



UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE BIOCÊNCIAS
DEPARTAMENTO DE ZOOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

PEDRO HENRIQUE DA PAIXÃO E SILVA

**TAXONOMIA INTEGRATIVA DE CAMARÕES-DE-ESTALO DO GÊNERO
SYNALPHEUS SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) DO NORDESTE
DO BRASIL**

Recife

2025

PEDRO HENRIQUE DA PAIXÃO E SILVA

**TAXONOMIA INTEGRATIVA DE CAMARÕES-DE-ESTALO DO GÊNERO
SYNALPHEUS SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) DO NORDESTE
DO BRASIL**

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

Área de Concentração: Biologia Animal

Orientador: Prof. Dr. Alexandre Oliveira de Almeida

Co-orientadora: Profa. Dra. Mariana Terossi Rodrigues

Recife

2025

Silva, Pedro Henrique da Paixão e.

Taxonomia integrativa de camarões-de-estalo do gênero *Synalpheus* Spence Bate, 1888 (Decapoda: Alpheidae) do Nordeste do Brasil / Pedro Henrique da Paixão e Silva. - Recife, 2025. 162f.: il.

Tese (Doutorado)- Universidade Federal de Pernambuco, Centro de Biociências, Programa de Pós-Graduação em Biologia Animal, 2025.

Orientação: Alexandre Oliveira de Almeida.

Coorientação: Mariana Terossi Rodrigues.

1. Camarões carídeos; 2. Arquipélago de Fernando de Noronha; 3. Gene 16S; 4. Gene COI; 5. Novos registros; 6. Camarões associados a esponja. I. Almeida, Alexandre Oliveira de. II. Rodrigues, Mariana Terossi. III. Título.

UFPE-Biblioteca Central

PEDRO HENRIQUE DA PAIXÃO E SILVA

**TAXONOMIA INTEGRATIVA DE CAMARÕES-DE-ESTALO DO GÊNERO
SYNALPHEUS SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) DO NORDESTE
DO BRASIL**

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

Aprovado em: 07/08/2025

BANCA EXAMINADORA



Documento assinado digitalmente

ALEXANDRE OLIVEIRA DE ALMEIDA

Data: 31/10/2025 15:54:02-0300

Verifique em <https://validar.iti.gov.br>

Prof. Dr. Alexandre Oliveira de Almeida (Orientador)

Universidade Federal de Pernambuco

Documento assinado digitalmente



PAULA BRAGA GOMES DE PEREZ

Data: 28/10/2025 17:54:45-0300

Verifique em <https://validar.iti.gov.br>

Prof^a. Dr^a. Paula Braga Gomes (Examinadora Interna)

Universidade Federal de Pernambuco

Documento assinado digitalmente



ISABELA RIBEIRO ROCHA DE MORAES

Data: 27/10/2025 11:07:53-0300

Verifique em <https://validar.iti.gov.br>

Prof^a. Dr^a. Isabela Ribeiro Rocha de Moraes (Examinadora Externa)

Universidade Federal do Rio Grande do Sul

Documento assinado digitalmente



JESSICA COLAVITE

Data: 27/10/2025 13:19:36-0300

Verifique em <https://validar.iti.gov.br>

Prof^a. Dr^a. Jessica Colavite (Examinadora Externa)

Museu de Zoologia da Universidade de São Paulo

Documento assinado digitalmente



PATRICIA SOUZA DOS SANTOS

Data: 30/10/2025 14:47:25-0300

Verifique em <https://validar.iti.gov.br>

Dr^a. Patricia Souza dos Santos (Examinadora Externa)

Dedico esta tese à minha querida esposa,
mãe, pai, amigos, familiares e, também, à
ciência.

AGRADECIMENTOS

Gostaria de agradecer, primeiramente, à Deus por, apesar das minhas falhas, sempre estar ao meu lado, me colocando em situações para que eu me torne mais forte e me auxiliando nos momentos de fraqueza, falta de inspiração e motivação na árdua jornada que é um doutorado.

Agradeço também à maravilhosa pessoa que é minha esposa. O que falar de Patricia (sem acento mesmo)... Ela é aquele tipo de pessoa que, mesmo estando nos piores dias, com todas as dificuldades e estresses da vida adulta, sempre, sem exceções, está aqui, ao meu lado, para me ajudar. Em todos esses 28 anos da minha vida, eu não me deparei com nenhuma pessoa, que não meu pai ou mãe, que acreditou tanto no meu potencial e, também, que viu o melhor que há em mim, o melhor que eu posso ser e o quanto eu posso crescer. Meu amor, tenha certeza que, se não fosse você, nenhuma linha dessa tese haveria de ser escrita. Você foi a melhor pessoa que poderia ter entrado na minha vida. Amo você!

Também agradeço à minha mãe, Helena Maria, e ao meu pai, José Jackson, por todo investimento, tempo e dedicação que puseram em minha educação. Mesmo tendo dificuldades, preferiam se apertar e viver com o mínimo do que deixar de me proporcionar a melhor educação que eles puderam naquele momento. E foi essa educação que me fez chegar a esse momento. Sem vocês, eu não estaria aqui, “papi” e “mami”. Também amo vocês, apesar de não externalizar isso em palavras com tanta frequência.

Não obstante, deixo um trecho dos agradecimentos para meu orientador, Alexandre Almeida, ou simplesmente “prôfi”. Foi uma longa jornada de muito aprendizado com o senhor. Lembro dos meus primeiros passos no laboratório, lá em 2016, começando a identificar *Alpheus* com auxílio de Guidomar e Patricia, seus pupilos na época. Lembro-me de, quando perguntei sobre a possibilidade de fazer iniciação científica, o senhor me apresentou uma proposta de projeto que, naquele momento, me parecia meio fora da realidade mas que, devido a isso, me fez trabalhar com os bichinhos que trabalho hoje: camarões associados a esponja, mais especificamente, “meus” amados *Synalpheus*. Sei que, se não fosse pelo senhor, eu também não estaria finalizando essa longa jornada. Foram dois anos de iniciação científica, mais um mestrado que transcorreu a pandemia do Covid – 19 e mais quatro anos de doutorado. Não vou mentir e dizer que, nesses quase dez anos, foi tudo um mar de rosas. Houve muitos momentos

em que “queimamos a mufa” para resolver algum aspecto dos projetos, momentos em que me desanimei, momentos em que me faltou inspiração, momentos em que me faltou, até mesmo, vontade de continuar. Mas o senhor, com toda sua calma, paciência e sabedoria, estava ali para me apoiar, me dar um direcionamento e mostrar que eu sou capaz. Sei, do fundo do coração, que poderia ter sido um orientando muito melhor e sei que falhei muitas vezes e, mais uma vez, agradeço por nunca teres saído do meu lado. Sempre terás um lugar muito especial na minha formação e, também, na minha vida e coração, “prôfi”.

Também gostaria de fazer um agradecimento especial a duas pessoas muito importantes nessa jornada que foi o meu doutorado: minha coorientadora, profa. Mariana Terossi (profa Mari) e Karmine. Se não fosse a cooperação, empenho, atenção e profissionalismo dessas duas mulheres, eu também não teria chegado no fim de meu doutorado. Convivi pouco com a profa Mari. A encontrei em três momentos, se não me falhe a memória: em um dos congressos de carcinologia aqui no Brasil, onde ela estava maravilhosamente bem fantasiada de Etevaldo (personagem do Castelo Rá-Tim-Bum), em uma outra visita que ela fez a Recife, em que estava grávida da sua segunda bebezinha, e no período em que ela me mostrou, presencialmente, o mundo da genética molecular. Esse último encontro foi o mais especial de todos, pela recepção que tive e por todo conhecimento que me foi passado. Sempre com muita calma e paciência, até mesmo nas dezenas de reuniões online que fiz com ela para tirar dúvidas e, também, fazer as análises moleculares, a profa Mari me mostrou o caminho das pedras do mundo molecular e se mostrou também uma das melhores coorientadoras que eu poderia ter tido. E Karmine... Conheci Karmine durante um período em que ela veio para Recife para fazer coletas das fêmeas ovígeras dela e, desde então, começamos uma dessas amizades que se iniciam e parece que você já conhecia a pessoa há muitos e muitos anos. Ela contagiou todo mundo do laboratório e, também, o pessoal do PPGBA com a energia maravilhosa que ela tem. Aqui em Recife, tivemos muitos momentos de risos, de boas conversas, de dificuldades das mais variadas com tudo que possa envolver trabalhar com larvas de crustáceos e, como é de se imaginar, momentos de tristeza, de choro mas, também, de superação e reconhecimento das nossas capacidades como pessoa e como pesquisadores. E esse companheirismo se mostrou mais uma vez quando ela abriu as portas da própria casa para que eu pudesse fazer esse “estágio em genética” em Porto Alegre. Eu já disse isso milhares de vezes a você, amiga, mas gostaria de deixar eternizado nesses agradecimentos: Karmine, você foi uma pessoa fundamental para a elaboração dessa tese e não há palavras que eu possa dizer que resumirão tudo que você fez por mim e, também, a grande mulher que você é! Muito obrigado!

Também deixo registrada minha gratidão aos integrantes do Laboratório de Biologia de Crustáceos da UFPE, ao atuais e aos da “velha guarda”, integrantes esses que, por vezes, convivi mais até do que minha própria família e que tive momentos maravilhosos! Gostaria de deixar um agradecimento especial, dentro desses integrantes, a Pati, Guido, Andressa, Renatinha, Aninha, Rodrigo, Whand, Joyce e Ramires, aqueles com quem mais convivi e, conseqüentemente, com quem criei laços de amizade mais fortes. Adoro vocês! Também agradeço a colaboração da equipe do Laboratório de Carcinologia da UFRGS, do Laboratório de Porífera da UFPE, da equipe do laboratório de crustáceos do MOUFPE e todos os outros laboratórios envolvidos. Fazendo parte desse corpo de laboratórios envolvidos, gostaria de tecer um agradecimento especial a Fabíola, técnica do MOUFPE, por toda paciência e solicitude nos momentos em que solicitei empréstimo de materiais do MOUFPE.

Agradeço também a todos os amigos e amigas que fizeram parte, de alguma forma, dessa jornada. Aos longínquos “Michoquinhos”, amigos desde a época da graduação e, alguns, desde a época do ensino médio, aos amigos de turma, amigos do bairro e amigos e amigas do PPGBA, especialmente uma figurinha muito especial na correria que é a vida num programa de pós-graduação de excelência como o PPGBA: Michelly Lira. Conheci Michelly no começo do mestrado, também no PPGBA e, desde então, não largamos um do outro no que se diz respeito aos perrengues da pós e, também, naquele apoio, mesmo que indireto, no dia a dia da pós. Dentro e fora do PPGBA, Michelly foi e ainda é um grande apoio e fonte de motivação e, acima de tudo, uma grande amiga!

Também agradeço ao PPGBA pelo apoio, a CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) pela concessão da bolsa de doutorado e a todos os órgãos de fomento e instituições envolvidas na tese: CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), FACEPE (Fundação de Amparo à Ciência e Tecnologia de Pernambuco), ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade).

Crustaceans exhibit the greatest diversity of body forms of any group of animals.

Brusca & Brusca

RESUMO

Os camarões-de-estalo do gênero *Synalpheus* formam um dos grupos mais numericamente abundantes e taxonomicamente diversos a habitar recifes de coral ao redor do mundo. Grande parte de sua diversidade conhecida encontra-se no Mar do Caribe, onde uma série de estudos sobre o grupo vem sendo realizados ao longo das últimas décadas. No Brasil, estudos sobre o gênero iniciaram com Spence Bate (1888), passando por vários outros. Uma série de estudos aponta a necessidade de revisão taxonômica devido ao reconhecimento de complexos de espécies e possíveis espécies crípticas no gênero. A presente tese está dividida em três capítulos que têm por objetivo revisar taxonomicamente os camarões do gênero *Synalpheus* no litoral do Nordeste do Brasil com o uso de uma abordagem integrativa. No primeiro capítulo, que objetivou elaborar um checklist com as espécies de *Synalpheus* no Nordeste do Brasil, um total de 1010 indivíduos de 26 espécies foram analisadas, havendo seis novos registros para o Atlântico Sul Ocidental (*S. barahonensis*, *S. belizensis*, *S. brevidactylus*, *S. corallinus*, *S. hoetjesi* e *S. kensleyi*) e treze extensões de distribuição/novos registros (*S. agelas*, *S. androsi*, *S. antillensis*, *S. dardeui*, *S. fritzmuelleri*, *S. hemphilli*, *S. herricki*, *S. pandionis*, *S. ruetzleri*, *S. tenuispina*, *S. townsendi*, *S. ubatuba* e *S. yano*) para a região, bem como a exclusão de registros duvidosos (*S. filidigitus*, *S. longicarpus*, *S. paraneptunus* e *S. rathbunae*). Com isso, a diversidade conhecida de *Synalpheus* para a região Nordeste passou de 27 para 29 espécies, enquanto a do Brasil foi de 29 para 31 espécies. No segundo capítulo, duas novas espécies de *Synalpheus* foram descritas baseadas em dados morfológicos e moleculares (gene 16S). *Synalpheus* sp. nov. 1 é morfológicamente semelhante a *S. herricki*, com uma diferenciação molecular de 5% entre os marcadores utilizados, enquanto *Synalpheus* sp. nov. 2 é similar morfológicamente a *S. ruetzleri*, com uma diferenciação molecular de 4–5% entre os marcadores utilizados. O terceiro capítulo visou avaliar o grau de estruturação populacional da espécie *S. hoetjesi* do Brasil e do Mar do Caribe, onde as análises de Máxima Verossimilhança, número, rede e diversidade haplotípicas, diversidade nucleotídica e variação genética usando o gene Citocromo Oxidase I, mostraram estruturação entre ambas populações. Os resultados desse estudo mostram a importância de abordagens integrativas para estudos sistemáticos e taxonômicos dentro do gênero.

Palavras-chave: camarões carídeos; Arquipélago de Fernando de Noronha; gene 16S; gene COI; novos registros; camarões associados a esponja.

ABSTRACT

Snapping shrimp of the genus *Synalpheus* represent one of the most numerically abundant and taxonomically diverse groups inhabiting coral reefs worldwide. Much of their known diversity occurs in the Caribbean Sea, where a series of studies on the group have been conducted over the past few decades. In Brazil, research on the genus began with Spence Bate (1888) and has since been followed by several other contributions. A growing number of studies have highlighted the need for taxonomic revision due to the recognition of species complexes and the occurrence of possible cryptic species within the genus. This thesis is divided into three chapters that aim to taxonomically review the *Synalpheus* shrimp from the northeastern coast of Brazil using an integrative approach. In the first chapter, which provides a checklist of *Synalpheus* species from northeastern Brazil, a total of 1,010 individuals representing 26 species were analyzed. Six species were recorded for the first time in the western South Atlantic (*S. barahonensis*, *S. belizensis*, *S. brevidactylus*, *S. corallinus*, *S. hoetjesi*, and *S. kensleyi*), and thirteen represented range extensions or new regional records (*S. agelas*, *S. androsi*, *S. antillensis*, *S. dardeai*, *S. fritzmuelleri*, *S. hemphilli*, *S. herricki*, *S. pandionis*, *S. ruetzleri*, *S. tenuispina*, *S. townsendi*, *S. ubatuba*, and *S. yano*). Additionally, doubtful records (*S. filidigitus*, *S. longicarpus*, *S. paraneptunus*, and *S. rathbunae*) were excluded. As a result, the known diversity of *Synalpheus* in northeastern Brazil increased from 27 to 29 species, and the total number of species known from Brazil rose from 29 to 31. In the second chapter, two new species of *Synalpheus* were described based on morphological and molecular data (16S gene). *Synalpheus* sp. nov. 1 is morphologically similar to *S. herricki*, with approximately 5% molecular divergence in the analyzed markers, whereas *Synalpheus* sp. nov. 2 closely resembles *S. ruetzleri*, showing 4–5% divergence. The third chapter aimed to assess the degree of population structure in *S. hoetjesi* from Brazil and the Caribbean Sea. Maximum Likelihood analyses, haplotype network and diversity estimates, nucleotide diversity, and genetic variation analyses using the Cytochrome Oxidase I gene all revealed genetic structuring between the two populations. Overall, the results of this study reinforce the importance of integrative approaches for systematic and taxonomic research within the genus *Synalpheus*.

Keywords: caridean shrimp; Fernando de Noronha Archipelago; 16S gene; COI gene; new records; sponge-associated shrimp.

LISTA DE FIGURAS

Artigo Científico 1

Figure 1 - Map of collection sites. The blue background indicates the Northeastern region of Brazil; the green area represents the Fernando de Noronha Archipelago; the red area represents the São Pedro e São Paulo Archipelago; black diamonds mark the sampling locations.

.....33

Figure 2 - Sampling locations of specimens of *Synalpheus* Spence Bate, 1888 analyzed in this study. A, Baía de Suape, Cabo de Santo Agostinho, Pernambuco; B, Praia dos Carneiros, Tamandaré, Pernambuco; C, Praia de Pontas de Pedra, Goiana, Pernambuco; D, Fernando de Noronha Archipelago, Pernambuco; E, São Pedro e São Paulo Archipelago, Rio Grande do Norte; F, Dredging on the continental shelf off Recife, Pernambuco. Photos: A, B, E—G.L. Bochini; C—T.E.R. Cavalcanti; D—K. Pasinato; F—P.H. Paixão.....36

Figure 3 - Substrates where the specimens of *Synalpheus* Spence Bate, 1888 analyzed in this study were found. A, Rhodoliths; B, Sediment; C, Sponge where the colony of *S. brooksi* Coutière, 1909 was found; D, Sponge morphotype where the possible communal groups of *S. hoetjesi* Hultgren, Macdonald & Duffy, 2010 and *S. ul* (Ríos & Duffy, 2007) were found, arrows indicate the presence of shrimps. Photos A–D: P.H. Paixão.....37

Figure 4 - *Synalpheus androsi* Coutière, 1909: female from the continental shelf off Recife, Pernambuco, Brazil [DZ/UFRGS 7050]. A, frontal region, dorsal view; B, third pereopod, left side, lateroventral view; C, major chela, right side, mesial view; D, same, lateral view. Scale bars: 0.5 mm42

Figure 5 - *Synalpheus barahonensis* Armstrong, 1949: female from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21870]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, left side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–F, 0.5 mm; G, 0.3 mm44

Figure 6 - *Synalpheus barahonensis* Armstrong, 1949: female from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21870]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A, 0.5 mm; B–E, 0.3 mm.45

Figure 7 - *Synalpheus belizensis* Anker & Tóth, 2008: female from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/UFRGS 7041]. A, frontal region, dorsal view; B, major chela, right side, mesial view; C, same, lateral view; D, minor chela, left side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–C, 1 mm; D–G, 0.5 mm48

Figure 8 - *Synalpheus belizensis* Anker & Tóth, 2008: female from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/UFRGS 7041]. A, pleon, left view; B, telson, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view. Scale bars: A, 1 mm; B–D, 0.5 mm..... 49

Figure 9 - *Synalpheus brevidactylus* Anker & Tóth, 2008: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21813]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, left side, lateral view; G, third pereopod, left side, lateral view. Scale bars: A, D, E, G, 0.5 mm; B, C, 1 mm; F, 0.3 mm.....55

Figure 10 - *Synalpheus brevidactylus* Anker & Tóth, 2008: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21813]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, third maxilliped, left side, lateral view. Scale bars: A, 1 mm; B–E, 0.3 mm 56

Figure 11 - *Synalpheus corallinus* Macdonald, Hultgren & Duffy, 2009: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21812]. A, frontal region, dorsal view; B, major chela, right side, mesial view; C, same, lateral view; D, minor chela, left side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–E, 0.5 mm; F, G, 0.3 mm 61

Figure 12 - *Synalpheus corallinus* Macdonald, Hultgren & Duffy, 2009: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21812]. A, pleon, right view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A, 1 mm; B–E, 0.3 mm 62

Figure 13 - *Synalpheus herricki* Coutière, 1909: male from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/UFRGS 7046]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–C, 1 mm; D, E, G, 0.5 mm; F, 0.4 mm. 67

Figure 14 - *Synalpheus herricki* Coutière, 1909: male from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/UFRGS 7046]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, third maxilliped, right side, lateral view. Scale bars: A, 1 mm; B, C, E, 0.4 mm; D, 0.5 mm 68

Figure 15 - *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010: female from Cabo de Santo Agostinho, Pernambuco, Brazil [MOUFPE 21530]. A, frontal region, dorsal view; B, major chela, right side, mesial view; C, same, lateral view; D, minor chela, left side mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A, D, E, 0.5 mm; B, C, F, G, 1 mm..... 69

Figure 16 - *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010: female from Cabo de Santo Agostinho, Pernambuco, Brazil [MOUFPE 21530]. A, pleon, left view; B, right uropod,

dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A, 1 mm; B–E, 0.5 mm 70

Figure 17 - *Synalpheus kensleyi* (Ríos & Duffy, 2007): male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21869]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A, D–G, 0.5 mm; B, C, 1 mm. 73

Figure 18 - *Synalpheus kensleyi* (Ríos & Duffy, 2007): male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21869]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A–C, E, 0.5 mm; D, 0.2 mm. 74

Figure 19 - Phylogram constructed from Maximum Likelihood for the 16S mitochondrial gene. The numbers at the nodes correspond to the support values considering 1000 bootstrap pseudo-replicas. Bold specimens indicate sequences obtained in the present study; sequences obtained from Genbank have accession numbers. Atl: Atlantic Ocean; PE: Pernambuco; SP: São Paulo. 85

Figure 20 - Maps with the distribution of new records of *Synalpheus* (*S. agelas*, *S. androsi*, *S. antillensis*, *S. barahonensis*, *S. belizensis*, *S. brevidactylus*, *S. corallinus*, *S. dardeui*, *S. fritzmuelleri*) for the coast in northeastern Brazil or Brazil. *Synalpheus fritzmuelleri* - also occurs in the São Pedro e São Paulo Archipelago, Helena Island, and Ascension Island. Blue dots = previous records; Red dots = new records..... 88

Figure 21 - Maps with the distribution of new records of *Synalpheus* (*S. hemphilli*, *S. herricki*, *S. hoetjesi*, *S. kensleyi*, *S. pandionis*, *S. ruetzleri*, *S. tenuispina*, *S. townsendi*, *S. ubatuba*, and *S. yano*) to the coast in northeastern Brazil or Brazil. *Synalpheus tenuispina* - also occurs in the São Pedro e São Paulo Archipelago. Blue dots = previous records; Red dots = new records. 89

Artigo Científico 2

Figure 1 - Phylogram constructed using Maximum Likelihood analysis of the 16S mitochondrial gene sequences for *Synalpheus* specimens. The node values represent the support values considering 1000 bootstrap pseudo-replicates. Values <50% are not shown. Atl: Atlantic Ocean; FN: Fernando de Noronha archipelago; PA: Pará. Bold indicates the new species. 116

Figure 2 - *Synalpheus* sp. nov. 1, male holotype, male individual from, from Laje Dois Irmãos, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48906). A, frontal region, dorsal view; B, same, lateral view; C, major chela, left side, mesial view; D, same, lateral view;

E, minor chela, right side, mesial view; F, same, lateral view. Scale bars: A–D, 1 mm; E, F, 0,5 mm 118

Figure 3 - *Synalpheus* sp. nov. 1, male holotype from, Laje Dois Irmãos, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48906). Mouthparts, A, mandible, right side; B, first maxilla, right side; C, second maxilla, right side; D, first maxilliped, right side; E, second maxilliped, right side; F, third maxilliped, right side. Scale bars: A–E, 0.2 mm; F, 0.4 mm. 119

Figure 4 - *Synalpheus* sp. nov. 1, male holotype from Fernando de Noronha Archipelago, Laje Dois Irmãos, Pernambuco, Brazil (MZUSP 48906). A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, second pereopod, right side, lateral view; F, third pereopod, right side, lateral view. Scale bars: A, 1 mm; B, C, E, 0.4 mm; D, F, 0.5 mm 121

Figure 5 - *Synalpheus* sp. nov. 2, male holotype from Buraco do Inferno, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48907). A, frontal region, dorsal view; B, same, lateral view; C, major chela, right side, mesial view; D, same, lateral view; E, minor chela, left side, mesial view; F, same, lateral view. Scale bars: A, B, E, F, 0.5 mm; C, D, 1 mm. 124

Figure 6. *Synalpheus* sp. nov. 2, male holotype from Buraco do Inferno, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48907). Mouthparts, A, mandible, right side; B, first maxilla, right side; C, second maxilla, right side; D, first maxilliped, right side; E, second maxilliped, right side; F, third maxilliped, right side. Scale bars: A–E, 0.2 mm; F, 0.5 mm. 126

Figure 7. *Synalpheus* sp. nov. 2, male holotype from Buraco do Inferno, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48907). A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, second pereopod, right side, lateral view; F, third pereopod, right side, lateral view. Scale bars: A, 1 mm; B, C, E, 0.4 mm; D, F, 0.5 mm 127

Artigo Científico 3

Figura 1 - Árvore filogenética para os espécimes de *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010 e outras espécies de *Synalpheus* usando a análise de Máxima Verossimilhança das sequências do gene COI mtDNA. Os valores nos nós representam os valores de suporte considerando 1000 pseudo-réplicas do bootstraps. Valores <50% não são mostrados.

Abreviação das localidades: BR - Brasil. Marcações em azul representam indivíduos de Pernambuco, Brasil; as vermelhas, os do Mar do Caribe 142

Figura 2: *Synalpheus hoetjesi*. Rede de haplótipos baseada na análise de Median-Joining do gene COI mtDNA, indicando a presença de cada haplótipo (H) encontrado na população (5 haplótipos em 12 espécimes). O tamanho do círculo é proporcional à frequência do haplótipo. Círculo preto representam os vetores médios. Diferentes cores representam diferentes localidades. Cada traço representa um passo mutacional..... 143

LISTA DE TABELAS

Artigo Científico 1

Table 1 - Diversity and distribution of alpheid shrimp of the genus *Synalpheus* Spence Bate, 1888 from Brazil. The acronyms refer to the locations of the new records (ASPSP—São Pedro e São Paulo Archipelago; FN—Fernando de Noronha Archipelago; BA—Bahia; MA—Maranhão; PE—Pernambuco; RN—Rio Grande do Norte; SE—Sergipe; Markings in bold refer to new records for the southwestern Atlantic while the “-” refers to records that were already known)..... 90

Artigo Científico 2

Table 1 - Specimens of *Synalpheus* Spence Bate, 1888 used in the genetic analysis. Atl: Atlantic..... 115

Table 2 - Pairwise genetic distance for the 16S gene between the new species and other specimens of *Synalpheus* Spence Bate, 1888 analyzed in the present study. Atl: Atlantic. 129

Artigo Científico 3

Tabela 1 - Espécimes de *Synalpheus* Spence Bate, 1888 utilizados nas análises genéticas. Nomes de espécies destacados em **negrito** representam as sequências que foram obtidas pelo presente trabalho..... 141

Tabela 2 - Matriz de distância genética do gene COI mtDNA entre espécimes de *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010 e outras espécies de *Synalpheus*..... 144

Tabela 3 - *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010. Análise de Variância Molecular (AMOVA). *Valores significantes, $p < 0,05$ 144

SUMÁRIO

INTRODUÇÃO	19
OBJETIVOS	26
OBJETIVO GERAL	26
OBJETIVOS ESPECÍFICOS	26
ESTRUTURAÇÃO DA TESE	27
ARTIGO CIENTÍFICO 1 – SHRIMPS OF THE GENUS <i>SYNALPHEUS</i> SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) FROM NORTHEAST BRAZIL REGION	28
ARTIGO CIENTÍFICO 2 - TWO NEW SPECIES OF SNAPPING SHRIMP <i>SYNALPHEUS</i> SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) REVEALED BY AN INTEGRATIVE APPROACH IN NORTHEAST BRAZIL	111
ARTIGO CIENTÍFICO 3 - ESTRUTURAÇÃO GENÉTICA EM <i>SYNALPHEUS HOETJESI</i> (DECAPODA: ALPHEIDAE): UMA ESPÉCIE COM DISTRIBUIÇÃO DISJUNTA NO ATLÂNTICO OCIDENTAL	136
CONSIDERAÇÕES FINAIS	156
REFERÊNCIAS	157

INTRODUÇÃO

Os crustáceos

Os crustáceos abrangem invertebrados amplamente conhecidos, como camarões, caranguejos, lagostas, lagostins, cracas e tatuzinhos-de-jardim, reunindo ainda alguns grupos menos conhecidos, como membros das classes Remipedia e Ostracoda. Com aproximadamente 70.000 espécies conhecidas e estimativas que indicam um número entre cinco e dez vezes superior ainda por ser descrito, este grupo apresenta a maior diversidade morfológica dentro do reino animal, além de ocupar uma ampla gama de habitats e apresentar grande variação de tamanho (Brusca *et al.*, 2018). Seus representantes estão presentes em todos os ambientes aquáticos do planeta, desde as regiões abissais até áreas costeiras rasas, incluindo também ambientes estuarinos, de água doce e o terrestre (Brusca *et al.*, 2018).

A ordem Decapoda reúne mais de 17.000 espécies, incluindo organismos familiares como camarões, caranguejos, lagostas e lagostins (De Grave *et al.*, 2023). A infraordem Caridea, pertencente à subordem Pleocyemata, e representa o táxon mais diverso entre os camarões, com cerca de 4.000 espécies conhecidas (De Grave *et al.*, 2023), com seus integrantes sendo caracterizados por apresentarem os primeiros e segundos pereiópodos quelados, ou ainda os apêndices torácicos quarto e quinto com quelas, pela sobreposição da segunda pleura sobre a primeira e a terceira, além das brânquias serem do tipo filobrânquias (Bauer, 2004).

Entre os carídeos, a família Alpheidae Rafinesque, 1815 é uma das mais diversas (De Grave *et al.*, 2023), com seus representantes sendo caracterizados pelos olhos serem parcial ou totalmente cobertos pela carapaça e pela ausência, ou presença discreta, do rostro (Chace, 1972). Esse táxon abriga cerca de 800 espécies (De Grave *et al.*, 2023), sendo o gênero *Alpheus* Fabricius, 1798 o mais diverso, com 344 espécies descritas (Santos *et al.*, 2024; WoRMS, 2025a), seguido de *Synalpheus* Spence Bate, 1888, com 173 espécies atualmente descritas (Anker *et al.*, 2012; Anker & Pachel, 2014; WoRMS, 2025b).

***Synalpheus*: características, história dos grupos e situação no Brasil**

Apesar de distribuída globalmente (Ríos & Duffy, 2007; Macdonald *et al.*, 2009; Hultgren *et al.*, 2010, 2011; De Grave & Fransen, 2011), uma expressiva concentração da diversidade de *Synalpheus* encontra-se no Oceano Atlântico, onde cerca de metade das espécies ocorre (Anker *et al.*, 2012). Esses camarões habitam desde ambientes estuarinos até regiões de

plataforma continental (Anker *et al.*, 2012; Almeida *et al.*, 2015). Além disso, é um dos táxons mais abundantes em número de indivíduos e com maior riqueza de espécies dentro da fauna críptica associada a recifes de coral ao redor do planeta (Bruce, 1976; Reed *et al.*, 1982; Snelgrove & Lewis, 1989; Duffy, 2002). Há registros também de espécies de *Synalpheus* de vida livre, associadas ao fundo marinho ou vivendo entre rochas, cascalho de coral e outros materiais biogênicos, bem como espécies associadas a macroalgas, recifes de coral, colônias de *Phragmatopoma* spp. e, também, em simbiose com ascídias, briozoários, equinodermos e poríferos. Representantes do gênero também ocorrem em manguezais, ocupando galerias na lama, espaços entre raízes de mangue e em madeiras perfuradas por vermes (Ríos & Duffy, 2007; Anker *et al.*, 2012).

Eles são caracterizados por não apresentar epipoditos nos pereiópodos e pelos dactílos dos apêndices não quelados serem biunguiculados (Chace, 1972). Em seus estudos, Coutière (1908; 1909) estabeleceu a existência de seis grupos dentro do gênero que, supostamente, possuem relações evolutivas mais íntimas: *S. brevicarpus*, *S. coutierei*, *S. comatularum*, *S. gambarelloides*, *S. neomeris* e *S. paulsoni*. Mais tarde, Banner & Banner (1975) concluíram que apenas três desses grupos, *S. brevicarpus*, *S. comatularum* e *S. gambarelloides*, apresentavam suporte morfológico suficiente para serem taxonomicamente utilizados. Hultgren *et al.* (2014), por meio de uma abordagem genética utilizando dois marcadores mitocondriais (COI e 16S) e dois nucleares (PEPCK e 18S), também verificaram a existência de suporte para os mesmos grupos. O grupo *S. comatularum* inclui espécies de camarões que vivem associadas, basicamente, a crinoides no Oceano Indo-Pacífico Oeste (Hultgren *et al.*, 2014), sendo caracterizado pela ausência do processo orbitorostral, pela região frontal da carapaça expandida, se estendendo consideravelmente além dos olhos, pelo rostro distintamente mais longo que os dentes orbitais, geralmente possuindo uma crístae e pela ausência de espinhos no mero do terceiro pereiópodo (Banner & Banner, 1975). *Synalpheus gambarelloides* é um grupo encontrado mundialmente, com maior parte de suas espécies sendo encontradas no Atlântico Ocidental (Hultgren *et al.*, 2014). O grupo é caracterizado por apresentar um tufo de cerdas (cerdas gambarelloides) na superfície extensora do dactílo da quela menor, utilizadas para fragmentar o tecido da esponja hospedeira, o qual é utilizado para varrer rapidamente os canais internos da esponja, o que é seguido pela ingestão dos fragmentos resultantes da abrasão (Banner & Banner, 1975; Duffy, 2003). Por fim, o grupo *S. brevicarpus* é encontrado nas Américas e no Pacífico Oriental e se diferencia do grupo *S. comatularum* pela extensão do rostro e dos dentes orbitais, os quais são mais longos em *S. comatularum*, e do grupo *S.*

gambarelloides por não apresentar o tufo de cerdas na superfície extensora do dátilo da quela menor (Banner & Banner, 1975).

Ríos & Duffy (2007), baseando-se em dados morfológicos, ecológicos e moleculares (Morisson et al., 2004), propuseram a elevação do grupo *S. gambarelloides* para um nível genérico, *Zuzalpheus* Ríos & Duffy, 2007, composto, naquele momento, por 34 espécies. Entretanto, Anker & De Grave (2008) propuseram a invalidação de *Zuzalpheus* e consequente sinonimização com *Synalpheus*, baseando-se em fatores como a ausência de trabalhos prévios a respeito do grupo que indiquem a necessidade da elevação de *S. gambarelloides* para o nível de gênero (Coutière, 1909; Banner & Banner, 1975; Dardeau, 1984; Chace, 1988) e na falta de uma comparação morfológica formal entre *S. gambarelloides* e *Synalpheus*. Outros fatores pontuados por Anker & De Grave (2008) para a invalidação *Zuzalpheus* foi o fato de sua diagnose apontar apenas três caracteres morfológicos, que não apresentam suporte significativo, e das variações presentes dentro de *S. gambarelloides* como, por exemplo, no complexo de espécies *Synalpheus paraneptunus* Coutière, 1909. Nas espécies deste complexo, as cerdas gambarelloides são esparsas, diferindo das cerdas encontradas de forma densa como descrito para *Zuzalpheus*, além de o estilocerito alcançar ou, até mesmo, ultrapassar a extremidade distal do primeiro artículo do pedúnculo antenular (vs. não alcançando a extremidade distal deste artículo em *Zuzalpheus*) (Anker & De Grave, 2008).

Ademais, duas das características elencadas por Ríos & Duffy (2007) para ... não estão presentes em todas as espécies de *S. gambarelloides*. Uma delas é o arranjo das cerdas gambarelloides na forma de densos feixes arranjados em uma série de linhas paralelas, havendo casos onde as cerdas são encontradas de forma esparsa na superfície do dátilo (Ríos & Duffy, 2007; Anker & De Grave, 2008). O outro caso se refere ao comprimento do estilocerito, descrito como não alcançando a margem distal do primeiro artículo do pedúnculo antenular; no entanto, existem casos em que o estilocerito alcança o final deste artículo (Ríos & Duffy, 2007; Anker & De Grave, 2008). Além disso, Anker & De Grave (2008) ainda comentam que análises moleculares feitas previamente por Morrison et al. (2004) não evidenciam separação entre *Zuzalpheus* e *Synalpheus*, o que tornaria *Synalpheus* sensu stricto um táxon parafilético.

Parte significativa da diversidade de *Synalpheus* encontra-se na região do Mar do Caribe (Hultgren et al., 2010; Anker et al., 2012). No Brasil, Spence Bate (1888) registrou indivíduos de *Synalpheus* pela primeira vez, também descrevendo *S. minus* (Say, 1818), previamente descrito como *Alpheus minus*. Posteriormente, Coutière (1909), registrou *S. antillensis* Coutière, 1909 (como *S. minus antillensis*) e, depois, Chace (1972) e Christoffersen (1979;

1980; 1998) reportaram várias espécies para o Brasil, como *S. apioceros* Coutière, 1909, *S. brevicarpus* Herrick, 1891, *S. brooksi* Coutière, 1909, *S. fritzmuelleri* Coutière, 1909, *S. hemphilli* Coutière, 1909, entre outras. Outros estudos elaboraram listagens de espécies, algumas das quais trouxeram novos registros e ilustrações de *Synalpheus*, como Almeida et al. (2012), registrando *S. ul* Ríos & Duffy, 2007, e Oliveira et al. (2015), com o primeiro registro de *S. dardeau* (Ríos & Duffy, 2007). Há também descrições de novas espécies, como *S. trinitatis* Anker, Tavares & Mendonça, 2016 (Anker et al., 2016) e *S. ubatuba* Mantelatto, França, Cunha & Almeida, 2023 (Mantelatto et al., 2023). Ademais, também há estudos que comentam sobre a necessidade de revisões em certos grupos taxonomicamente problemáticos, como *S. apioceros*, *S. brevicarpus* e *S. brooksi* e *S. paraneptunus* (e.g. Almeida et al., 2007; Anker et al., 2012; Anker & Pachelles, 2014), o que evidencia a necessidade de mais abordagens taxonômicas envolvendo material da costa brasileira.

Organização social e aspectos biológicos em *Synalpheus*

As formas de organização social encontradas em *Synalpheus* vão variar a depender de certos parâmetros, como o enviesamento reprodutivo, o comportamento social cooperativo, a sobreposição de gerações e o próprio tamanho do agrupamento (Wilson, 1971; Sherman *et al.*, 1995; Bourke, 1999). O enviesamento reprodutivo descreve o grau de desigualdade na reprodução entre indivíduos do mesmo sexo dentro de um grupo, ou seja, o quanto determinados machos e fêmeas reproduzem no agrupamento (Vehrencamp, 1983; Rubenstein, 2012). Em colônias de *Synalpheus*, esse enviesamento é variável, com algumas espécies possuindo várias fêmeas reprodutivas com embriões, indicando baixo enviesamento, enquanto outras apresentam apenas uma fêmea reprodutora, o que caracteriza alto enviesamento reprodutivo (Hultgren *et al.*, 2017).

Já o comportamento social cooperativo engloba ações coordenadas entre membros do grupo, que trazem benefícios para outros integrantes do agrupamento (Hultgren *et al.*, 2017). Em insetos, é comum observar esse comportamento na forma de defesa e cuidado com os jovens, por exemplo (Wilson, 1971; Hultgren *et al.*, 2017). Em *Synalpheus*, embora não haja evidência direta de cuidado parental, a presença frequente de juvenis de *S. brooksi* Coutière, 1909 ao lado de fêmeas ovígeras e machos em esponjas sugere algum nível de interação ou proteção (Hultgren *et al.*, 2017).

Por sua vez, a sobreposição de gerações ocorre quando indivíduos geneticamente relacionados e de diferentes idades compõem um mesmo agrupamento. Essa característica foi observada em várias espécies de *Synalpheus*, com indivíduos de distintos tamanhos convivendo dentro de uma esponja e reagindo a intrusos (Hultgren *et al.*, 2017). Tal comportamento foi sustentado pela presença de aloenzimas no DNA de *S. regalis* Duffy, 1996a (Duffy, 1996b), e em *S. brooksi*, através de análises de microssatélites (Rubenstein *et al.*, 2008).

Além disso, o tamanho do agrupamento refere-se ao número de indivíduos de uma espécie que compartilham o mesmo hospedeiro, frequentemente esponjas (Hultgren & Duffy, 2010). Esse número está fortemente relacionado ao tamanho do hospedeiro, no qual esponjas menores, como as que crescem entre cascalhos de coral, frequentemente abrigam apenas um casal de camarões (Hultgren & Duffy, 2010), enquanto esponjas maiores podem abrigar de dezenas a centenas de indivíduos (Anker *et al.*, 2012).

Os representantes de *Synalpheus* podem ser encontrados formando pares heterossexuais, considerada a condição ancestral de pareamento sexual dentro de Alpheidae (Knowlton, 1980; Mathews, 2002). Entre os táxons que exibem esse pareamento, comportamentos comumente registrados incluem defesa conjunta do território, construção de tocas e confrontos com outros indivíduos, tanto da mesma espécie quanto de espécies diferentes (Mathews, 2002; Duffy, 2007). Apesar dos conflitos, diferentes espécies de *Synalpheus* podem coexistir em grandes esponjas, embora geralmente em pequenos grupos formados por apenas um ou poucos pares (Hultgren *et al.*, 2017).

Assim como em outros gêneros de Alpheidae, fêmeas de *Synalpheus* que formam pares heterossexuais carregam entre dezenas e centenas de embriões que, posteriormente, darão origem a larvas livre-natantes que se afastam dos genitores logo após a eclosão e migram para a coluna d'água (Dobkin, 1965; Duffy & Macdonald, 2010). Essa estratégia reprodutiva inviabiliza a sobreposição de gerações, uma vez que os descendentes não permanecem no mesmo refúgio e não recebem qualquer tipo de cuidado parental após a eclosão (Hultgren *et al.*, 2017).

Esse mesmo tipo de liberação larval também é observado em várias espécies que formam grupos comunais, como *S. carpenteri* Macdonald & Duffy, 2006, *S. herricki* Coutière, 1909 e *S. longicarpus* (Herrick, 1891). Nesses grupos, machos e fêmeas adultos reproduzem-se igualmente, por consequência, apresentando baixo enviesamento reprodutivo (Hultgren *et al.*, 2017). Nesse tipo de agrupamento, foi observada a presença de pares heterossexuais dentro dos mesmos canais das esponjas hospedeiras, o que sugere formação de diferentes pares

reprodutivos com tolerância entre os membros do par. Porém, interações agressivas observadas entre outros indivíduos da mesma espécie, que compartilham o mesmo hospedeiro, indicam baixa complacência com outros integrantes do agrupamento (Hultgren *et al.*, 2017). Esse tipo de organização social, aparentemente, representa um estágio intermediário entre as espécies eussociais e aquelas que formam pares.

A eussocialidade, por sua vez, é um fenômeno raro em ambientes marinhos e foi documentada apenas para algumas espécies de *Synalpheus* associadas obrigatoriamente a esponjas (Duffy, 1996b; Hultgren *et al.*, 2017), o que reforça a ideia de que esse tipo de hospedeiro foi essencial para a evolução desse comportamento (Hultgren *et al.*, 2017). Nessas espécies, observam-se características como alto enviesamento reprodutivo, sobreposição de gerações e defesa cooperativa do hospedeiro, especialmente em certas espécies em que aspectos comportamentais puderam ser observados, além da formação de agrupamentos numerosos (Hultgren *et al.*, 2017). Pelo menos nove espécies Atlânticas ocidentais do grupo *S. gambarelloides* formam colônias eussociais (Hultgren *et al.*, 2017), mas há registros de espécies eussociais fora dessa região geográfica e também, aparentemente, fora do grupo *S. gambarelloides*, com ocorrências na Indonésia (Didderen *et al.*, 2006), no leste da África (Banner & Banner, 1983) e no Mar Vermelho (Banner & Banner, 1981).

Dispersão larval e genética populacional

O conhecimento sobre como a dispersão larval ocorre é importante para avaliar a conectividade entre populações marinhas, incluindo as de crustáceos. De forma geral, espera-se que espécies que possuem alto poder de dispersão larval apresentem maiores conexões entre suas populações, sobretudo quando se trata de similaridades genéticas (Palumbi, 1992; Ituarte *et al.*, 2012). Tal conectividade pode ser definida como a grandeza que há no intercâmbio entre populações, sendo fundamental para a compreensão de aspectos relacionados à dinâmica populacional, estrutura genética e biogeografia de várias espécies (Cowen *et al.*, 2006). Se as larvas têm capacidade de dispersão por longas distâncias, é de se esperar que as mesmas atuem tanto como agentes de colonização quanto promotoras de fluxo gênico entre populações geograficamente distantes. Esse fluxo é, em grande parte, determinado pela interação entre a habilidade de dispersão larval e as correntes oceânicas durante a fase planctônica (Scheltema, 1971; Hamasaki *et al.*, 2015). Entretanto, apesar de algumas espécies possuírem larvas com elevados tempos de desenvolvimento e potencial de dispersão, elas podem apresentar estruturação populacional elevada (Bowen *et al.*, 2006; Kelly & Palumbi, 2010). Isso sugere

que, em ambientes marinhos e costeiros, a estrutura genética das populações nem sempre reflete a capacidade dispersiva das larvas (Burton, 1983; Ituarte et al., 2012; Wieman et al., 2014).

