NE, E e SE, congruente com as barreiras encontradas entre as distribuições de *C. dubia s.s.* e *C. brasiliensis* **comb. nov.**, cujo limite encontra-se na foz do rio Paraguaçu, que deságua na Baía de Todos os Santos (BA). A diferenciação entre as espécies de *Chondrochelia* e das populações de *A. marcuzzii* 'continent' exatamente na mesma região mostra a importância histórica de eventos climáticos para a distribuição das espécies.

Em relação à estruturação populacional em *C. brasiliensis* **comb. nov.**, é possível observar a diferenciação das populações de Boipeba (BOI), Trancoso (TRA) e Abrolhos (ABR) com relação às populações do sudeste e sul [Arraial do Cabo (ARR), Cabo Frio (CF), Ilha Grande (IG), Alcatrazes (ALC) e Bombinhas (BOM)], encontrada também dentro de *A. marcuzzii* 'continent', também separada em leste e sudeste. No caso de *A. marcuzzii* 'continent', a distribuição da espécie é menor, e limita-se até a região norte do estado de São Paulo. Tal estruturação sugere uma barreira próxima à cadeia

Vitória-Trindade/ Plateau de Abrolhos, comumente observada para organismos marinhos, como os ácaros marinhos *Agauopsis legionium* e *Rhombognathus levigatoides* (Pepato et al. 2019) e a alga parda *Colpomenia sinuosa* (Martins et al. 2022a), correspondente também com a latitude da foz do Rio Doce (Martins et al. 2022a). Ambas as barreiras da foz do rio Paraguaçu quanto a cadeia Vitória-Trindade são conhecidas por limitar a distribuição de populações e espécies marinhas (Martins et al. 2022b).

Considerando a separação de linhagens pela foz do rio Paraguaçu, os tempos de divergência estimados para a diversificação de *C. dubia s.s.* e *C. brasiliensis* **comb. nov.** foram de ~14.95 Ma, enquanto a divergência das populações NE e E de *A. marcuzzii* 'continent' foram estimadas em ~10.72 Ma. Assim, a proximidade nos tempos estimados (não idênticos possivelmente pela falta de dados fósseis de linhagens viventes, estimativas de taxas evolutivas únicas para Peracarida sem levar em consideração o tempo de geração de cada espécie) sugere que os mesmos eventos tenham isolado as populações de *C. dubia/C. brasiliensis* e *A. marcuzzii* no Mioceno.

Enquanto isso, a barreira gerada pela cadeia Vitória-Trindade esteve exposta em períodos de glaciação máxima e diminuição do nível do mar, alterando assim a direção das correntes (Martins et al. 2022). Já a foz do Rio Doce, assim como a foz do Rio Paraguaçu, pode funcionar como uma barreira permanente e determinante na distribuição de linhagens mais ou menos adaptadas a mudanças na salinidade, temperatura, e nutrientes dissolvidos.

De acordo com os tempos de divergência das populações de *C. dubia/C. brasiliensis* e *A. marcuzzii,* eventos distintos possivelmente levaram ao isolamento das populações. Apesar da concordância geográfica na estruturação populacional das espécies, tanto a ordem dos eventos de separação NE vs E+SE no complexo *C. dubi*a e NE+E vs SE em *A. marcuzzii* 'continent', quanto a diferença nos tempos de divergência (*C. brasiliensis*: SE e E ~3.53 Ma; *A. marcuzzii* 'continent': ~14.3 Ma) sugerem uma região instável, sujeita a distintas separações temporais.

Deste modo, tentamos avaliar quais variáveis abióticas poderiam estar influenciando na estruturação das populações, a partir de uma abordagem de testes de isolamento-por-ambiente (isolation-by-environment, IBE) para ambos complexos. Enquanto não foi observado nenhum indício de IBE para *C. brasiliensis*, sete variáveis foram identificadas pela análise de IBE para *A. marcuzzii* 'continent'. Observamos que as variações genômicas NE vs SE em *A. marcuzzi* podem ser explicadas pelas variações ambientais, uma vez que as localidades mais ao sul tendem a estar sujeitas a maiores alterações de temperatura e a águas mais turbulentas. Esta diferenciação também é concordante com a geomorfologia, na qual as localidades do sudeste são constituídas por recifes rochosos, enquanto as localidades NE e E são compostas principalmente por recifes biogênicos.

Dentro das diferenças entre as histórias evolutivas dos complexos *C. dubia* e *A. marcuzzii*, a que chama mais a atenção foi a separação das linhagens de 'continent' e 'islands' recuperada em *A. marcuzzii*, padrão não observado para *C. dubia s.l.* Os fatores que levaram a tais resultados ainda são desconhecidos, e, possivelmente, trabalhos futuros experimentais e comparativos entre as duas espécies possam explicar os resultados apresentados na presente tese.

2) Biogeografia global de Peracarida associados a macroalgas

Ao analisarmos a filogenia e biogeografia de dois grupos distintos com distribuição cosmopolita, observamos que, tanto o gênero de tanaidáceos *Synapseudes*, quanto a família de anfípodes Ampithoidae, ambos presentes em macroalgas, possuíram ancestrais distribuídos na região do Indo-Pacífico. Esta região, conhecida pela grande diversidade de espécie, também foi recuperada como área das espécies ancestrais de algas pardas (Bringloe et al. 2020), corroborando a hipótese de que a diversificação de invertebrados associados a macroalgas se deu a partir da irradiação do grupo hospedeiro.

Com relação aos eventos de dispersão para o Oceano Atlântico, observamos que ambos os táxosns possuem padrões de dispersão semelhantes, sendo que múltiplas dispersões ocorreram, mas, nos dois casos, um clado de *Synapseudes* e um de Ampithoidae (*Foscampithoe*) dispersaram inicialmente ao Oceano Atlântico, onde foram sujeitos a processos de especiação.

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ANEXOS

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada *Delimitação de espécies, filogeografia comparativa e conectividade de Peracarida (Crustacea: Eumalacostraca) associados a Sargassum no Brasil com ênfase em populações insulares*, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 16 de dezembro de 2022

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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada “ ***Delimitação de espécies, filogeografia comparativa e conectividade de Peracarida (Crustacea: Eumalacostraca) associados a Sargassum no Brasil com ênfase em populações insulares*** ”, desenvolvida no Programa de Pós-Graduação em Biologia Animal do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

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