Por se tratar do principal meio de transporte passivo de larvas planctônicas, a atuação de correntes oceânicas é outro fator determinante para o grau de conexão entre populações marinhas (Burton & Feldman, 1982; Burton, 1983). Devido a esse fator abiótico, pode haver favorecimento da dispersão em larga escala, possibilitando o fluxo gênico entre regiões geográficas distantes, inclusive transpassando barreiras oceânicas, ou mesmo a retenção dessas larvas no local onde eclodiram, diminuindo a sua dispersão e, conseqüentemente, a homogeneização das populações de determinada espécie (Santana *et al.*, 2018). Outros fatores por trás da forma como a dispersão dessas espécies ocorrerá são temperatura, salinidade, luz, disponibilidade de alimento e duração do ciclo larval, parâmetros que influenciarão na composição, abundância e diversidade dessas espécies (Anger, 2001; Strathmann *et al.*, 2002; Gibson, 2003; Landeira *et al.*, 2010). Todavia, vale salientar que, mesmo que apresentem elevado potencial dispersivo, esses organismos podem exibir diferentes níveis de estruturação populacional devido a combinação de vários fatores, como barreiras históricas ao fluxo gênico, barreiras ecológicas (e.g., predação, competição e limitação de recursos), barreiras físicas, além do comportamento larval frente a esses estímulos (Burton, 1983; Barber *et al.*, 2000; Hellberg *et al.*, 2002; Palumbi, 2003; Shanks *et al.*, 2003). Além desses fatores, há evidências de que aspectos biológicos também restrinjam a dispersão de espécies marinhas, resultando em padrões de estruturação populacional semelhantes aos modelos de isolamento por distância ou *stepping-stone* (Hellberg, 1994).

OBJETIVOS

OBJETIVO GERAL

Revisar, taxonomicamente e com uma abordagem integrativa, os camarões do gênero *Synalpheus* no litoral do Nordeste do Brasil.

OBJETIVOS ESPECÍFICOS

- Prover um checklist das espécies de *Synalpheus* que ocorrem no Nordeste do Brasil;
- Descrever e delimitar duas novas espécies do grupo *Synalpheus gambarelloides* do Nordeste do Brasil, baseada em dados moleculares e morfológicos;
- Investigar a extensão da estruturação genética previamente observada em *S. hoetjesi* a partir de análises envolvendo o gene mitocondrial COI.

ESTRUTURAÇÃO DA TESE

A tese está dividida em três capítulos, os quais têm por objetivo revisar taxonomicamente os camarões do gênero *Synalpheus* no litoral do Nordeste do Brasil. O capítulo 1 foi publicado na revista “*Zootaxa*” e teve por objetivo prover um checklist atualizado das espécies de *Synalpheus* do Nordeste do Brasil baseadas na revisão de literatura existente, análise de material recentemente coletado e de material advindo de uma das coleções mais importantes da região, o Museu de Oceanografia Prof. Petrônio Alves Coelho, Universidade Federal de Pernambuco, trazendo uma atualização da diversidade conhecida do gênero na região. O capítulo 2 será submetido também para a “*Zootaxa*” e tem por objetivo descrever duas espécies pertencentes ao grupo *Synalpheus gambarelloides* do Nordeste do Brasil, baseada em dados moleculares e morfológicos. Por fim, o capítulo 3 será submetido na revista “*Marine and Freshwater Research*” e tem por objetivo investigar a extensão da estruturação genética previamente observada em *S. hoetjesi* a partir de análises envolvendo o gene mitocondrial COI, evidenciando a diferenciação existente entre essas populações.

ARTIGO CIENTÍFICO 1 – SHRIMPS OF THE GENUS *SYNALPHEUS* SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) FROM NORTHEAST BRAZIL REGION

Manuscrito publicado na revista *Zootaxa* (2025)

Referência: Shrimps of the genus *Synalpheus* Spence Bate, 1888 (Decapoda: Alpheidae) from Northeast Brazil region. *Zootaxa*, 5666(1), 1-52.

doi: <https://doi.org/10.11646/zootaxa.5666.1.1>

Abstract

The aim of this study was to provide a commented catalogue of the snapping shrimp species belonging to the genus *Synalpheus* Spence Bate, 1888 from Northeast Brazil region, a 3,300 kilometers long tropical coast. The material examined was collected from various sites along the coast of the state of Pernambuco, as well as from the archipelagos of Fernando de Noronha and São Pedro e São Paulo. Additionally, specimens deposited in the crustacean collection of the Museu de Oceanografia Prof. Petrônio Alves Coelho (MOUFPE) were also examined. A total of 1010 individuals belonging to 26 species were analyzed. This study provides six new records for the southwestern Atlantic [*Synalpheus barahonensis* Armstrong, 1949, *S. belizensis* Anker & Tóth, 2008, *S. brevidactylus* Anker & Tóth, 2008, *S. corallinus* Macdonald, Hultgren & Duffy, 2009, *S. hoetjesi* Hultgren, Macdonald & Duffy, 2010, and *S. kensleyi* (Ríos & Duffy, 2007)] and 13 range extensions/new records [(*S. agelas* Pequegnat & Heard, 1979, *S. androsi* Coutière, 1909, *S. antillensis* Coutière, 1909, *S. dardeau* (Ríos & Duffy, 2007), *S. fritzmuelleri* Coutière, 1909, *S. hemphilli* Coutière, 1909, *S. herricki* Coutière, 1909, *S. pandionis* Coutière, 1909, *S. ruetzleri* Macdonald & Duffy, 2006, *S. tenuispina* Coutière, 1909, *S. townsendi* Coutière, 1909, *S. ubatuba* Mantelatto, França, Cunha & Almeida, 2023, and *S. yano* (Ríos & Duffy, 2007))] along the Brazilian coast. Some of these records were confirmed using molecular data (ribosomal 16S gene). Moreover, comments regarding doubtful records in the study area (*S. filidigitus* Armstrong, 1949, *S. longicarpus* (Herrick, 1891), *S. paranephtunus* Coutière, 1909, and *S. rathbunae* Coutière, 1909) are also provided. Taking into account the exclusion of the doubtful records, our data increases from 27 to 29, and from 29 to 31 species, recorded in the study area and along the Brazilian coast, respectively.

Keywords: caridean shrimps, Fernando de Noronha Archipelago, new records, southwestern Atlantic, sponge-associated fauna.

Introduction

Synalpheus Spence Bate, 1888 comprises a set of small-sized and cryptic caridean shrimp species, including both free-living forms and commensals associated with corals, sea anemones, sea urchins, and particularly, crinoids and sponges (Bruce 1976; VandenSpiegel et al. 1998; Duffy & Macdonald 1999; Anker et al. 2012). *Synalpheus* shrimps represent one of the most abundant and diverse groups within the cryptic coral reef fauna worldwide (Bruce 1976; Reed et al. 1982; Chace 1989; Snelgrove & Lewis 1989; Duffy 2003). Members of the *Synalpheus gambarelloides* group exhibit a symbiotic relationship with sponges, feeding on host tissue or food particles circulating through the sponge's channels (Dardeau 1984; Duffy 1996a; Ríos & Duffy, 2007; Hultgren & Duffy 2010). Members of this group are characterized by a dense brush of setae on the dorsal surface of the minor chela of the dactylus (Banner & Banner 1975), used to fragment the host's tissue by rapidly sweeping the sponge's internal canals and then ingesting them (Duffy 2003). These distinctive traits highlight the biological importance of *Synalpheus* species, particularly within their ecological niches.

Synalpheus species also exhibit a diverse range of social organization that can vary based on demographic characteristics, such as group size and the number of reproductive females in each colony (Chak et al. 2017). Species that form heterosexual pairs live as solitary breeding pairs, and this pairing behavior probably represents the ancestral state of social organization within alpheidids (Knowlton 1980; Hultgren et al. 2017). Communal species inhabit sponges in groups of multiple unrelated breeding pairs, with an approximately equal sex ratio of adult males and females. However, the social behaviors of these groups are not well understood (Hultgren et al. 2017). Eusocial species typically consist of one or a few queens and hundreds of non-reproductive workers, likely siblings and offspring of the queen (Duffy 1996b). Worker shrimps defend their host sponge against intruders and, in some species, exhibit both behavioral and morphological changes (Duffy 1996b; Duffy et al. 2002; Tóth & Duffy 2005, 2008; Chak et al. 2015). Additionally, “subsocial” groups have been reported, where immature offspring remain in the host sponge under the mother's care, forming a group of related individuals that do not reproduce and display less developed social behaviors (Michener 1969; Boomsma 2009; Anker et al. 2012).

Synalpheus is the second-largest genus in terms of species richness within the family Alpheidae, comprising 173 valid species, nearly half of them found in the Atlantic Ocean (De Grave & Fransen 2011; Anker et al. 2012; Anker & Pachtelle 2014; WoRMS 2025). Many of

the most recent studies on the genus have been carried out in the Caribbean Sea, a region that harbors a significant portion of the known *Synalpheus* species richness (e.g., Anker et al. 2012; Cházaro-Olvera & Vázquez-López 2014; Cházaro-Olvera *et al.* 2017; De Grave & Anker 2017; Velásquez *et al.* 2017; Ashrafi & Hultgren 2022). In Brazil, research on the group started with Spence Bate (1888), who described *S. minus* (Say, 1818) (as *Alpheus minus*), with the type locality in the state of Bahia, and Coutière (1909), who recorded of *S. antillensis* Coutière, 1909 (as *S. minus antillensis*) also in Bahia. After several decades without any update to the Brazilian *Synalpheus* fauna, Chace (1972) and Christoffersen (1979, 1980, 1998) documented several species to the area, such as *S. apioceros* Coutière, 1909, *S. brevicarpus* Herrick, 1891, *S. brooksi* Coutière, 1909, *S. fritzmueelleri* Coutière, 1909, *S. hemphilli* Coutière, 1909, among others. Other contributions to the Brazilian fauna include species checklists, which often report new records and provide illustrations of local specimens [e.g., *S. ul* (Ríos & Duffy, 2007) by Almeida *et al.* (2012); *S. dardeau* (Ríos & Duffy, 2007) by Oliveira *et al.* (2015)]. There are also studies describing new species, such as *S. maxillispinus* Anker & Pachelles, 2014, from Abrolhos Archipelago, Bahia (Anker & Pachelles, 2014), *S. trinitatis* Anker, Tavares & Mendonça, 2016, described from Trindade Island, Espírito Santo (Anker et al. 2016), and *S. ubatuba* Mantelatto, França, Cunha & Almeida, 2023, described from São Paulo and Bahia (Mantelatto et al. 2023). Finally, some studies highlight the need for taxonomic revision of potential species complexes, such as *S. minus* and *S. apioceros* (Almeida *et al.* 2007; Anker *et al.* 2012; Anker & Pachelles 2014).

Currently, 29 species of *Synalpheus* have been recorded from the Brazilian coast. Some of them have been widely recorded (e.g., *S. apioceros* and *S. minus*), whereas others have been recorded only once (e.g., *S. curacaoensis* Schmitt, 1924; *S. filidigitus* Armstrong, 1949, *S. paranepetunus* Coutière, 1909) (Christoffersen 1979, 1998; Ramos- Porto *et al.* 1996; Bezerra & Coelho 2006; Coelho *et al.* 2006; Coelho-Filho 2006; Almeida *et al.* 2012; Anker *et al.* 2012, 2016; Mantelatto *et al.* 2023). However, many of these records require confirmation. This uncertainty stems from the morphological similarities among certain species, which may represent complexes of cryptic species (Anker *et al.* 2012). Additionally, some records were published without illustrations of diagnostic features or detailed morphological descriptions, further complicating species verification.

Northeast Brazil encompasses a vast tropical coastline spanning approximately 3,300 kilometers, extending from western Maranhão to southern Bahia. This region includes notable

archipelagos such as São Pedro e São Paulo (0°55'N 29°20'W), Fernando de Noronha (03°51'N 35°25'W), and Abrolhos (18°19'N 39°40'W), along with the Rocas Atoll (3°45'–3°56'S 33°37'–33°56'W) and the North Chain seamounts (01°00'–04°00'S 37°00'–39°00'W; 03°00'–04°30'S 32°00'–37°00'W) (Coelho *et al.* 2008). This coastal area includes diverse ecosystems, including sandy beaches, estuaries, mangroves, seagrass beds, and coral reefs (Brasil n.d., n.p.; Cerqueira *et al.* 2018). Many of these habitats host a rich diversity of sponges (Muricy & Moraes 1998; Moraes *et al.* 2003), which provide ideal conditions for the occurrence of *Synalpheus*. To date, 27 species of *Synalpheus* have been recorded in this region (e.g., Chace 1972; Christoffersen 1979, 1998; Ramos-Porto *et al.* 1996; Bezerra & Coelho 2006; Coelho *et al.* 2006; Coelho-Filho 2006; Ríos & Duffy, 2007; Anker *et al.* 2012, 2016; Anker & Pachelle 2014). Despite this environmental richness, the diversity of *Synalpheus* in the area is likely underestimated. This study aims to provide an updated checklist of *Synalpheus* species from Northeast Brazil, based on a review of existing literature, the analysis of recently collected material, and material deposited in the most important crustacean collection of the region, the Museu de Oceanografia Prof. Petrônio Alves Coelho, Universidade Federal de Pernambuco. Additionally, we provide illustrations and molecular data to support our findings, along with a discussion of uncertain records.

Material and Methods

Sampling of new material was conducted primarily at various locations in the state of Pernambuco, including Baía de Suape in the municipality of Cabo de Santo Agostinho, Praia dos Carneiros in Tamandaré, Praia de Ponta de Pedras in Goiana, and the continental shelf off Recife, within an approximate 35 kilometer wide segment from the coast. Additional collections were made in the Fernando de Noronha Archipelago and the São Pedro e São Paulo Archipelago (Fig. 1). To account for the ecological diversity of *Synalpheus*, multiple sampling methods were employed, ensuring a thorough representation of the diverse substrates that these organisms inhabit. Figure 2 shows the main collection methods and sampling locations.

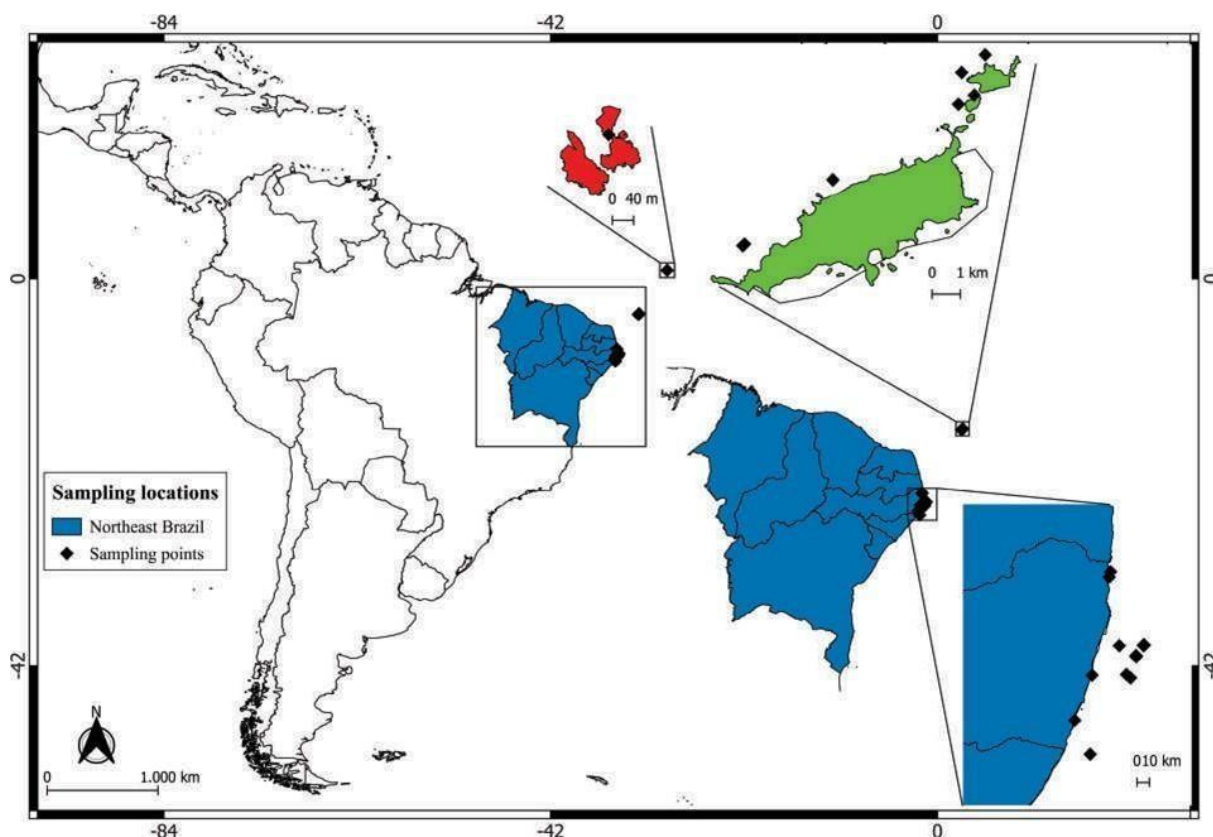


FIGURE 1. Map of collection sites. The blue background indicates the Northeastern region of Brazil; the green area represents the Fernando de Noronha Archipelago; the red area represents the São Pedro e São Paulo Archipelago; black diamonds mark the sampling locations.

SCUBA diving was used to collect sponges and other substrates, such as coral rubble, dead corals, coralline algae, seagrass banks, and perforated rocks, with potential to harbor *Synalpheus* shrimps at Baía de Suape, Praia de Carneiros, and Fernando de Noronha, as well as to install artificial refuge structures (ARS) at Baía de Suape and Praia de Carneiros. The ARS were placed at depths of 3 to 5 meters in reef areas sheltered from wave action and retrieved after approximately three months. Adapted from Almeida *et al.* (2018a), the ARS consisted of cube-shaped cages (25×25 cm) made of plastic canvas, filled with five sets of three plastic tubes (flat conduits; 1.5 cm in diameter), plus five sets of three plastic tubes (plain conduits; 2 cm in diameter), 10 plastic tubes (plain conduit; 2.5 cm in diameter), and six sets of three 25×25 cm plastic screens (“sombrite”). All plastic tubes were 12 cm long. The structures were secured to rocks with ropes and wrapped in plastic bags during retrieval to prevent shrimp loss. Sampling in Fernando de Noronha was conducted at depths ranging from 4 to 24 meters. At Praia de Ponta de Pedras, samples were collected via free diving at depths of up to one meter. Substrates, primarily sponges, were sorted and fragmented on a sieve using tweezers. The extracted shrimps were separated, preserved in 70% alcohol, and labeled appropriately.

Collections on the continental shelf off Recife were conducted using a motorized vessel 10 m long and 3 m wide, equipped with a dredging system. A trawl dredge measuring 80×40×75 cm (Fig. 2F) was employed to sample material at depths ranging from 50 to 65 meters. Sampling occurred at 32 stations across three campaigns: Campaign I (REC I) on February 7, 2018, with 13 stations; Campaign II (REC II) on February 27, 2018, with 11 stations; and Campaign III (REC III) on May 10, 2018, with 8 stations. The average dredging time was 10 minutes but varied depending on how long it took to fill the dredge. The most common substrates collected included sponges, calcareous algae, coral rubble, rhodoliths, and sand of varying grain sizes (Fig. 3). After each dredging, the material was placed in insulated containers, labeled, and transported to the laboratory. The endolithic fauna was carefully extracted by fragmenting the substrates using a hammer and chisel.

The sampled material was deposited in the collections of the Museu de Oceanografia Prof. Petrônio Alves Coelho, Universidade Federal de Pernambuco (MOUFPE), and in the Coleção de Crustáceos do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul (DZ/UFRGS). Material obtained from different sponges was catalogued under separate accession numbers, even when collected at the same locality and on the same date. This was done in order to preserve the association data between the shrimps and their respective hosts. The specimens deposited at the MOUFPE, obtained from several localities along the Northeast Brazil states (Maranhão, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Sergipe and Bahia) as well as in São Pedro e São Paulo and Fernando de Noronha, were also analyzed and included therein. New records of *Synalpheus* species for the study area are highlighted in bold in the distribution section of the Results. Additionally, this study incorporates literature records published up to 2024, excluding unpublished sources (e.g., theses) and conference proceedings. Doubtful species records were evaluated (see ‘Misidentifications and Doubtful Records’ in the Discussion section) and excluded from the checklist. The ‘Ecology’ section of the Results includes information from the literature (e.g., hosts, sociobiology, bathymetry) as well as complementary data obtained in the present study. Depth records representing new bathymetric ranges are also indicated in bold within the ‘Ecology’ section.

Shrimps were identified based on available taxonomic keys (e.g., Chace 1972; Abele & Kim 1986; Anker *et al.* 2012) and original species descriptions. We used “cf.” [e.g., *S. cf. brevicarpus* (Herrick, 1891)] when the material examined in this study presented significant morphological variations regarding the species description. In some cases, information such as

geographic coordinates and collection date and depth was missing (e.g. in cases of material from environmental consultancy activities deposited at the MOUFPE collection).

In *Synalpheus* species, the *appendix masculina* is absent from the endopod of the second pleopods, a structure that typically distinguishes males from females in many caridean shrimps (Bauer 2004). Therefore, sex determination in this study relied on alternative characteristics. These included the presence of an ovigerous mass beneath the pleon and/or ovigerous setae, features exclusive to females (Bauer 2004), as well as the shape of the pleura on the first pleonal segment, which is rounded in females and ventrodistally projected or hook-shaped in males (Banner & Banner 1975). Specimens were categorized as males (M), ovigerous females (OV), non-ovigerous females (F), or as individuals with sex not-identified (NI) if they were damaged and lacked a pleon. Additionally, the abbreviations (St.) and (m) were used to denote station of collection and meters, respectively.

To prepare the drawings, the shrimps were placed on a Petri dish containing 70% alcohol and photographed under a stereomicroscope using an image capture system (Leica EZ4). Subsequently, the images were transferred to CorelDRAW software version 21.0.0.593 for vectorization.

For some species, we obtained DNA sequences that aided in their identification. DNA extraction was performed from the pleonal muscle of the specimens using a Qiagen Extraction Kit, following the manufacturer's recommendations. A segment of approximately 600 base pairs from the 16S mtDNA gene was amplified from the extracted DNA using a polymerase chain reaction (PCR) with the primers 16Sbr (CCGGTCTGAACTCAGATCACGT) and 16Sar (CGCCTGTTTATCAAAAACAT) (Palumbi & Benzie 1991). PCR was performed under the following conditions: initial denaturation at 95°C for 5 min; annealing in 40 cycles of 95°C for 45 s, 46°C for 45 s, 72°C for 1 min, and final extension at 72°C for 3 min. The reagents used in PCR and their respective quantities per sample were: betaine (5µl), dNTP (4µl), buffer (3µl), MgCl₂ (3µl), primers (1µl of each), and Taq DNA polymerase (0.5µl). The PCR products were purified using the ExoSAP-IT Kit, following the manufacturer's recommendations, and sent to the company ACTGENE Análises Moleculares Ltda. for sequencing. Sequences of both DNA strands were obtained, and the consensus sequence was determined using the Bioedit 7.0.5 computer program (Hall 2005) and manually checked to correct any non-specific readings, as

necessary. The obtained sequences were compared with sequences available in GenBank using the BLAST tool (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>).

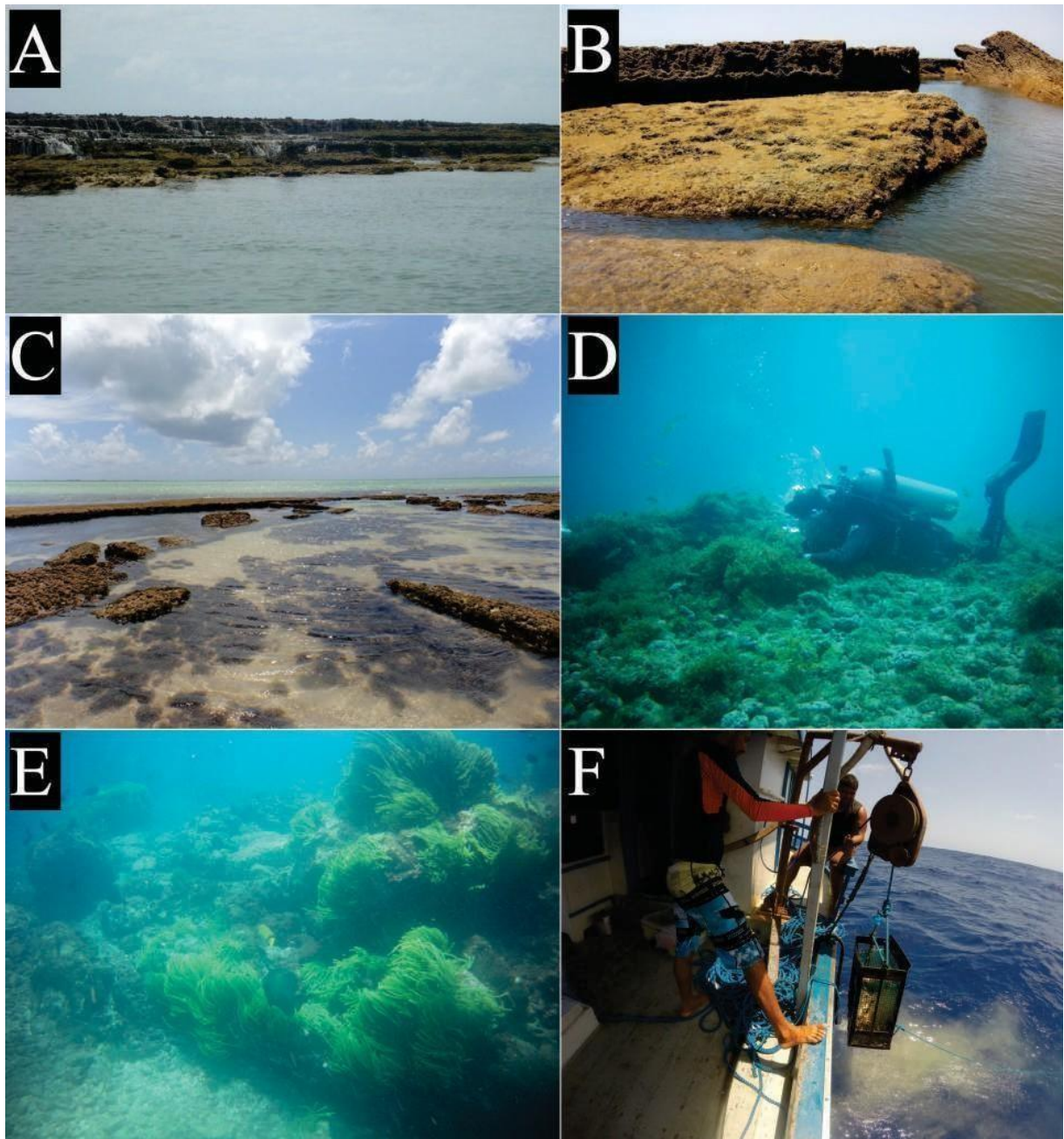


FIGURE 2. Sampling locations of specimens of *Synalpheus* Spence Bate, 1888 analyzed in this study. A, Baía de Suape, Cabo de Santo Agostinho, Pernambuco; B, Praia dos Carneiros, Tamandaré, Pernambuco; C, Praia de Pontas de Pedra, Goiana, Pernambuco; D, Fernando de Noronha Archipelago, Pernambuco; E, São Pedro e São Paulo Archipelago, Rio Grande do Norte; F, Dredging on the continental shelf off Recife, Pernambuco. Photos: A, B, E—G.L. Bochini; C—T.E.R. Cavalcanti; D—K. Pasinato; F—P.H. Paixão.

Sequences from morphologically similar species were obtained from GenBank to construct a phylogram. The final sequences were aligned using the Muscle method (Edgar 2004), implemented on the Cyberinfrastructure for Phylogenetic Research (CIPRES) platform

(Miller *et al.* 2010). A Maximum Likelihood analysis was performed using the RAxML program (Stamatakis 2014), implemented on the CIPRES platform with the GTR standard model. The consistency of the topologies was measured using the bootstrap method, and the tree was visualized and edited using the Mega 7 software (Kumar *et al.* 2016). Only support values above 50% were shown. The new sequences were deposited in GenBank and the accession numbers are provided in the phylogram.

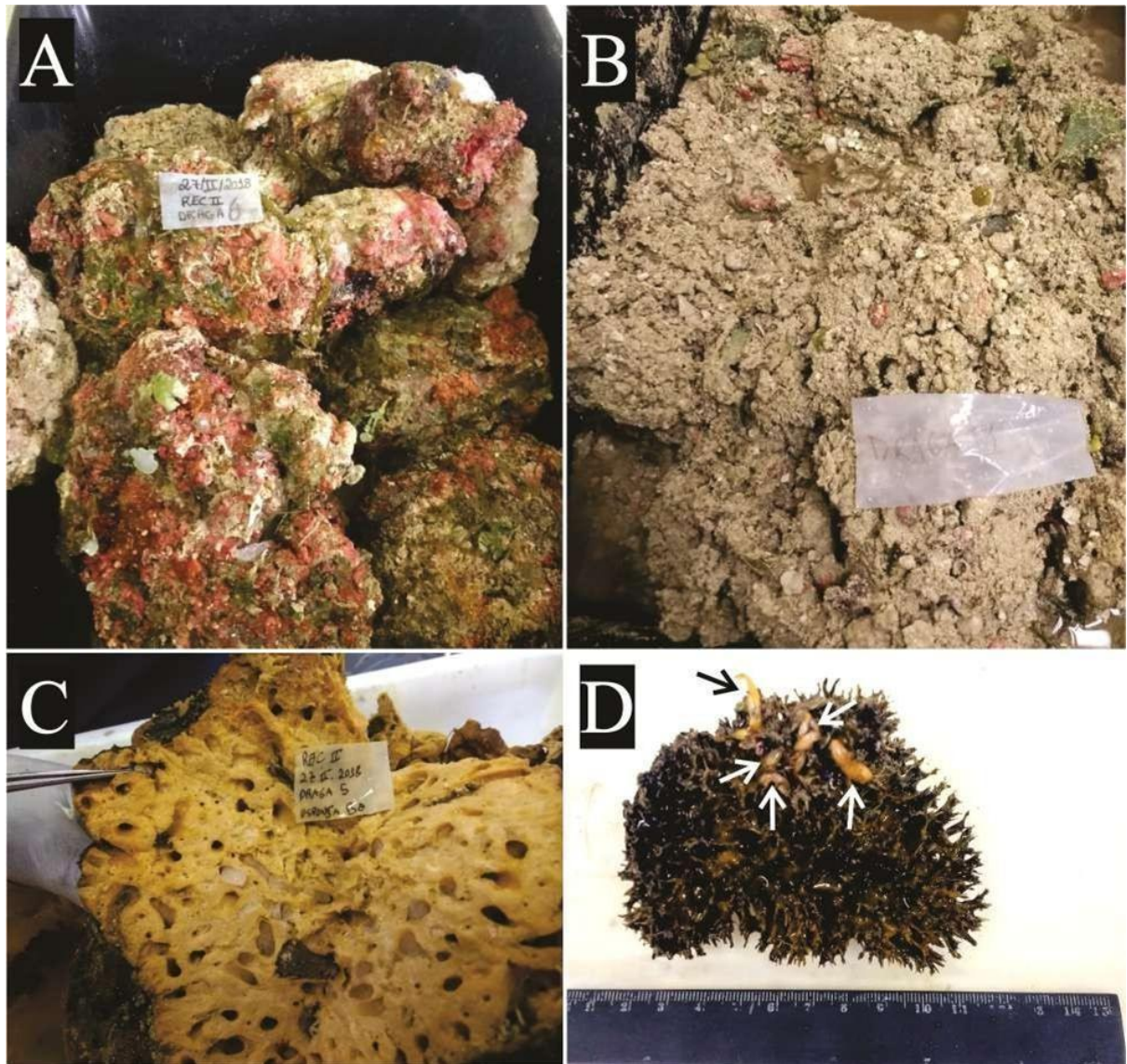


FIGURE 3. Substrates where the specimens of *Synalpheus* Spence Bate, 1888 analyzed in this study were found. A, Rhodoliths; B, Sediment; C, Sponge where the colony of *S. brooksi* Coutière, 1909 was found; D, Sponge morphotype where the possible communal groups of *S. hoetjesi* Hultgren, Macdonald & Duffy, 2010 and *S. ul* (Ríos & Duffy, 2007) were found, arrows indicate the presence of shrimps. Photos A–D: P.H. Paixão.

Results

A total of 1010 individuals from 26 different species were analyzed.

Alpheidae Rafinesque, 1815

***Synalpheus* Spence Bate, 1888**

***Synalpheus* cf. *africanus* Crosnier & Forest, 1965**

Material examined: None.

Description: Anker *et al.* (2012).

Distribution: Eastern Atlantic: São Tomé and Príncipe. Western Atlantic: Panama (Bocas del Toro), Dominican Republic (Bayahibe), Aruba and Brazil (Rocas Atoll) (Anker *et al.* 2012).

Ecology: In cavities of dead eroded corals and in coralline algae; in heterosexual pairs; up to 2 m (Anker *et al.* 2012).

Remarks: The amphi-Atlantic *S. africanus* is morphologically very similar to *S. tenuispina* (Coutière, 1909) (see Anker *et al.* 2012). However, Anker *et al.* (2012) reported genetic differences between specimens from São Tomé and Príncipe (a male and an ovigerous female) and a typical *S. africanus* specimen from the eastern Atlantic. Additionally, the authors noted that materials from Rocas Atoll, Aruba, and Panama exhibit characteristics more consistent with *S. africanus* than *S. tenuispina*, particularly regarding the length of the scaphocerite and the shape of the rostrum (Anker *et al.* 2012). Specimens from these regions were also found to be significantly smaller than the type material of *S. tenuispina*. According to Anker *et al.* (2012), a more comprehensive study, encompassing both morphological and genetic analysis, must be conducted to address the taxonomic issues associated with these taxa.

***Synalpheus agelas* Pequegnat & Heard, 1979**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 27.ii.2018, 8°13'52.1"S 34°37'39.1"W, 50.8 m depth, in sponge, DZ/UFRGS 7049; 1 M, same data as DZ/UFRGS 7049, in sponge, MOUFPE 21542; Fernando de Noronha: 2 M, 6 F, Ressureta, 19.vi.2019,

03°49.191'S 32°23.847'W, 8.0 m depth, in sponge, DZ/UFRGS 6710; 2 M, 3 F, Cagaras, 25.vi.2022, 03°50.933'S 32°26.178'W, 13.0 m depth, in sponge, DZ/UFRGS 7025; 1 M, 3 F, Ressureta, 25.vi.2022, 03°50.933'S 32°26.178'W, 8.0 m depth, in sponge, DZ/UFRGS 7028; 3 M, 3 OV, 5 F, Buraco do Inferno, 26.vi.2022, 03°48.968'S 32°23.577'W, 12.0 m depth, in sponge, DZ/UFRGS 7029; 10 M, 3 OV, 6 F, Ilha do Meio, 26.vi.2022, 03°49.015'S 32°23.549'W, 11.0 m depth, in sponge, DZ/UFRGS 7035; 6 M, 4 OV, 2 F, Ponta da Sapata, 30.vi.2022, 03°51.892'S 32°27.965'W, 11.0 m depth, in sponge, DZ/UFRGS 7040; 9 M, 4 OV, 1 F, Laje Dois Irmãos, 30.vi.2022, 03°51.859'S 32°27.934'W, 17.0 m depth, in sponge, DZ/UFRGS 7044.

Description: Pequegnat & Heard (1979), Ríos & Duffy (2007), and Anker *et al.* (2012).

Distribution: Gulf of Mexico, Puerto Rico, Cuba, Belize, Jamaica, Panama, Curaçao, Barbados, and Brazil (**Fernando de Noronha**, Rocas Atoll, seamounts of North Chain, Trindade & Martin Vaz Archipelago, and from Amapá to Espírito Santo) (Coelho-Filho 2006; Ríos & Duffy, 2007; Hultgren *et al.* 2011; Anker *et al.* 2012, 2016; this study).

Ecology: In coral reefs, coral rubble, and similar habitats in sublittoral areas with sponges abundant; commonly inhabiting sponges of the genus *Agelas* Duchassaing & Michelotti, 1864 (Anker *et al.* 2016); forming heterosexual pairs; 5–80 m (Anker *et al.* 2016; this study). Sampled at continental shelf off Recife (DZ/UFRGS 7049; MOUFPE 21542) in a substrate of sediment, macroalgae, coral rubble, and sponges.

Remarks: The examined material was sampled at a depth of 8 m in Fernando de Noronha and between 50.8 and 80 m on the continental shelf off Recife, extending the bathymetric range of this species from 56 m (Anker *et al.* 2016) to 80 m. One specimen (male, DZ/UFRGS 7044) exhibited a slight morphological variation in the fixed finger of the major chela, which was much shorter than the dactylus (vs. slightly shorter in length in Pequegnat & Heard 1979) (see Pequegnat & Heard 1979, Figs. 3A, B).

***Synalpheus androsi* Coutière, 1909 (Fig. 4)**

Material examined: Maranhão—Turiaçu: 1 M, Nordeste Expedition II, St. 111/112, MOUFPE 12510; Pernambuco—Continental Shelf off Recife: 1 M, 1 OV, 10.v.2018, 08°23'04.3"S

34°40'07''W, 80.0 m depth, in sponge, DZ/UFRGS 7050; Bahia—Salvador: 1 M, Almirante Saldanha Expedition, St. 1981, 23.ix.1968, 13°48.5'S 38°48.5'W, 49.0 m depth, MOUFPE 9212.

Description: Coutière (1909), Ríos & Duffy (2007), Anker & Pachelle (2014).

Distribution: Bahamas (Andros Island), Belize (Carrie Bow Cay), Jamaica, Barbados and Brazil (**Maranhão, Pernambuco**, Bahia and Espírito Santo: Vitória-Trindade chain) (Coutière, 1909; Dardeau 1984; Coelho *et al.* 2006; Ríos & Duffy, 2007; Macdonald *et al.* 2009; Hultgren *et al.* 2011; Anker & Pachelle 2014; this study).

Ecology: In association with sponges [e.g., *Aiolochoira crassa* (Hyatt, 1875), *Hyattella intestinalis* Lamarck, 1814, *Hymeniacidon caerulea* Pulitzer-Finali, 1986]; solitarily or in heterosexual pairs; 14–**80 m** (Anker & Pachelle 2014; Ríos & Duffy, 2007; this study). Sampled at the continental shelf off Recife (DZ/UFRGS 7050) in association with an unidentified sponge.

Remarks: *Synalpheus androsi* can be identified by the distinct morphology of the third pair of pereopods, which display a noticeable concavity on the flexor margins of the merus, carpus, and propodus (see Fig. 4B) (Coutière, 1909; Ríos & Duffy, 2007). This study extends the known bathymetric range of the species from 55 m (Anker & Pachelle 2014) to 80 m.

***Synalpheus antillensis* Coutière, 1909**

Material examined: Maranhão—Turiaçu: 1 M, Almirante Saldanha Expedition, St. 1751, 06.xi.1967, 00°37.0'S 44°40.0'W, 44.0 m depth, MOUFPE 8795; Pernambuco—Goiana: 1 M, 1 OV, Praia de Pontas de Pedra, 07°37'00''S 34°48'51''W, 1.0 m depth, in the sponge *Haliclona implexiformis* Hechtel, 1965, MOUFPE 21600; Sergipe—2 M, Plataforma Pcm11 Pós. Face Externa Pé: Fora Superfície Externa, MOUFPE 15791; Bahia—1 M, Nordeste Expedition III, St. 181, MOUFPE 13050.

Description: Coutière (1909), as *Synalpheus minus antillensis*, and Anker *et al.* (2012).

Distribution: Gulf of Mexico (off Texas), Caribbean Sea (from Yucatan Peninsula to Venezuela), and Brazil (Abrolhos, Rocas Atoll, Trindade Island, **Maranhão** and from Ceará to São Paulo) (Anker *et al.* 2012, 2016; Soledade *et al.* 2015; this study).

Ecology: In coral reefs, coral rubble, coralline algae, and sponges (e.g., *Ircinia* sp.); mostly in heterosexual pairs; intertidal to 42 m (Anker *et al.* 2012, 2016). The material from Goiana, Pernambuco (MOUFPE 21600), was found in heterosexual pairs inhabiting coral rubble and sponges (*H. implexiformis*).

Remarks: This species is recorded in association with the sponge *H. implexiformis* for the first time.

***Synalpheus apioceros* Coutière, 1909**

Material examined: Maranhão—São José de Ribamar: 1 F, Praia de Araçagi, MOUFPE 9111; Pernambuco—Cabo de Santo Agostinho: 2 F, Baía de Suape, 8°21'54"S 34°56'50"W, MOUFPE 21871; Goiana: 1 M, 1 OV, Milênio Project, St. 03, Rio Carrapicho, 11.ii.2004, MOUFPE 15783; 1 M, Praia de Pontas de Pedra, 07°37'00"S 34°48'51"W, 1.0 m depth, MOUFPE 21873; Ilha de Itamaracá: 1 M, MOUFPE 8897; Paulista: 1 M, Praia de Maria Farinha, MOUFPE 8788; Continental Shelf off Recife: 1 M, 07.ii.2018, 8°08'51.5"S 34°34'08.0"W, 65.0 m depth, in sponge, MOUFPE 21803.

Description: Coutière (1909) and Anker *et al.* (2012).

Distribution: USA (Florida), Gulf of Mexico, Bahamas, Caribbean Sea, Suriname, and Brazil (from Amapá to Santa Catarina and seamounts of the North Chain) (Chace 1972; Lemaitre 1984; Christoffersen 1998; Coelho-Filho 2006; Anker *et al.* 2012).

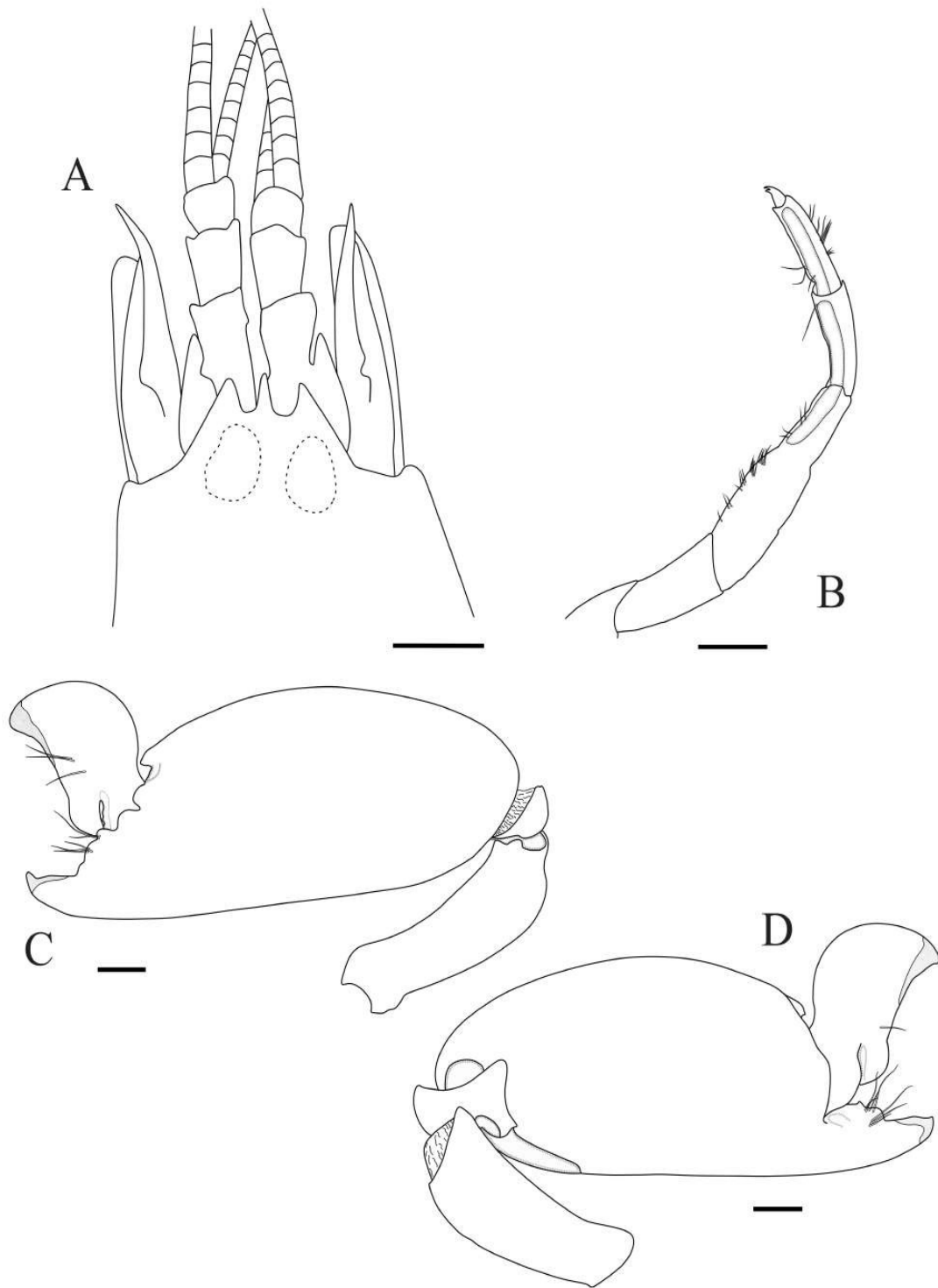


FIGURE 4. *Synalpheus androsi* Coutière, 1909: female from the continental shelf off Recife, Pernambuco, Brazil [DZ/UFRGS 7050]. A, frontal region, dorsal view; B, third pereopod, left side, lateroventral view; C, major chela, right side, mesial view; D, same, lateral view. Scale bars: 0.5 mm.

Ecology: On rocky shores with high concentration of sponges, ascidians and coral rubble; in crevices of coral rocks, among ascidians, bryozoans and sponges; in mangrove areas, either among the roots or in shipworm- perforated mangrove wood; mostly in heterosexual pairs; intertidal to **65 m** (Pequegnat & Ray 1974; Rodríguez 1980; Anker *et al.* 2012; this study).

Remarks: The present study extends the known bathymetric depth of *S. apioceros* from 20 m (Pequegnat & Ray 1974) to 65 m. This species exhibits notable morphological variation and has been suggested as a potential species complex (Anker *et al.* 2012). Further studies are required to comprehensively assess the extent of morphological variation within what is currently recognized as *S. apioceros*.

***Synalpheus barahonensis* Armstrong, 1949 (Figs. 5, 6)**

Material examined: Pernambuco—Continental Shelf off Recife: 2 M, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, DZ/UFRGS 7066 (genetic voucher, GenBank access PV273119); 1 F, same data as DZ/UFRGS 7066, in sponge, MOUFPE 21870.

Description: Armstrong (1949).

Distribution: Dominican Republic, Panama, **Brazil (Pernambuco)** (Armstrong, 1949; Duffy 1992; this study).

Ecology: In association with the coral *Agaricia agaricites* Linnaeus, 1758, and in coral rubble (Armstrong, 1949; Duffy 1992); **50.6 m** (Dardeau 1984; De Grave & Anker 2017; this study). Sampled at continental shelf off Recife (DZ/UFRGS 7066; MOUFPE 21870) in association with unidentified sponges.

Remarks: *Synalpheus barahonensis* is characterized by the presence of four articles in the carpus of the second pair of pereopods (Fig. 5F), the basicerite unarmed dorsally, and a ventrolateral spine almost equal in length to the distolateral tooth of the scaphocerite (Fig. 5A; Armstrong, 1949, Fig. 7). Additional characters include the tip of the ultimate article of the third maxilliped bearing a series of setae (Fig. 6D) [vs. a set of spiniform setae, as in most *Synalpheus* species (Ríos & Duffy, 2007; Anker *et al.* 2012)], and the second to fifth pleurae of males tapering to a sharp point ventrally (Armstrong, 1949; Dardeau 1984). The species is considered rare (De Grave & Anker 2017) and remains poorly understood in terms of biological aspects. This study represents the first record of *S. barahonensis* in the southwestern Atlantic, and provides the initial data on its depth range (50.6 m), and offers the first 16S gene sequence information for the species.

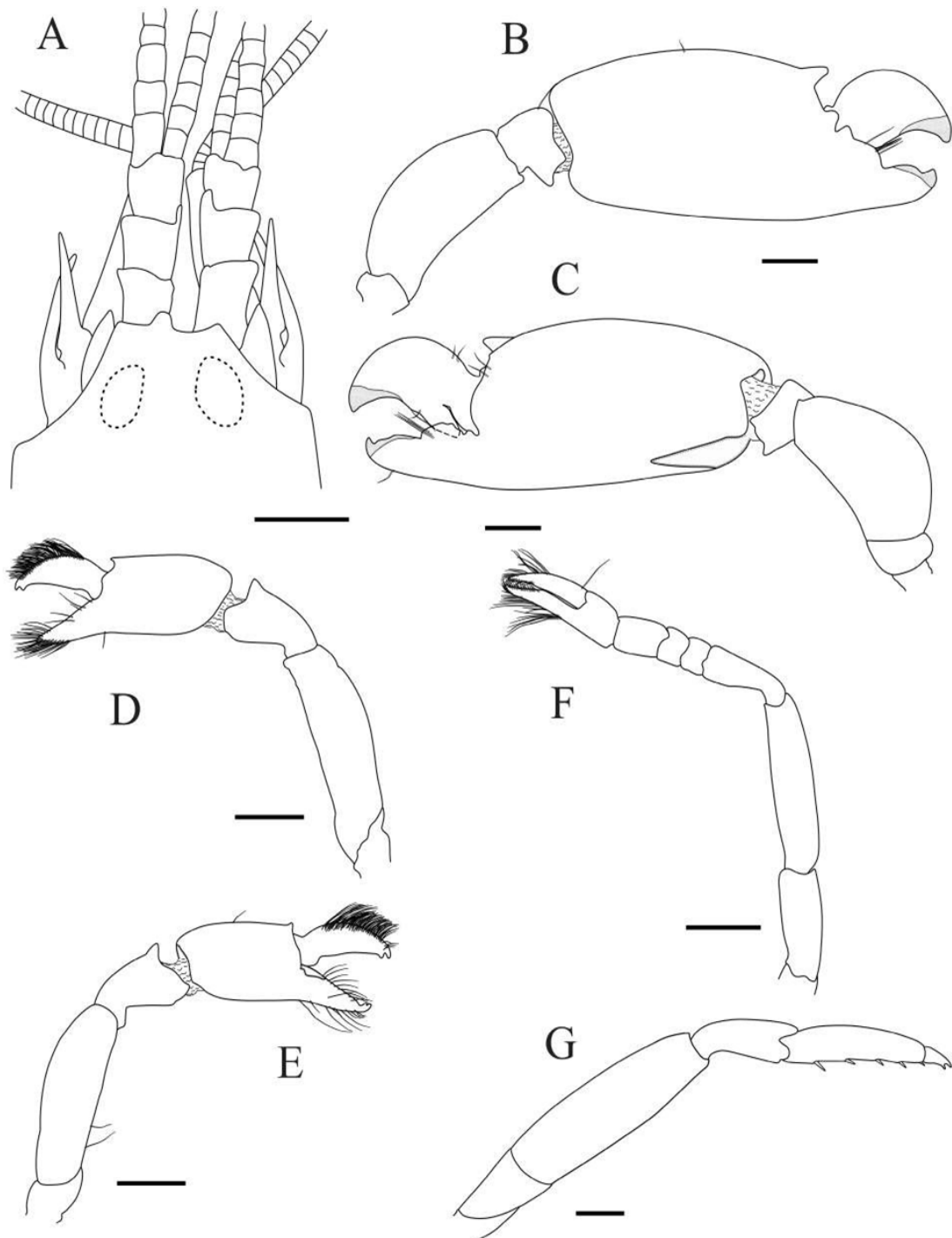


FIGURE 5. *Synalpheus barahonensis* Armstrong, 1949: female from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21870]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, left side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–F, 0.5 mm; G, 0.3 mm.

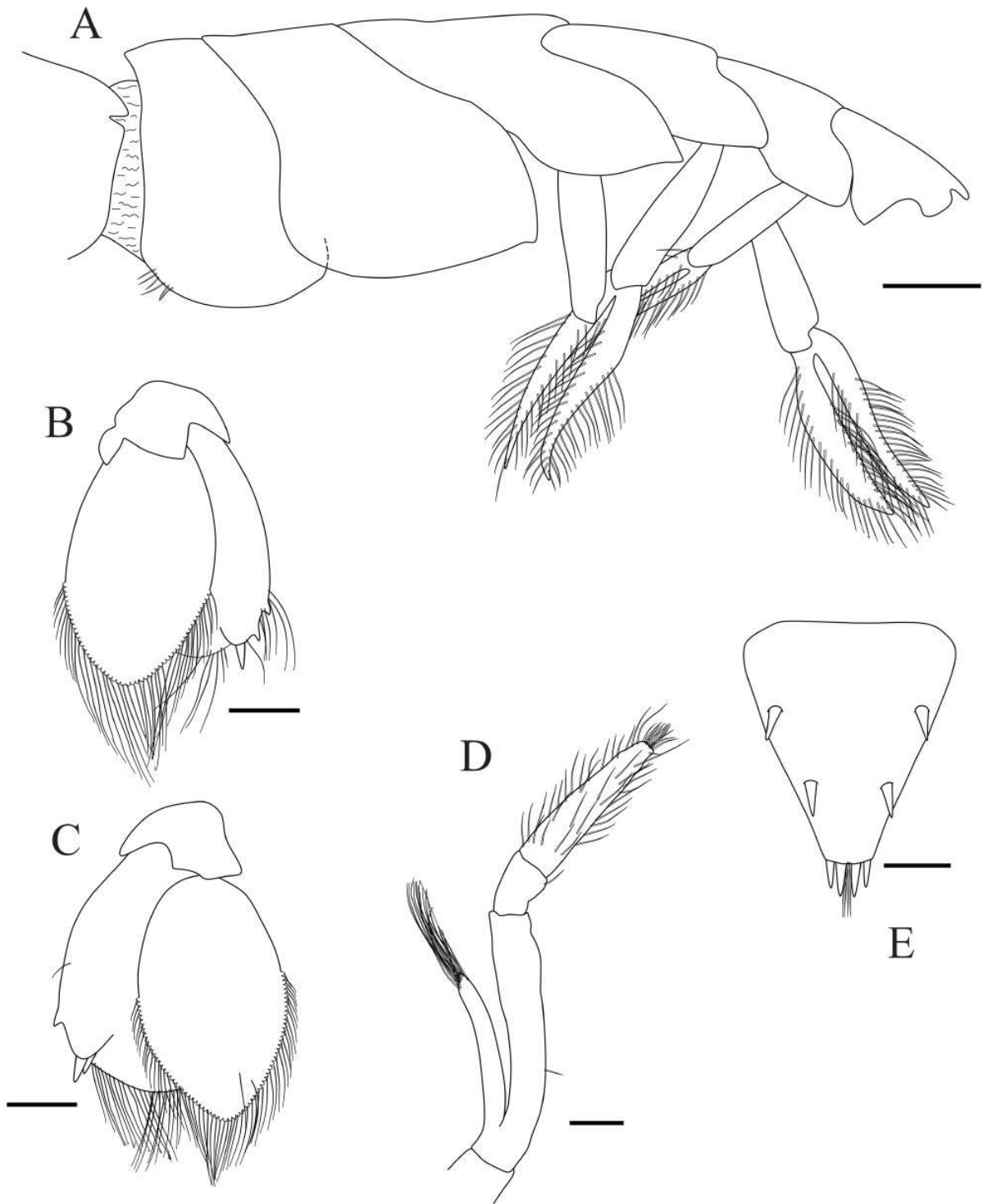


FIGURE 6. *Synalpheus barahonensis* Armstrong, 1949: female from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21870]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A, 0.5 mm; B–E, 0.3 mm.

***Synalpheus belizensis* Anker & Tóth, 2008 (Figs. 7, 8)**

Material examined: Pernambuco—Continental Shelf off Recife: 1 F, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, in sponge, DZ/UFRGS 7051; Fernando de Noronha: 1 F, Ponta da Sapata, 30.vi.2022, 03°51.892'S 32°27.965'W, 11.0 m depth, in sponge, DZ/UFRGS 7041.

Description: Anker & Tóth (2008).

Distribution: Belize, Jamaica, Curaçao, Barbados and **Brazil (Fernando de Noronha and Pernambuco)**

(Anker & Tóth, 2008; Macdonald *et al.* 2009; Hultgren *et al.* 2010, 2011; this study).

Ecology: Often in association with sponges (e.g., *Xestospongia* sp.) or coral rubble with sponges (Anker & Tóth, 2008; Hultgren *et al.* 2010); records of co-occurrence in the same host sponge with individuals of the *S. paraneptunus* complex (*S. bocas* Anker & Tóth, 2008, and *S. duffyi* Anker & Tóth, 2008) (Macdonald *et al.* 2009); in heterosexual pairs; 12–**50.6 m** (Anker & Tóth, 2008; this study). The material analyzed (DZ/UFRGS 7041, 7051) was found in unidentified sponges.

Remarks: *Synalpheus belizensis* belongs to the *S. paraneptunus* complex, which also includes *S. bocas*, *S. brevidactylus* Anker & Tóth, 2008, *S. duffyi*, *S. microneptunus* Hultgren, Macdonald & Duffy, 2011, *S. maxillispinus*,

S. paraneptunus, and *S. riosi* Anker & Tóth, 2008 (Anker & Pachellet 2014). The species is characterized by a rostrum and orbital teeth subequal in length, proximally broadened and tapering distally; the stylocerite surpassing the distal margin of the first antennular segment; the presence of a scaphocerite blade (Fig. 7A); the carpus of the second pereopod having five articles, the first approximately four times as long as the second (Fig. 7F) (Anker & Tóth, 2008). Additional distinguishing characters include the fixed and movable fingers of the minor chela excavated on the cutting edge, with the dorsal surface of the dactylus with scattered gambarelloid setae (Figs. 7D, E); the distal tip of the third maxilliped bearing a set of spiniform setae (Fig. 8D), and the uropodal exopod armed with a distolateral tooth (Fig. 8C) (Anker & Tóth, 2008; Anker *et al.* 2012). Anker & Tóth (2008) initially stated that the scaphocerite blade is absent in *S. belizensis*. However, their figures 12A and B, illustrate its presence, which is also mentioned in other sections of the text. Interestingly, the male paratype of the species differs from the holotype by having longer orbital teeth, by the absence of scaphocerite blade on the left side, but a small blade on the right side and by the slightly longer second antennular segment (Anker & Tóth, 2008). Hultgren *et al.* (2010) documented additional variations in scaphocerite blade development, ranging from 50% to 80% of the scaphocerite lateral spine's length. The

following variations were observed in our material: one individual (1 F, DZ/UFRGS 7041) has the dactylus of the major chela as long as the fixed finger, and a slightly longer distodorsal spine (Figs. 7B, C) (vs. dactylus of the major chela subequal to fixed finger and a shorter distodorsal spine; see Anker & Tóth, 2008, figs. 11A–C); another individual (1 F, DZ/UFRGS 7051) has slightly longer rostrum and orbital hoods (vs. not produced rostrum and orbital hoods), major chela fingers squared (vs. rounded/pointed major chela fingers), and distodorsal region of the major chela with a very short and rounded tubercle (vs. distodorsal region of the major chela with a sharp and directed anteriorly spine) (see Anker & Tóth, 2008, figs. 12A, B, and 11A–C). These variations were identified by Anker & Tóth (2008) as intraspecific, but further sampling and molecular analyses are necessary to determine the full extent of morphological variability within the species. This study represents the first record of *S. belizensis* in the southwestern Atlantic and extends its known bathymetric distribution from 12 m (Anker & Tóth, 2008) to 50.6 m.

***Synalpheus bousfieldi* Chace, 1972**

Material examined: None.

Description: Chace (1972), Dardeau (1984), Macdonald & Duffy (2006), Ríos & Duffy (2007), and Anker *et al.* (2012).

Distribution: Bahamas, Gulf of Mexico, Caribbean Sea, and Brazil (Rocas Atoll) (Chace 1972; Ríos & Duffy, 2007; Hultgren *et al.* 2010, 2011; Anker *et al.* 2012).

Ecology: On bottoms with abundance of coral rubble and sponges [e.g., *H. intestinalis*, *H. caerulea*, *ectyoplasia ferox* (Duchassaing & Michelotti, 1864), cited in Ríos & Duffy (2007) as *Hymeniacidon amphilecta*, *A. crassa*, cited in Ríos & Duffy (2007) as *Pseudoceratina crassa*] (Ríos & Duffy, 2007; see Table 1 in Anker *et al.* 2012 for more records); in heterosexual pairs or in groups composed of several adult individuals in an approximately equal sex ratio; 5–20 m (Ríos & Duffy, 2007; Anker *et al.* 2012).

Remarks: *Synalpheus bousfieldi*, along with *S. brooksi*, *S. carpenteri* Macdonald & Duffy, 2006, *S. chacei* Duffy, 1998, *S. corallinus* Macdonald, Hultgren & Duffy, 2009, *S. plumosetosus* Macdonald, Hultgren & Duffy, 2009, *S. ruetzleri* Macdonald & Duffy, 2006, and *S. thele* Macdonald, Hultgren & Duffy, 2009, belongs to the *S. brooksi* complex (Ríos & Duffy, 2007; Macdonald *et al.* 2009; Anker *et al.* 2012). In Brazil, *S. bousfieldi* has been reported from

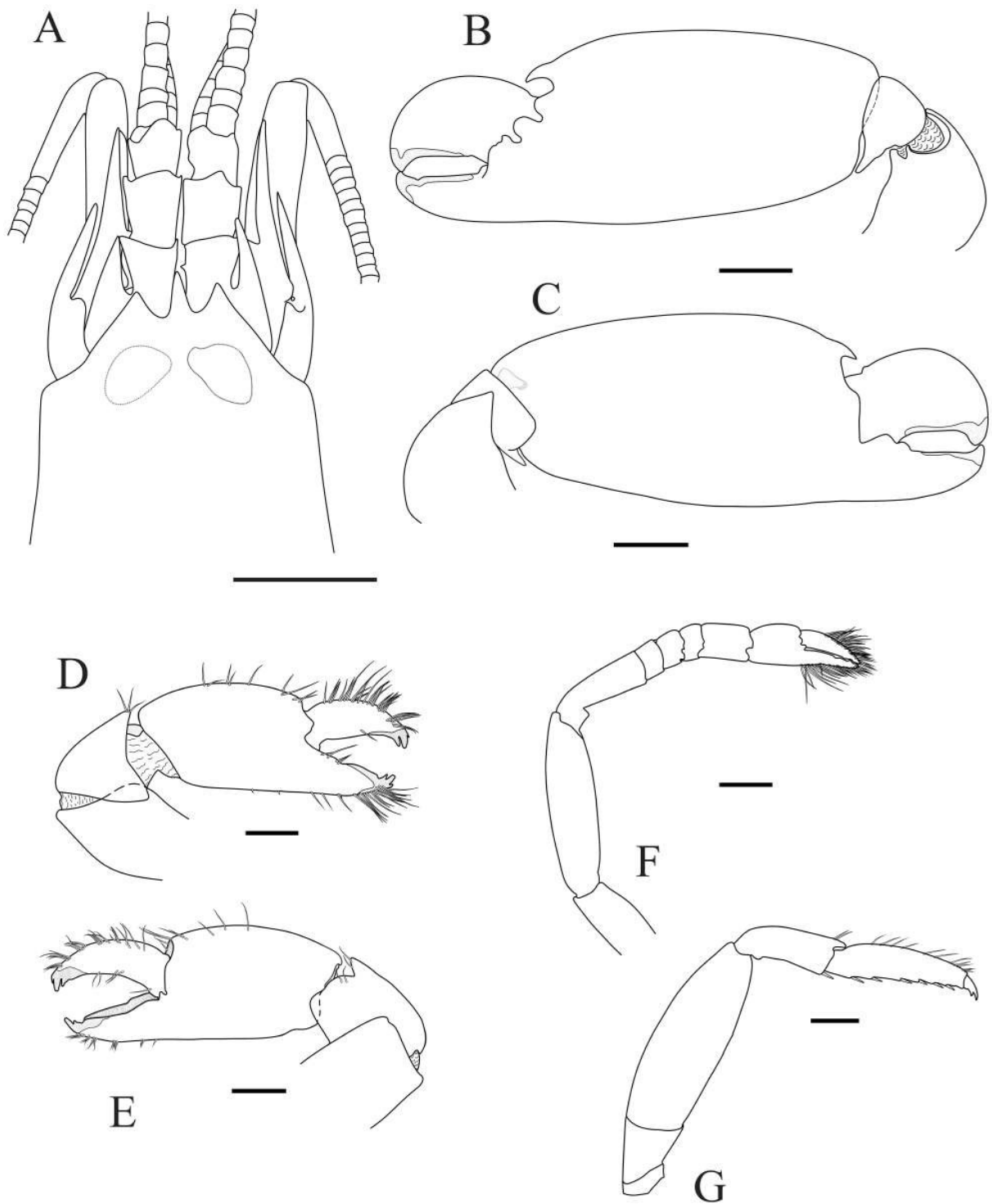


FIGURE 7. *Synalpheus belizensis* Anker & Tóth, 2008: female from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/UFRGS 7041]. A, frontal region, dorsal view; B, major chela, right side, mesial view; C, same, lateral view; D, minor chela, left side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–C, 1 mm; D–G, 0.5 mm.

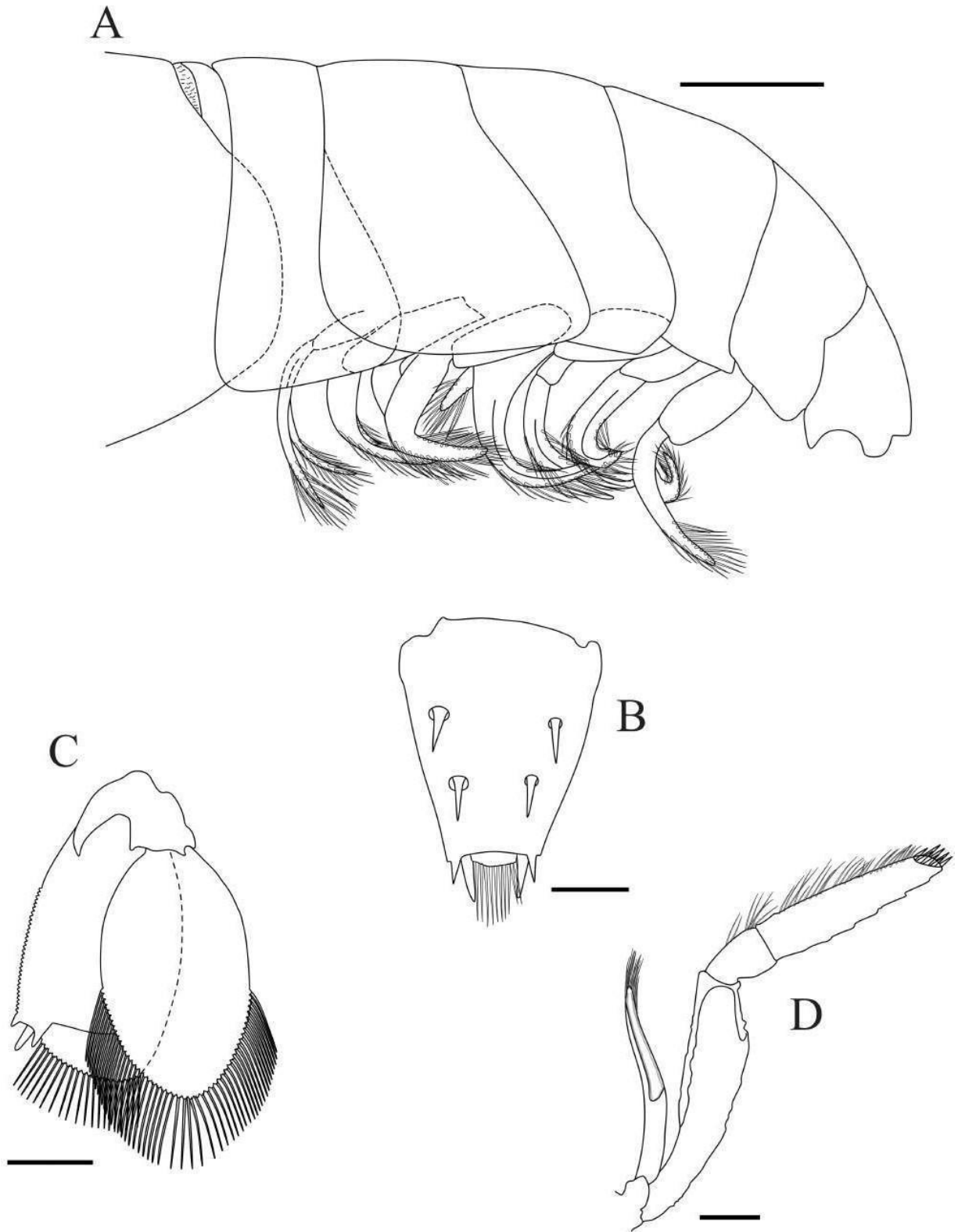


FIGURE 8. *Synalpheus belizensis* Anker & Tóth, 2008: female from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/UFRGS 7041]. A, pleon, left view; B, telson, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view. Scale bars: A, 1 mm; B–D, 0.5 mm.

Amapá to Ceará (Christoffersen 1979; Coelho-Filho 2006) and Rocas Atoll (Anker *et al.* 2012). Records of this species in different studies (e.g., Ríos & Duffy, 2007; Hultgren *et al.* 2010, 2011) consistently cite Christoffersen (1979) as the reference for Brazilian records. However, the author did not provide any specific comments regarding its occurrence in Brazil. Similarly, Coelho-Filho (2006) reported the species from Ceará, but did not include illustrations or detailed morphological remarks of the analyzed material. In the present study, no specimens of *S. bousfieldi* were found. Conversely, Anker *et al.* (2012) provided illustrations and accession numbers for material collected at Rocas Atoll, offering a more reliable record. Based on this evidence, the distribution of *S. bousfieldi* should be considered confirmed only for the Rocas Atoll.

***Synalpheus cf. brevicarpus* (Herrick, 1891)**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 27.ii.2018, 8°13'52.1"S 34°37'39.1"W,

50.8 m depth, in sponge, MOUFPE 21537; 1 M, same data as MOUFPE 21537, MOUFPE 21555; Sergipe—3 M, Plataforma Pdo 2 Face Externa Pé:Terra Fundo, 30.x.2000, MOUFPE 15787.

Description: Herrick (1891), as *Alpheus saulcyi f. brevicarpus* Herrick, 1891, and Coutière (1909).

Distribution: Bermuda, USA (Florida), Gulf of Mexico, Bahamas, West Indies, Panama, Venezuela, and Brazil (from Ceará to Rio Grande do Sul) (Christoffersen 1979, 1998; Bezerra & Coelho 2006; Cházaro-Olvera & Vázquez-López 2014; Velásquez *et al.* 2017; as references as *S. brevicarpus*).

Ecology: Muddy and sandy bottoms, coral rubble, and under rocks; in association with sponges (e.g., *Ircinia* sp., *Haliclona* sp., *Spongia* sp., and *Zygomyscale* sp.), ascidians, and in reefs of *Phragmatopoma* sp.; intertidal to 51 m (Christoffersen 1979; Velásquez *et al.* 2017).

Remarks: *Synalpheus brevicarpus* belongs to the *S. brevicarpus* complex, which includes the eastern Pacific *S. digueti* Coutière, 1909 and *S. pinkfloydi* Anker, Hultgren & De Grave, 2017, and the western Atlantic *S. antillensis*, *S. minus*, and *S. ubatuba* (Anker *et al.* 2017; Mantelatto *et al.* 2023). Santos *et al.* (2012), when analyzing material identified as *S. cf.*

brevicarpus, found two distinct color patterns, suggesting the presence of at least two species in southern Bahia. However, part of their material (e.g., the specimen with the pinkish color pattern on the major chela, Fig. 4D) was mistakenly attributed to *S. antillensis* (see Soledade *et al.* 2015). Almeida *et al.* (2018b) also reported two color patterns in specimens of *S. brevicarpus* from São Paulo: one with the distal portion of the palm and fingers of the major chela exhibiting a pink/orange coloration (*S. cf. brevicarpus* - pink/orange chela) and another with a green/blue coloration (*S. cf. brevicarpus* - green/blue chela). Mantelatto *et al.* (2023) subsequently described the *S. cf. brevicarpus* (green/blue chela) material from São Paulo as a new species, *S. ubatuba*. Based on color pattern, part of the material from Bahia initially referred to as *S. cf. brevicarpus* by Almeida *et al.* (2012) and Santos *et al.* (2012) was also reassigned to *S. ubatuba*. Additionally, Mantelatto *et al.* (2023) identified the *S. cf. brevicarpus* (pink/orange chela) material analyzed by Almeida *et al.* (2018b) as corresponding to *S. minus*. Mantelatto *et al.* (2023) highlighted some morphological differences between *S. ubatuba* and *S. brevicarpus*, such as the morphology of the basicerite, which in the former is armed with a long, strong distoventral tooth (vs. dorsal margin with a short, subacute point in *S. brevicarpus*), and the distolateral tooth of the scaphocerite, which is as long as the antennular peduncle in *S. ubatuba* (vs. not reaching the end of the antennular peduncle in *S. brevicarpus*). These same morphological differences were observed in the material examined in this study. Additionally, the coloration of the major chelae could not be assessed due to pigment dilution caused by ethanol preservation, nor could molecular analyses be conducted. Given the uncertainty surrounding the identity of the material, *S. brevicarpus* was not excluded from the checklist.

***Synalpheus brevidactylus* Anker & Tóth, 2008 (Figs. 9, 10)**

Material examined: Pernambuco—Continental Shelf off Recife: 1 OV, 27.ii.2018, 8°13'52.1"S 34°37'42.7"W, 50.0 m depth, in sponge, DZ/UFRGS 7052; 1 OV, same data as DZ/UFRGS 7052, MOUFPE 21815; 1 M, 27.ii.2018, 8°13'36.8"S 34°37'41.9"W, 51.0 m depth, in sponge, MOUFPE 21813; 1 M, 27.ii.2018, 8°13'52.1"S 34°37'41.2"W, 51.8 m depth, in sponge, DZ/UFRGS 7053.

Description: Anker & Tóth (2008).

Distribution: Panama and **Brazil (Pernambuco)** (Anker & Tóth, 2008; this study).

Ecology: Associated with the sponges *Neopetrosia subtriangularis* (Duchassaing, 1850) and *Calyx podatypa* (Laubenfels, 1934), growing on substrates such as coral rubble and

seagrass; in heterosexual pairs; 1–51.8 m (Anker & Tóth, 2008; this study). Sampled at the continental shelf off Recife (all lots cited above) in association with sponges, on coral rubble and algae bottom, at depths from 50–51.8 m.

Remarks: *Synalpheus brevidactylus* is characterized by a rostrum distinctly longer than the orbital teeth, broad at the base and tapering to the tip; by the fixed and movable fingers of the minor chela excavated on the cutting edges, with the dactylus bearing scattered gambarelloid setae on dorsal surface; by the uropodal exopod armed with two to three lateral teeth (Figs. 10B, C); and by the telson presenting a longitudinal median depression (Fig. 10D) (Anker & Tóth, 2008; Anker *et al.* 2012; this study). Additional diagnostic characters are: the carpus of the second pair of pereopods divided into five articles, with the first four times as long as the second (Fig. 9F), the third maxilliped ending in a set of six or seven spiniform setae (Fig. 10E), and the palm of the major chela is approximately three times as long as the fingers (Anker & Tóth, 2008). The material examined revealed morphological variations when compared to the original description of the species. For instance, a male specimen (MOUFPE 21813) exhibited a rostrum and orbital teeth that were subequal in length, with the rostrum being narrower (vs. rostrum longer and broader than the orbital teeth) (for comparison, see Fig. 9A and Anker & Tóth, 2008, Fig. 8A). The fingers of the major chela were strongly unequal in length, with the dactylus being square/rounded and longer than the fixed finger (vs. dactylus slightly longer and more bulging than the fixed finger) (see Figs. 9B, C, and Anker & Tóth, 2008, Figs. 8C, E). Additionally, the distodorsal tooth of the basicerite is slightly more acute (vs. distodorsal margin of the basicerite with a subacute point). The blade of the scaphocerite is longer, extending beyond the ventrolateral tooth of the basicerite and reaching the end of the distolateral tooth of the scaphocerite (vs. blade of scaphocerite reaching the end of the ventrolateral tooth of the basicerite and halfway to the distolateral tooth of the scaphocerite) (for comparison, see Fig. 9A and Anker & Tóth, 2008, Fig. 8A). In another specimen (1 OV, MOUFPE 21815), the tooth of the right orbital hood is partially fused to the rostrum (vs. typical tridentate front) and the uropodal exopod had three fixed teeth on the right side and two on the left (vs. uropodal exopod with three or four fixed teeth in both sides) (see Anker & Tóth, 2008, Figs. 8I, K). This study provides the first record of *S. brevidactylus* in the southwestern Atlantic and expands its known bathymetric distribution from 3 (Anker & Tóth, 2008) to 51.8 m.

***Synalpheus brooksi* Coutière, 1909**

Material examined: Maranhão—Turiaçu: 4 M, Almirante Saldanha Expedition, St. 1749 A, 06.xi.1967, 00°03.0'S 44°32.3'W, 63.0 m depth, MOUFPE 8746; Ceará—Acaraú: 3 M, 1 OV,

1 F, Almirante Saldanha Expedition, St. 1710, 27.x.1967, 02°39.5'S 39°46.0'W, 17.0 m depth, MOUFPE 8743; 5 M, same data as MOUFPE 8743, MOUFPE 8756; Fortaleza: 1 M, Parque Estadual Marinho da Pedra da Risca do Meio, 15.vii.2004, in *Monanchora arbuscula*, MOUFPE 21868; Paracuru: 1 M, Almirante Saldanha Expedition, St. 1708 A, 22.x.1967, 02°44.3'S 39°04.0'W, 54.0 m depth, MOUFPE 8762; 1 OV, Almirante Saldanha Expedition, St. 1701, MOUFPE 8741; 49 M, Pavasas Expedition - DG 03, 19.vii.1987, MOUFPE 8749; Pernambuco—Fernando de Noronha: 1 M, Buraco do Inferno, 18.vi.2019, 03°48.968'S 32°23.577'W, 13.0–15.0 m depth, in sponge, DZ/UFRGS 6712; 1 M, same data as DZ/ UFRGS 6712, DZ/UFRGS 6713; 1 M, 2 OV, Cagarras, 25.vi.2022, 03°50.933'S 32°26.178'W, 13.0 m depth, in sponge, DZ/UFRGS 7026; 4 M, 2 OV, Buraco do Inferno, 26.vi.2022, 03°48.968'S 32°23.577'W, 12.0 m depth, in sponge, DZ/UFRGS 7030; 2 M, 2 F, Ilha do Meio, 26.vi.2022, 03°49.015'S 32°23.549'W, 11.0 m depth, in sponge, DZ/UFRGS 7036; 1 M, Ponta da Sapata, 30.vi.2022, 03°51.892'S 32°27.965'W, 11.0 m depth, in sponge, DZ/ UFRGS 7042; 1 M, Laje Dois Irmãos, 30.vi.2022, 03°51.859'S 32°27.934'W, 17.0 m depth, in sponge, DZ/UFRGS 7045; Continental Shelf off Recife: 45 M, 7 F, 2 NI, 27.ii.2018, 8°13'33.0''S 34°37'40.3''W, 50.6 m depth, in sponge, MOUFPE 21816; 2 M, 10.v.2018, 08°23'04.3''S 34°40'07''W, 80.0 m depth, in sponge, MOUFPE 21818; 1 M, same data as MOUFPE 21818, MOUFPE 21825; 2 M, same data as MOUFPE 21818, MOUFPE 21826; 2 M, same data as MOUFPE 21818, MOUFPE 21842; 1 M, same data as MOUFPE 21818, MOUFPE 21855; 1 M, 07.ii.2018, 8°08'43.7''S 34°34'22.6''W, 54.0 m depth, MOUFPE 21559; 1 M, same data as MOUFPE 21559, in rhodoliths, MOUFPE 21564; 1 M, 10.v.2018, 08°21'34.9''S 34°41'53.3''W, 50.8 m depth, in sponge, MOUFPE 21791; 1 M, 27.ii.2018, 8°13'52.1''S 34°37'41.2''W, 51.8 m depth, MOUFPE 21549; Ilha de Itamaracá: 11 M, 17.i.1969, 7°49'S 34°49'13''W, 0.8 m depth, MOUFPE 8753; Recife: 18 M, 4 F, 2 NI, Boa Viagem, 24.xi.1964, in sponge, MOUFPE 8757.

Description: Macdonald & Duffy (2006) and Anker *et al.* (2012).

Distribution: USA (Florida), Gulf of Mexico, Bahamas, Caribbean Sea, Suriname and Brazil (Fernando de Noronha, Abrolhos, and from Amapá to Bahia) (Chace 1972; Christoffersen 1979, 1998; Ríos & Duffy, 2007; Alves *et al.* 2008; Anker *et al.* 2012; Soledade *et al.* 2015).

Ecology: Coral reef areas, associated with coral rubble, calcareous algae, seagrass banks, and sponges (e.g., *Agelas* sp., *Ircinia* sp., *Lissodendoryx* sp., and *Spheciospongia* sp.); in heterosexual pairs, associated with *H. caerulea*; also forming “subsocial” groups, with densities varying from 10 to 1000 individuals, with few ovigerous females among them (Ríos & Duffy,

2007); intertidal to 82.3 m, most commonly up to 10 m (Christoffersen 1979; Dardeau 1984; Ríos & Duffy, 2007; Anker *et al.* 2012). Ecological notes regarding our material, especially those related to association with sponges, are provided in the remarks and in the Discussion section.

Remarks: *Synalpheus brooksi* is one of the most widely distributed species of *Synalpheus* in the western Atlantic (Macdonald & Duffy 2006; Anker *et al.* 2012). The specimen from Parque Estadual Marinho da Pedra da Risca do Meio, Fortaleza, Ceará, previously cited by Bezerra & Coelho (2006) as *S. townsendi* (without access number), actually correspond to *S. brooksi* (MOUFPE 21868) (this study). Some morphological variations were observed in our material in comparison to the redescription provided by Dardeau (1984). In three females (1 OV, MOUFPE 8741; 1 OV, and 1 F, MOUFPE 8743), the pleura of the third and fourth segments are rounded (vs. third and fourth pleura subrectangular to tapered) (Dardeau 1984, Fig. 12C). One of these females (OV, MOUFPE 8741) exhibited only one pair of dorsal spiniform setae on the telson (vs. typically two pairs; see Dardeau 1984, Fig. 12F), two distolateral teeth on the uropodal exopod (vs. one distolateral tooth; see Dardeau 1984, Fig. 12F), and the rostrum and orbital hoods were poorly produced, with the tridentate front being wider than long (vs. produced rostrum and orbital hoods, with tridentate front being longer than wide; see Dardeau 1984, Fig. 12A)

Interestingly, eight males carried embryos on their pleopods (1 M, MOUFPE 8746; 4 M, MOUFPE 8749; 2 M, MOUFPE 8753; 1 M, MOUFPE 21816), a surprising observation given the absence of ovigerous setae and the presence of pleura characteristics typical of *Synalpheus* males. This behavior has been previously reported for this species by Coutière (1909), Chace (1972), Dardeau (1984), and Anker *et al.* (2012). Notably, ovigerous females were found in the same jars as these males, suggesting a potential collective caregiving behavior for offspring within “subsocial” groups. Ethological studies are needed to further investigate this phenomenon.

We recorded a possible subsocial group with a total of 54 specimens associated with a sponge (Fig. 3C) on the continental shelf off Recife, Pernambuco (MOUFPE 21816). Among them, two individuals (1 M and 1 F) possessed two pairs of minor chelae. Additionally, one *S. herricki* specimen (1 M, DZ/UFRGS 7067) was found co-occurring within the same sponge host. Parasitism was also observed, with some individuals exhibiting gill chambers infested by bopyrid isopods (1 M and 1 F, MOUFPE 21816) and pleons parasitized by rhizocephalans (MOUFPE 8746).

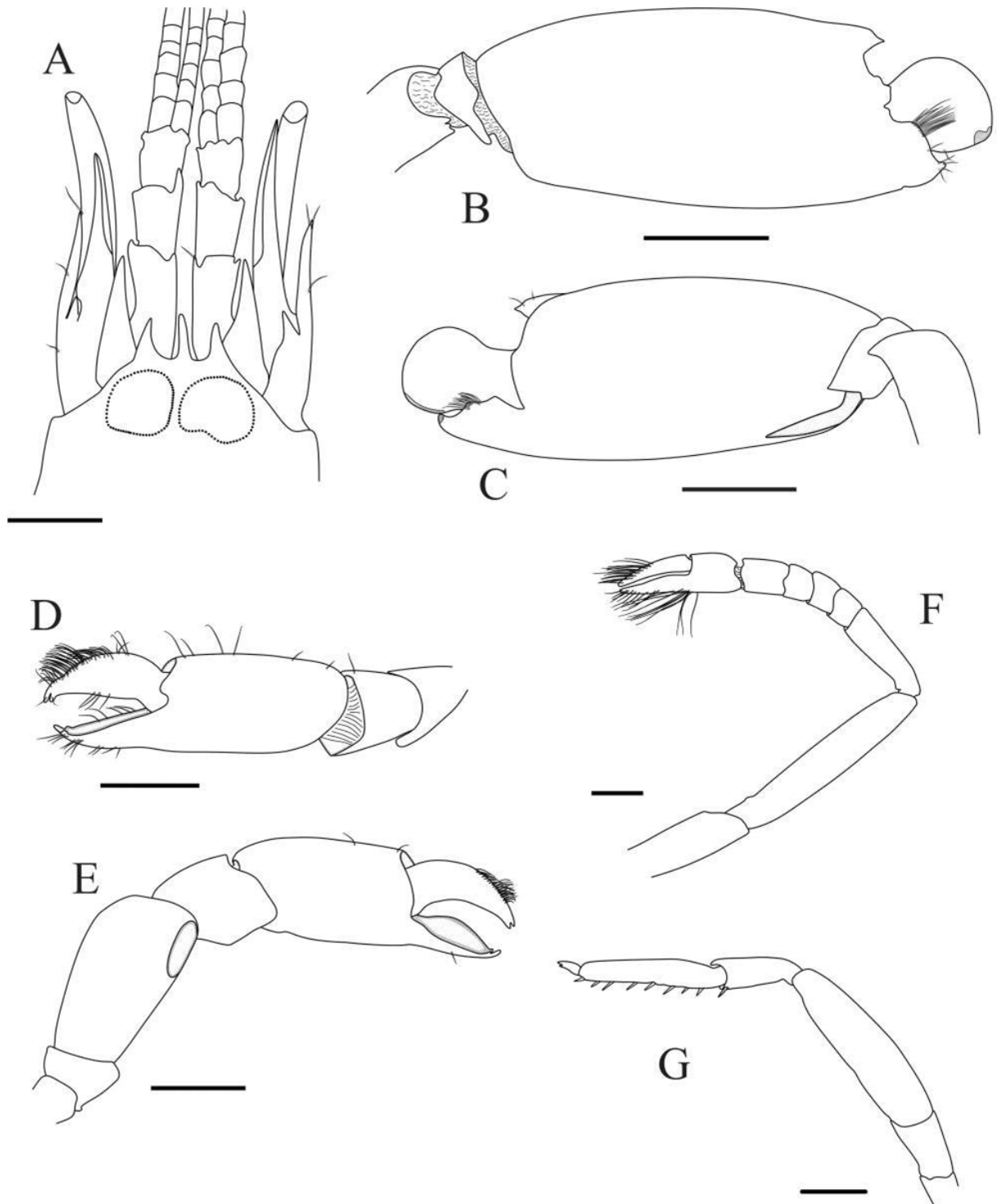


FIGURE 9. *Synalpheus brevidactylus* Anker & Tóth, 2008: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21813]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, left side, lateral view; G, third pereopod, left side, lateral view. Scale bars: A, D, E, G, 0.5 mm; B, C, 1 mm; F, 0.3 mm.

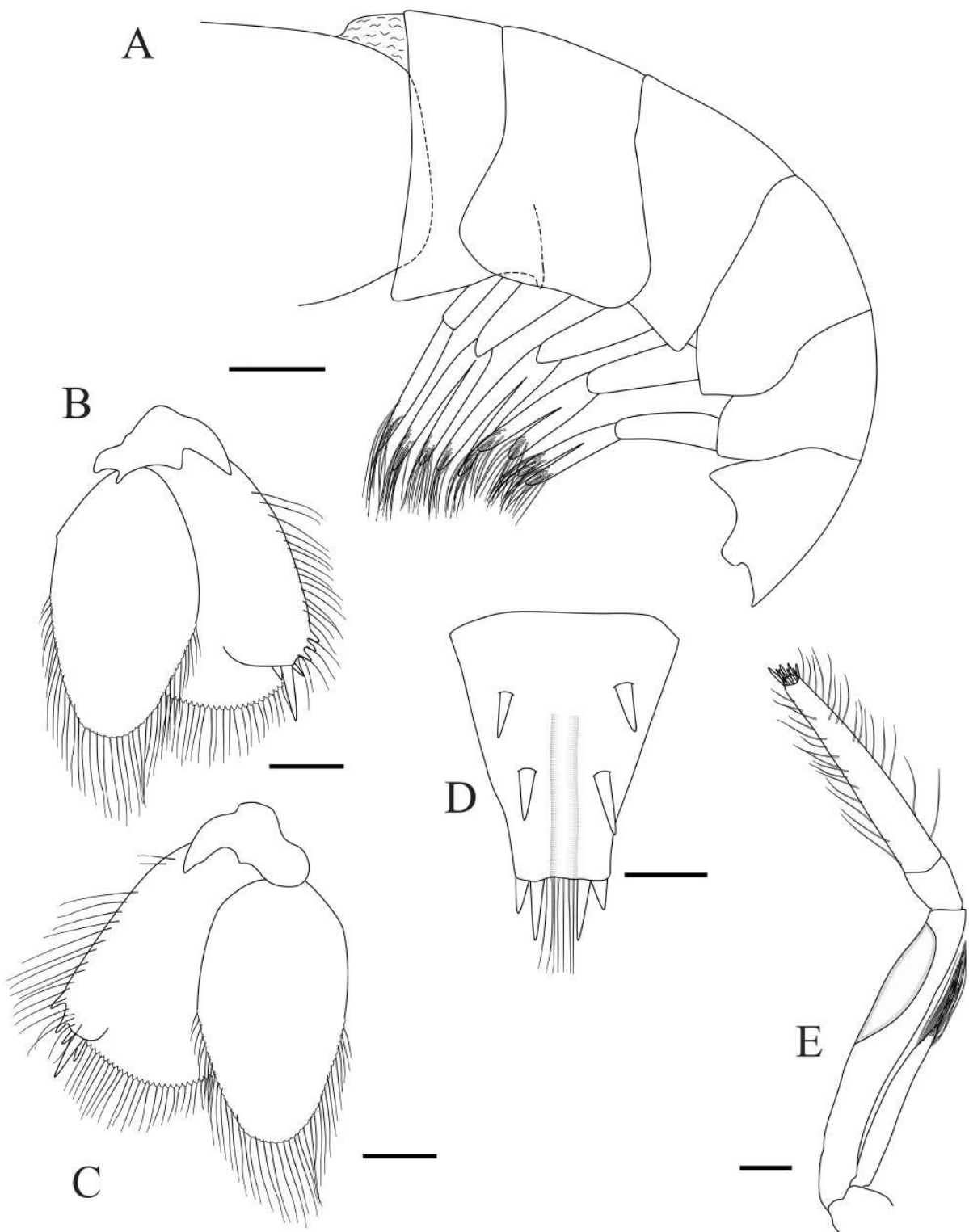


FIGURE 10. *Synalpheus brevidactylus* Anker & Tóth, 2008: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21813]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, third maxilliped, left side, lateral view. Scale bars: A, 1 mm; B–E, 0.3 mm.

***Synalpheus corallinus* Macdonald, Hultgren & Duffy, 2009 (Figs. 11, 12)**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, in sponge, MOUFPE 21814; 1 M, 27.ii.2018, 8°13'52.1"S 34°37'41.2"W, 51.8 m depth, in sponge, MOUFPE 21812.

Description: Macdonald *et al.* (2009).

Distribution: Jamaica (Discovery Bay) and **Brazil (Pernambuco)** (Macdonald *et al.* 2009; this study).

Ecology: In sponges, associated with *H. intestinalis* (Macdonald *et al.* 2009); in heterosexual pairs; **50.6–51.8 m** (Macdonald *et al.* 2009; Anker *et al.* 2012; this study). Sampled at the continental shelf off Recife (all lots cited above) in association with sponges, on coral rubble and algae bottom.

Remarks: *S. corallinus* is part of the *S. brooksi* complex (morphological differences regarding other species of the complex were discussed by Macdonald *et al.* 2009, Tab. 3, p. 12, Figs. 5–9). Our material agrees well with the description provided by Macdonald *et al.* (2009) (for comparison, see description and figures in Macdonald *et al.* 2009 and Figs. 11, 12 herein). The present study provides the first information regarding depth range for the species (50.6–51.8 m), as well as the first record of the species beyond its type locality (Discovery Bay, Jamaica), significantly expanding its known distribution.

***Synalpheus dardeau* (Ríos & Duffy, 2007)**

Material examined: Pernambuco—Tamandaré: 1 M, Carneiros, 20.vii.2019, 8°41'32"S 35°4'25"W, 3.5 m depth, in sponge, MOUFPE 21620.

Description: Ríos & Duffy (2007) and Oliveira *et al.* (2015).

Distribution: USA (North Carolina, Florida), Belize, Panama, Curaçao, and Brazil (**Pernambuco** and Bahia) (Ríos & Duffy, 2007; Hultgren *et al.* 2010; Anker *et al.* 2012; Oliveira *et al.* 2015; this study).

Ecology: In sponges [*Spheciospongia vesparium* (Lamarck, 1815), *Lissodendoryx colombiensis* Zea & van Soest, 1986, and *Ircinia* cf. *strobilina* (Lamarck, 1816)]; on seagrass banks, among roots in mangroves with a high abundance of sponges; in heterosexual pairs;

shallow waters to 65 m (Ríos & Duffy, 2007; Hultgren *et al.* 2010; Anker *et al.* 2012; Oliveira *et al.* 2015). Sampled in association with a sponge (unidentified).

Remarks: Oliveira *et al.* (2015) highlighted differences between their material and the type series of the species, interpreting these as intraspecific variations (for more details, see Oliveira *et al.* 2015, Remarks and Fig. 2, and Ríos & Duffy, 2007, Figs. 3–6). The material analyzed in this study is consistent with the variations reported by Oliveira *et al.* (2015). Furthermore, with the new record, this study fills a gap in the species' known distribution along the Brazilian coast.

Synalpheus fritzmuelleri (Coutière, 1909)

Material examined: Rio Grande do Norte—São Pedro e São Paulo Archipelago: 3 F, 10 m depth, in an ARS, DZ/ UFRGS 7068; 1 F, 0.1 m depth, in coral, DZ/UFRGS 7069; Paraíba—João Pessoa: 1 M, in coral reef, MOUFPE 8898; 1 M, 1 OV, Praia de Cabo Branco, 23.iii.2023, under rocks, DZ/UFRGS 7054; Pernambuco—Fernando de Noronha: 2 M, MOUFPE 8793; Cabo de Santo Agostinho: 1 F, 16.vi.2015, MOUFPE 21857; 2 M, Calhetas, 27.iv.1990, MOUFPE 8877; 2 M, 2 OV, 5 F, Calhetas, 27.iii.1990, MOUFPE 8882; 1 M, 1 OV, 1 F, Calhetas, 03.xii.1990, 7°50'S 34°49'W, 1.0–3.0 m depth, MOUFPE 8888; 1 F, Calhetas, 09.viii.1990, MOUFPE 8894; 1 M, Calhetas, 25.v.1990, MOUFPE 8900; 1 OV, Calhetas, MOUFPE 8906; 2 M, Gaibu, MOUFPE 8809; 1 M, 1 OV, 1 F, Gaibu, 17.ix.1989, MOUFPE 8883; 2 M, 1 OV, Praia do Paiva, 13.viii.2015, MOUFPE 21859; 1 M, Praia do Paiva, 05.vii.2007, under rocks, MOUFPE 15457; 1 M, 1 OV, Praia do Paraíso, 28.xi.2019, 8°21'54"S 34°56'50"W, under rocks, MOUFPE 21863; 2 M, Baía de Suape, 05.vi.1998, 8°21'54"S 34°56'50"W, MOUFPE 13156; 1 OV, Baía de Suape, 09.i.1970, 7°49'S 34°48'W, 1.2 m depth, MOUFPE 8892; Goiana: 1 OV, Milênio Project St. 03, Rio Carrapicho, 11.ii.2004, MOUFPE 15781; 1 M, 1 OV, Praia de Pontas de Pedra, 07°37'00"S 34°48'51"W, 1.0 m depth, associated with *Dysidea etheria* Laubenfels, 1936, MOUFPE 21601; 1 F, same data as MOUFPE 21601, associated with *Amphimedon compressa* Duchassaing & Michelotti, 1864, MOUFPE 21602; Ilha de Itamaracá: 1 M, Ilha de Itamaracá, St. 06, 08.i.1989, 7°43'36"S 34°49'24"W, 3.7 m depth, MOUFPE 8878; 1 M, 1 F, Ilha de Itamaracá, St. 91, 1990, 7°35'58"S 34°48'33"W, 10.5 m depth, MOUFPE 8879; 1 M, 2 OV, Ilha de Itamaracá, St. 46, 1990, 7°43'36"S 34°49'24"W, 3.7 m depth, MOUFPE 8880; 2 M, 1 OV, 2 NI, Ilha de Itamaracá, St. 92, 03.xii.1990, 7°36'S 34°48'W, 0.15–0.65 m depth, MOUFPE 8886; 1 M, 2

OV, Ilha de Itamaracá, St. 74, MOUFPE 8889; 1 M, 1 OV, Ilha de Itamaracá, St. 11, MOUFPE 8891; 1 OV, Ilha de Itamaracá, St. 41, 09.i.1970, 7°51'S 34°49'W, 3.9 m depth, MOUFPE 8893; 1 OV, Ilha de Itamaracá, St. 30, MOUFPE 8895; 1 OV, Ilha de Itamaracá, St. 89, 03.xii.1990, 7°36'08"S 34°48'33"W, 0.6 m depth, MOUFPE 8899; Jaboatão dos Guararapes: 1 M, 1 OV, 1 F, Candeias, 16.ix.1989, MOUFPE 8876; 3 M, 3 OV, 1 F, Piedade, 18.iii.1969, 7°45'36"S 34°48'00"W, 1.65 m depth, in coral reef, MOUFPE 8890; 1 M, Piedade, 22.xi.1968, MOUFPE 8902; Recife: 1 F, Praia de Boa Viagem, 05.i.2008, DZ/UFRGS 7055; 1 F, Praia de Boa Viagem, 05.i.2008, MOUFPE 21872; Sirinhaém: 1 M, 1 F, Ilha de Santo Aleixo, MOUFPE 13442; 1 M, Ilha de Santo Aleixo, MOUFPE 13515; 4 M, 3 F, Ilha de Santo Aleixo, 05.vi.2015, MOUFPE 21858; Tamandaré: 1 OV, Praia de Carneiros, 06.vi.2019, 8°41'32"S 35°4'25"W, 2.0 m depth, under rocks, MOUFPE 21594; 1 M, Praia de Carneiros, iv.1998, MOUFPE 10563; 1 OV, 1 F, Praia de Carneiros, 08.iv.1997, MOUFPE 10566; Sergipe—2 M, 2 F, Plataforma Pdo2 Posição Face Externa Pé Fora Da Superfície, MOUFPE 15360; 2 M, 4 OV, Plataforma Pcb4 Face, 01.xi.2000, MOUFPE 15770; 3 M, 1 F, Plataforma Pcm5 Pós: Face Externa Pé: Terra Superfície, MOUFPE 15771; 5 M, 5 OV, Plataforma Pcb4 Face Externa Fora Fundo, 01.xi.2000, MOUFPE 15772; 2 M, Plataforma PCM11 Pós Face Externa Pé:Fora Superfície Externa, MOUFPE 15773; 2 M, 2 OV, 3 F, Plataforma Pd02 Face Externa Terra Meio, 30.x.2000, MOUFPE 15776; 1 M, 1 OV, Plataforma Pcm5 Face Externa Pé: Fora Superfície, 30.x.2000, MOUFPE 15780; 1 M, Plataforma Pcb4 Face Externa Terra Superfície, 01.xi.2000, MOUFPE 15782; Bahia—1 M, BCAM 40 GAR 256 R3C2 (environmental consultancy activity), xii.2008, MOUFPE 15774; 1 F, Bioincrustação P15S R2C2 (environmental consultancy activity), xii.2008, MOUFPE 15775; 1 F, Bioincrustação P25S R1C2 (environmental consultancy activity), xii.2008, MOUFPE 15777; 1 OV, Bioincrustação P45S R3C2 (environmental consultancy activity), xii.2008, MOUFPE 15778; 1 OV, Bioincrustação P210S R3CR (environmental consultancy activity), MOUFPE 15779.

Description: Coutière (1909), Williams (1984), and Anker *et al.* (2012).

Distribution: USA (North Carolina to Florida), Gulf of Mexico, Honduras, Belize, Panama, Cuba, Jamaica, Dominican Republic, Colombia, Aruba, Venezuela, Saint Martin, Barbados, Bermuda, Brazil (Abrolhos, **Fernando de Noronha**, Rocas Atoll, São Pedro e São Paulo Archipelago, Trindade & Martin Vaz Archipelago, and from Ceará to Santa Catarina), Santa Helena and Ascension Islands (Anker *et al.* 2012 and references therein; 2016; Santos *et al.* 2012 and references therein; Soledade *et al.* 2015; this study).

Ecology: Under rocks, in clusters of coralline algae, among roots in mangroves, in reefs of *Phragmatopoma* sp., and in association with cnidarians, bryozoans, and sponges (e.g. *Amphimedon* sp., *Aplysina* sp., *Dysidea* sp., *Ircinia* sp.); in heterosexual pairs; shallow waters to 51 m (Williams 1984; Frick *et al.* 2003; Anker *et al.* 2012; Cházaro-Olvera & Vázquez-López 2014; Almeida *et al.* 2015; this study). Also on gas platforms in the Colombian Caribbean region and on mussel farming lines in Santa Catarina (Macedo *et al.* 2012; Gracia *et al.* 2013). Part of the material examined was collected in coral and under rocks. Herein, we provide the first record of the species in the sponge *Dysidea etheria*.

Remarks: *Synalpheus fritzmulleri* is one of the most common species of *Synalpheus* in the western Atlantic, with multiples records along the Brazilian coast (e.g., Christoffersen 1979, 1998; Anker *et al.* 2012; Santos *et al.* 2012; Soledade *et al.* 2015). *Synalpheus fritzmulleri* is a possible species complex (Anker *et al.* 2012). A comprehensive study must be conducted to clarify the taxonomic status of the species, including the status of its three junior synonyms, originally described as varieties: *S. f. caribaea* Verrill, 1922, from Dominica Island; *S. f. carolinensis* Verrill, 1922, from North Carolina, USA; and *S. f. elongatus* Coutière, 1909, from Florida, USA (Coutière, 1909; Verrill 1922; Anker *et al.* 2012).

***Synalpheus hemphilli* Coutière, 1909**

Material examined: Ceará—2 M, Parque Estadual Marinho da Pedra da Risca do Meio, associated with *Callyspongia* (*Cladochalina*) *aculeata* (Linnaeus 1759), 22.0 m depth, MOUFPE 18389; Rio Grande do Norte—Natal: 1 M, Almirante Saldanha Expedition, St. 1657, 08.x.1967, 05°33.4'S 35°0.02'W, 52.0 m depth, MOUFPE 8778.

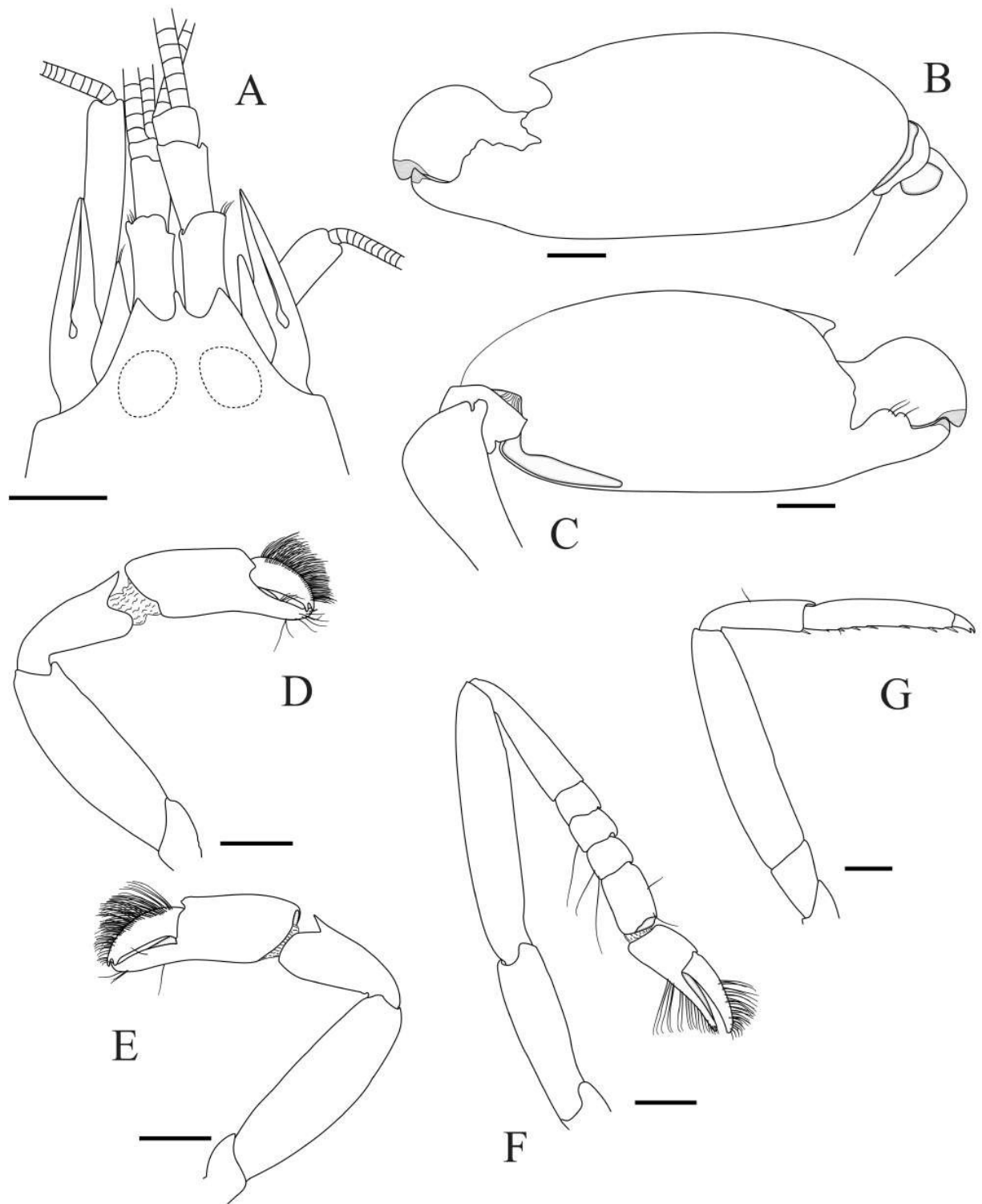


FIGURE 11. *Synalpheus corallinus* Macdonald, Hultgren & Duffy, 2009: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21812]. A, frontal region, dorsal view; B, major chela, right side, mesial view; C, same, lateral view; D, minor chela, left side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–E, 0.5 mm; F, G, 0.3 mm.

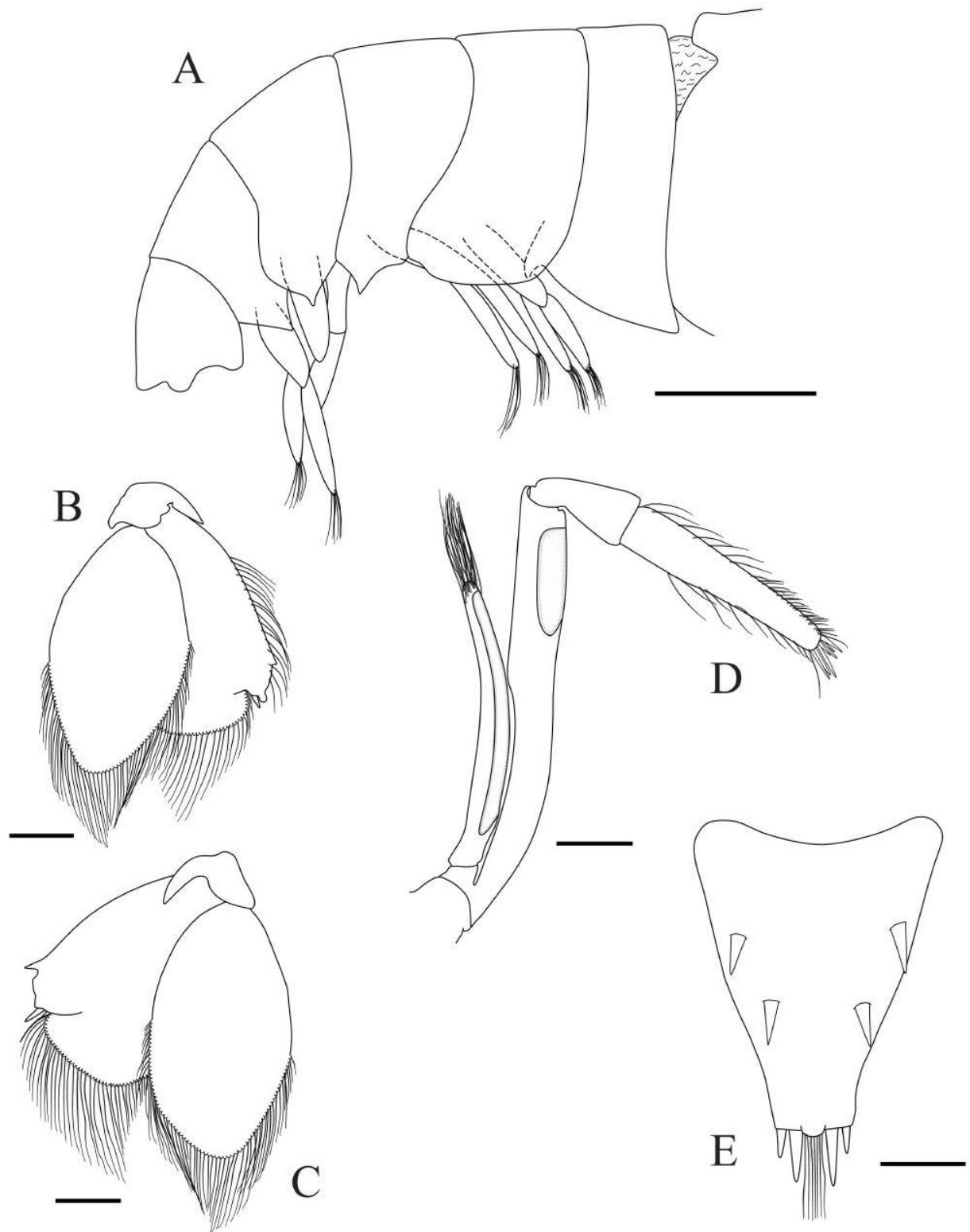


FIGURE 12. *Synalpheus corallinus* Macdonald, Hultgren & Duffy, 2009: male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21812]. A, pleon, right view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A, 1 mm; B–E, 0.3 mm.

Description: Coutière (1909), Verrill (1922), and Anker *et al.* (2012).

Distribution: Bermuda, USA (from North Carolina to Florida), Gulf of Mexico, Curaçao, Bonaire, Panama, Cuba, Venezuela, and Brazil (Abrolhos, Ceará, **Rio Grande do Norte**, and Bahia) (Christoffersen 1979, 1988; Rodríguez 1980; Bezerra & Coelho 2006, Anker *et al.* 2012; this study).

Ecology: In shallow reefs and adjacent areas and seagrass (Christoffersen 1979). Associated with sponges [e.g., *Callyspongia* (*Cladochalina*) *aculeata*, *Haliclona* sp.], dead corals, rocks and *Phragmatopoma* sp. reefs; in heterosexual pairs; 1–51 m (Chace 1956a; Hazlett 1962; Knowlton 1970; Christoffersen 1979; Bezerra & Coelho 2006; Anker *et al.* 2012; Velásquez *et al.* 2017; this study).

Remarks: The present study, with the new record (Rio Grande do Norte), fills a gap in the species distribution along the Brazilian coast.

***Synalpheus herricki* Coutière, 1909 (Figs. 13, 14)**

Material examined: Ceará—1 M, 3 OV, 1 F, Almirante Saldanha Expedition, St. 1701 A, 21.x.1967, 01°57.0'S 37°45.0'W, 57.0 m depth, MOUFPE 8742; Pernambuco—Fernando de Noronha: 2 M, Laje Dois Irmãos, 17.vi.2019, 03°51.859'S 32°27.934'W, 15.0 m depth, in sponge, DZ/UFRGS 6708; 1 M, same data as DZ/UFRGS 6708, DZ/ UFRGS 6709; 3 M, Cagarras, 25.vi.2022, 03°50.933'S 32°26.178'W, 13.0 m depth, in sponge, DZ/UFRGS 7027; 4 M, 2 F, Buraco do Inferno, 26.vi.2022, 03°48.968'S 32°23.577'W, 12.0 m depth, in sponge, DZ/UFRGS 7032; 1 OV, 1 F, Ilha do Meio, 26.vi.2022, 03°49.015'S 32°23.549'W, 11.0 m depth, in sponge, DZ/UFRGS 7038; 1 F, Ponta da Sapata, 30.vi.2022, 03°51.892'S 32°27.965'W, 11.0 m depth, in sponge, DZ/UFRGS 7043; 11 M, 3 OV, 1 F, Laje Dois Irmãos, 30.vi.2022, 03°51.859'S 32°27.934'W, 17.0 m depth, DZ/UFRGS 7046; Continental Shelf off Recife: 2 M, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, in sponge, DZ/UFRGS 7067; Sergipe—4 M, 1 OV, MOUFPE 8754.

Description: Coutière (1909), Dardeau (1984), Ríos & Duffy (2007), Anker *et al.* (2012).

Distribution: USA (Florida), Gulf of Mexico, Mexico, Belize, Saint Martin, Panama (Bocas del Toro), Curaçao, and Brazil (Rocas Atoll, Fernando de Noronha, Ceará, **Pernambuco**, and **Sergipe**) (Chace 1972; Dardeau 1984; Ríos & Duffy, 2007; Hultgren *et al.* 2010; Anker *et al.* 2012; De Grave & Anker 2017; Horch *et al.* 2024; this study).

Ecology: In sponges [e.g., *Agelas dispar* Duchassaing & Michelotti, 1864, *A. crassa*, *Hymeniacion amplexa* Laubenfels, 1936, *H. intestinalis*, and *Ircinia* sp.]; near coral reefs with an abundance of this type of host; in heterosexual pairs; from 5–73 m (Dardeau 1984; Rodríguez 1986; Ríos & Duffy, 2007; Anker *et al.* 2012).

Remarks: *Synalpheus herricki* can be distinguished from other western Atlantic *Synalpheus* by the ventral margins of the third and fourth pleurae of males having a “W” shape (see Dardeau 1984, Fig. 30C) and by the dactylus of the major chela ending in a distinct spine directed ventrally, which is separated from the rest of the dactylus by a somewhat subtriangular notch (Fig. 13B) (Dardeau 1984; Ríos & Duffy, 2007). Anker *et al.* (2012) documented several variations in specimens of *S. herricki* from Rocas Atoll, such as the absence of the rostrum and well-developed orbital teeth, in the number and position of spiniform setae of telson and in the shape of pleonal segment. The individuals sampled in Fernando de Noronha, Pernambuco, and Sergipe, presented some morphological variations compared to the original description by Coutière (1909) and the redescription by Dardeau (1984). These variations include the fingers of the second pair of pereopods being longer than the palm (vs. as long as the palm) (Fig. 13F; Dardeau 1984, fig. 28C), and the absence of a sinus between the anterior and posterior portions of the third to fifth pleurae (vs. sinus present) (Fig. 14A; Dardeau 1984, fig. 30C). These variations highlight the need for integrative approaches to more accurately characterize the range of morphological differences within the species.

***Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010 (Figs. 15, 16)**

Material examined: Pernambuco—Goiana: 2 M, 2 OV, Praia de Catuama, 20.i.2023, 7°39'18.6"S 34°49'28.1"W, 1.5 m depth, in sponge, DZ/UFRGS 7057; Cabo de Santo Agostinho: 4 M, Baía de Suape, 16.viii.2019, 8°21'54"S 34°56'50"W, 3.5 m depth, in sponge, MOUFPE 21521; 8 M, 1 OV, same data as MOUFPE 21521, associated with *echinodictyum dendroides* Hechtel, 1983, MOUFPE 21513; 2 M, same data as MOUFPE 21521, MOUFPE 21510; 2 M, same data as MOUFPE 21521, in sponge, MOUFPE 21523; 5 M, same data as MOUFPE 21521, in sponge, MOUFPE 21508; 6 M, same data as MOUFPE 21521, in sponge, MOUFPE 21522; 5 M, same data as MOUFPE 21521, in sponge, MOUFPE 21509; 8 M, Baía de Suape, 21.iii.2019, 8°21'54"S 34°56'50"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21581; 2 M, same data as MOUFPE 21581, MOUFPE 21585; 6 M, 2 OV, same

data as MOUFPE 21581, DZ/UFRGS 7056; 1 M, 1 OV, same data as MOUFPE 21581, DZ/UFRGS 7056; 6 M, same data as MOUFPE 21581, MOUFPE 21589; 4 M, 1 OV, Baía de Suape, 26.x.2018, 8°21'54"S 34°56'50"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21579; 6 M, same data as MOUFPE 21579, MOUFPE 21583; 1 M, same data as MOUFPE 21579, MOUFPE 21584; 2 M, same data as MOUFPE 21579, MOUFPE 21587; 35 M, 4 OV, 1 F, same data as MOUFPE 21579, in unidentified sponge, MOUFPE 21603; 1 OV, same data as MOUFPE 21579, MOUFPE 21526; 1 OV, same data as MOUFPE 21579, MOUFPE 21528; 1 OV, same data as MOUFPE 21579, MOUFPE 21530; 9 M, 2 OV, Baía de Suape, 26.iv.2018, 8°21'54"S 34°56'50"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21861; Tamandaré: 1 M, 1 OV, Praia de Carneiros, 06.vi.2019, 8°41'32"S 35°4'25"W, 2.0 m depth, in sponge, MOUFPE 21595; 1 OV, same data as MOUFPE 21595, in rocks, MOUFPE 21596; 1 M, 1 OV, same data as MOUFPE 21595, in rocks, MOUFPE 21597; 2 M, Praia de Carneiros, 20.vii.2019, 8°41'32"S 35°4'25"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21610; 5 M, Praia de Carneiros, 20.vii.2019, 8°41'32"S 35°4'25"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21612; 1 M, same data as MOUFPE 21612, MOUFPE 21619; 1 M, 1 OV, same data as MOUFPE 21612, MOUFPE 21622; 2 M, same data as MOUFPE 21612, MOUFPE 21611; 37 M, 3 OV, Praia de Carneiros, 22.iii.2019, 8°41'32"S 35°4'25"W, 3.5 m depth, associated with *e. dendroides*, DZ/UFRGS 7058 (genetic voucher, genbank access PV273116, PV273117); 2 M, 3 OV, 1 F, same data as DZ/UFRGS 7058, MOUFPE 21860.

Description: Hultgren, Macdonald & Duffy (2010).

Distribution: Panama (Bocas del Toro), Curaçao, Barbados, Venezuela, and **Brazil (Pernambuco)** (Hultgren *et al.* 2010, 2011; Hultgren & Duffy 2011; Anker *et al.* 2012; Rodríguez *et al.* 2020).

Ecology: Shallow regions of coral reefs, on rocks or in sponges (e.g., *Agelas* sp., *Hyattella* sp., *Xestospongia* sp.); in heterosexual pairs; shallow waters to 15 m (Hultgren *et al.* 2010; Anker *et al.* 2012; this study). Here, we record *S. hoetjesi* for the first time in association with the sponge *e. dendroides*. Ecological notes regarding our material are provided in the Remarks and in the Discussion section.

Remarks: *Synalpheus hoetjesi* is characterized by the rostrum subequal in length although narrower than the orbital teeth, by the orbital teeth rounded to triangular (Fig. 15A), by the ventrolateral tooth of the basicerite and the distolateral tooth of the scaphocerite being

subequal in length (Fig. 15A), by the lateral margin of the uropodal exopod with four to six teeth (in addition to the spiniform setae) (Fig. 16B) and by the mesial spiniform setae on the posterior margin of the telson much thicker than the lateral (Fig. 16D) (Hultgren *et al.* 2010). Although previous studies (e.g., Hultgren *et al.* 2010; Anker *et al.* 2012) have reported *S. hoetjesi* in heterosexual pairs, we observed *S. hoetjesi* in aggregations ranging from 3 to 46 individuals by host sponge, with varying proportions of males and females. It is also noteworthy that, as reported by Anker *et al.* (2012), specimens of *S. ul*, a species very similar to *S. hoetjesi*, were found at the same collection site and in the same species of sponge (Fig. 3D). *Synalpheus hoetjesi* differs from *S. ul* by the thickness of the spiniform setae on the posterior margin of the telson, with the mesial more robust than lateral in *S. hoetjesi* (vs. mesial and lateral with approximately the same thickness in *S. ul*) (see Hultgren *et al.* 2010, Fig. 9). Hultgren *et al.* (2010) reported morphological variations in the spiniform setae of *S. hoetjesi* according to the sponge species in which these individuals were found, with mesial and lateral approximately the same thickness (see Hultgren *et al.* 2010, Fig. 9). In this study, one male specimen from Praia de Carneiros, Tamandaré (MOUFPE 21619), have four articles in both carpus of the second pereopod, instead of five, as described for the species (Hultgren *et al.* 2010). This variation may suggest morphological plasticity in *S. hoetjesi*, although the potential influence of the host sponge on shrimp morphology was not evaluated in this study. Here, we report the first record and provide 16S gene sequences for the species in the southwestern Atlantic, showing a 99.5% similarity to sequences from individuals found in the Caribbean Sea (Barbados, Curaçao, and Panama) (phylogram Fig. 19) (see more details in the discussion).

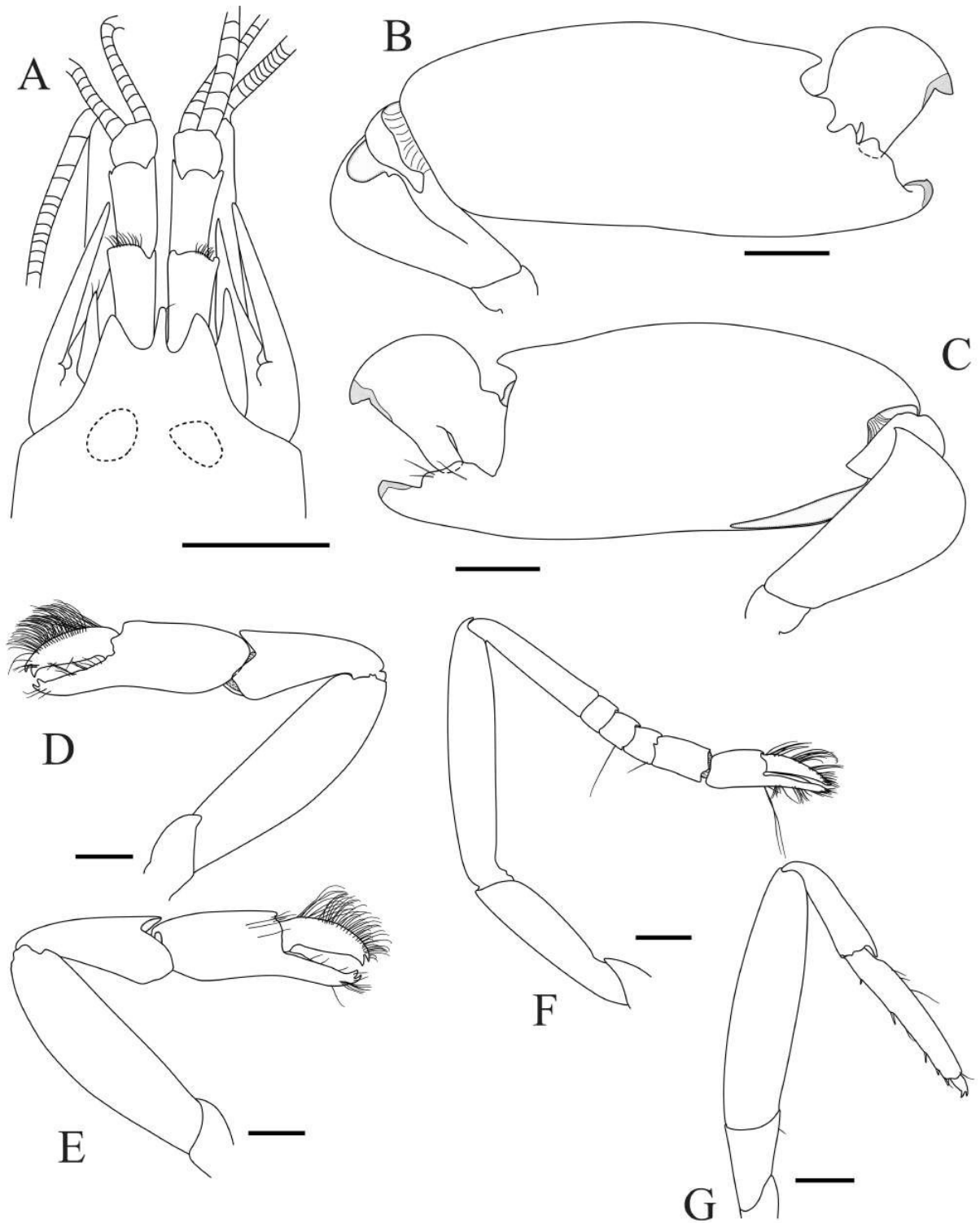


FIGURE 13. *Synalpheus herricki* Coutière, 1909: male from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/ UFRGS 7046]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A–C, 1 mm; D, E, G, 0.5 mm; F, 0.4 mm.

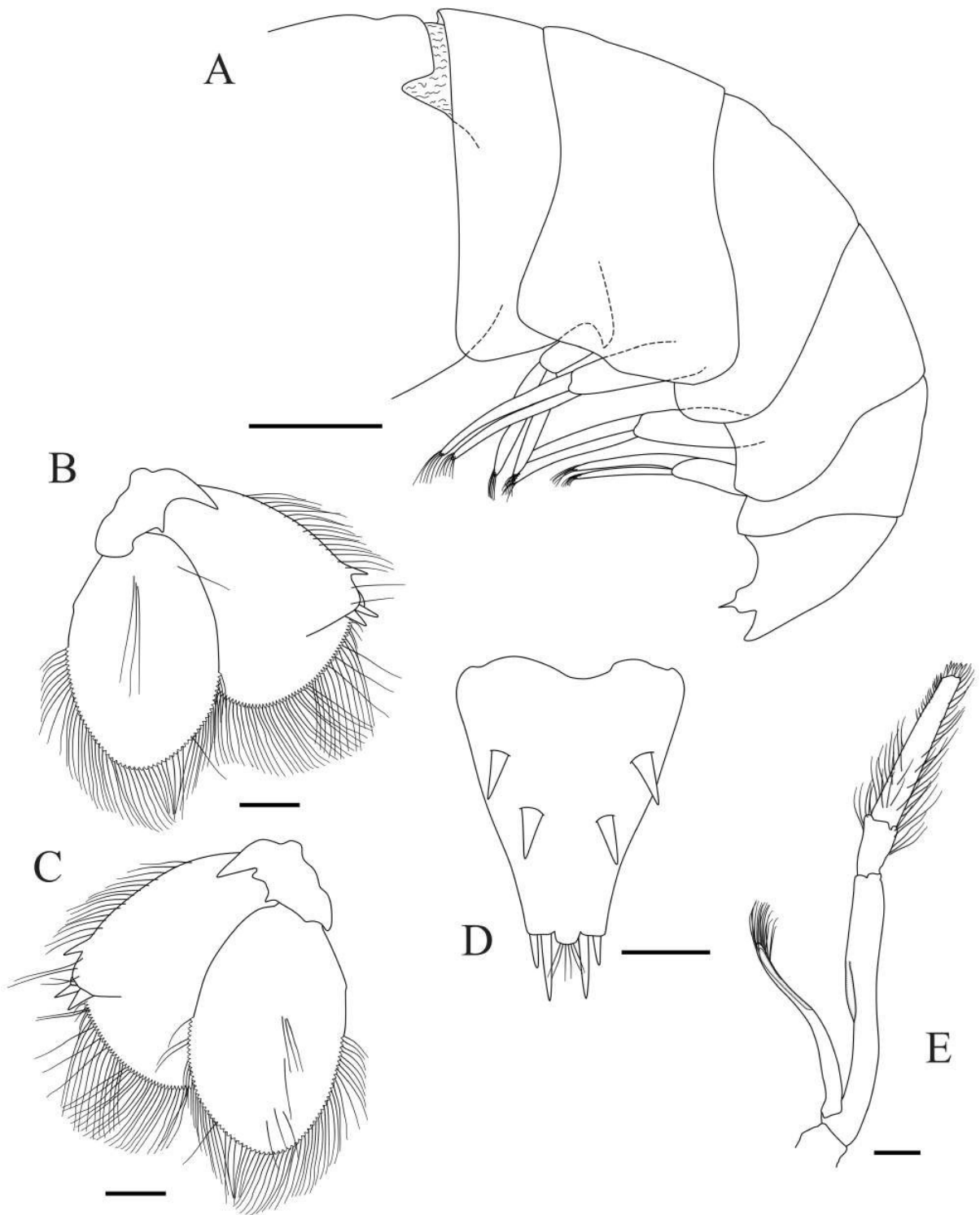


FIGURE 14. *Synalpheus herricki* Coutière, 1909: male from the Fernando de Noronha Archipelago, Pernambuco, Brazil [DZ/ UFRGS 7046]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, third maxilliped, right side, lateral view. Scale bars: A, 1 mm; B, C, E, 0.4 mm; D, 0.5 mm.

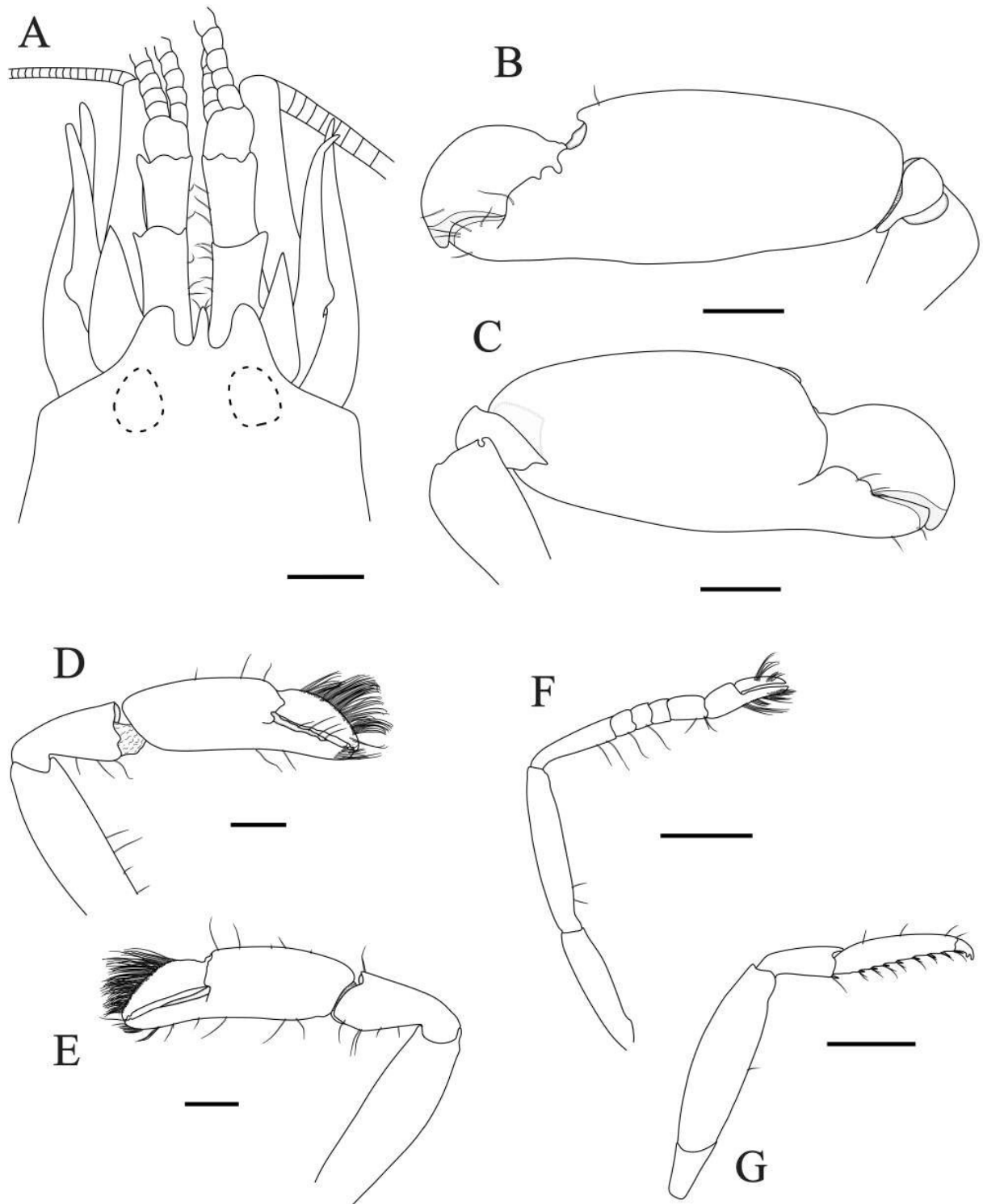


FIGURE 15. *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010: female from Cabo de Santo Agostinho, Pernambuco, Brazil [MOUFPE 21530]. A, frontal region, dorsal view; B, major chela, right side, mesial view; C, same, lateral view; D, minor chela, left side mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A, D, E, 0.5 mm; B, C, F, G, 1 mm.

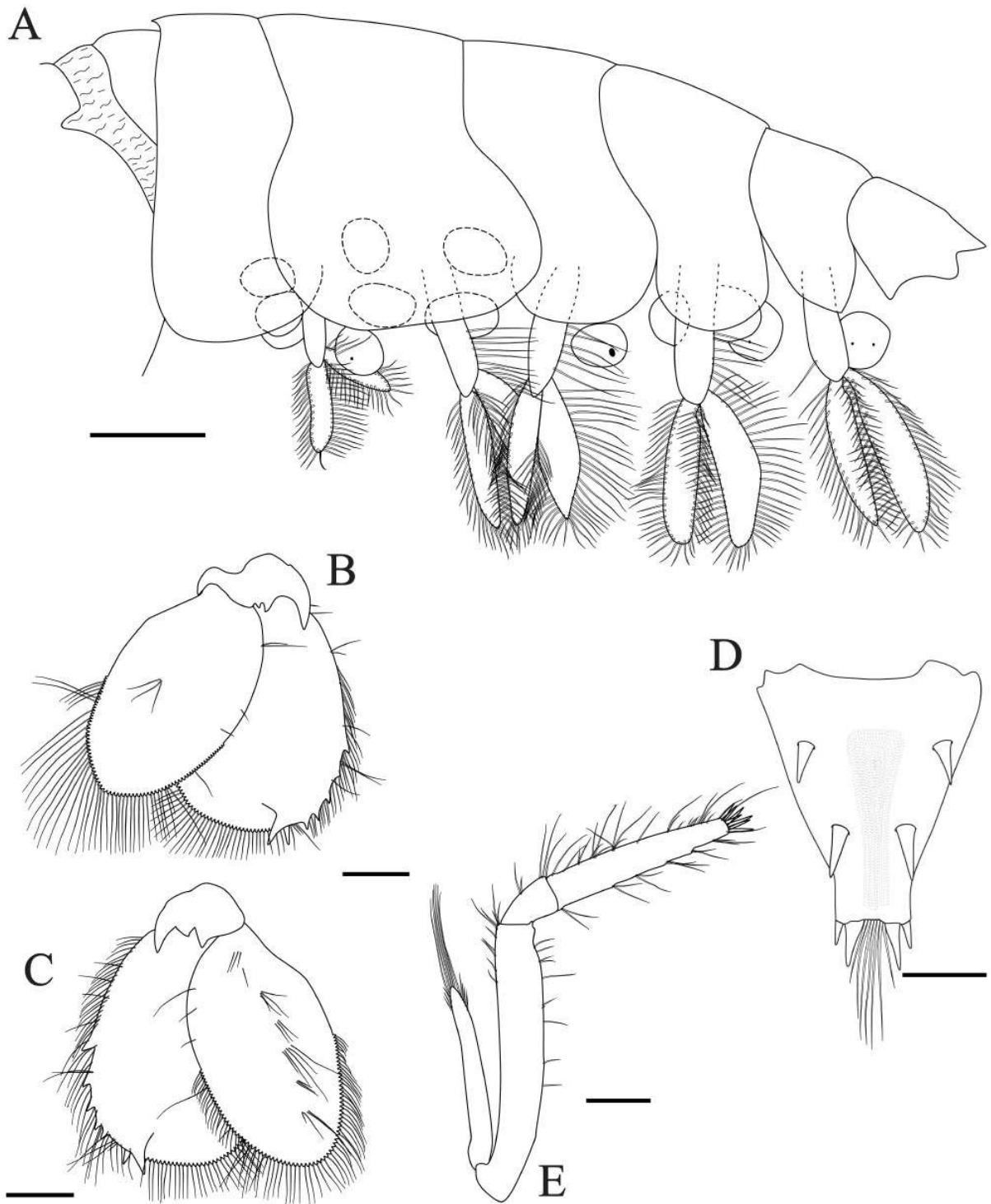


FIGURE 16. *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010: female from Cabo de Santo Agostinho, Pernambuco, Brazil [MOUFPE 21530]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A, 1 mm; B–E, 0.5 mm.

***Synalpheus kensleyi* (Ríos & Duffy, 2007) (Figs. 17, 18)**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 1 OV, 07.ii.2018, 8°08'53.0"S 34°34'07.4"W, 68.0 m depth, in coral rubble, MOUFPE 21869; 1 M, 07.ii.2018, 8°08'44.2"S 34°34'23.2"W, 55.0 m depth, DZ/ UFRGS 7059; Ilha de Itamaracá: 1 M, Forte Orange, 28.iv.1950, in sponge, MOUFPE 15807.

Description: Ríos & Duffy (2007).

Distribution: Belize (Carrie Bow Cay), Dominican Republic (Bayahibe), Panama (Bocas del Toro), and **Brazil (Pernambuco)** (Ríos & Duffy, 2007; Anker *et al.* 2012; this study).

Ecology: Associated with the sponges *H. intestinalis*, *H. caerulea*, and an unidentified yellow tubular sponge; in heterosexual pairs; shallow reefs with abundance of sponges; depths up to 2–68 m (Ríos & Duffy, 2007; Anker *et al.* 2012; this study). Sampled in coral rubble and sponges.

Remarks: *Synalpheus kensleyi* is characterized by the rostrum narrower and slightly longer than the orbital teeth, the dorsal margin of the basicerite bearing an acute spine, by its ventrolateral tooth reaching half-length of the distolateral tooth of the scaphocerite (Fig. 17A), by the major chela massive, with dactylus slightly exceeding the fixed finger and the distodorsal margin of the palm with a prominent tubercle with a spine directed downwards (see Ríos & Duffy, 2007, fig. 20A). The species is considered rare and has been previously recorded only in the Caribbean (Anker *et al.* 2012; De Grave & Anker 2017). In this study, we provide the first record from the southwestern Atlantic. A male specimen from the continental shelf off Recife (MOUFPE 21869) has a more globose major chela, with dactylus noticeably longer than the fixed finger and more squared/rounded in shape (vs. more cylindrical/ rectangular major chela, with dactylus slightly longer than the fixed finger and more elongated) (for comparison see Figs. 17B, C and illustration of type material by Ríos & Duffy, 2007, fig. 20). The present study expands the known bathymetric distribution for the species from 2 (Ríos & Duffy, 2007) to 68 m.

***Synalpheus maxillispinus* Anker & Pachelle, 2014**

Material examined: None.

Description: Anker & Pachelle (2014).

Distribution: Brazil (Bahia and Espírito Santo) (Anker & Pachelle 2014).

Ecology: In sponges; 15–50 m (Anker & Pachelle 2014).

Remarks: *Synalpheus maxillispinus* is part of the *S. paraneptunus* complex, and is morphologically similar to

S. bocas and *S. belizensis* (Anker & Pachelle 2014). For a detailed comparison and distinction among these species, refer to Anker & Tóth (2008) and Anker & Pachelle (2014).

***Synalpheus minus* (Say, 1818)**

Material examined: Paraíba—1 M, Akaroa Expedition, St. 03, 08°56'15"S 34°57'40"W, MOUFPE 15788; Pernambuco—Continental Shelf off Recife: 1 F, 27.ii.2018, 8°13'52.1"S 34°37'39.1"W, 50.8 m depth, in sponge, MOUFPE 21541; Ilha de Itamaracá: 1 M, Ilha de Itamaracá, St. 01, Forte Orange, MOUFPE 8789; 1 M, Forte Orange, 27.i.1990, MOUFPE 8789.

Description: Coutière (1909) and Christoffersen (1979).

Distribution: Bermuda and from USA (North Carolina) to Brazil (Abrolhos and from Ceará to São Paulo) (Christoffersen 1979, 1998; Almeida *et al.* 2018b; this study).

Ecology: Among rocks, in coralline rocks with algae, in calcareous algae, reefs of *Phragmatopoma* sp., and in association with ascidians and sponges (e.g., *Callyspongia* sp., *Ircinia* sp., *Hymeniacidon* sp., *Pseudoceratina* sp., *Xestospongia* sp.); in heterosexual pairs; intertidal to 85 m (Christoffersen 1979; Anker *et al.* 2012).

Remarks: *Synalpheus minus* is part of the *S. brevicarpus* complex, as mentioned above.

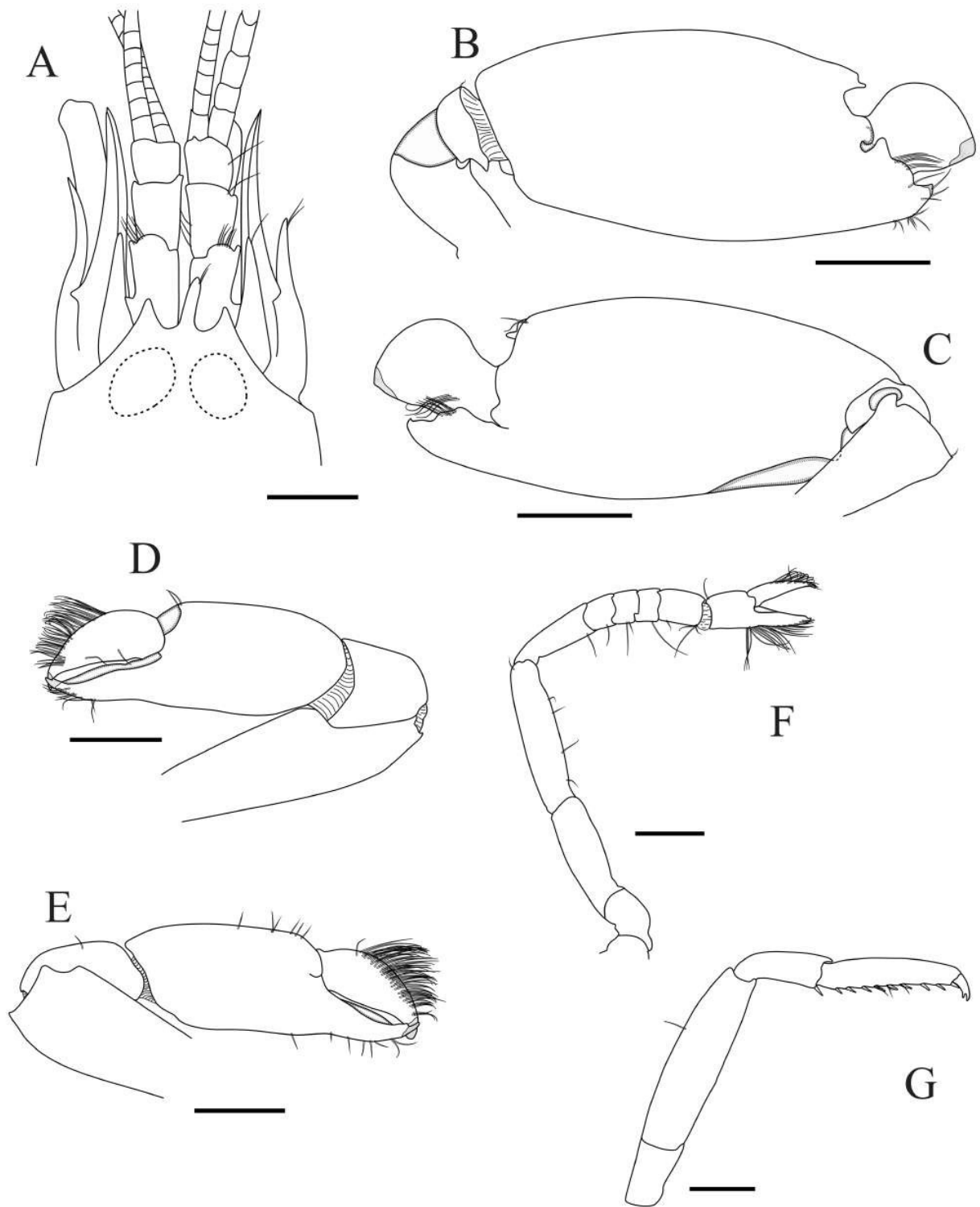


FIGURE 17. *Synalpheus kensleyi* (Ríos & Duffy, 2007): male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21869]. A, frontal region, dorsal view; B, major chela, left side, mesial view; C, same, lateral view; D, minor chela, right side, mesial view; E, same, lateral view; F, second pereopod, right side, lateral view; G, third pereopod, right side, lateral view. Scale bars: A, D–G, 0.5 mm; B, C, 1 mm.

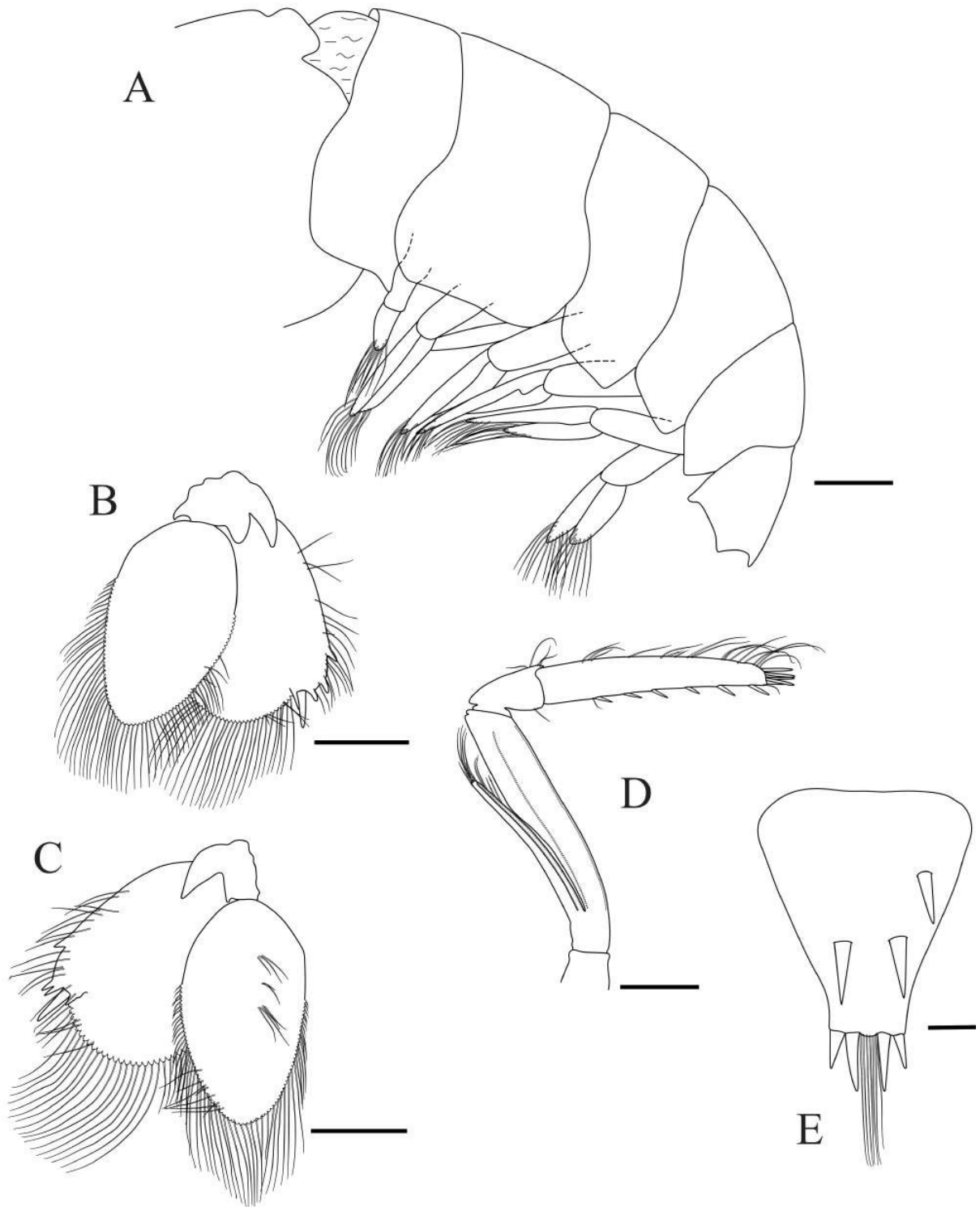


FIGURE 18. *Synalpheus kensleyi* (Ríos & Duffy, 2007): male from the continental shelf off Recife, Pernambuco, Brazil [MOUFPE 21869]. A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, third maxilliped, right side, lateral view; E, telson, dorsal view. Scale bars: A–C, E, 0.5 mm; D, 0.2 mm.

***Synalpheus pandionis* Coutière, 1909**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 07.ii.2018, 8°08'43.7"S 34°34'22.6"W, 54.0 m depth, MOUFPE 21546; Recife: 2 M, 08°09'7"S 34°45'0"W, 31.5 m depth, MOUFPE 15389.

Description: Coutière (1909), Dardeau (1984), Ríos & Duffy (2007), and Anker *et al.* (2012).

Distribution: USA (Florida), Gulf of Mexico, Bahamas, Cuba, Mexico, Honduras, Panama, Puerto Rico, Virgin Islands, Curaçao, Barbados, and Brazil (Ceará and **Pernambuco**) (Anker *et al.* 2012 and references therein; Cházaro-Olvera *et al.* 2017; this study).

Ecology: Shallow reefs and marine substrates, in sponges [*Lissodendoryx* cf. *strongylata* van Soest, 1984, *L. colombiensis*, *Agelas clathrodes* (Schmidt, 1870), *H. intestinalis*, *e. ferox*, and *A. crassa*]; in heterosexual pairs; shallow waters to 80 m (Ríos & Duffy, 2007; Anker *et al.* 2012; Cházaro-Olvera *et al.* 2017; De Grave & Anker 2017).

Remarks: *S. pandionis* was previously known from Brazil based on a single record from Ceará (Anker *et al.* 2012). Here, we extend its southern range in the western Atlantic.

***Synalpheus ruetzleri* Macdonald & Duffy, 2006**

Material examined: Pernambuco—Fernando de Noronha: 4 M, 1 OV, 2 F, Buraco do Inferno, 18.vi.2019, 03°48.968'S 32°23.577'W, 13.0–15.0 m depth, in sponge, DZ/UFRGS 7073; 3 M, Ilha do Meio, 18.vi.2019, 03°49.015'S 32°23.549'W, 12.0 m depth, in sponge, DZ/UFRGS 6705; 2 M, Ressureta, 19.vi.2019, 03°49.191'S 32°23.847'W, 8.0 m depth, in sponge, DZ/UFRGS 7070; 2 M, Ponta da Sapata, 17.vi.2019, 03°51.892'S 32°27.965'W, 8.0 m depth, in sponge, DZ/UFRGS 6707; Continental Shelf off Recife: 1 M, 10.v.2018, 08°21'34.9"S 34°41'53.3"W, 50.8 m depth, in sponge, MOUFPE 21794; 1 F, same data as MOUFPE 21794, MOUFPE 21793.

Description: Macdonald & Duffy (2006), Ríos & Duffy (2007), and Anker & Pachelle (2014).

Distribution: Belize, Panama, and Brazil (**Fernando de Noronha**, Ceará, and **Pernambuco**) (Macdonald & Duffy 2006; Ríos & Duffy, 2007; Anker & Pachelles 2014; this study).

Ecology: Obligatory symbiont of sponges (*A. dispar*, *H. cf. caerulea*, and unidentified sponge species); in heterosexual pairs; shallow waters to **50.8 m** (Macdonald & Duffy 2006; Ríos & Duffy, 2007; Anker & Pachelles 2014, as *S. cf. ruetzleri*; this study). Sampled at Fernando de Noronha (DZ/UFRGS 6705, 6707, 7070, 7073) and continental shelf off Recife (MOUFPE 21793, 21794) in association with sponges (unidentified).

Remarks: *Synalpheus ruetzleri* is part of the *S. brooksi* complex (Macdonald & Duffy 2006) and, as described by Macdonald & Duffy (2006), exhibits an extensive morphological variation, complicating its identification within the complex. The first record of the species from Brazil was provided by Anker & Pachelles (2014), from Ceará, where the material was identified as *S. cf. ruetzleri* due to differences from the type material (for more details, see Remarks of *S. cf. ruetzleri* in Anker & Pachelles 2014). Our material agrees with the description provided by Macdonald & Duffy (2006), except for one male (DZ/UFRGS 6710) that exhibited four articles in the carpus of the second pair of pereopods (vs. five articles in the holotype) (see Macdonald & Duffy 2006, fig. 11G). The present study expands the known range of the species in the southwestern Atlantic, as well as its bathymetric distribution, from less than 20 m (Anker & Pachelles 2014) to 50.8 m.

***Synalpheus sanctithomae* Coutière, 1909**

Material examined: Pernambuco—Fernando de Noronha: 1 M, Buraco do Inferno, 26.vi.2022, 03°48.968'S 32°23.577'W, 12.0 m depth, in sponge, DZ/UFRGS 7033; 1 F, Ilha do Meio, 26.vi.2022, 03°49.015'S 32°23.549'W, 11.0 m depth, in sponge, DZ/UFRGS 7039; Continental Shelf off Recife: 3 M, 1 OV, 2 F, 07.ii.2018, 8°08'43.7"S 34°34'22.6"W, 54.0 m depth, MOUFPE 21785; 1 M, 1 OV, 07.ii.2018, 8°09'06.8"S 34°34'28.4"W, 53.0 m depth, MOUFPE 21786; 1 M, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, in sponge, MOUFPE 21540; 1 F, 10.v.2018, 08°21'34.9"S 34°41'53.3"W, 50.8 m depth, in sponge, MOUFPE 21795; 1 F, 10.v.2018, 08°23'04.3"S 34°40'07"W, 80.0 m depth, in sediment, MOUFPE 21789; 1 M, same data as MOUFPE 21789, in sponge, MOUFPE 21829; 1 M, 1 NI, same data as MOUFPE 21789, in sponge, MOUFPE 21827; 1 OV, same data as MOUFPE 21789, in sponge, MOUFPE 21828; 1 M, 1 F, same data as MOUFPE 21789, in sponge, MOUFPE 21819; 1 M, same data as MOUFPE 21789, in sponge, MOUFPE 21832; 1 M, same

data as MOUFPE 21789, in sponge, MOUFPE 21838; 1 M, 1 F, same data as MOUFPE 21789, in sponge, MOUFPE 21823; 1 OV, same data as MOUFPE 21789, in sponge, MOUFPE 21839; 1 M, same data as MOUFPE 21789, in sponge, MOUFPE 21840; 3 M, 1 F, same data as MOUFPE 21789, in sponge, MOUFPE 21835; 1 M, same data as MOUFPE 21789, in sponge, MOUFPE 21846; 1 M, same data as MOUFPE 21789, in sponge, MOUFPE 21850; 1 M, 1 F, same data as MOUFPE 21789, in sponge, MOUFPE 21841; 1 F, same data as MOUFPE 21789, in sponge, MOUFPE 21843; 1 M, 1 F, same data as MOUFPE 21789, in sponge, MOUFPE 21845.

Description: Coutière (1909), Dardeau (1984), and Ríos & Duffy (2007).

Distribution: USA (Florida), Caribbean Sea, and Brazil (Rocas Atoll, Almirante Saldanha Seamounts, Trindade Island, and from Pernambuco to Bahia) (Christoffersen 1979; Ríos & Duffy, 2007; Anker *et al.* 2016).

Ecology: Coral reefs or on sea bottom with abundance of perforated rocks and calcareous algae; in association with sponges (e.g., *Agelas* sp., *Hyattella* sp., *Hymeniacidon* sp., and *Lissodendoryx* sp.) (Ríos & Duffy, 2007); in heterosexual pairs; more commonly from 1–20 m, with records at 80 m (this study) and 105 m (Anker *et al.* 2012, 2016).

Remarks: *Synalpheus sanctithomae* is morphologically similar to *S. mcclendoni* Coutière, 1910, differing from the latter species by the fingers of major chela being not curved (vs. curved mesially in *S. mcclendoni*) (for comparison, see Coutière, 1909, fig. 35K, for *S. sanctithomae*, and Dardeau 1984, fig. 38L, for *S. mcclendoni*) (Anker *et al.* 2012). The record of *S. sanctithomae* by Bezerra & Coelho (2006) from Ceará has been reassigned to *S. townsendi* (Anker *et al.* 2012). Hultgren *et al.* (2010) documented morphological variations in the species, including the number of setae on distal margin of telson (ranging from 2 to 7) and the presence of a row of setae on the major chela dactyl (vs. major chela dactyl without row of setae) (see Coutière, 1909, fig. 35K). A male specimen from the continental shelf off Recife (MOUFPE 21850) examined in this study fits the diagnostic features in the description, but exhibited three pairs of dorsal spiniform setae on the telson (vs. two pair of dorsal spiniform setae) (see Coutière, 1909, fig. 35T).

***Synalpheus scaphoceris* Coutière, 1910**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 10.v.2018, 08°21'34.9"S 34°41'53.3"W, 50.8 m depth, in sponge, MOUFPE 21790; Brazil, Bahia—Porto Seguro: 1 M, Praia de Mutá, 25.ix.2011, associated with *Millepora alcicornis* Linnaeus, 1785, MOUFPE 21865.

Description: Dardeau (1984) and Anker *et al.* (2012).

Distribution: Bermuda, USA (Florida), Gulf of Mexico, Caribbean Sea, and Brazil (from Pernambuco to São Paulo) (Pequegnat & Ray 1974; Dardeau 1986; Duffy 1992; Christoffersen 1998; Anker *et al.* 2012).

Ecology: Shallow coral reefs and adjacent areas; coral and rock cavities, mangroves with perforated trunks, on the coral *M. alcicornis*; in heterosexual pairs; shallow waters to **50.8 m** (Schmitt 1924; Dardeau 1986; Anker *et al.* 2012; Santos *et al.* 2012). Sampled in association with sponge (this study).

Remarks: *Synalpheus scaphoceris* is one of the most common species found on coral reefs in the Caribbean, but it is rarely encountered along the Brazilian coast (Anker *et al.* 2012). The species can be differentiated from the morphologically similar *S. townsendi* by presenting several red chromatophores distributed across its body (see Anker *et al.* 2012, fig. 44) (vs. restricted to the region between the eyes in *S. townsendi*; see Anker *et al.* 2012, fig. 46), by the ventral process of the rostrum being strongly produced (see Dardeau 1986, fig. 3C) (vs. short in *S. townsendi*; see Hermoso-Salazar *et al.* 2005, fig. 1B), by the absence of a distodorsal tooth on the major chela (see Dardeau 1986, fig. 2G) (vs. major chela with a strong, sharp, distodorsal tooth in *S. townsendi*) (Dardeau 1986; Hermoso-Salazar *et al.* 2005; Anker *et al.* 2012). The present study extends the bathymetric distribution of the species from 20 (Anker *et al.* 2012) to 50.8 m, and provides the first record of association of *S. scaphoceris* with a sponge.

***Synalpheus tenuispina* Coutière, 1909**

Material examined: Rio Grande do Norte—São Pedro e São Paulo Archipelago: 1 F, 30 m depth, MOUFPE 13565; Pernambuco—Ilha de Itamaracá: 1 M, 1 F, Ilha de Itamaracá, St. 01, MOUFPE 8897.

Description: Anker & Pachelle (2014).

Distribution: Brazil (São Pedro e São Paulo Archipelago, Rio Grande do Norte, Pernambuco, Rio de Janeiro, São Paulo, and Santa Catarina) (Anker & Pachelle 2014; this study).

Ecology: Dwelling in pier growth or in crevices of polychaete reefs, on *Schizoporella* sp. bryozoan colonies; in heterosexual pairs; shallow waters to 45 m (Anker & Pachelle 2014; Almeida *et al.* 2018b).

Remarks: *Synalpheus tenuispina* is endemic to the Brazilian coast. Caribbean records (e.g., Abele 1976; Martínez-Iglesias *et al.* 1993, 1996) have been reassigned to *Synalpheus* cf. *africanus* (Anker & Pachelle 2014). This study extends the northern known range of the species.

***Synalpheus townsendi* Coutière, 1909**

Material examined: Maranhão—Turiacu: 1 F, Nordeste Expedition II, St. 111/112, MOUFPE 12510; Ceará—Camocim: 1 F, Almirante Saldanha Expedition, St. 1722, 29.x.1967, 02°13.5'S 40°43.5'W, 53.0 m depth, MOUFPE 8948; Pernambuco—Fernando de Noronha: 1 F, Buraco do Inferno, 26.vi.2022, 03°48.968'S 32°23.577'W, 12.0 m depth, in sponge, DZ/UFRGS 7034; 1 OV, Laje Dois Irmãos, 30.vi.2022, 03°51.859'S 32°27.934'W, 17.0 m depth, in sponge, DZ/UFRGS 7047; 1 F, Ilha do Meio, 18.vi.2019, 03°49.015'S 32°23.549'W, 12.0 m depth, in sponge, DZ/UFRGS 7072; 1 F, Ressureta, 19.vi.2019, 03°49.191'S 32°23.847'W, 8.0 m depth, in sponge, DZ/UFRGS 7071; Continental Shelf off Recife: 1 M, 07.ii.2018, 8°08'51.5"S 34°34'08.0"W, 65.0 m depth, in sponge, MOUFPE 21797; 1 OV, same data as MOUFPE 21797, MOUFPE 21798; 1 M, same data as MOUFPE 21797, MOUFPE 21799; 1 M, same data as MOUFPE 21797, MOUFPE 21800; 1 M, same data as MOUFPE 21797, MOUFPE 21801; 1 NI, same data as MOUFPE 21797, MOUFPE 21802; 1 M, same data as MOUFPE 21797, MOUFPE 21804; 1 M, same data as MOUFPE 21797, MOUFPE 21805; 1 M, same data as MOUFPE 21797, MOUFPE 21806; 1 M, same data as MOUFPE 21797, MOUFPE 21807; 1 OV, same data as MOUFPE 21797, MOUFPE 21809; 1 OV, 10.v.2018, 08°21'34.9"S 34°41'53.3"W, 50.8 m depth, in sponge, MOUFPE 21796; 1 F, same data as MOUFPE 21796, MOUFPE 21792; 1 OV, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, in sponge, MOUFPE 21536; 1 M, 27.ii.2018, 8°13'52.1"S 34°37'39.1"W, 50.8 m depth, in sponge, MOUFPE 21543; 1 F, 27.ii.2018, 8°13'52.1"S 34°37'41.2"W, 51.8 m depth, in sponge, MOUFPE 21538; 1 M, same data as MOUFPE 21538, in sponge, MOUFPE 21539; 1 M, 1 F, same data as MOUFPE 21538, in sponge, MOUFPE 21535; 1 F, 27.ii.2018, 8°13'52.1"S

34°37'42.7"W, 50.0 m depth, in sponge, DZ/UFRGS 7060; 1 M, same data as DZ/UFRGS 7060, MOUFPE 21568; 1 OV, same data as DZ/UFRGS 7060, MOUFPE 21576; 1 F, 10.v.2018, 08°23'04.3"S 34°40'07"W, 80.0 m depth, in sponge, MOUFPE 21830; 1 M, 1 OV, same data as MOUFPE 21830, MOUFPE 21821; 1 NI, same data as MOUFPE 21830, MOUFPE 21820; 1 M, 1 OV, same data as MOUFPE 21830, MOUFPE 21847; 1 F, same data as MOUFPE 21830, MOUFPE 21831; 1 M, 1 OV, same data as MOUFPE 21830, MOUFPE 21848; 1 OV, same data as MOUFPE 21830, MOUFPE 21817; 1 M, 1 OV, same data as MOUFPE 21830, MOUFPE 21852; 1 OV, same data as MOUFPE 21830, MOUFPE 21822; 1 OV, same data as MOUFPE 21830, MOUFPE 21824; 1 OV, same data as MOUFPE 21830, MOUFPE 21856; 1 F, same data as MOUFPE 21830, MOUFPE 21836; 1 F, same data as MOUFPE 21830, MOUFPE 21844; 1 M, same data as MOUFPE 21830, MOUFPE 21837; 1 M, 1 F, 1 NI, same data as MOUFPE 21830, MOUFPE 21833; 1 M, same data as MOUFPE 21830, MOUFPE 21851; 1 M, same data as MOUFPE 21830, MOUFPE 21853; 1 M, same data as MOUFPE 21830, MOUFPE 21854; 2 M, same data as MOUFPE 21830, MOUFPE 21834; 2 M, same data as MOUFPE 21830, MOUFPE 21849; 1 M, same data as MOUFPE 21830, in sediment, MOUFPE 21787; 1 F, 07.ii.2018, 8°08'43.7"S 34°34'22.6"W, 54.0 m depth, in coral rubble, MOUFPE 21569; 1 F, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, MOUFPE 21562; 1 F, 27.ii.2018, 8°13'25.4"S 34°37'43.2"W, 51.0 m depth, MOUFPE 21573; 1 M, 27.ii.2018, 8°13'52.1"S 34°37'39.1"W, 50.8 m depth, MOUFPE 21574; 1 F, 27.ii.2018, 8°13'52.1"S 34°37'41.2"W, 51.8 m depth, MOUFPE 21551; 1 M, same data as MOUFPE 21551, MOUFPE 21552; 1 F, same data as MOUFPE 21551, MOUFPE 21553; 1 F, same data as MOUFPE 21551, MOUFPE 21554; 1 F, same data as MOUFPE 21551, MOUFPE 21556; 1 M, same data as MOUFPE 21551, MOUFPE 21557; 1 M, same data as MOUFPE 21551, MOUFPE 21558; 1 M, same data as MOUFPE 21551, MOUFPE 21561; 1 F, same data as MOUFPE 21551, MOUFPE 21565; 1 M, same data as MOUFPE 21551, MOUFPE 21570; 1 M, same data as MOUFPE 21551, MOUFPE 21571; 1 M, same data as MOUFPE 21551, MOUFPE 21572; 1 M, same data as MOUFPE 21551, MOUFPE 21575; Recife: 1 M, 08°09'7"S 34°45'0"W, 31.5 m depth, MOUFPE 15392; 1 M, same data as MOUFPE 15392, MOUFPE 15389; Bahia—Abrolhos: 2 M, Ilha de Santa Bárbara, 31.viii.2013, in dead coral, MOUFPE 21866; 1 M, 1 OV, Ilha de Santa Bárbara, 31.viii.2013, in sponge, MOUFPE 21867.

Description: Coutière (1909), Williams (1984), and Anker *et al.* (2012).

Distribution: Bermuda, USA (from North Carolina to Florida), Gulf of Mexico, Honduras, Panama, Jamaica, Curaçao, and Barbados to Brazil (Rocas Atoll, **Fernando de**

Noronha, Trindade & Martin Vaz Archipelago, **Maranhão**, and from Ceará to São Paulo) (Hermoso-Salazar *et al.* 2005; Anker *et al.* 2012, 2016; Soledade *et al.* 2015; Almeida *et al.* 2018b; this study).

Ecology: Reef areas with abundance of sponges, *Phragmatopoma* sp., reef cavities, or dead corals (e.g. *Oculina* sp., *Porites* sp., *Siderastrea* sp., *Mussismilia* sp.); calcareous algae and ascidians, in mangroves, worm-perforated wood, and sponges; in heterosexual pairs; shallow waters to 102 m (Rouse 1970; Gore *et al.* 1978; Rodríguez 1980; Reed *et al.* 1982; Duffy 1992; Anker *et al.* 2012; 2016). Sampled herein in sediment, coral rubble, dead coral and sponges.

Remarks: *Synalpheus townsendi* is a common and widely distributed species throughout the western Atlantic, with numerous records along the Brazilian coast (Anker *et al.* 2012). One specimen collected from the continental shelf off Recife carried a rhizocephalan pleonal parasite (MOUFPE 21821). The material from Parque Estadual Marinho da Pedra da Risca do Meio, Fortaleza, previously reported by Bezerra & Coelho (2006), has been reidentified as *S. brooksi* (see *S. brooksi* section).

***Synalpheus ubatuba* Mantelatto, França, Cunha & Almeida, 2023**

Material examined: Pernambuco—Continental Shelf off Recife: 1 M, 07.ii.2018, 8°08'51.5"S 34°34'08.0"W, 65.0 m depth, in sponge, MOUFPE 21808; Sergipe—2 M, 3 OV, Plataforma Pcb4 Face Externa Fora Fundo, 01.xi.2000, MOUFPE 15790; 1 M, Plataforma Pcm11 Pós Face Externa Pé: Fora Superfície Externa, MOUFPE 15791; 1 OV, Plataforma Pd02 Face Externa Terra Meio, 30.x.2000, MOUFPE 15792; 1 M, Plataforma Pcb4 Face Externa Terra Superfície, 01.xi.2000, MOUFPE 15793; 1 M, 1 OV, Plataforma Pcm5 Pós: Face Externa Pé: Terra Superfície, MOUFPE 15794.

Description: Mantelatto *et al.* (2023).

Distribution: Brazil (**Pernambuco**, **Sergipe**, Bahia and São Paulo) (Mantelatto *et al.* 2023; this study).

Ecology: Under rocks, dead coral rubble and on dead parts of *M. alcicornis* in association with the bryozoan *Schizoporella errata* (Waters, 1878) and the sponge *Amphimedon viridis* Duchassaing & Michelotti, 1864; 2–65 m (Almeida *et al.* 2012, as *S. cf. brevicarpus*;

2018, as *S. cf. brevicarpus* (green/blue chela); Santos *et al.* 2012, as *S. cf. brevicarpus*; Mantelatto *et al.* 2023; this study).

Remarks: *Synalpheus ubatuba* belongs to the *S. brevicarpus* complex (Mantelatto *et al.* 2023; see remarks in the *S. cf. brevicarpus* section). The occurrence of *S. ubatuba* in the Northeast region has been confirmed in localities in southern Bahia (Mantelatto *et al.* 2023). The present study expands the known bathymetric distribution for the species from 8 (Mantelatto *et al.* 2023) to 65 m.

***Synalpheus ul* (Ríos & Duffy, 2007)**

Material examined: Pernambuco—Goiana: 1 M, 1 OV, Praia de Catuama, 20.i.2023, 7°39'18.6"S 34°49'28.1"W, 1.5 m depth, in sponge, MOUFPE 21811; Cabo de Santo Agostinho: 7 M, 2 OV, 1 F, Baía de Suape, 15.viii.2022, 8°21'54"S 34°56'50"W, 3.5 m depth, in sponge, MOUFPE 21784; 1 M, 1 OV, Baía de Suape, 16.viii.2019, 8°21'54"S 34°56'50"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21511; 1 M, 1 OV, same data as MOUFPE 21511, in unidentified sponge, MOUFPE 21512; 4 M, 1 OV, same data as MOUFPE 21511, MOUFPE 21517; 1 M, 1 OV, same data as MOUFPE 21511, MOUFPE 21514; 5 M, 1 OV, same data as MOUFPE 21511, MOUFPE 21518; 2 M, 1 OV, same data as MOUFPE 21511, in unidentified sponge, MOUFPE 21520; 1 M, 1 OV, same data as MOUFPE 21511, in unidentified sponge, MOUFPE 21516; 3 M, same data as MOUFPE 21511, in unidentified sponge, MOUFPE 21515; 3 M, 1 OV, same data as MOUFPE 21511, in unidentified sponge, MOUFPE 21519; 3 M, 1 OV, Baía de Suape, 26.x.2018, 8°21'54"S 34°56'50"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21593; 6 M, same data as MOUFPE 21593, MOUFPE 21588; 1 OV, same data as MOUFPE 21593, MOUFPE 21582; 1 M, 1 OV, same data as MOUFPE 21593, MOUFPE 21529; 1 M, 1 OV, same data as MOUFPE 21593, MOUFPE 21586; 1 M, 1 OV, same data as MOUFPE 21593, MOUFPE 21591; 1 M, same data as MOUFPE 21593, MOUFPE 21527; 1 OV, same data as MOUFPE 21593, MOUFPE 21531; 2 OV, same data as MOUFPE 21593, MOUFPE 21524; 1 M, 1 OV, same data as MOUFPE 21593, MOUFPE 21592; 1 M, same data as MOUFPE 21593, MOUFPE 21533; 1 M, 1 OV, same data as MOUFPE 21593, MOUFPE 21604; 3 M, 3 OV, same data as MOUFPE 21593, in unidentified sponge, MOUFPE 21862; 1 M, 2 OV, Baía de Suape, 21.iii.2019, 8°21'54"S 34°56'50"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE

21578; 2 M, 1 OV, same data as MOUFPE 21578, MOUFPE 21580; 1 M, 1 OV, same data as MOUFPE 21578, MOUFPE 21525; 2 M, 2 OV, same data as MOUFPE 21578, MOUFPE 21534; 1 M, 1 OV, same data as MOUFPE 21578, MOUFPE 21532; 1 M, 1 OV, same data as MOUFPE 21578, MOUFPE 21590; 1 M, 2 F, Praia do Paraíso, 23.ix.2022, 8°21'54"S 34°56'50"W, associated with *e. dendroides*, DZ/UFRGS 7048; Tamandaré: 1 M, 1 OV, Praia de Carneiros, 06.vi.2019, 8°41'32"S 35°4'25"W, 2.0 m depth, in sponge, MOUFPE 21598; 27 M, 13 OV, 2 F, Praia de Carneiros, 22.iii.2019, 8°41'32"S 35°4'25"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21599 (genetic voucher, genbank access PV273118); 2 M, 1 OV, Praia de Carneiros, 20.vii.2019, 8°41'32"S 35°4'25"W, 3.5 m depth, associated with *e. dendroides*, MOUFPE 21606; 2 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21607; 1 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21605; 1 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21608; 1 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21609; 1 F, same data as MOUFPE 21606, MOUFPE 21616; 1 OV, same data as MOUFPE 21606, MOUFPE 21624; 2 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21623; 1 M, 1 F, same data as MOUFPE 21606, MOUFPE 21625; 1 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21613; 1 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21614; 2 M, same data as MOUFPE 21606, MOUFPE 21615; 2 M, same data as MOUFPE 21606, MOUFPE 21617; 1 OV, same data as MOUFPE 21606, MOUFPE 21810; 3 M, 1 OV, same data as MOUFPE 21606, MOUFPE 21618.

Description: Ríos & Duffy (2007), Almeida *et al.* (2012), and Anker *et al.* (2012).

Distribution: Belize, Panama, Jamaica, Dominican Republic, Saint Martin, Barbados, Curaçao, and Brazil (Pernambuco, Alagoas, Sergipe and Bahia) (Hultgren *et al.* 2011; Almeida *et al.* 2012; Anker & Pachelle 2014; Barros-Alves *et al.* 2015).

Ecology: In shallow reefs; associated with rubble and seagrass banks with abundance of sponges, and substrates covered by bryozoans; obligate symbiont of sponges (e.g., *Hymeniacidon* sp., *Hyattella* sp., *Lissodendoryx* sp., *Xestospongia* sp.); in heterosexual pairs (see Remarks below); shallow waters to 52 m (Ríos & Duffy, 2007; Anker *et al.* 2012; Anker & Pachelle 2014).

Remarks: Anker *et al.* (2012) stated that *S. ul* forms heterosexual pairs; however, groups ranging from 2–6 to 42 individuals, with varying proportions of males and females, were observed in the same host sponge (see Discussion section for details). Some organisms were parasitized in the gill chamber by bopyrid isopods (1 OV, MOUFPE 21518; 1 M, MOUFPE 21525; 1 OV, MOUFPE 21862).

Morphological variations were observed in our material. In some specimens (1 M, MOUFPE 21529; 6 M, MOUFPE 21599), the mesial spiniform setae on the posterior margin of the telson were slightly longer and broader than the lateral, as previously reported by Hultgren *et al.* (2010).

Herein, we provide the first 16S gene sequences for the species in the southwestern Atlantic. Our sequences are identical to sequences of specimens collected in the Caribbean Sea (Barbados and Panama) (Fig. 19) (detailed in Discussion section).

***Synalpheus yano* (Ríos & Duffy, 2007)**

Material examined: Pernambuco—Continental Shelf off Recife: 1 OV, 27.ii.2018, 8°13'52.1"S 34°37'41.2"W, 51.8 m depth, in sponge, DZ/UFRGS 7062; 1 M, same data as DZ/UFRGS 7062, MOUFPE 21547; 1 M, 10.v.2018, 08°23'04.3"S 34°40'07"W, 80.0 m depth, in sponge, DZ/UFRGS 7061; 1 M, same data as DZ/UFRGS 7061, in sediment, MOUFPE 21788; 1 M, 07.ii.2018, 8°08'43.7"S 34°34'22.6"W, 54.0 m depth, in rhodoliths, MOUFPE 21563; 1 M, 07.ii.2018, 8°08'44.2"S 34°34'23.2"W, 55.0 m depth, MOUFPE 21545; 1 OV, same data as MOUFPE 21545, MOUFPE 21548; 1 M, 27.ii.2018, 8°13'52.1"S 34°37'42.7"W, 50.0 m depth, MOUFPE 21566; 1 M, same data as MOUFPE 21566, MOUFPE 21567; 1 F, same data as MOUFPE 21566, MOUFPE 21560; 1 M, 27.ii.2018, 8°13'33.0"S 34°37'40.3"W, 50.6 m depth, MOUFPE 21577; 1 OV, 27.ii.2018, 8°13'25.4"S 34°37'43.2"W, 51.0 m depth, MOUFPE 21544; 1 M, 27.ii.2018, 8°13'52.1"S 34°37'39.1"W, 50.8 m depth, MOUFPE 21550; Tamandaré: 2 M, xii.1972, MOUFPE 8864; Bahia—Camamu: 1 M, Baía de Camamu, MOUFPE 21864.

Description: Ríos & Duffy (2007) and Anker *et al.* (2012).

Distribution: Gulf of Mexico, Belize, Panama, Jamaica, and Brazil (Ceará, Pernambuco, and Bahia) (Ríos & Duffy, 2007; Anker *et al.* 2012; Anker & Pachelle 2014; this study).

Ecology: In shallow reefs and nearby areas with abundance of gravel and sponges; nearby mangroves and seagrass banks; symbiont of *Lissodendoryx* cf. *strongylata*, *L. colombiensis*, *H. caerulea*, and *C. podatypa*; in heterosexual pairs; 1–80 m (Ríos & Duffy, 2007; Anker *et al.* 2012; this study). Material from the continental shelf off Recife sampled in rhodoliths, sediment and sponges.

Remarks: *Synalpheus yano* is characterized by a square to broadly rounded orbital teeth and the absence of a scaphocerite blade, which is reduced in other members of the group (Ríos & Duffy, 2007; Anker *et al.* 2012). Morphological variations have been previously reported in *S. yano*, particularly in males sampled in Panama and analyzed by Anker *et al.* (2012), where the orbital teeth were more triangular. The rostrum was missing in one specimen analyzed in this study (1 M, MOUFPE 8864).

Synalpheus yano has been reported on the Brazilian coast only from Ceará. Herein, we expand the southern known range of the species in the western Atlantic as well as its bathymetric distribution from 3 (Anker *et al.* 2012) to 80 m.

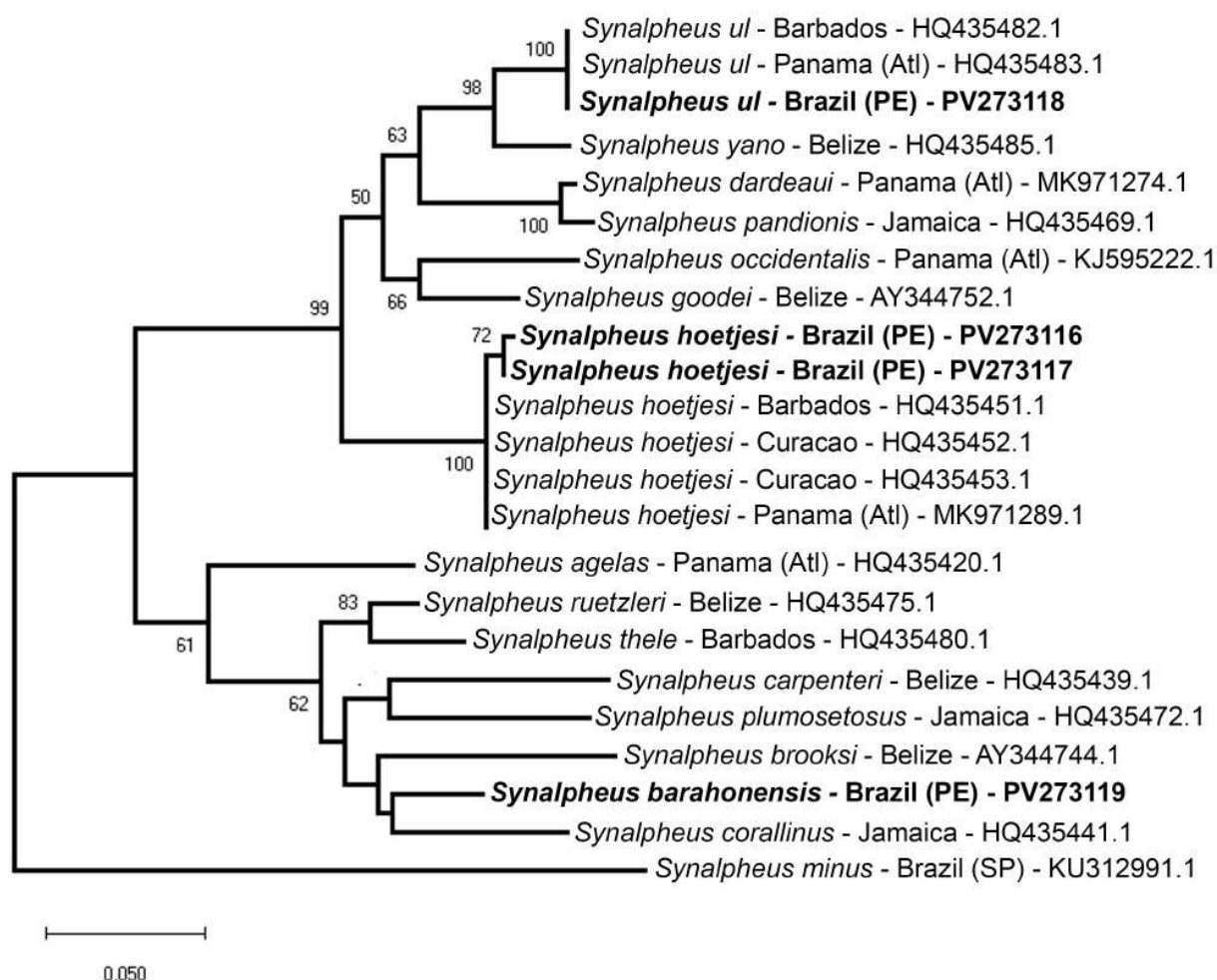


FIGURE 19. Phylogram constructed from Maximum Likelihood for the 16S mitochondrial gene. The numbers at the nodes correspond to the support values considering 1000 bootstrap pseudo-replicas. Bold specimens indicate sequences obtained in the present study; sequences obtained from Genbank have accession numbers. Atl: Atlantic Ocean; PE: Pernambuco; SP: São Paulo.

Discussion

Synalpheus diversity in the study area

Of the 27 species that have been recorded from Northeast Brazil, 20 were analyzed in the present study. We have not examined material of *S. cf. africanus*, *S. bousfieldi*, *S. filidigitus*, *S. longicarpus*, *S. maxillispinus*, *S. paranepetunus* and *S. rathbunae* (Table 1). The present study provides six new records for the southwestern Atlantic (*S. barahonensis*, *S. belizensis*, *S. brevidactylus*, *S. corallinus*, *S. hoetjesi*, and *S. kensleyi*) and 13 range extensions/new records from Brazil (*S. agelas*, *S. androsi*, *S. antillensis*, *S. dardeauui*, *S. fritzmuelleri*, *S. hemphilli*, *S. herricki*, *S. pandionis*, *S. ruetzleri*, *S. tenuispina*, *S. townsendi*, *S. ubatuba*, and *S. yano*) (Figs. 20, 21), increasing the known diversity of *Synalpheus* in the study area, excluding the four doubtful records (see below), to 29 species.

Most of the new records in this study involve species collected from calcareous substrates on the outer continental shelf off Recife, Pernambuco (*S. androsi*, *S. barahonensis*, *S. belizensis*, *S. brevidactylus*, *S. corallinus*, *S. herricki*, *S. kensleyi*, *S. pandionis*, *S. ruetzleri*, and *S. yano*), the majority of which are sponge-associated. Sampling in underexplored areas and substrates, particularly on the continental shelf, often yields new records, extensions of known bathymetric distributions, as demonstrated in this study, and the discovery of new taxa (e.g., Soledade *et al.* 2019). Additionally, new records for species inhabiting shallow coastal waters (*S. dardeauui*, *S. hoetjesi*, *S. kensleyi*, *S. pandionis*, *S. tenuispina*, and *S. yano*) were also documented. These findings are attributed to the scarcity of studies focusing on the genus in the region and the taxonomic challenges associated with identifying certain species, besides the employment of advanced sampling techniques such as artificial refuge structures (ARS), diving, and dredging (Hultgren *et al.* 2010; Anker *et al.* 2012, 2016).

With the addition of six new records from the southwestern Atlantic and excluding the misidentifications and doubtful records discussed below, the number of *Synalpheus* species currently known from the Brazilian coast is 31 (Table 1).

Sequences of the 16S gene for *S. barahonensis*, *S. hoetjesi*, and *S. ul* were compared with other *Synalpheus* sequences available in GenBank to confirm their identification (Fig. 19). The sequence for *S. barahonensis* represents the first of this gene to be deposited in GenBank, rendering comparisons with other populations unfeasible at the moment.

Conversely, the 16S sequences for *S. hoetjesi* and *S. ul* are the first reported from the southwestern Atlantic. As noted earlier, the sequences of *S. ul* specimens from Brazil (PE) were found to be identical to those from the southern Caribbean (Barbados and Panama), suggesting recent connectivity between Brazil and the Caribbean Sea (Fig. 19). In the case of *S. hoetjesi*, although the two sequences from Praia dos Carneiros (*S. hoetjesi*–Brazil, PE) clustered with those from the Caribbean (Panama, Barbados, and Curaçao) in a well-supported clade, a subdivision within the clade was observed. This subdivision separated the Brazilian specimens from their Caribbean counterparts into two distinct lineages. Furthermore, a genetic difference of 0.5% between these lineages was detected, suggesting small genetic variations between *S. hoetjesi* populations (Kimura & Weiss 1964; Avise 2000).

Misidentifications and doubtful records

Synalpheus filidigitus has been recorded in Ceará by Bezerra & Coelho (2006), in association with the sponge *A. crassa*. However, Anker *et al.* (2012) commented that this material possibly belongs to *S. brooksi*. Moreover, no specimens of this species were found in our study. Consequently, the occurrence of the species in Brazilian waters remains uncertain and requires further confirmation. For these reasons, *S. filidigitus* was not included in this checklist.

Synalpheus longicarpus has been recorded in Brazil by Gomes Corrêa (1972) in Bahia and Christoffersen (1979) from Paraíba to Rio de Janeiro. However, Christoffersen (1979) noted that the material examined by Gomes Corrêa (1972) actually corresponds to *S. brooksi*. Additionally, Anker & Pachelle (2014) highlighted that the records of *S. longicarpus* mentioned by Christoffersen (1979) and possibly in other studies are based on misidentified specimens. They also indicated that some specimens analyzed by Christoffersen (1979) from Pernambuco, previously identified as *S. longicarpus*, were, in fact, *S. ul*. Given this complex scenario and the absence of material of this species in our study, the occurrence of *S. longicarpus* in Brazil remains uncertain and was not included in the checklist.

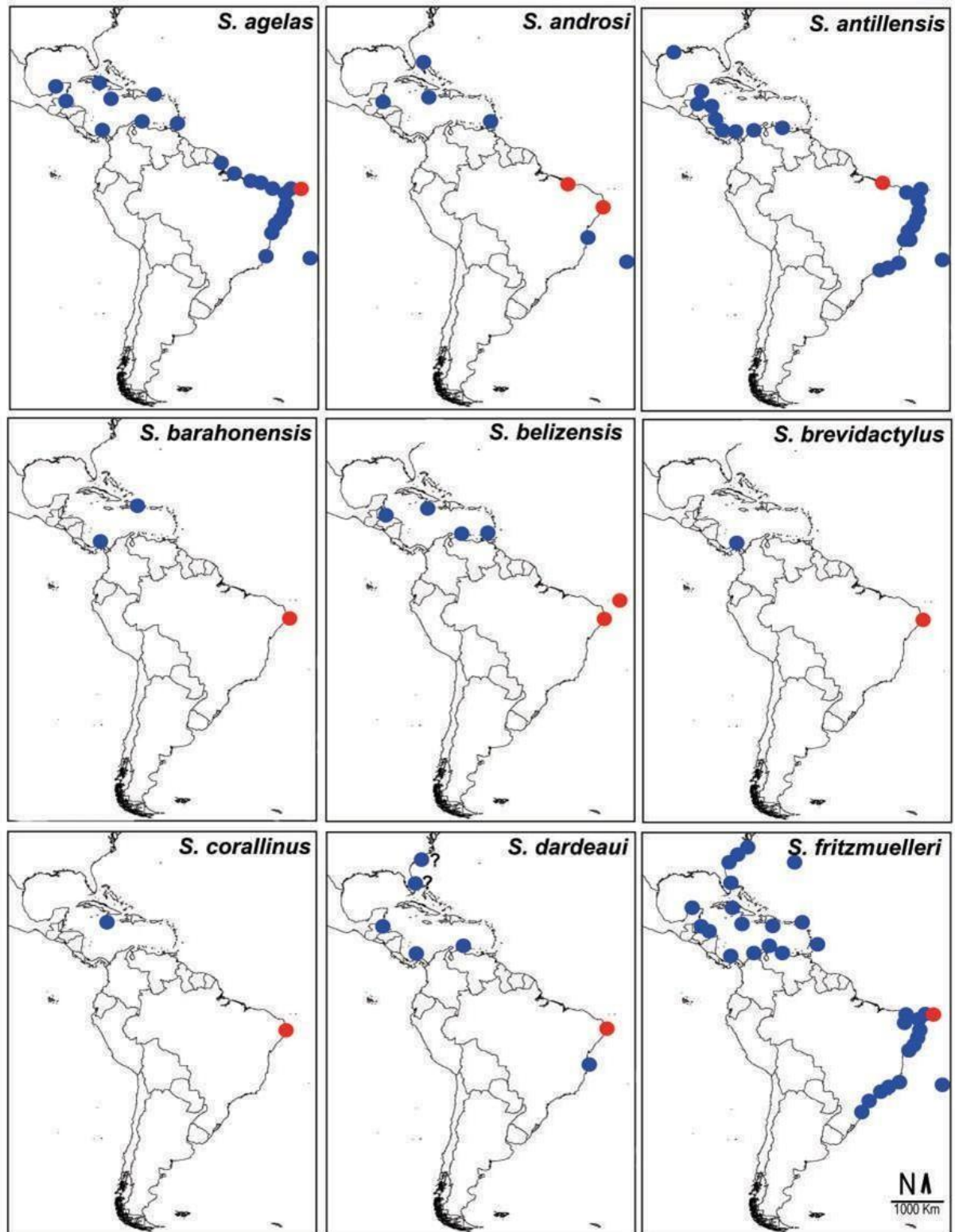


FIGURE 20. Maps with the distribution of new records of *Synalpheus* (*S. agelas*, *S. androsi*, *S. antillensis*, *S. barahonensis*, *S. belizensis*, *S. brevidactylus*, *S. corallinus*, *S. dardeau*, *S. fritzmuelleri*) for the coast in northeastern Brazil or Brazil. *Synalpheus fritzmuelleri* - also occurs in the São Pedro e São Paulo Archipelago, Helena Island, and Ascension Island. Blue dots = previous records; Red dots = new records.

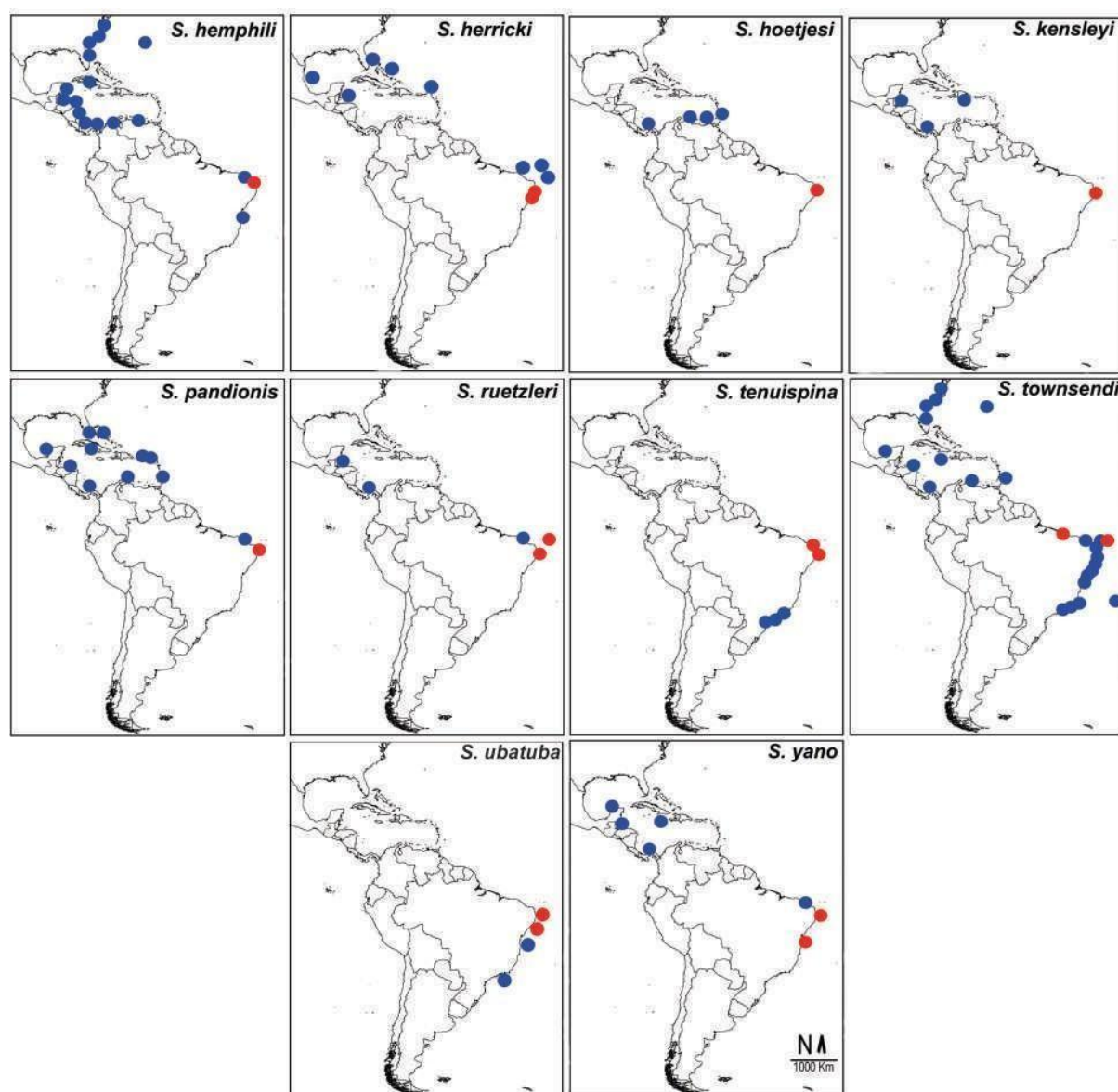


FIGURE 21. Maps with the distribution of new records of *Synalpheus* (*S. hemphilli*, *S. herricki*, *S. hoetjesi*, *S. kensleyi*, *S. pandionis*, *S. ruetzleri*, *S. tenuispina*, *S. townsendi*, *S. ubatuba*, and *S. yano*) to the coast in northeastern Brazil or Brazil. *Synalpheus tenuispina* - also occurs in the São Pedro e São Paulo Archipelago. Blue dots = previous records; Red dots = new records.

Table 1. Diversity and distribution of alpheid shrimp of the genus *Synalpheus* Spence Bate, 1888 from Brazil. The acronyms refer to the locations of the new records (ASPSP—São Pedro e São Paulo Archipelago; FN—Fernando de Noronha Archipelago; BA—Bahia; MA—Maranhão; PE—Pernambuco; RN—Rio Grande do Norte; SE—Sergipe; Markings in bold refer to new records for the southwestern Atlantic while the “-” refers to records that were already known).

<i>Synalpheus</i> Species	Distribution in the western Atlantic	New Records	References
<i>Synalpheus</i> cf. <i>africanus</i>	Panama (Bocas del Toro), Dominican Republic (Bayahibe), Aruba and Brazil (Rocas Atoll)	-	Anker <i>et al.</i> (2012)
<i>Synalpheus agelas</i>	Gulf of Mexico, Puerto Rico, Cuba, Belize, Jamaica, Panama, Curaçao, Barbados and Brazil (Fernando de Noronha, Rocas Atoll, seamounts of North Chain, Trindade & Martin Vaz Archipelago, and from Amapá to Espírito Santo)	FN	Coelho-Filho (2006); Coelho <i>et al.</i> (2006); Ríos & Duffy (2007); Hultgren <i>et al.</i> (2011); Anker <i>et al.</i> (2012, 2016); this study
<i>Synalpheus androsi</i>	Bahamas (Andros Island), Belize (Carrie Bow Cay), Jamaica, Barbados and Brazil (Maranhão, Pernambuco, Bahia and Espírito Santo: Vitória-Trindade chain)	MA and PE	Coutière (1909); Dardeau (1984); Coelho <i>et al.</i> (2006); Ríos & Duffy (2007); Macdonald <i>et al.</i> (2009); Hultgren <i>et al.</i> (2011); Anker & Pachellet (2014); this study
<i>Synalpheus antillensis</i>	Gulf of Mexico (off Texas), Caribbean Sea (from Yucatan Peninsula to Venezuela) and Brazil (Abrolhos, Rocas MA Atoll, Trindade Island, Maranhão, and from Ceará to São Paulo)	MA	Coutière (1909); Chace (1956b); Anker <i>et al.</i> (2012, 2016); Soledade <i>et al.</i> (2015)
<i>Synalpheus apioceros</i>	USA (Florida), Gulf of Mexico, Bahamas, Caribbean Sea, Suriname and -	-	Chace (1972); Lemaitre (1984); Christoffersen (1998); Coelho-Filho

	Brazil (from Amapá to Santa Catarina and seamounts of North Chain)		(2006); Anker <i>et al.</i> (2012)
<i>Synalpheus barahonensis</i>	Dominican Republic, Panama, Brazil (Pernambuco)	PE	Armstrong (1949); Duffy (1992); this study
<i>Synalpheus belizensis</i>	Belize, Jamaica, Curaçao, Barbados and Brazil (Fernando de Noronha and Pernambuco)	FN and PE	Anker & Tóth (2008); Macdonald <i>et al.</i> (2009); Hultgren <i>et al.</i> (2010, 2011); this study
<i>Synalpheus bousfieldi</i>	Bahamas, Gulf of Mexico, Caribbean Sea and Brazil (Rocas Atoll)	-	Chace (1972); Dardeau (1984); Martínez-Iglesias <i>et al.</i> (1996); Coelho <i>et al.</i> (2006); Ríos & Duffy (2007) [as <i>Zuzalpheus bousfieldi</i> Chace, 1972]; Hultgren <i>et al.</i> (2010, 2011); Anker <i>et al.</i> (2012)
<i>Synalpheus brevicarpus</i>	Bermuda, USA (Florida), Gulf of Mexico, Bahamas, West Indies, Panama, Venezuela and Brazil (from Ceará to Rio Grande do Sul)	-	Christoffersen (1979, 1998); Bezerra & Coelho (2006); Cházaro- Olvera & Vázquez-López (2014); Velásquez <i>et al.</i> (2017)
<i>Synalpheus brevidactylus</i>	Panama and Brazil (Pernambuco)	PE	Anker & Tóth (2008); this study
<i>Synalpheus brooksi</i>	USA (Florida), Gulf of Mexico, Bahamas, Caribbean Sea, Suriname and Brazil (Fernando de Noronha, Abrolhos and from Amapá to Bahia)	-	Chace (1972); Christoffersen (1979, 1998); Ríos & Duffy (2007); Anker <i>et al.</i> (2012); Soledade <i>et al.</i> (2015); this study
<i>Synalpheus corallinus</i>	Jamaica (Discovery Bay) and Brazil (Pernambuco)	PE	Macdonald <i>et al.</i> (2009); this study
<i>Synalpheus curacaoensis</i>	Curaçao, Mexico, Colombia, and Brazil (Pará)	-	Schmitt (1924); Coelho <i>et al.</i> (2006);

			Prüsmann & Palacio (2008); Hernández <i>et al.</i> (2010)
<i>Synalpheus dardeau</i>	USA (North Carolina, Florida), Belize, Panama, Curaçao, and Brazil (Pernambuco and Bahia)	PE	Ríos & Duffy (2007); Hultgren <i>et al.</i> (2010); Anker <i>et al.</i> (2012); Oliveira <i>et al.</i> (2015); this study
<i>Synalpheus fritzmuelleri</i>	USA (North Carolina to Florida), Gulf of Mexico, Honduras, Belize, Panama, Cuba, Jamaica, Dominican Republic, Colombia, Aruba, Venezuela, Saint Martin, Barbados, Bermuda, Brazil (Abrolhos, Fernando de Noronha, Rocas Atoll, São Pedro and São Paulo, Archipelago of Trindade & Martim Vaz, and from Ceará to Santa Catarina), Santa Helena Island, Ascension Island	FN	Anker <i>et al.</i> (2012) and references therein; Santos <i>et al.</i> (2012) and references therein; Soledade <i>et al.</i> (2015); Anker <i>et al.</i> (2016); this study
<i>Synalpheus hemphilli</i>	Bermuda, USA (from North Carolina to Florida), Gulf of Mexico, Curaçao, Bonaire, Panama, Cuba, Venezuela, and Brazil (Abrolhos, Ceará, Rio Grande do Norte, and Bahia)	RN	Coutière (1909); Verrill (1922); Rodríguez (1980); Christoffersen (1979, 1998); Bezerra & Coelho (2006); Anker <i>et al.</i> (2012); this study
<i>Synalpheus herricki</i>	USA (Florida), Gulf of Mexico, Mexico, Belize, Saint Martin, Panama (Bocas del Toro), Curaçao, and Brazil (Rocas Atoll, Fernando de Noronha, Ceará, Pernambuco, and Sergipe)	PE and SE	Chace (1972); Dardeau (1984); Ríos & Duffy (2007); Anker <i>et al.</i> (2012); Cházaro-Olvera <i>et al.</i> (2017); Horch <i>et al.</i> (2024)
<i>Synalpheus hoetjesi</i>	Panama (Bocas del Toro), Curaçao, Barbados, Venezuela, and Brazil (Pernambuco)	PE	Hultgren <i>et al.</i> (2010, 2011); Hultgren & Duffy (2011); Anker <i>et al.</i> (2012); Rodríguez <i>et al.</i> (2020); this study

<i>Synalpheus kensleyi</i>	Belize (Carrie Bow Cay), Dominican Republic (Bayahibe), Panama (Bocas del Toro) and Brazil (Pernambuco)	PE	Ríos & Duffy (2007); Anker <i>et al.</i> (2012); this study
<i>Synalpheus maxillispinus</i>	Brazil (Bahia and Espírito Santo)	-	Anker & Pachelle (2014)
<i>Synalpheus minus</i>	Bermuda and from USA (North Carolina) to Brazil (Abrolhos, Maranhão and from Ceará to São Paulo)	-	Spence Bate (1888); Rathbun (1900); Christoffersen (1979, 1980, 1998); Fausto-Filho (1980); Ramos-Porto <i>et al.</i> (1996); Masunari <i>et al.</i> (1998); Coelho <i>et al.</i> (2002); Bezerra & Coelho (2006)
<i>Synalpheus pandionis</i>	USA (Florida), Gulf of Mexico, Bahamas, Cuba, Mexico, Honduras, Panama, Puerto Rico, Virgin Islands, Curaçao, Barbados, and Brazil (Ceará and Pernambuco)	PE	Coutière (1909); Zimmer (1913); Schmitt (1935); Chace (1972); Dardeau (1984); Rodríguez (1986); Coelho <i>et al.</i> (2006); Ríos & Duffy (2007); Anker <i>et al.</i> (2012); Cházaro-Olvera <i>et al.</i> 2017; this study
<i>Synalpheus ruetzleri</i>	Panama, Belize, and Brazil (Fernando de Noronha, Ceará, and Pernambuco)	FN and PE	Macdonald & Duffy (2006); Ríos & Duffy (2007); Anker & Pachelle (2014) (as <i>Synalpheus</i> cf. <i>ruetzleri</i>); this study
<i>Synalpheus sanctithomae</i>	USA (Florida), Caribbean Sea, and Brazil (Rocas Atoll, Almirante Saldanha Seamounts, Trindade Islands, from Pernambuco to Bahia)	-	Christoffersen (1979, 1998); Nogueira (2003); Bezerra & Coelho (2006); Ríos & Duffy (2007); Anker <i>et al.</i> (2012, 2016)
<i>Synalpheus scaphoceris</i>	Bermuda, USA (Florida), Gulf of Mexico, Caribbean	-	Chace (1956b); Pequegnat & Ray

	Sea, and Brazil (from Pernambuco to São Paulo)		(1974); Duffy (1992); Christoffersen (1979, 1998); Dardeau (1986); Anker <i>et al.</i> (2012)
<i>Synalpheus tenuispina</i>	Brazil (São Pedro and São Paulo, Rio Grande do Norte, Pernambuco, Rio de Janeiro, São Paulo, and Santa Catarina)	ASPSP, RN, and PE	Coelho & Ramos (1972); Riul <i>et al.</i> (2008); Anker & Pachelles (2014); this study
<i>Synalpheus townsendi</i>	Bermuda, USA (from North Carolina to Florida), Gulf of Mexico, Honduras, Panama, Jamaica, Curaçao and Brazil (Rocas Atoll, Fernando de Noronha, Trindade and Martim Vaz Islands, Maranhão, and from Ceará to São Paulo)	FN and MA	Christoffersen (1980); Ramos-Porto <i>et al.</i> (1996); Hermoso-Salazar <i>et al.</i> (2005); Anker <i>et al.</i> (2012, 2016); Soledade <i>et al.</i> (2015); Almeida <i>et al.</i> (2018); this study
<i>Synalpheus trinitatis</i>	Brazil (Trindade and Martim Vaz)	-	Anker <i>et al.</i> (2016)
<i>Synalpheus ubatuba</i>	Brazil (Pernambuco, Sergipe, Bahia and São Paulo)	PE and SE	Mantelatto <i>et al.</i> (2023); this study.
<i>Synalpheus ul</i>	Belize, Panama, Jamaica, Dominican Republic, Saint Martin, Barbados, Curaçao, and Brazil (Pernambuco, Alagoas, Sergipe, and Bahia)	-	Hultgren <i>et al.</i> (2011); Almeida <i>et al.</i> (2012); Anker & Pachelles (2014); Barros-Alves <i>et al.</i> (2015)
<i>Synalpheus yano</i>	Gulf of Mexico, Belize, Panama, Jamaica, and Brazil (Ceará, Pernambuco, and Bahia)	PE and BA	Ríos & Duffy (2007); Anker <i>et al.</i> (2012); Anker & Pachelles (2014); this study

The only record of *S. paraneptunus* from Brazilian waters (Fernando de Noronha) was reported by Coelho- Filho (2006). However, the author did not provide any illustration or detailed morphological descriptions of the material. Anker & Tóth (2008) and De Grave & Anker (2017) noted that *S. paraneptunus* is reliably known only from its type locality (Morrosquillo, Colombia), and that all records beyond this location likely pertain to other

species within the *S. paraneptunus* complex, including some undescribed species and *S. paraneptunus* itself. In our study, we found two species belonging to the *S. paraneptunus* complex (*S. belizensis* and *S. brevidactylus*), neither of which correspond to *S. paraneptunus sensu stricto*. Coelho-Filho (2006) also provided, without any illustrations or morphological details, the first record of *S. rathbunae* from Brazilian waters (seamounts of North Chain, Fernando de Noronha and Ceará). Alves *et al.* (2008) included the species in a checklist of decapods from Fernando de Noronha, based on the Coelho Filho's (2006) record. However, we did not encounter any specimens of *S. rathbunae* in our study. Given the lack of confirmatory evidence, we consider the occurrence of *S. paraneptunus* and *S. rathbunae* in Brazil as doubtful and they were not included in the checklist.

Notes on shrimp-sponge association

Synalpheus species are frequently found in association with sponges (Ríos & Duffy, 2007; Hultgren *et al.* 2010; Anker *et al.* 2012, 2016; Anker & Pachelle 2014), a pattern also observed in many of the specimens reported here. This association is particularly notable in the *S. gambarelloides* group (Ríos & Duffy, 2007), which exhibits eusocial groupings (Hultgren *et al.* 2017). In the present study, *S. hoetjesi* and *S. ul* were observed forming possible communal groupings within their sponge hosts. Additionally, both species were found cohabiting the same host in 15 different sponge specimens. Records of *Synalpheus* species cohabiting the same host sponges are rare. Examples include *S. belizensis* and *S. microneptunus* inhabiting the canals of *Neopetrosia proxima* (Duchassaing & Michelotti, 1864)—cited as *Xestospongia proxima* in Hultgren *et al.* (2011)—and *S. dardeau* sharing the canals of *Spheciospongia vesparium* with *S. brooksi* and *S. pectiniger* Coutière, 1907 (Ríos & Duffy, 2007 Hultgren *et al.* 2011). Such communal groupings have been reported in other *Synalpheus* species, including *S. longicarpus*, *S. pectiniger*, and *S. thele*. Interestingly, individuals of some species observed in this study, such as *S. dardeau* and *S. yano*, were found living solitarily, despite communal behavior being documented in related taxa (Hultgren *et al.* 2017). However, further research is needed to confirm whether the groupings observed in *S. hoetjesi* and *S. ul* represent true communal structures.

Another noteworthy observation is the presence of 54 specimens of *S. brooksi* within a single sponge host. This species is known to form “subsocal” groupings with a sex ratio strongly skewed towards males (Ríos & Duffy, 2007), comprising tens to thousands of

individuals (Pearse 1932, 1950). *Synalpheus brooksi* appears to exhibit an intermediate social structure between the ancestral condition of heterosexual pairings typical of Alpheidae and eusociality (Duffy *et al.* 2000). Interestingly, two individuals within this grouping were observed with two minor chelae instead of the usual major and minor chelae. This trait, also noted in the eusocial *S. filidigitus* (Duffy & MacDonald 1999), raises the possibility that this grouping might exhibit eusociality. However, additional evaluations of key characteristics, such as overlapping generations, division of labor, and cooperative social behavior (Wilson 1971; Sherman *et al.* 1995), are required to confirm whether *S. brooksi* exhibits truly eusocial organization.

Acknowledgments

We would like to thank CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for the financial assistance granted to MT (Universal 421193/2018-2, PQ 311340/2021-0), AOA (PQ 311217/2022-2), GLB (DCR- 300067/2018-6), and KP (doctoral scholarship Proc. 140066/2021-7); to FACEPE (Fundação de Amparo à Ciência e Tecnologia de Pernambuco) for the aid granted to GLB (APQ-0196-2.04/16) and to PHP (master's scholarship Process IBPG-1407-2.04/18); to CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for the financial assistance granted to PHP (doctoral scholarship Proc. 88887.611870/2021-00, Finance code 001); to FAPERGS (Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul) or the aid granted to MT (24/2551-0001357-1); to ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade) for authorizations for collections in the archipelagos (66478), granted to MT, and on the coastal areas of Pernambuco (58697-1), granted to GLB; to the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio NGI Noronha) and the Autarquia Territorial Distrito Estadual de Fernando de Noronha—ATDEFN for all logistical support during the fieldwork in Fernando de Noronha; to Amanda Horch and Isabela Moraes for helping to collect and sort animals in the Fernando de Noronha; to the Laboratório de Porifera (LABPOR) at UFPE for identifying the sponges; to the Museu de Oceanografia Prof. Petrônio Alves Coelho (MOUFPE) at UFPE, especially the curator of the Crustacean Collection, Dr. Jessor Fidelis de Souza Filho, and Dr. Fabíola M. Marques do Couto-Cahu, for lending *Synalpheus* material. Finally, we are grateful to the anonymous reviewers for the

corrections and suggestions that improved the manuscript. The English version of this paper was prepared using DeepL and ChatGPT and later revised by the authors.

References

- Abele, L.G. (1976) Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panama. *Marine Biology*, 38, 263–278. <https://doi.org/10.1007/BF00388939>
- Abele, L.G. & Kim, W. (1986) An illustrated guide to the marine decapod crustaceans of Florida. *Florida Department of environmental Regulation, Technical Series*, 8 (1), 1–225.
- Almeida, A.O., Boehs, G., Araújo-Silva, C.L. & Bezerra, L.E.A. (2012) Shallow-water caridean shrimps from southern Bahia, Brazil, including the first record of *Synalpheus ul* (Ríos & Duffy, 2007) (Alpheidae) in the southwestern Atlantic Ocean. *Zootaxa*, 3347 (1), 1–35. <https://doi.org/10.11646/zootaxa.3347.1.1>
- Almeida, A.O., Guerrazzi, M.C. & Coelho, A. (2007) Stomatopod and decapod crustaceans from Camamu Bay, state of Bahia, Brazil. *Zootaxa*, 1553 (1), 1–45. <https://doi.org/10.11646/zootaxa.1553.1.1>
- Almeida, A.O., Santos, S., Soledade, G.O., Santos, J.P. & Pérez, C.D. (2015) New invertebrate host records (Porifera and Cnidaria) for some caridean shrimps in estuaries of north-eastern Brazil. *Marine Biodiversity Records*, 8, e38. <https://doi.org/10.1017/S1755267215000111>
- Almeida, A.O., Terossi, M., Buranelli, R.C., Castilho, A.L., Costa, R.C., Zara, F.J. & Mantelatto, F.L. (2018b) Checklist of decapods (Crustacea) from the coast of São Paulo State (Brazil) supported by integrative molecular and morphological data: II. Infraorder Caridea: family Alpheidae. *Zootaxa*, 4450 (3), 331–358. <https://doi.org/10.11646/zootaxa.4450.3.2>
- Almeida, A.S., Barros-Alves, S.P., Hirose, G.L. & Alves, D.F.R. (2018a) Reproductive output of the ornamental shrimp *Lysmata vittata* (Stimpson, 1860) (Decapoda: Caridea) in wild populations and under different maturation diets. *Invertebrate Reproduction & Development*, 62, 257–267. <https://doi.org/10.1080/07924259.2018.1509903>

- Alves, M.D.L., Ramos-Porto, M. & Viana, G.F.S. (2008) Checklist of the decapods (Crustacea) from the Fernando de Noronha Archipelago, Brazil. *Zootaxa*, 1881 (1), 43–68. <https://doi.org/10.11646/zootaxa.1881.1.2>
- Anker, A., Hultgren, K.M. & De Grave, S. (2017) *Synalpheus pinkfloydi* sp. nov., a new pistol shrimp from the tropical eastern Pacific (Decapoda: Alpheidae). *Zootaxa*, 4254 (1), 111–119. <https://doi.org/10.11646/zootaxa.4254.1.7>
- Anker, A. & Pachelle, G. (2014) Taxonomic notes on some Brazilian species of *Synalpheus* Spence Bate, 1888, with new records and description of a new species (Decapoda, Alpheidae). *Zootaxa*, 3815 (2), 215–232. <https://doi.org/10.11646/zootaxa.3815.2.3>
- Anker, A., Pachelle, G., De Grave, S. & Hultgren, K.M. (2012) Taxonomic and biological notes on some Atlantic species of the snapping shrimp genus *Synalpheus* Spence Bate, 1888 (Decapoda, Alpheidae). *Zootaxa*, 3598 (1), 1–96. <https://doi.org/10.11646/zootaxa.3598.1.1>
- Anker, A., Tavares, M. & Mendonça, J.B. (2016) Alpheid shrimps (Decapoda: Caridea) of the Trindade & Martin Vaz Archipelago, off Brazil, with new records, description of a new species of *Synalpheus* and remarks on zoogeographical patterns in the oceanic islands of the tropical southern Atlantic. *Zootaxa*, 4138 (1), 1–58. <https://doi.org/10.11646/zootaxa.4138.1.1>
- Anker, A. & Tóth, E. (2008) A preliminary revision of the *Synalpheus paraneptunus* Coutière, 1909 species complex (Crustacea: Decapoda: Alpheidae). *Zootaxa*, 1915 (1), 1–28. <https://doi.org/10.11646/zootaxa.1915.1.1>
- Armstrong, J.C. (1949) New Caridea from the Dominican Republic. *American Museum Novitates*, 1410, 1–27.
- Ashrafi, H. & Hultgren, K.M. (2022) Integrative methods resolve taxonomy and relationships of snapping shrimps in the genus *Synalpheus* (Decapoda: Alpheidae) collected during the MNHN ‘Madibenthos’ expedition. *Invertebrate Systematics*, 36, 389–418. <https://doi.org/10.1071/IS21057>
- Avise, J.C. (2000) *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, 447 pp. <https://doi.org/10.2307/j.ctv1nzfgj7>
- Banner, D.M. & Banner, A.H. (1975) The alpheid shrimp of Australia. Part 2: the genus *Synalpheus*. *Records of the Australian Museum*, 29 (12), 267–389. <https://doi.org/10.3853/j.0067-1975.29.1975.389>

- Barros-Alves, S.D., Alves, D.F.R., Silva, S.L.R.D., Guimarães, C.R. & Hirose, G.L. (2015) New records of decapod crustaceans from the coast of Sergipe state, Brazil. *Check List*, 11, 1768. <https://doi.org/10.15560/11.5.1768>
- Bauer, R.T. (2004) *Remarkable shrimps: adaptations and natural history of the carideans*. University of Oklahoma Press, Norman, Oklahoma, 282 pp.
- Bezerra, L.E.A. & Coelho, A. (2006) Crustáceos associados a esponjas no litoral do Estado do Ceará, Brazil. *Revista Brasileira de Zoologia*, 23, 699–702. <https://doi.org/10.1590/S0101-81752006000300012>
- Boomsma, J.J. (2009) Lifetime monogamy and the evolution of eusociality. *Philosophical transactions of the Royal Society B: Biological Sciences*, 364, 3191–3207. <https://doi.org/10.1098/rstb.2009.0101>
- Brasil. Ministério do meio ambiente. O Desafio. s/d. Available from: <https://antigo.mma.gov.br/gestao-territorial/projeto-terramar/o-desafio.html> (accessed 5 February 2024)
- Bruce, A.J. (1976) Coral Reef Caridea and “Commensalism”. *Micronesica*, 12 (1), 83–98.
- Cerqueira, A.C., Milani, I.C.B. & Pinheiro, A.A.L. (2018) Mapeamento das estruturas de defesa litorânea e mitigação de processos erosivos em Pernambuco-Brasil. In: *Recursos Hídricos: gestão, planejamento e técnicas de pesquisa*. Editora Científica Digital, São Paulo, pp. 151–158.
- Chace Jr., F.A. (1956a) Crustáceos decápodos y estomatópodos del Archipiélago de los Roques e Isla de la Orchila. In: Sociedad de Ciencias Naturales La Salle (Ed.), *Archipiélago de Los Roques y la Orchila*. Sociedad de Ciencias Naturales La Salle, Editorial Sucre, Caracas, pp. 145–168.
- Chace Jr., F.A. (1956b) Decapod crustaceans from St. Helena, South Atlantic. *Proceedings of the United States National Museum*, 118, 622–662.
- Chace Jr., F.A. (1972) The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). *Smithsonian Contributions to Zoology*, 98, 1–179. <https://doi.org/10.5479/si.00810282.98>
- Chace Jr, F.A. (1989) The Caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine expedition, 1907-1910, Part 5: Family Alpheidae. *Smithsonian Contributions to Zoology*, 46, 1–99. <https://doi.org/10.5479/si.19436696.391.1>

- Chak, S.T.C., Duffy, J.E., Hultgren, K.M. & Rubenstein, D.R. (2017) Evolutionary transitions towards eusociality in snapping shrimps. *Nature ecology & evolution*, 1, 96. <https://doi.org/10.1038/s41559-017-0096>
- Chak, S.T.C, Rubenstein, D.R. & Duffy, J.E. (2015) Social control of reproduction and breeding monopolization in the eusocial snapping shrimp *Synalpheus elizabethae*. *the American Naturalist*, 186, 660–668. <https://doi.org/10.1086/683132>
- Cházaro-Olvera, S., Hernández-Vidal, G.A., Ortiz, M. & Winfield, I. (2017) Primer registro de la asociación de *Synalpheus herricki* y *S. pandionis* con *Aiolochoira crassa* en el parque nacional arrecife Puerto Morelos, Quintana Roo, México. *Revista de Biología Marina y Oceanografía*, 52, 617–620. <https://doi.org/10.4067/S0718-19572017000300017>
- Cházaro-Olvera, S.C. & Vázquez-López, H. (2014) Asociación de *Synalpheus* (Decapoda, Alpheidae) con Esponjas Del Parque Marino Nacional Sistema Arrecifal Veracruzano, Sw Del Golfo De México. *Biocyt: Biología, Ciencia y tecnología*, 7, 465–473. <https://doi.org/10.22201/fesi.20072082.2014.7.76133>
- Christoffersen, M.L. (1979) Decapod Crustacea: Alpheoidea. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962). I. 36, *Annales de l'Institut Océanographique, Monaco*, 55 (Supplement), 297–377.
- Christoffersen, M.L. (1980) *taxonomia e distribuição geográfica dos Alpheoidea (Crustacea, Decapoda, Natantia) do Brasil, Uruguai e norte da Argentina, incluindo considerações sobre a divisão do sul do continente em províncias biogeográficas marinhas*. Unpublished Ph.D. Thesis, University of São Paulo, São Paulo, 467 pp.
- Christoffersen, M.L. (1998) Malacostraca. Eucarida. Caridea. Crangonoidea and Alpheoidea (Except Glyphocrangonidae and Crangonidae). In: Young, S. (Ed.), *Catalogue of Crustacea of Brazil*. Museu Nacional, Rio de Janeiro, pp. 351–372.
- Coelho, P.A., Almeida, A.O. & Bezerra, L.E.A. (2008) Checklist of the marine and estuarine Brachyura (Crustacea: Decapoda) of northern and northeastern Brazil. *Zootaxa*, 1956 (1), 1–58. <https://doi.org/10.11646/zootaxa.1956.1.1>
- Coelho, P.A., Almeida, A.O., Souza-Filho, J.F., Bezerra, L.E.A. & Giraldes, B.W. (2006) Diversity and distribution of the marine and estuarine shrimps (Dendrobranchiata, Stenopodidea and Caridea) from North and Northeast Brazil. *Zootaxa*, 1221 (1), 41–62. <https://doi.org/10.11646/zootaxa.1221.1.5>

- Coelho, P.A. & Ramos, M.A. (1972) A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes de 5°N e 39°S. *trabalhos Oceanográficos da Universidade Federal de Pernambuco*, 13, 133–236. <https://doi.org/10.5914/tropocean.v13i1.2555>
- Coelho-Filho, P.A. (2006) Checklist of the decapods (Crustacea) from the outer continental shelf and seamounts from Northeast of Brazil—REVIZEE Program (NE III). *Zootaxa*, 1184 (1), 1–27. <https://doi.org/10.11646/zootaxa.1184.1.1>
- Coutière, H. (1907) Sur la présence de mâles en excès chez deux espèces de Synalphees. *Comptes Rendus des Séances de la Société Biologique*, 62, 610–612.
- Coutière, H. (1909) The American species of snapping shrimps of the genus *Synalpheus*. *Proceedings of the United States National Museum*, 36, 1–93. <https://doi.org/10.5479/si.00963801.36-1659.1>
- Coutière, H. (1910) The snapping shrimps (Alpheidae) of the Dry Tortugas, Florida. *Proceedings of the United States National Museum*, 37, 485–487. <https://doi.org/10.5479/si.00963801.37-1716.485>
- Crosnier, A. & Forest, J. (1965) Note préliminaire sur les Alpheidae recueillis par la Calypso dans l'Atlantique oriental tropical. *Bulletin du Muséum national d'Histoire naturelle*, 36, 602–610.
- Dardeau, M.R. (1984) *Synalpheus* shrimps (Crustacea: Decapoda: Alpheidae). I. The Gambarelloides group, with a description of a new species. *Memoirs of the Hourglass Cruises*, 7, 1–125.
- Dardeau, M.R. (1986) Redescription of *Synalpheus scaphoceris* Coutière, 1910 (Decapoda: Alpheidae) with new records from the Gulf of Mexico. *Journal of Crustacean Biology*, 6, 491–496. <https://doi.org/10.1163/193724086X00334>
- De Grave, S. & Anker, A. (2017) An annotated checklist of marine caridean and stenopodidean shrimps (Malacostraca: Decapoda) of the Caribbean coast of Panama. *Nauplius*, 25, 1–40. <https://doi.org/10.1590/2358-2936e2017015>
- De Grave, S. & Fransen, C.H.J.M. (2011) Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zoologische Mededelingen*, 85, 195–588.
- Duchassaing, F. (1850) *Animaux radiaires des Antilles*. Plon Frères, Paris, 35 pp.

Duchassaing, F. & Michelotti, G. (1864) Spongiaires de la mer Caraïbe. *Natuurkundige verhandelingen van de Hollandsche maatschappij der wetenschappen te Haarlem*, 21, 1–124. <https://doi.org/10.5962/bhl.title.11943>

Duffy, J.E. (1992) Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Marine ecology Progress Series*, 90, 127–138. <https://doi.org/10.3354/meps090127>

Duffy, J.E. (1996a) *Synalpheus regalis*, new species, a sponge-dwelling shrimp from the Belize Barrier Reef, with comments on host specificity in *Synalpheus*. *Journal of Crustacean Biology*, 16, 564–573. <https://doi.org/10.1163/193724096X00603>

Duffy, J.E. (1996b) Eusociality in a coral-reef shrimp. *Nature*, 381, 512–514. <https://doi.org/10.1038/381512a0>

Duffy, J.E. (1998) On the frequency of eusociality in snapping shrimps (Decapoda: Alpheidae), with description of a second eusocial species. *Bulletin of Marine Science*, 62, 387–400.

Duffy, J.E. (2003) The ecology and evolution of eusociality in sponge-dwelling shrimp. In: *Genes, Behavior and evolution in Social Insects*. University of Hokkaido Press, Sapporo, pp. 1–38. <https://doi.org/10.1093/acprof:oso/9780195179927.003.0018>

Duffy, J.E. & Macdonald, K.S. (1999) Colony structure of the social snapping shrimp *Synalpheus filidigitus* in Belize. *Journal of Crustacean Biology*, 19, 283–292. <https://doi.org/10.1163/193724099X00097>

Duffy, J.E., Morrison, C. & Rios, R. (2000) Multiple origins of eusociality among spongedwelling shrimps (*Synalpheus*). *Evolution*, 54, 503–516. <https://doi.org/10.1111/j.0014-3820.2000.tb00053.x>

Duffy, E.J., Morrison, C.L. & Macdonald, K.S. (2002) Colony defense and behavioral differentiation in the eusocial shrimp

Synalpheus regalis. *Behavioral ecology and Sociobiology*, 51, 488–495. <https://doi.org/10.1007/s00265-002-0455-5>

Edgar, R.C. (2004) Muscle: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797. <https://doi.org/10.1093/nar/gkh340>

- Fausto-Filho, J. (1980) Crustáceos estomatópodos e decápodos dos substratos de cascalho do Nordeste Brasileiro. *Ciência Agrônômica*, 10, 109–124. <https://doi.org/10.32360/acmar.v18i1-2.31586>
- Frick, M.G., Mason, A., Williams, K.L., Andrews, K. & Gerstung, H. (2003) Epibionts of hawksbill turtles in a Caribbean nesting ground: a potentially unique association with snapping shrimp (Crustacea: Alpheidae). *Marine turtle Newsletter*, 99, 8–11.
- Gomes Corrêa, M.M. (1972) Contribuição ao conhecimento da fauna do Arquipélago de Abrolhos, Bahia, Brasil. 2—Lista preliminar de crustáceos decápodos. *Boletim do Museu de História Natural Zoologia, Belo Horizonte*, 15, 1–19.
- Gore, R.H., Scotto, L.E. & Becker, L.J. (1978) Studies on decapod crustacea from the Indian River Lagoon region of Florida. IV. Community composition, stability and trophic partitioning in decapod crustaceans inhabiting some subtropical sabellariid worm reefs. *Bulletin of Marine Science*, 28, 221–248.
- Gracia, C., Cruz, N., Borrero, G., Báez, D. & Santodomingo, N. (2013) Diversity of marine invertebrates associated to gas platforms in La Guajira (Colombian Caribbean Sea). *Boletín de Investigaciones Marinas y Costeras-INVEMAR*, 42, 361–386. <https://doi.org/10.25268/bimc.invemar.2013.42.2.56>
- Hall, T. (2005) BioEdit 7.0.5. North Carolina State University, Department of Microbiology. Available from: <http://www.mbio.ncsu.edu/BioEdit/bioedit.html>
- Hazlett, B.A. (1962) Aspects of the biology of snapping shrimp (*Alpheus* and *Synalpheus*). *Crustaceana*, 4, 82–83. <https://doi.org/10.1163/156854062X00094>
- Hechtel, G.J. (1965) A systematic study of the Demospongiae of Port Royal, Jamaica. *Bulletin of the Peabody Museum of Natural History*, 20, 1–103.
- Hechtel, G.J. (1983) New species of marine Demospongiae from Brazil. *Iheringia (Zoologia)*, 63, 58–89.
- Hernández, C., Álvarez, F. & Villalobos, J.L. (2010) Crustáceos asociados a sustrato duro en la zona intermareal de Montepío, Veracruz, México. *Revista Mexicana de Biodiversidad*, 81, 141–151. <https://doi.org/10.22201/ib.20078706e.2010.0.217>
- Hermoso-Salazar, M., Wicksten, M. & Morrone, J.J. (2005) Redescriptions and taxonomic notes on species of the *Synalpheus townsendi* Coutière, 1909 complex (Decapoda: Caridea: Alpheidae). *Zootaxa*, 1027 (1), 1–26. <https://doi.org/10.11646/zootaxa.1027.1.1>

- Herrick, F.H. (1891) *Alpheus*: a study in the development of Crustacea. In: Brooks, W.K. & Herrick, F.H. (Eds.), *the embryology and metamorphosis of the Macroura: Memoirs of the National Academy of Sciences, Washington*, 5, pp. 370–463.
- Horch, A.P., Williams, J.D. & Terossi, M. (2024) A new species of *Parapleurocrypta* Chopra, 1923 (Isopoda, Epicaridea, Bopyridae) parasitizing shrimps of the genus *Synalpheus* Spence Bate, 1888 (Decapoda, Caridea, Alpheidae) from the Fernando de Noronha archipelago, Brazil. *Zoological Studies*, 63, 13. <https://doi.org/10.6620/ZS.2024.63-13>
- Hultgren, K.M. & Duffy, J.E. (2010) Sponge host characteristics shape the community structure of their shrimp associates. *Marine ecology Progress Series*, 407, 1–12. <https://doi.org/10.3354/meps08609>
- Hultgren, K.M. & Duffy, J.E. (2011) Multi-locus phylogeny of sponge-dwelling snapping shrimp (Caridea: Alpheidae: *Synalpheus*) supports morphology-based species concepts. *Journal of Crustacean Biology*, 31, 352–360. <https://doi.org/10.1651/10-3382.1>
- Hultgren, K., Duffy, J.E. & Rubenstein, D.R. (2017) Sociality in shrimps. In: Rubenstein, D.R. & Abbot, P. (Eds.), *Comparative Social evolution*. Cambridge University Press, Cambridge, pp. 224–249. <https://doi.org/10.1017/9781107338319.009>
- Hultgren, K.M., Macdonald, K.S.III & Duffy, J.E. (2010) Sponge-dwelling snapping shrimps of Curaçao, with descriptions of three new species. *Zootaxa*, 2372 (1), 221–262. <https://doi.org/10.11646/zootaxa.2372.1.20>
- Hultgren, K.M., Macdonald, K.S.III & Duffy, J.E. (2011) Sponge-dwelling snapping shrimps (Alpheidae: *Synalpheus*) of Barbados, West Indies, with a description of a new eusocial species. *Zootaxa*, 2834 (1), 1–16. <https://doi.org/10.11646/zootaxa.2834.1.1>
- Hyatt, A. (1875) Revision of the North American Poriferae, with Remarks upon Foreign Species. Part I. *Memoirs of the Boston Society of Natural History*, 2, 399–408.
- Kimura, M. & Weiss, G.H. (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics*, 49, 561–576. <https://doi.org/10.1093/genetics/49.4.561>
- Knowlton, N. (1980) Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. *evolution*, 34, 161–173. <https://doi.org/10.1111/j.1558-5646.1980.tb04802.x>

- Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and evolution*, 33, 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lamarck, J.B.M. 1814 (1813) Sur les polypiers empâtés. *Annales du Museum National d'Histoire Naturelle*, 20, 29–458. Lamarck, J.B.M. 1815 (1814) Suite des polypiers empâtés. *Mémoires du Muséum d'Histoire Naturelle, Paris*, 1, 69–80 + 162–168 + 331–340.
- Lamarck, J.B.M. (1816) *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent. Vol. 2.* Verdière. J.B. Baillière, Libraire, Paris, 568 pp. <https://doi.org/10.5962/bhl.title.40014>
- Laubenfels, M.W. (1934) New sponges from the Puerto Rican dee. *Smithsonian Miscellaneous Collections*, 91, 1–28. Laubenfels, M.W. (1936) *A Discussion of the Sponge Fauna of the Dry tortugas in Particular and the West Indies in General, with Material for a Revision of the Families and Orders of the Porifera.* Carnegie Institute of Washington Publication, Washington, D.C., 225 pp.
- Lemaitre, R. (1984) Decapod crustaceans from Cay Sal Bank, Bahamas, with notes on their zoogeographic affinities. *Journal of Crustacean Biology*, 4, 425–447. <https://doi.org/10.2307/1548042>
- Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. editio decima, reformata. tomus I. 10th Revised edition.* Laurentius Salvius, Holmiae, 824 pp. <https://doi.org/10.5962/bhl.title.559>
- Linnaeus, C. (1759) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. tomus II. editio Decima, Reformata.* Typis Ioannis Thomae, Vindobonae, 4 + 559 pp. [pp. 1–4 + 825–1384] <https://doi.org/10.5962/bhl.title.37256>
- Macdonald, K.S.III & Duffy, J.E. (2006) Two new species of sponge-dwelling snapping shrimp from the Belizean Barrier Reef, with a synopsis of the *Synalpheus brooksi* species complex. *American Museum Novitates*, 3543, 1–22. [https://doi.org/10.1206/0003-0082\(2006\)3543\[1:TNSOSS\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)3543[1:TNSOSS]2.0.CO;2)

- Macdonald, K.S.III, Hultgren, K. & Duffy, J.E. (2009) The sponge-dwelling snapping shrimps (Crustacea, Decapoda, Alpheidae, *Synalpheus*) of Discovery Bay, Jamaica, with descriptions of four new species. *Zootaxa*, 2199 (1), 1–57. <https://doi.org/10.11646/zootaxa.2199.1.1>
- Macedo, B.D., Masunari, S. & Corbetta, R. (2012) Crustáceos decápodos associados às cordas de cultivo do mexilhão *Perna perna* (Linnaeus, 1758) (Mollusca, Bivalvia, Mytilidae) na Enseada da Armação do Itapocoroy, Penha-SC. *Biota Neotropica*, 12, 185–195. <https://doi.org/10.1590/S1676-06032012000200018>
- Mantelatto, F.L., França, N.F., Cunha, A.M. & Almeida, A.O. (2023) Molecular data highlight cryptic diversity and reveal a new species in the *Synalpheus brevicarpus* (Herrick 1891) complex (Decapoda: Caridea: Alpheidae) in the Western Atlantic. *Journal of Crustacean Biology*, 43, ruad076. <https://doi.org/10.1093/jcbiol/ruad076>
- Martínez-Iglesias, J.C., Carvacho, A. & Ríos, R. (1996) Catálogo de los carídeos marinos (Crustacea, Decapoda, Caridea) de las aguas someras de Cuba. *Avicennia*, 4/5, 27–40.
- Martínez-Iglesias, J.C., Gómez, O., Carvacho, A. & Ríos, R. (1993) Nuevos registros de crustáceos decápodos (Crustacea:Decapoda) en la plataforma marina de Cuba. *Avicennia*, 1993, 9–13.
- Masunari, S., Oliveira, E. & Kowalczyk, G.L. (1998) Crustacea Decapoda da praia rochosa da Ilha do Farol, Matinhos, Paraná. I: Distribuição temporal de densidade das populações. *Revista Brasileira de Zoologia*, 15, 219–239. <https://doi.org/10.1590/S0101-81751998000100020>
- Michener, C.D. (1969) Comparative social behavior of bees. *Annual Review of entomology*, 14 (1), 299–342. <https://doi.org/10.1146/ANNUREV.EN.14.010169.001503>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *2010 gateway computing environments workshop (GCE)*, November 1010. IEEE, New Orleans, Louisiana, pp. 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Moraes, F.C., Vilanova, E. & Muricy, G. (2003) Distribuição das esponjas (Porifera) na reserva biológica do Atol das Rocas, Nordeste do Brasil. *Arquivos do Museu Nacional*, 61, 13–22.

Muricy, G. & Moraes, F.C. (1998) Marine sponges of Pernambuco state, NE Brazil. *Revista Brasileira de Oceanografia*, 46, 213–217. <https://doi.org/10.1590/S1413-77391998000200009>

Nogueira, J.M.M. (2003) Fauna living in colonies of *Mussismilia hispida* (Verrill) (Cnidaria: Scleractinia) in four south-eastern Brazil islands. *Brazilian Archives of Biology and technology*, 46, 421–432. <https://doi.org/10.1590/S1516-89132003000300014>

Oliveira, M., Santos, S. & Almeida, A.O. (2015) First record of the sponge-dwelling shrimp *Synalpheus dardeau* (Crustacea: Decapoda: Alpheidae) in the south-western Atlantic. *Marine Biodiversity Records*, 8, e51. <https://doi.org/10.1017/S1755267215000251>

Palumbi, S.R. & Benzie, J. (1991) Large mitochondrial DNA differences between morphologically similar penaeid shrimp. *Molecular Marine Biology and Biotechnology*, 1, 27–34.

Pearse, A.S. (1932) Inhabitants of certain sponges at Dry Tortugas. (Papers from Tortugas Laboratory 28). *Carnegie Institution of Washington Publication*, 435, 119–122.

Pearse, A.S. (1950) Notes on the inhabitants of certain sponges at Bimini. *ecology*, 31, 149–151. <https://doi.org/10.2307/1931369>

Pequegnat, L.H. & Heard, R.W. (1979) *Synalpheus agelas*, new species of snapping shrimp from the Gulf of Mexico and Bahama Islands (Decapoda: Caridea: Alpheidae). *Bulletin of Marine Science*, 29, 110–116.

Pequegnat, L.H. & Ray, J. (1974) Crustacea and other arthropods. In: Bright, T.J. & Pequegnat, L.H. (Eds.), *Biota of the Fest Flower Garden Bank*. Gulf Publishers Co., Houston, Texas, pp. 232–261.

Prüsmann, J. & Palacio, J. (2008) Colonización de moluscos y crustáceos en raíces de mangle rojo en una laguna costera de la punta norte del golfo de Morrosquillo. *Gestión y Ambiente*, 11, 77–86.

Pulitzer-Finali, G. (1986) A collection of West Indian Demospongiae (Porifera). In appendix, a list of the Demospongiae hitherto recorded from the West Indies. *Annali del Museo civico di storia naturale Giacomo Doria*, 86, 65–216.

Rafinesque, C.S. (1815) *Analyse de la Nature ou tableau de l'Univers et des corps organisés*. Aux deipens de l'auteur, Palerme, 224 pp. <https://doi.org/10.5962/bhl.title.106607>

- Ramos-Porto, M., Torres, M.F.A. & Viana, G.F.S. (1996) Crustáceos decápodos coletados durante as Expedições Nordeste III e Pavaas I (Penaeidea e Caridea). *trabalhos Oceanográficos da Universidade Federal de Pernambuco*, 24, 211–227. <https://doi.org/10.5914/tropocean.v24i1.2709>
- Rathbun, M.J. (1900) Results of the Branner-Agassiz expedition to Brazil. I. The decapod and stomatopod Crustacea. *Proceedings of the Washington Academy of Sciences*, 2, 133–156.
- Reed, J.K., Gore, R.H., Scotto, L.E. & Wilson, K.A. (1982) Studies on decapod Crustacea from the Indian River region of Florida, XXI Community composition, structure, areal and trophic relationships of decapods associated with shallow-and deep-water *Oculina varicosa* coral reefs. *Bulletin of Marine Science*, 32, 761–786.
- Ríos, R. & Duffy, J.E. (2007) A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of *Zuzalpheus*, new genus, and six new species. *Zootaxa*, 1602 (1), 1–89. <https://doi.org/10.11646/zootaxa.1602.1.1>
- Riul, P., Rodrigues, F.M.A., Xavier-Filho, E.S., Santos, R.G., Leonel, R.M. & Christoffersen, M.L. (2008) Macrocrustaceans from Ponta do Cabo Branco, João Pessoa, Paraíba, Brazil, the easternmost point of South America. *Revista Nordestina de Biologia*, 19, 3–13.
- Rodríguez, B. (1986) Los camarones (Crustacea, Decapoda, Natantia) del Parque Nacional Archipiélago de los Roques. Trabajo especial de grado para optar al título de licenciado en biología, Universidad Central de Venezuela, 350 pp.
- Rodríguez, G. (1980) *Crustáceos decápodos de Venezuela*. Instituto Venezolano de Investigaciones Científicas, Caracas, 494 pp.
- Rodríguez, P., Lira, C., Muñoz, N. & Morales, D. (2020) Crustáceos decápodos de la playa El Amparo, isla de Coche, Venezuela. I. Suborden Dendrobranchiata e Infraordenes Stenopodidea y Caridea. *Acta Biológica Venezuelica*, 40, 171–209.
- Rouse, W.L. (1970) Littoral Crustacea from southwest Florida. *Quarterly Journal of Florida Academy of Sciences*, 32, 127–152.
- Santos, S., Soledade, G.O. & Almeida, A.O. (2012) Decapod crustaceans on dead coral from reef areas on the coast of Bahia, Brazil. *Nauplius*, 20, 145–169. <https://doi.org/10.1590/S0104-64972012000200007>

Say, T. (1818) An account of the Crustacea of the United States, part 5. *Journal of the Academy of Natural Sciences at Philadelphia*, 1, 235–253.

Schmidt, O. (1870) *Grundzüge einer Spongien-Fauna des atlantischen Gebietes*. Wilhelm Engelmann, Leipzig, 88 pp. Schmitt, W.L. (1924) The Macruran, Anomuran and Stomatopod Crustacea. *Bijdragen tot de kennis der fauna van Curaçao. Resultaten eener reis van Dr. C.J. van der Horst in 1920. Bijdragen tot de Dierkunde*, 23, 61–81.

Schmitt, W.L. (1935) Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands. *Science Survey of Porto Rico (New York Academy of Sciences)*, 15, 125–227.

Sherman, W., Lacey, E.A., Reeve, H.K. & Keller, L. (1995) The eusociality continuum. *Behavioral ecology*, 6, 102–108. <https://doi.org/10.1093/beheco/6.1.102>

Snelgrove, R. & Lewis, J.B. (1989) Response of a coral-associated crustacean community to eutrophication. *Marine Biology*, 101, 249–257. <https://doi.org/10.1007/BF00391464>

Soledade, G.O., Fonseca, M.S. & Almeida, A.O. (2015) Shallow-water stenopodidean and caridean shrimps from Abrolhos Archipelago, Brazil: new records and updated checklist. *Zootaxa*, 3905 (1), 52–68. <https://doi.org/10.11646/zootaxa.3905.1.3>

Soledade, G.O., Terossi, M., Scioli, J.A., Mantelatto, F.L. & Almeida, A.O. (2019) A new western Atlantic snapping shrimp of the *Alpheus macrocheles* group (Caridea, Alpheidae) revealed by morphological, molecular and color data. *European Journal of Taxonomy*, 581, 1–21. <https://doi.org/10.5852/ejt.2019.581>

Spence Bate, C. (1888) Report on the Crustacea Macrura collected by the Challenger during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76. *Zoology*, 24 (52), i–xc + 1–942, pls. 1–150. <https://doi.org/10.5962/bhl.title.6513>

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>

Tóth, E. & Duffy, J.E. (2005) Coordinated group response to nest intruders in social shrimp. *Biology Letters*, 1, 49–52. <https://doi.org/10.1098/rsbl.2004.0237>

Tóth, E. & Duffy, J.E. (2008) Influence of sociality on allometric growth and morphological differentiation in sponge-dwelling alpheid shrimp. *Biological Journal of the Linnean Society*, 94, 527–540. <https://doi.org/10.1111/j.1095-8312.2008.01013.x>

- VandenSpiegel, D., Eeckhaut, I. & Jangoux, M. (1998) Host selection by *Synalpheus stimpsoni* (De Man), an ectosymbiotic shrimp of comatulid crinoids, inferred by a field survey and laboratory experiments. *Journal of experimental Marine Biology and ecology*, 225, 185–196. [https://doi.org/10.1016/S0022-0981\(97\)00222-0](https://doi.org/10.1016/S0022-0981(97)00222-0)
- Van Soest, R.W.M. (1984) Marine sponges from Curaçao and other Caribbean localities. Part III. Poecilosclerida. In: Hummelinck, W. & Van der Steen, L.J. (Eds.), *Studies on the Fauna of Curaçao and other Caribbean Islands*, 66, pp. 1–167.
- Velásquez, M., Vera-Caripe, J. & Lira, C. (2017) Crustáceos decápodos asociados a arrecifes de *Phragmatopoma* sp. (Polychaeta: Sabellariidae) en Playa El Horcón, Isla Margarita, Venezuela. *Saber, Universidad de Oriente, Venezuela*, 29, 249–266.
- Verrill, A.E. (1922) Decapod Crustacea of Bermuda. Part II. Macrura. *transactions of the Connecticut Academy of Arts and Sciences*, 26, 1–179. <https://doi.org/10.5962/bhl.title.23648>
- Waters, A.W. (1878) The use of opercula in the determination of the cheilostomatous Bryozoa. *Proceedings of the Manchester Literary and Philosophical Society*, 18, 8–11. <https://doi.org/10.14284/170>
- Williams, A.B. (1984) *Shrimps, lobsters and crabs of the Atlantic Coast of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Cambridge, 550 pp. <https://doi.org/10.2307/1352125>
- Wilson, E. (1971) *the Insect Societies*. Belknap Press of Harvard University, Cambridge, Massachusetts, 548 pp.
- WoRMS (2025) *Synalpheus* Spence Bate, 1888. Available from: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106982> (accessed 7 July 2025)
- Zea, S. & Van Soest, R.W.M. (1986) Three new species of sponges from the Colombian Caribbean. *Bulletin of Marine Science*, 38, 355–365.
- Zimmer, C. (1913) Westindische Decapoden, 1: Die Familie Alpheidae. *Zoologische Jahrbücher*, 11, 381–412.

**ARTIGO CIENTÍFICO 2 - TWO NEW SPECIES OF SNAPPING SHRIMP
SYNALPHEUS SPENCE BATE, 1888 (DECAPODA: ALPHEIDAE) REVEALED BY
AN INTEGRATIVE APPROACH IN NORTHEAST BRAZIL**

Capítulo a ser submetido na Zootaxa; Fator de Impacto: 1.091; Percentil: 47%; Qualis CAPES A4.

Abstract

This study describes two new species of *Synalpheus* Spence Bate, 1888, belonging to the *S. gambarelloides* group, from the northeastern coast of Brazil, based on morphological characteristics and molecular data (16S rRNA gene). The descriptions are based on materials from the oceanic island of Fernando de Noronha Archipelago, the continental shelf off Recife (Pernambuco state), and on the coast of Sergipe state. *Synalpheus* sp. nov. 1 is morphologically similar to *S. herricki* Coutière, 1909, but can be distinguished by the number of teeth on incisor process of the mandible, length of dactylus of minor chela, the distodorsal projection of the major chela, length of fingers of second pereopods, and morphology of pleurae, and 0.05 of molecular distance between both species. *Synalpheus* sp. nov. 2 closely resembles *S. ruetzleri* Macdonald & Duffy, 2006, differing on the length of the lateral spines on the basicerite and scaphocerite, the distodorsal projection of the major chela, the morphology of the third pereopods, and the fingers of the minor chela, with a molecular variation of 0.04—0.05 between both species.

Keywords: Fernando de Noronha Archipelago; Continental shelf; Pernambuco; 16S gene.

Introduction

Alpheidae Rafinesque, 1815 is one of the most diverse within Decapoda, comprising over 700 species distributed worldwide. It includes both deep-sea and predominantly shallow-water species inhabiting a wide range of microhabitats (Anker et al. 2006; De Grave & Fransen 2011; WoRMS 2025). *Alpheus* Fabricius, 1798, and *Synalpheus* Spence Bate, 1888 are the most speciose genera in Alpheidae and exhibit significant taxonomic challenges, including the presence of multiple species complexes (Anker et al. 2012; Almeida et al. 2016). Consequently, taxonomic studies targeting alpheids increased in recent years, particularly through integrative approaches that combine morphological, molecular, and ecological data to address these issues (Hultgren & Duffy 2010, 2011; Almeida et al. 2013; Bracken-Grissom & Felder 2014; Dehghani et al. 2019; Santos et al. 2019; Soledade et al. 2019; Ashrafi et al. 2020; Chack et al. 2020; Ashrafi & Hultgren 2022; Santos et al. 2024).

Synalpheus has 173 species currently described, approximately two-fifths of which are recorded from the Atlantic Ocean (De Grave & Fransen 2011; Anker et al. 2012; Anker & Pachelle 2014; Almeida et al. 2018; WoRMS 2025). The group of obligate sponge-dwelling symbionts called *Synalpheus gambarelloides* Coutière, 1909 is the most speciose within the genus. Research on this group has led to the recognition and description of numerous species (Ríos & Duffy 2007; Macdonald et al. 2009; Hultgren et al. 2010, 2011; Anker et al. 2012; Ashrafi & Hultgren 2022).

This study describes two new species of the *S. gambarelloides* group from northeastern Brazil, based on morphological and molecular data. The specimens were collected from the Fernando de Noronha Archipelago, the continental shelf off Recife (Pernambuco state), and the coast of Sergipe state. Moreover, this study updates the distribution ranges of *S. herricki* Coutière, 1909, previously reported for Pernambuco and Sergipe (Paixão et al. 2025), and *S. ruetzleri* Macdonald & Duffy, 2006, previously reported for Fernando de Noronha Archipelago (Paixão et al. 2025) (for more details, see Remarks of *Synalpheus* sp. nov. 1 and *Synalpheus* sp. nov. 2).

Material and Methods

Sampling on the continental shelf off Recife was conducted approximately 35 kilometers from the coast, using a motorized vessel (10 m in length and 3 m in width) equipped with a trawl dredge measuring 80×40×75 cm, used to collect samples at depths between 50 and 65 meters. A total of 32 stations were sampled over three campaigns: Campaign I (REC I) on February 7, 2018, comprising 13 stations; Campaign II (REC II) on February 27, 2018, comprising 11 stations; and Campaign III (REC III) on May 10, 2018, comprising 8 stations. The dredging was carried out at a depth of approximately 50 m for a duration of 10 minutes. In the Fernando de Noronha Archipelago, SCUBA dives were performed at depths ranging from 11 to 17 m to collect potential sponge hosts of the shrimp. In both cases, the collected substrates were labeled and placed in plastic tubes for later processing in the laboratory. There, they were fragmented over sieves using tweezers and scissors. Shrimps were sorted and preserved in 70% ethanol. The specimens were deposited in the Coleção de Crustáceos do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul (DZ/UFRGS) and in the Coleção de Crustáceos do Museu de Oceanografia Prof. Petrônio Alves Coelho (MOUFPE), Universidade Federal de Pernambuco (see type material and examined material lists).

Specimens were initially identified using the identification key provided by Anker et al. (2012), and subsequently compared with morphologically similar species (*S. herricki* and *S. ruetzleri*) deposited in the MOUFPE collection, including their original descriptions and redescriptions (e.g., Coutière 1909; Chace 1972; Dardeau 1984; Macdonald & Duffy 2006). Sex determination was based on the presence of an ovigerous mass beneath the pleon and/or ovigerous setae, features exclusive to females (Bauer 2004), as well as the shape of the pleura on the first pleonal segment, which is rounded in females and ventrodistally projected or hook-shaped in males (Banner & Banner 1975). Specimens were classified as males (m), ovigerous females (ovf), or non-ovigerous females (f).

For the preparation of the illustrations, specimens were photographed under a stereomicroscope equipped with an image capture system (Leica EZ4). The resulting images were then imported into CorelDRAW (version 21.0.0.593), where they were vectorized for illustration purposes.

The procedures for DNA extraction, amplification of a small fragment of 16S ribosomal gene, purification, and sequencing followed the protocols described by Paixão et al. (2025). The primers 16Sbr (CCGGTCTGAACTCAGATCACGT) and 16Sar (CGCCTGTTTATCAAAAACAT) (Palumbi & Benzie 1991) were used, with initial

denaturation at 95°C for 5 min; annealing in 40 cycles of 95°C for 45 s, 46°C for 45 s, 72°C for 1 min, and final extension at 72°C for 3 min. The newly obtained sequences were deposited in GenBank. Additional sequences were retrieved from GenBank for comparative purposes (Table 1). Sequence alignment was performed using BioEdit 7.2.5 (Hall, 1999), and phylogenetic reconstruction was conducted in MEGA 11.0.11 (Tamura et al., 2021) using the Maximum Likelihood method and using the GTR (General Time Reversible) substitution model. Node support was assessed by bootstrap analysis with 1,000 replicates, and only values above 50% were shown.

Table 1. Specimens of *Synalpheus* Spence Bate, 1888 used in the genetic analysis. Atl: Atlantic.

Species	Location	Accession number
<i>Alpheus petronioi</i> Almeida, Terossi & Mantelatto, 2014	Pará (Brazil)	KF667545
<i>Synalpheus agelas</i> Pequegnat & Heard, 1979	Belize	HQ435419
<i>Synalpheus agelas</i> Pequegnat & Heard, 1979	Flórida (EUA)	AY344734
<i>Synalpheus brooksi</i> Coutière, 1909	Panamá (Atl)	AY344745
<i>Synalpheus brooksi</i> Coutière, 1909	Belize	AY344744
<i>Synalpheus herricki</i> Coutière, 1909	Belize	AY344754
<i>Synalpheus</i> sp. nov. 1	Fernando de Noronha Archipelago, Pernambuco (Brazil)	Pendente
<i>Synalpheus ruetzleri</i> Macdonald & Duffy, 2006	Panamá (Atl)	HQ435476
<i>Synalpheus ruetzleri</i> Macdonald & Duffy, 2006	Belize	HQ435475
<i>Synalpheus</i> sp. nov. 2	Fernando de Noronha Archipelago, Pernambuco (Brazil)	Pendente
<i>Synalpheus sanctithomae</i> Coutière, 1909	Belize	AY344768

Results

In addition to the sequences of one specimen of *Synalpheus* sp. nov. 1 and one of *Synalpheus* sp. nov. 2, nine sequences of related taxa were included (Macdonald & Duffy 2006;

Anker et al. 2012; Hultgren et al. 2014). Both species described in this study are molecularly distinct from other taxa within the genus (for further details, see the Remarks sections of the new species and Table 2).

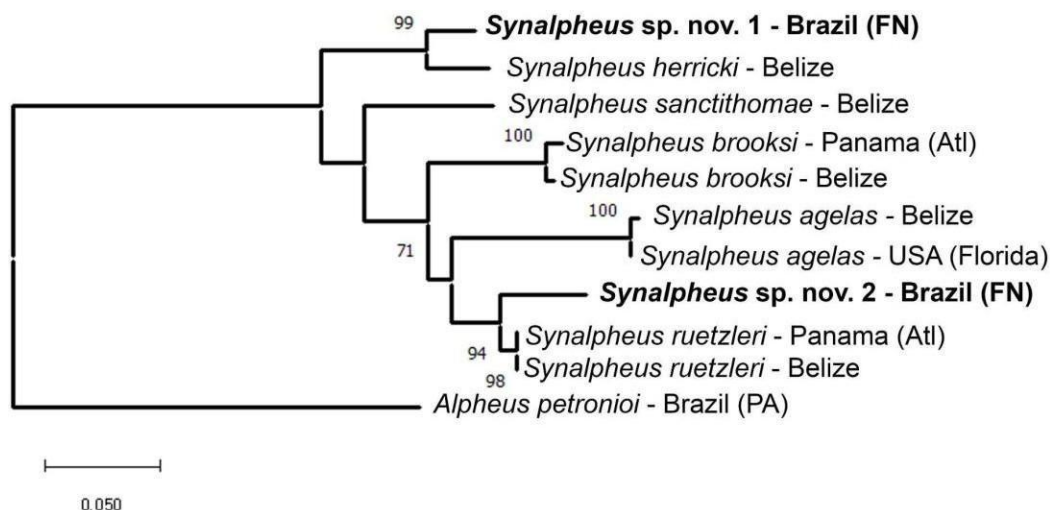


Figure 1. Phylogram constructed using Maximum Likelihood analysis of the 16S mitochondrial gene sequences for *Synalpheus* specimens. The node values represent the support values considering 1000 bootstrap pseudo-replicates. Values <50% are not shown. Atl: Atlantic Ocean; FN: Fernando de Noronha archipelago; PA: Pará. Bold indicates the new species.

Systematics

Alpheidae Rafinesque, 1815

Synalpheus Spence Bate, 1888

Synalpheus sp. nov. 1

Synalpheus herricki—Horch et al., 2024: 4, 5, 10, 11 (not *S. herricki*); Paixão et al., 2025: 17, 24, 26, 27, 39, 41, 44, Figs. 13, 14, and 21, Table 1, material from Pernambuco and Sergipe (not *S. herricki*)

Type material: Brazil, Pernambuco, Fernando de Noronha Archipelago, Laje Dois Irmãos, 03°50'40.2"S 32°26'34.6"W, in sponge—Holotype, m, 30.vi.2022, 17 m deep, coll. I. Moraes, K. Pasinato & M. Terossi, MZUSP 48906 (removed from DZ/UFRGS 7046); Paratypes, 2 m, 17.vi.2019, 11 m deep, coll. G. Bochini & K. Pasinato, DZ/UFRGS 6708; 1 m, 17.vi.2019, 11 m deep, coll. G. Bochini & K. Pasinato, DZ/UFRGS 6709; 10 m, 3 ovf, 1 f, 30.vi.2022, 17 m deep, coll. I. Moraes, K. Pasinato & M. Terossi, DZ/UFRGS 7046.

Additional material examined. Brazil, Pernambuco—Fernando de Noronha Archipelago, in sponge, coll. I. Moraes, K. Pasinato & M. Terossi: 4 m, 2 f, Buraco do Inferno, 03°48'14.7"S 32°23'12.4"W, 26.vi.2022, 12 m deep, DZ/UFRGS 7032; 3 m, Cagaras, 03°48'32.6"S 32°23'50.9"W, 25.vi.2022, 13 m deep, DZ/UFRGS 7027; 1 ovf, 1 f, Ilha do Meio, 03°49'11.5"S 32°23'50.8"W, 26.vi.2022, 11 m deep, DZ/UFRGS 7038; 10 m, 3 ovf, 1 f, Laje Dois Irmãos, 03°50'40.2"S 32°26'34.6"W, 30.vi.2022, 17 m deep, DZ/UFRGS 7046; 1 f, Ponta da Sapata, 03°51'53.5"S 32°27'57.9"W, 30.vi.2022, 11 m deep, DZ/UFRGS 7043; Continental Shelf off Recife: 2 m, 08°13'33.0"S 34°37'40.3"W, 27.ii.2018, 50.6 m deep, in sponge, DZ/UFRGS 7067; Brazil, Sergipe—4 m, 1 ovf, Station AL-SE, MOUFPE 8754.

Comparative material. *Synalpheus herricki* Coutière, 1909: Ceará—1 m, 3 ov, 1 f, Almirante Saldanha Expedition, St. 1701 A, 21.x.1967, 01°57.0'S 37°45.0'W, 57.0 m depth, MOUFPE 8742.

Description. Body subcylindrical; carapace smooth, with pterygostomial region produced into bluntly acute angle (Fig. 2A), and posterior margin with cardiac notch distinct (Fig. 2A). Rostrum narrower than ocular hoods, ventrally convex in lateral view, slightly longer than ocular hoods and distally turned upward (Figs. 2A—B). Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly triangular, laterally convex, separated from rostrum by deep adrostral sinus (Fig. 2A). Ocular process produced into a fingerlike structure. Ocellar beak in lateral view not rodlike. Stylocerite slender; mesial margin convex; tip acute; distinctly shorter than distal margin of first segment of antennular peduncle (Fig. 2A); this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. Basicerite without spine on dorso-lateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite (Fig. 2A). Scaphocerite with blade absent, and with robust, acute lateral spine with lateral margin slightly concave, not overreaching antennular peduncle; mesial projection at base of scaphocerite present (Fig. 2A).

Mouthparts typical as figured (Fig. 3A—F). Mandible with 6 marginal teeth on incisor process (Fig. 3A). Palp of maxilliped 1 consisting of 2 segments (Fig. 3B). Maxilliped 3 with distal circlet of spines on distal segment, and without ventro-distal spine on antepenultimate segment (Fig. 3F).

Major pereopod 1 massive, fingers clearly less than half length of palm; fixed finger distinctly shorter than dactyl; in ventral view, outer face of fixed finger without lateral protuberance; dactylus with distinct subterminal V-shaped notch on flexor margin. Palm of

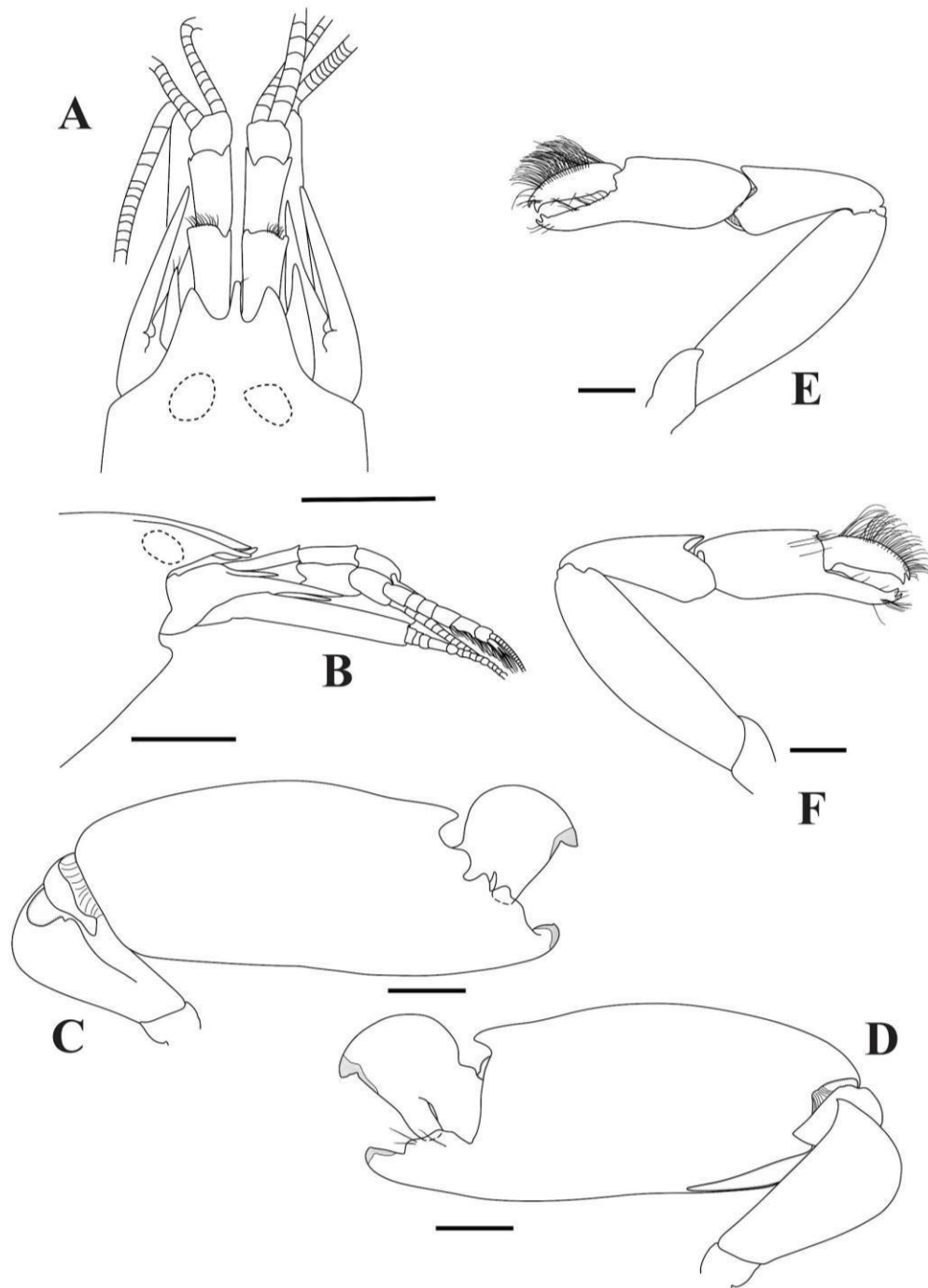


Figure 2: *Synalpheus* sp. nov. 1, male holotype, male individual from, from Laje Dois Irmãos, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48906). A, frontal region, dorsal view; B, same, lateral view; C, major chela, left side, mesial view; D, same, lateral view; E, minor chela, right side, mesial view; F, same, lateral view. Scale bars: A–D, 1 mm; E, F, 0.5 mm.

chela with distal superior margin produced into projecting blunt or subacute distal tooth. Carpus very short and broad. Merus extensor margin strongly convex, with distal angular projection (Figs. 2C–D).

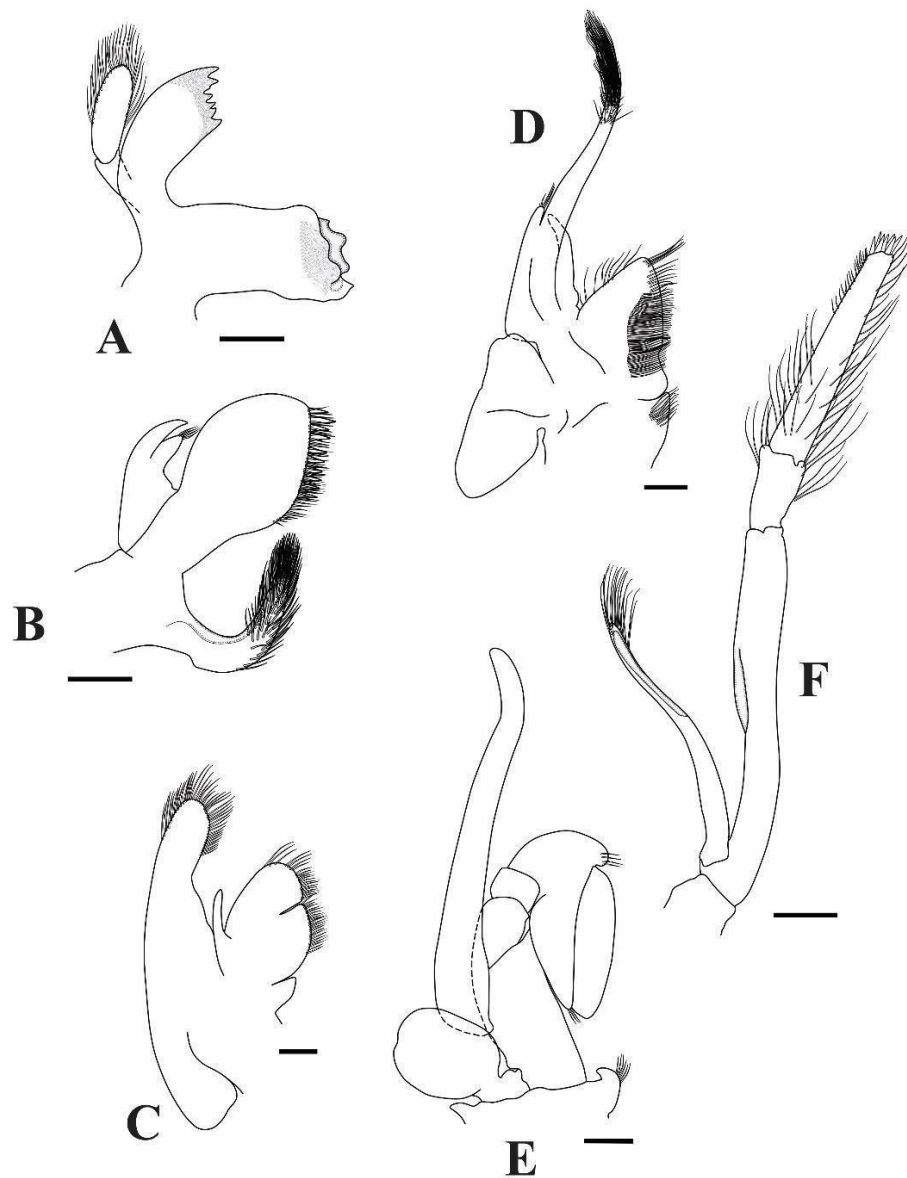


Figure 3. *Synalpheus* sp. nov. 1, male holotype from, Laje Dois Irmãos, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48906). Mouthparts, A, mandible, right side; B, first maxilla, right side; C, second maxilla, right side; D, first maxilliped, right side; E, second maxilliped, right side; F, third maxilliped, right side. Scale bars: A–E, 0.2 mm; F, 0.4 mm.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactylus with flexor margin straight, blade-like, with two distinct distal teeth, subequal in length, and parallel to dactylus axis; transverse dorsal setal combs on

extensor surface of dactylus very conspicuous; fixed finger with flexor margin straight, blade-like, and 2 distinct teeth subequal in length (Figs. 2E—F). Extensor margin of merus convex, ending in obtuse angle.

Figure 3. *Synalpheus* sp. nov. 1, male holotype from, Laje Dois Irmãos, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48906). Mouthparts, A, mandible, right side; B, first maxilla, right side; C, second maxilla, right side; D, first maxilliped, right side; E, second maxilliped, right side; F, third maxilliped, right side. Scale bars: A–E, 0.2 mm; F, 0.4 mm.

Pereiopod 2 (Fig. 4E) with carpus 5-segmented, distinctly longer than merus; proximal article subequal to combined lengths of distal 4. Fingers longer than palm.

Pereiopod 3 slender; dactylus biunguiculate, with subequal teeth; merus without movable spines on flexor margin; mesial lamella on coxa present. Flexor margin of propodus armed with movable spines (Fig. 4F). Pereiopod 4 similar to third, but shorter. Pereiopod 5 similar to fourth; propodus with several oblique rows of setae in distal 2/3; carpus unarmed; merus unarmed, subequal in length to propodus.

Pleura 1 (Fig. 4A) of male with posterior corner acutely produced ventrally; second pleura of male rounded to obtuse; pleura 3 with posteroventral angle pointed; pleura 4–5 square rounded (Fig. 4A). Pleopod 1 of male, with many terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson elongate, considerably broader anteriorly than posteriorly, concave in posterior; dorsal surface armed with 2 pairs of strong spines, anterior pair situated midway between posterior pair and anterior margin; posterior margin armed with 2 pairs of unequal spines; space between distal spines equal or less than one third of distal margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush absent. Uropods with single fixed tooth on outer margin of exopod.

Type locality: Laje Dois Irmãos, Fernando de Noronha, Pernambuco, Brazil (03°50'40.2"S 32°26'34.6"W).

Distribution: Western Atlantic—Brazil: Pernambuco (Fernando de Noronha Archipelago and continental shelf off Recife) and Sergipe states (present study).

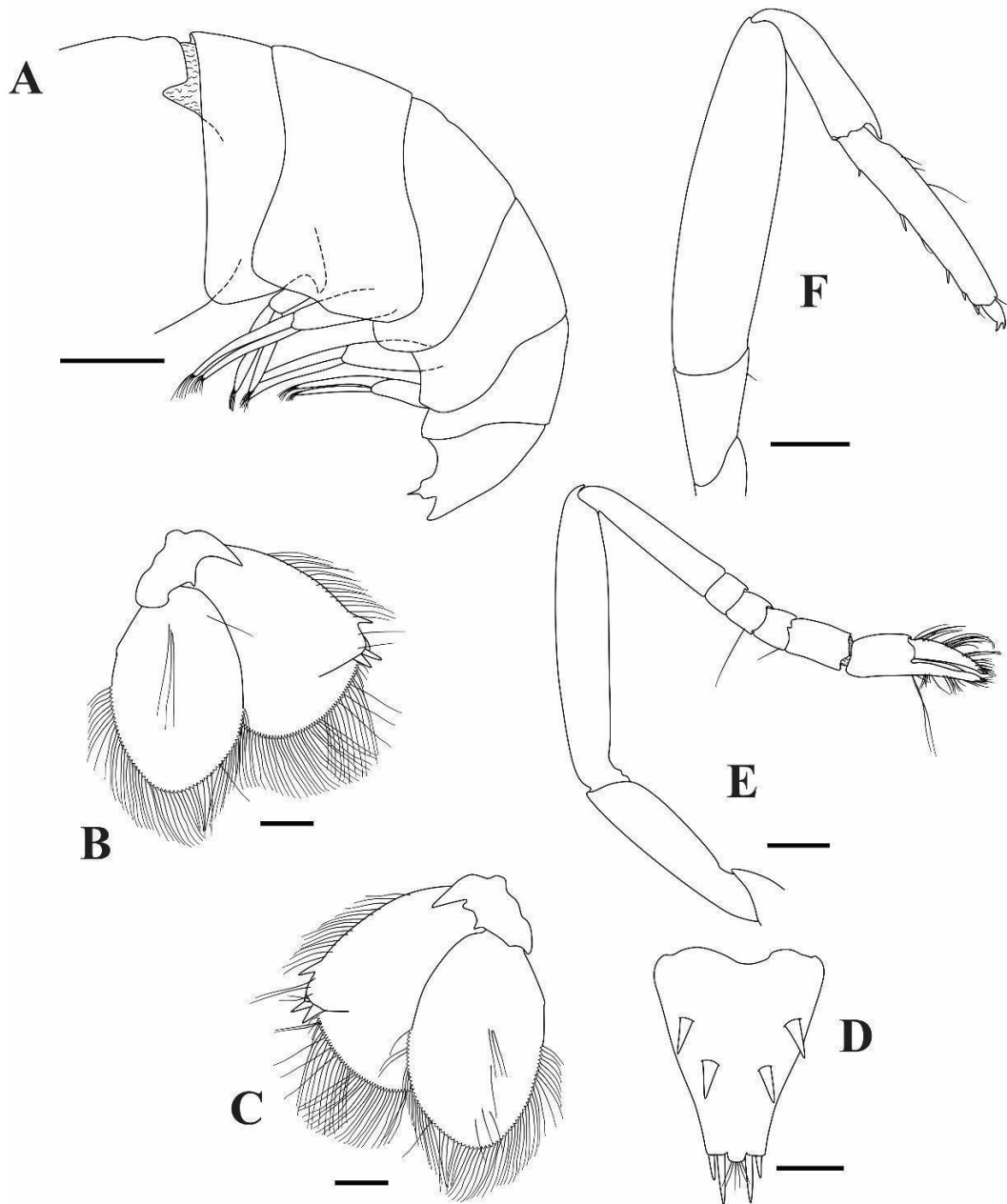


Figure 4. *Synalpheus* sp. nov. 1, male holotype from Fernando de Noronha Archipelago, Laje Dois Irmãos, Pernambuco, Brazil (MZUSP 48906). A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, second pereopod, right side, lateral view; F, third pereopod, right side, lateral view. Scale bars: A, 1 mm; B, C, E, 0.4 mm; D, F, 0.5 mm.

Ecology: *Synalpheus* sp. nov. 1 is found in association with sponges, from 11 to 50.6 m. Specimens from Fernando de Noronha parasitized by the bopyrid isopod *Parapleurocrypta duofratres* Horsch, Williams & Terossi, 2024 (see Horsch et al., 2024, as *S. herricki*).

Remarks: *Synalpheus* sp. nov. 1 is very similar to *S. herricki* (Paixão et al. 2025) as well as the members of the *Synalpheus brooksi* Coutière, 1909 species complex, which includes *S. bousfieldi* Chace, 1972, *S. brooksi*, *S. carpenteri* Macdonald & Duffy, 2006, *S. chacei* Duffy, 1998, *S. corallinus* Macdonald, Hultgren & Duffy, 2009, *S. plumosetosus* Macdonald, Hultgren & Duffy, 2009, *S. ruetzleri*, and *S. thele* Macdonald, Hultgren & Duffy, 2009 (Ríos & Duffy 2007; Anker et al. 2012). These species are characterized by a rostrum narrower than the ocular hoods, a long ventrolateral spine and a sharp lateral spine on the scaphocerite. In addition, the scaphocerite blade is absent or weakly developed (except in *S. ruetzleri*, where it is well developed), the distal superior margin of the major cheliped bears a produced or blunt tooth, and the dactylus of the minor cheliped has a dense dorsal setal brush on its extensor surface (Dardeau 1984; Ríos & Duffy 2007; Macdonald et al. 2009; Anker et al. 2012). *Synalpheus* sp. nov. 1 and *S. herricki* can be readily distinguished from other members of the genus by the dactylus of the major cheliped, separated from the rest of the dactylus by a more or less deep subtriangular notch (Fig. 2C, D) (Dardeau 1984; Anker et al. 2012). *Synalpheus* sp. nov. 1 differs from *S. herricki* by the mandible with 6 marginal teeth on incisor process (Fig. 3A) (vs. 7 marginal teeth in *S. herricki*), by the dactylus of the major chela being distinctly longer than the fixed finger (Fig. 2B, C) (vs. the fixed finger being almost as long as the dactylus in *S. herricki*), by the distodorsal region of the palm being produced into a projecting subacute distal tooth (Fig. 2B, C) (vs. produced into tapering acute spine in *S. herricki*) (see Dardeau 1984, figs 27—30). In addition, the fingers of the second pereopod are longer than the palm (Fig. 4E) (vs. equal in length to the palm in *S. herricki*). Pleurae 3—5 are posteriorly ventrally pointed or square rounded (Fig. 4A) (vs. pleurae 3—5 with progressively shallower sinuses ventrally between anterior and posterior margins in *S. herricki*) (see Dardeau 1984, Figs. 27—30).

Synalpheus sp. nov. 1 was reported by Horch et al. (2024) and Paixão et al. (2025), as *S. herricki*, with records from Laje Dois Irmãos, Ponta da Sapata, Buraco do Inferno, Cagaras, Ressureta, and Ilha do Meio in the Fernando de Noronha Archipelago, the continental shelf off Recife (Pernambuco), and the state of Sergipe (Horch et al., 2024; Paixão et al. 2025). In their material, Paixão et al. (2025) had already noted the presence of morphological variations that suggested the existence of a distinct species and highlighted the need for integrative approaches to assess the degree of differentiation. The Maximum Likelihood analysis recovered *Synalpheus* sp. nov. 1 as sister lineage to a specimen of *S. herricki* from Belize (Fig. 1). Molecular divergence was further supported by pairwise genetic distances, with a divergence of 0.26 from the outgroup (*A. petronioi*), 0.13 from *S. brooksi* (a representative of the *S. brooksi*

complex), and 0.05 from *S. herricki* (Table 2). This study also updates the distribution of *S. herricki* in Brazil, which had previously been expanded to include the Fernando de Noronha Archipelago and the states of Pernambuco and Sergipe (Horch et al. 2024; Paixão et al. 2025), but is now restricted to Atol das Rocas and the state of Ceará (Anker et al. 2012).

***Synalpheus* sp. nov. 2**

Synalpheus ruetzleri—Paixão et al., 2025: 1, 33, 39, 41 (not *S. ruetzleri*)

Type material: Brazil, Pernambuco, Fernando de Noronha Archipelago, Buraco do Inferno, 03°48'14.7"S 32°23'12.4"W, in sponge—Holotype, m, 26.vi.2022, 12 m deep, coll. I. Moraes, K. Pasinato & M. Terossi, MZUSP 48907 (removed from DZ/UFRGS 7073); Paratype, 3m, 1 ovf, 2 f, same data as holotype, DZ/UFRGS 7073.

Additional material examined. Brazil, Pernambuco—Fernando de Noronha Archipelago, in sponge, coll. I. Moraes, K. Pasinato & M. Terossi: 2 m, Ilha do Meio, 03°49'11.5"S, 32°23'50.8"W, 26.vi.2022, 12 m deep, DZ/UFRGS 6705; 1 m, Ponta da Sapata, 03°51'53.5"S 32°27'57.9"W, 30.vi.2022, 8 m deep, DZ/UFRGS 6707.

Comparative material. *Synalpheus ruetzleri* Macdonald & Duffy, 2006: Continental Shelf off Recife: 1 m, 10.v.2018, 08°21'34.9"S 34°41'53.3"W, 50.8 m depth, in sponge, MOUFPE 21794; 1 f, same data as MOUFPE 21794, MOUFPE 21793.

Description. Body form subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle (Fig. 5B), and posterior margin with cardiac notch distinct (Fig. 7A). Rostrum slightly longer than orbital teeth, and strongly narrower (Fig. 5A), distally upturned (Fig. 5B); margins in dorsal view, straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by a U-shaped adrostral sinus (Fig. 5B). Stylocerite acute, with blunt tip; mesial margin concave, subtly surpassing midpoint of first segment of antennular peduncle (Figs. 5A, B). Basicerite without dorsal spine on dorsomesial corner, with longer lateral spine, not reaching distal half of third segment of antennular peduncle (Fig. 5A). Scaphocerite with subtle blade; acute lateral spine robust, with lateral margin slightly concave, slightly surpassing basicerite spine, reaching proximal end of third antennular peduncle; mesial projection at base of scaphocerite present (Fig. 5A).

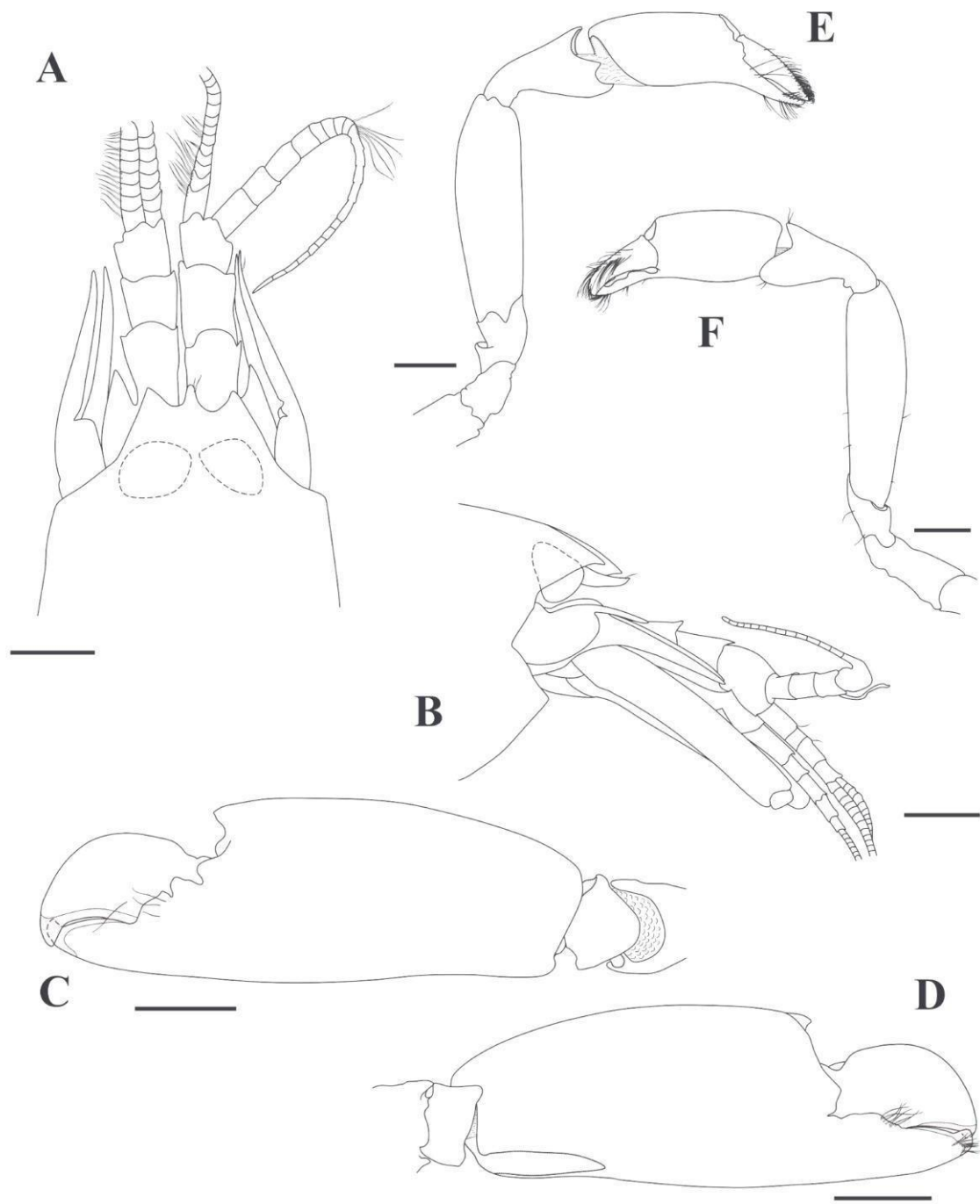


Figure 5. *Synalpheus* sp. nov. 2, male holotype from Buraco do Inferno, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48907). A, frontal region, dorsal view; B, same, lateral view; C, major chela, right side, mesial view; D, same, lateral view; E, minor chela, left side, mesial view; F, same, lateral view. Scale bars: A, B, E, F, 0.5 mm; C, D, 1 mm.

Mouthparts typical as figured (Fig. 6A—F). Mandible with 7 marginal teeth on incisor process (Fig. 6A). Palp of maxilliped 1 consisting of 2 segments (Fig. 6B). Maxilliped 3 with three distal spines on distal segment, and without ventro-distal spine on antepenultimate segment (Fig. 6F).

Major pereopod 1 (Fig. 5C, D) massive, fingers clearly shorter than half length of palm; fixed finger slightly shorter than dactyl. Palm of chela with distal superior margin protuberance, slightly curved upward in mesial view, toward dactyl.

Minor pereopod 1 (Fig. 5E, F) with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactylus with flexor margin straight, bladelike, with 1 distinct distal teeth; transverse dorsal setal brush on dactylus, very conspicuous; fixed finger with flexor margin straight, bladelike, and 1 distinct teeth.

Pereopod 2 (Fig. 7E) with carpus 5-segmented, subequal to merus. Both fingers ending in narrow, straight tooth.

Pereopod 3 (Fig. 7F) slender; dactylus biunguiculate, with flexor unguis clearly thicker than extensor; propodus with row of 8 mobile spines on flexor margin and one distal mobile spines flanking base of dactylus; carpus with distal mobile spine on flexor margin; merus almost 4 times longer than wide, without movable spines on flexor margin; mesial lamella on coxa present. Pereopod 4 similar to third, slightly weaker. Pereopod 5 similar to fourth, but smaller; propodus with only 2 spines on flexor margin, transverse combs of stout setae on ventral face; carpus without distal spine.

Pleura 1 (Fig. 7A) of male with posterior corner distinctly produced posteriorly into sharp projection; second pleura of male broadly rounded; third to fifth pleura of male progressively acute, but not pointed.

Pleopod 1 of male with 2 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating in distal half; appendix interna present on second to fifth male pleopods. Appendix interna present on second to fifth male pleopods.

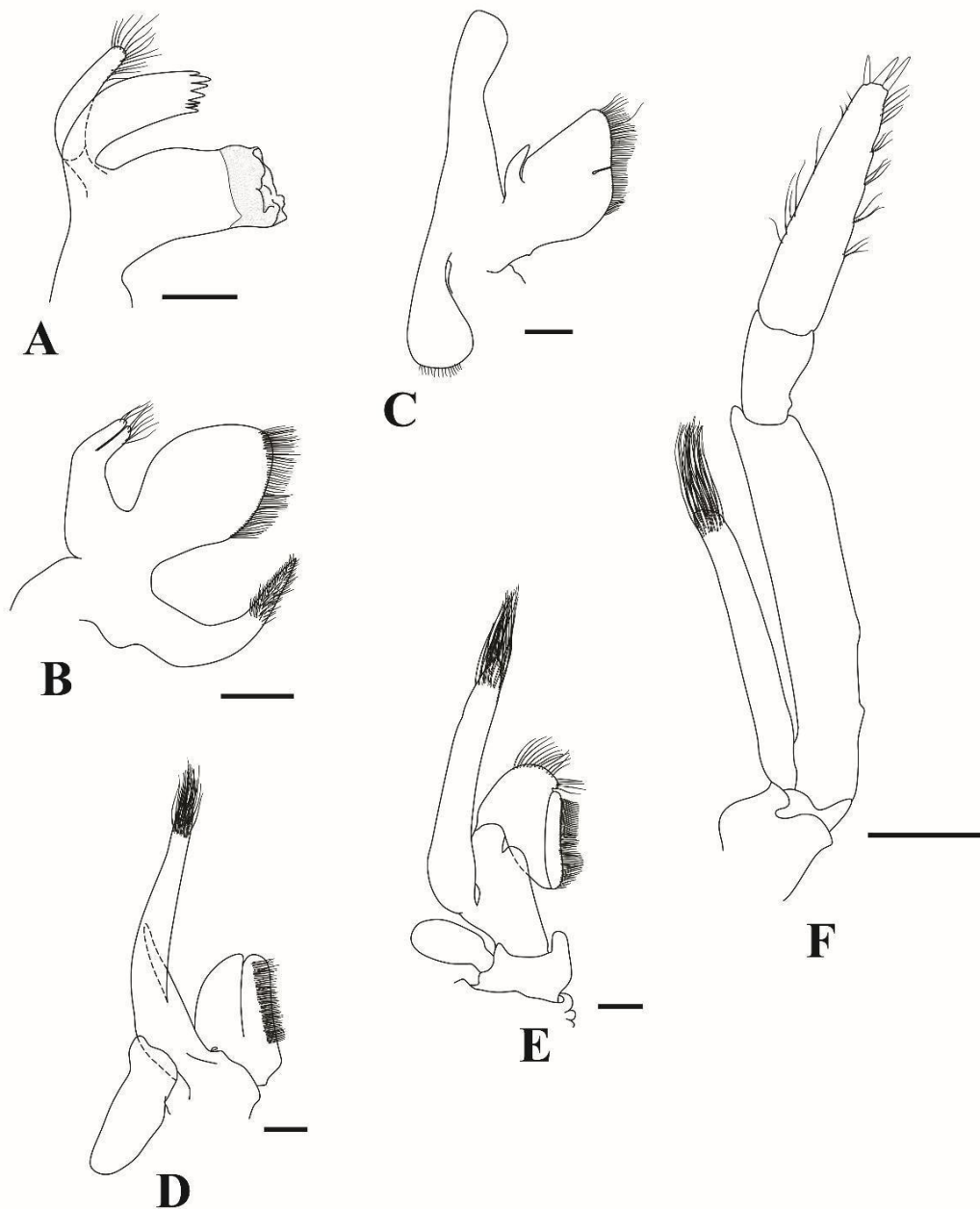


Figure 6. *Synalpheus* sp. nov. 2, male holotype from Buraco do Inferno, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48907). Mouthparts, A, mandible, right side; B, first maxilla, right side; C, second maxilla, right side; D, first maxilliped, right side; E, second maxilliped, right side; F, third maxilliped, right side. Scale bars: A–E, 0.2 mm; F, 0.5 mm.

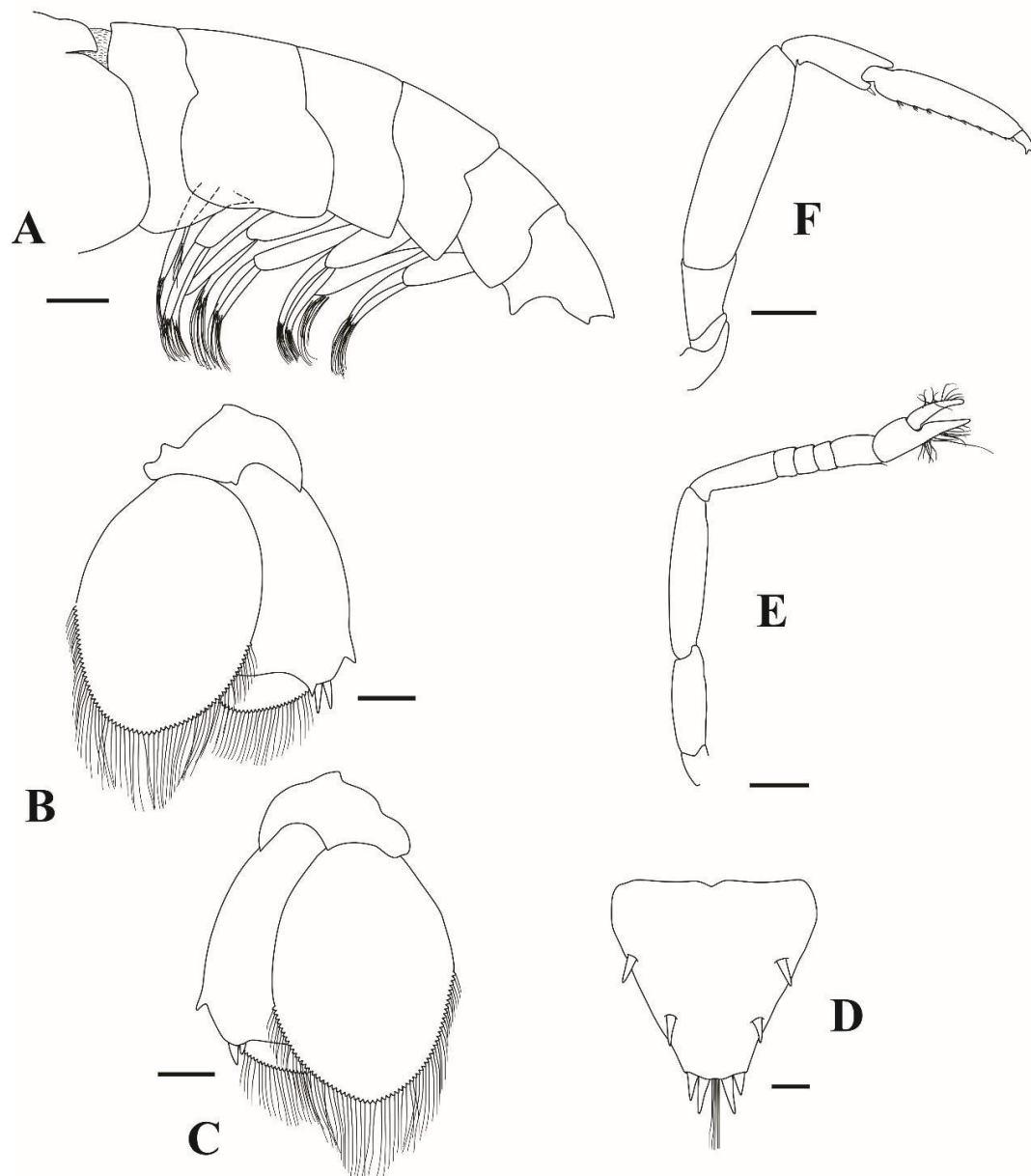


Figure 7. *Synalpheus* sp. nov. 2, male holotype from Buraco do Inferno, Fernando de Noronha Archipelago, Pernambuco, Brazil (MZUSP 48907). A, pleon, left view; B, right uropod, dorsal view; C, left uropod, dorsal view; D, telson, dorsal view; E, second pereopod, right side, lateral view; F, third pereopod, right side, lateral view. Scale bars: A, 1 mm; B, C, E, 0.4 mm; D, F, 0.5 mm.

Telson (Fig. 7D) with marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, postanal setal brush absent. Uropods with single fixed tooth on outer margin of exopod, distinctly spaced from the mobile spine, which is longer and more slender than adjacent inner fixed tooth.

Type locality: Buraco do Inferno, Fernando de Noronha, Pernambuco, Brazil (03°48'14.7"S 32°23'12.4"W).

Distribution: Western Atlantic — Brazil: Pernambuco (Fernando de Noronha Archipelago) (present study).

Ecology: *Synalpheus* sp. nov. 2 is found in association with sponges, from 8 to 12 m deep.

Remarks: *Synalpheus* sp. nv. 2 is morphologically similar to members of the *S. brooksi* complex. It differs from all species in this group, except *S. ruetzleri*, by the presence of a subtle scaphocerite blade (Fig. 5A). *Synalpheus* sp. nv. 2 differs from *S. ruetzleri* by the lateral spine of basicerite not reaching the distal end of the third antennular peduncle (Fig. 5A) (vs. lateral spine of basicerite reaching the distal end of third antennular peduncle in *S. ruetzleri*), lateral spine of scaphocerite reaching proximal end of third antennular peduncle (Fig. 5A) (vs. slightly overreaching antennular peduncle in *S. ruetzleri*), distodorsal protuberance of major pereopod not being secondarily produced distally, slightly curved upward (Fig. 5C, D) (vs. distodorsal protuberance of major pereopod secondarily produced distally, slightly curved downward in *S. ruetzleri*) (see Macdonald & Duffy 2006, Figs. 8—13). In addition, the minor pereopod fingers end in a single tooth (Fig. 5E, F) (vs. with two distinct distal teeth in *S. ruetzleri*), pereopod 3 with flexor margin of propodus with 8 mobile spines and one distal mobile spine at the base of dactylus, with flexor unguis slightly ticker than extensor (Fig. 7F) (vs. flexor margin of propodus with 7 mobile spines, one pair of distal mobile spines at the base of dactylus and flexor unguis clearly ticker than extensor in *S. ruetzleri*) (see Macdonald & Duffy 2006, Figs. 8—13).

Synalpheus sp. nov. 2 was reported by Paixão et al. (2025), as *S. ruetzleri*, from Buraco do Inferno, Ilha do Meio, and Ponta da Sapata in the Fernando de Noronha Archipelago. Pairwise genetic distances also supported the distinctiveness of *Synalpheus* sp. nov. 2, with divergence values of 0.28 from the outgroup (*A. petronioi*), 0.10 from *S. sanctithomae*, and 0.04

and 0.05 from *S. ruetzleri* specimens from Panama and Belize, respectively (Table 2). This study also updates the distribution of *S. ruetzleri* in Brazil, previously expanded to include the Fernando de Noronha Archipelago (Paixão et al. 2025), but is now restricted to states of Ceará and Pernambuco (Anker & Pachelle 2014; Paixão et al. 2025).

Table 2: Pairwise genetic distance for the 16S gene between the new species and other specimens of *Synalpheus* Spence Bate, 1888 analyzed in the present study. Atl: Atlantic. FN: Archipelago Fernando de Noronha.

Specimens	1	2	3	4	5	6	7	8	9	10	11
1 <i>Synalpheus agelas</i> (Belize)											
2 <i>Synalpheus agelas</i> (Florida, EUA)	0.00										
3 <i>Synalpheus brooksi</i> (Panama, Atl)	0.11	0.11									
4 <i>Synalpheus brooksi</i> (Belize)	0.12	0.12	0.01								
5 <i>Synalpheus herricki</i> (Belize)	0.16	0.17	0.14	0.15							
6 <i>Synalpheus</i> sp. nov. 1 (FN, Brazil)	0.15	0.15	0.13	0.13	0.05						
7 <i>Synalpheus ruetzleri</i> (Belize)	0.09	0.09	0.08	0.09	0.14	0.13					
8 <i>Synalpheus ruetzleri</i> (Panama, Atl)	0.09	0.10	0.08	0.08	0.13	0.12	0.00				
9 <i>Synalpheus</i> sp. nov. 2 (FN, Brazil)	0.11	0.12	0.10	0.10	0.15	0.13	0.05	0.04			
10 <i>Synalpheus sanctithomae</i> (Belize)	0.13	0.13	0.12	0.13	0.12	0.11	0.10	0.10	0.10		
11 <i>Alpheus petronioi</i> (Pará, Brazil)	0.25	0.26	0.27	0.27	0.27	0.26	0.25	0.27	0.28	0.26	

Discussion

In this study, we describe two new species of *Synalpheus* from Brazil (Fernando de Noronha Archipelago, Pernambuco, and Sergipe), based on morphological and molecular data. Both species belong to the *Synalpheus brooksi* complex. When describing two species within this complex, Macdonald & Duffy (2006) noted that it is taxonomically problematic due to the morphological similarity among species and high intraspecific variation, particularly among conspecifics inhabiting different sponge hosts and geographically distinct locations. Differentiation among members of the complex relies on subtle morphological traits such as the shape of the frontal region (whether shallow or normal), presence or absence of the scaphocerite blade, distribution and shape of gambarelloides setae, morphology of the distodorsal projection of the major pereopod, and also the coloration of embryos (Macdonald et al. 2009).

Maximum Likelihood analysis reinforced the morphological findings, grouping *Synalpheus* sp. nov. 1 with *S. herricki*, albeit in different lineages, as well as *Synalpheus* sp. nov. 2 and *S. ruetzleri*, also in distinct lineages (Fig. 1).. Hultgren et al. (2014) established

genetic divergence thresholds for delimiting cryptic species within the *Synalpheus gambarelloides* group. However, their assessment was based on the mitochondrial COI gene as a molecular marker. In the present study, molecular divergence between *Synalpheus* sp. nov. 1 and *Synalpheus* sp. nov. 2 and their respective morphologically similar species (*S. herricki* and *S. ruetzleri*) were processed using mitochondrial 16S gene and ranged from 0.04 to 0.05. Although these values are relatively low when compared to those reported by Hultgren et al. (2014) (mean genetic divergence between sister species: $8.14\% \pm 1.41$; mean interspecific divergence: $19.57\% \pm 0.21$), the integration of molecular and morphological evidence supports of both species recognition.

In addition to describing two new species of *Synalpheus*, thereby increasing the known diversity of these shrimps in Brazil from 30 to 32 species (Paixão et al. 2025, and references therein), the present study highlights the importance of integrative approaches in the taxonomy of the group, particularly within taxonomically challenging complexes such as the *S.s brooksi* complex. Although *Synalpheus* is currently recognized as the second most diverse genus within Alpheidae (Anker et al. 2012), this finding suggests that its actual diversity may still be underestimated. Moreover, the results presented here emphasize the significance of legally protected areas, such as the Fernando de Noronha Archipelago, in revealing the high potential these regions hold for the discovery of undescribed species.

Acknowledgments

We would like to thank CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for the financial assistance granted to MT (Universal 421193/2018-2, PQ 311340/2021-0), AOA (PQ 311217/2022-2); to FACEPE (Fundação de Amparo à Ciência e Tecnologia de Pernambuco) for the aid granted to PHP (master's scholarship Process IBPG-1407-2.04/18); to CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for the financial assistance granted to PHP (doctoral scholarship Proc. 88887.611870/2021-00, Finance code 001); to ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade) for authorizations for collections in the archipelagos (66478), granted to MT, and on the coastal areas of Pernambuco (58697-1); to Amanda Horch, Gabriel Bochini, Isabela Moraes and Karmine Pasinato for collecting and sorting animals in the Fernando de Noronha; to the Museu de Oceanografia Prof. Petrônio Alves Coelho (MOUFPE) at UFPE, especially the curator of

the Crustacean Collection, Dr. Jesser Fidelis de Souza Filho, and Dr. Fabíola M. Marques do Couto-Cahu, for lending *Synalpheus* material. The English version of this paper was prepared using DeepL and ChatGPT and later revised by the authors.

References

- Almeida, A.O., Terossi, M., Araújo-Silva, C.L. & Mantelatto, F.L. (2013) Description of *Alpheus buckupi* spec. nov., a new amphi-Atlantic snapping shrimp (Caridea: Alpheidae), based on morphological and molecular data. *Zootaxa*, 3652 (4), 437–452.
- Almeida, A.O.; Terossi, M.; Mantelatto, F.L. (2014). Morphology and DNA analyses reveal a new cryptic snapping shrimp of the *Alpheus heterochaelis* Say, 1818 (Decapoda: Alpheidae) species complex from the western Atlantic. *Zoosystema*. 36 (1), 53-71.
- Almeida, A.O., Terossi, M., Buranelli, R.C., Castilho, A.L., Costa, R.C., Zara, F.J., & Mantelatto, F.L. (2018) Checklist of decapods (Crustacea) from the coast of São Paulo State (Brazil) supported by integrative molecular and morphological data: II. Infraorder Caridea: family Alpheidae. *Zootaxa*, 4450(3), 331-358.
- Anker, A., Ah Yong, S.T., Noel, P.Y. & Palmer, A.R. (2006) Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. *Evolution*, 60, 2507–2528.
- Anker, A. & Pachelle, G. (2014) Taxonomic notes on some Brazilian species of *Synalpheus* Spence Bate 1888, with new records and description of a new species (Decapoda, Alpheidae). *Zootaxa*, 3815 (2), 215–232.
- Anker, A., Pachelle, G., De Grave, S. & Hultgren, K.M. (2012) Taxonomic and biological notes on some Atlantic species of the snapping shrimp genus *Synalpheus* Spence Bate 1888 (Decapoda, Alpheidae). *Zootaxa*, 3598, 1–96.
- Ashrafi, H. & Hultgren, K.M. (2022) Integrative methods resolve taxonomy and relationships of snapping shrimps in the genus *Synalpheus* (Decapoda: Alpheidae) collected during the MNHN ‘Madibenthos’ expedition. *Invertebrate Systematics*, 36: 389–418.

- Ashrafi, H., Sari, A. & Naderloo, R. (2020) A new sponge-dwelling species of *Synalpheus* Spence Bate, 1888 (Decapoda: Caridea: Alpheidae) from the Persian Gulf. *Zootaxa*, 4861: 338–348.
- Bauer, R.T. (2004) Remarkable shrimps: adaptations and natural history of the carideans. *University of Oklahoma Press, Norman*, 282 pp.
- Banner, D.M. & Banner, A.H. (1975) The alpheid shrimp of Australia. Part 2: the genus *Synalpheus*. *Records of the Australian Museum*, 29 (12), 267–389.
- Bracken-Grisson, H. & Felder, D.L. (2014) Provisional revision of American snapping shrimp allied to *Alpheus floridanus* Kingsley, 1878 (Crustacea: Decapoda: Alpheidae) with notes on *A. floridanus africanus*. *Zootaxa*, 3895 (4), 451–491.
- Chace Jr., F.A. (1972) The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). *Smithsonian Contributions to Zoology*, 98, 1–179.
- Chak, S.T.C., Barden, P. & Baeza, J.A. (2020) The complete mitochondrial genome of the eusocial sponge dwelling snapping shrimp *Synalpheus microneptunus*. *Scientific Reports*, 10: 7744.
- Coutière, H. (1909) The American species of snapping shrimps of the genus *Synalpheus*. *Proceedings of the United States National Museum*, 36, 1–93.
- De Grave, S. & Fransen, C.H.J.M. (2011) Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zoologische Mededelingen*, 85, 195–588.
- Dardeau, M.R. (1984) *Synalpheus* shrimps (Crustacea: Decapoda: Alpheidae). I. The Gambarelloides group, with a description of a new species. *Memoirs of the Hourglass Cruises*, 7, 1–125.
- Duffy, J.E. (1998) On the frequency of eusociality in snapping shrimps (Decapoda: Alpheidae), with description of a second eusocial species. *Bulletin of Marine Science*, 62, 387–400.
- Fabricius, J.C. (1798) Supplementum Entomologiae Systematicae. Proft et Storch, Hafniae, 572 pp.

- Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser.*, 41, 95 - 98.
- Horch, A.P., Williams, J.D., & Terossi, M. (2024) A New Species of *Parapleurocrypta* Chopra, 1923 (Isopoda, Epicaridea, Bopyridae) Parasitizing Shrimps of the Genus *Synalpheus* Spence Bate, 1888 (Decapoda, Caridea, Alpheidae) from the Fernando de Noronha Archipelago, Brazil. *Zoological Studies*, 62, e13.
- Hultgren, K.M., MacDonald, K.S. III & Duffy, J.E. (2010) Sponge-dwelling snapping shrimps of Curacao, with descriptions of three new species. In: De Grave, S. & Fransen, C.H.J.M. (eds), Contributions to Shrimp Taxonomy. *Zootaxa*, 2372: 221–262.
- Hultgren, K., MacDonald, K.S. III & Duffy, J.E. (2011) Sponge dwelling snapping shrimps (Alpheidae: *Synalpheus*) of Barbados, West Indies, with a description of a new eusocial species. *Zootaxa*, 2834: 1–16.
- Hultgren, K.M., Hurt, C., & Anker, A. (2014) Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). *Molecular Phylogenetics and Evolution*, 77, 116-125.
- Macdonald, K.S. III. & Duffy, J.E. (2006) Two new species of sponge-dwelling snapping shrimp from the Belizean Barrier Reef, with a synopsis of the *Synalpheus brooksi* species complex. *American Museum Novitates*, 3543, 1–22. [https://doi.org/10.1206/0003-0082\(2006\)3543\[1:TNSOSS\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)3543[1:TNSOSS]2.0.CO;2)
- Macdonald, K.S. III, Hultgren, K. & Duffy, J.E. (2009) The sponge-dwelling snapping shrimps (Crustacea, Decapoda, Alpheidae, *Synalpheus*) of Discovery Bay, Jamaica, with descriptions of four new species. *Zootaxa*, 2199, 1–57.
- Mantelatto, F.L., Carvalho, F.L., Simões, S.M., Negri, M., Souza-Carvalho, E.A. & Terossi, M. (2016) New primers for amplification of cytochrome c oxidase subunit I barcode region designed for species of Decapoda (Crustacea). *Nauplius*, 24, 1 – 4.
- Palumbi, S.R. & Benzie, J. (1991) Large mitochondrial DNA differences between morphologically similar penaeid shrimp. *Molecular Marine Biology and Biotechnology*, 1, 27–34.

- Pequegnat, L. H. & Heard, R. W. (1979). *Synalpheus agelas*, new species of snapping shrimp from the Gulf of Mexico and Bahama Islands (Decapoda: Caridea: Alpheidae). *Bulletin of Marine Science*, 29(1), 110-116.
- Rafinesque, C.S. (1815) *Analyse de la Nature ou Tableau de l'Univers et des corps organisés. Palerme*, 1–224.
- Ramos-Tafur, G.E. & Franke-Ante, R. (2019) *Synalpheus amintae* sp. nov., a new species of sponge-dwelling snapping shrimp (Crustacea: Decapoda: Alpheidae) from Parque Nacional Natural Isla Gorgona, Pacific Coast of Colombia. *Zootaxa*, 4646: 173–188.
- Ríos, R. & Duffy, J.E. (2007) A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of *Zuzalpheus*, new genus, and six new species. *Zootaxa*, 1602, 1–89.
- Santos, P.S., Terossi, M., Mantelatto, F.L., & Almeida, A.O. (2019) Using integrative taxonomy to establish the status of *Alpheus peasei* (Armstrong, 1940) (Decapoda: Alpheidae) as a single species throughout its distribution. *Zootaxa*, 4629(1), 51-68.
- Soledade, G.O., Terossi, M., Scioli, J.A., Mantelatto, F.L. & Almeida, A.O. (2019) A new western Atlantic snapping shrimp of the *Alpheus macrocheles* group (Caridea, Alpheidae) revealed by morphological, molecular and color data. *European Journal of Taxonomy*. 581: 1–21.
- Spence Bate, C. (1888) Report on the Crustacea Macrura collected by the Challenger during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76. *Zoology*, 24 (52), i–xc, 1–942, pl. 1–150.
- Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: molecular evolutionary genetics analysis version 11. *Molecular biology and evolution*, 38 (7), 3022 - 3027.
- WoRMS (2024a). Alpheidae Rafinesque, 1815. Available on: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106776>. Accessed in: March 20, 2024.

WoRMS (2025). *Synalpheus* Spence Bate, 1888. Available on: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106982>. Accessed in: July 07, 2025.

ARTIGO CIENTÍFICO 3 - ESTRUTURAÇÃO GENÉTICA EM *SYNALPHEUS HOETJESI* (DECAPODA: ALPHEIDAE): UMA ESPÉCIE COM DISTRIBUIÇÃO DISJUNTA NO ATLÂNTICO OCIDENTAL

Artigo a ser submetido na Marine and Freshwater Research; Fator de Impacto: 2.263; Percentil: 76%; Qualis CAPES A2.

Resumo

Synalpheus hoetjesi, além de ter uma distribuição disjunta, apresenta uma sutil diferenciação genética entre as populações do Caribe e do Brasil, com base na análise do gene mitocondrial 16S. Tendo em vista o uso do gênero como modelo em estudos genéticos, sua importância ambiental e a tal divergência, o objetivo do estudo foi avaliar a extensão dessa estruturação, a partir da análise do gene mitocondrial COI. Os camarões do Brasil foram coletados na Praia de Carneiros, Tamandaré, e na Praia de Catuama, Goiana, ambas no estado de Pernambuco, associadas a esponjas. Extrações do gene COI foram realizadas para calcular o número de haplótipos, a diversidade nucleotídica e haplotípica, a variação genética e a rede de haplótipos, em comparação às sequências depositadas no GenBank. Os resultados mostram uma variação de 2,8% entre as sequências de *S. hoetjesi* do Caribe e do Brasil, separando-as em duas populações distintas. O mesmo resultado foi encontrado na rede de haplótipos. A Análise de Variância Molecular mostrou uma variação de 92,3% entre as populações, quando não estruturadas hierarquicamente, e de 82,9% entre os grupos, quando estruturadas em duas populações. Apesar da divergência genética encontrada na espécie, ela é menor do que a divergência média interespecífica dentro do grupo *Synalpheus gambarelloides*. Por fim, sua distribuição disjunta pode estar atrelada à pluma dos rios Amazonas e Orinoco, apesar da existência de sistemas recifais entre o Mar do Caribe e o Brasil.

Palavras-chave: Mar do Caribe; Pernambuco; COI; Divergência genética; Pluma Amazonas-Orinoco.

Introdução

Ao contrário do que acontece com espécies terrestres, considera-se que exista uma elevada conectividade populacional e, conseqüentemente, um alto fluxo gênico entre populações marinhas (Aulsebrook, 2000; Cowen et al., 2000), muito devido à sua ampla distribuição geográfica, ao seu grande poder de dispersão e a seus extensos períodos de desenvolvimento larval (Cowen et al., 2000). Ademais, barreiras geográficas são menos óbvias em ambientes marinhos em comparação aos terrestres, onde a ação das correntes marítimas propiciaram a conectividade entre as populações, promovendo sua homogeneização (Cowen et al., 2000). Todavia, uma série de estudos mostraram níveis consideráveis de diferenciação genética em espécies com um elevado poder de dispersão (Taylor & Hellberg, 2003; Baums et al., 2005; Arnaud-Haond et al., 2008; Baeza & Fuentes, 2013).

No ambiente marinho, fatores como o tipo de desenvolvimento larval (se direto ou indireto), o tempo que a larva passa no ambiente pelágico e o seu comportamento (Cowen et al., 2000, 2006; Teske et al., 2007), isolamento pela distância (Planes & Fauvelot, 2002), tempo de geração (Rolán-Alves et al., 1995), adaptação local (Riginos & Nachman, 2001) e processos oceanográficos podem reduzir ou favorecer o fluxo gênico entre as localidades (Cowen et al., 2000, 2006; White et al., 2010) estando envolvidos na conectividade e estruturação populacional. Por outro lado, padrões de distribuição disjunta nesse ambiente podem ser explicados pela combinação da ação das correntes oceânicas, das características topológicas do assoalho marinho, das plumas advindas de águas continentais e da capacidade de dispersão dos organismos em diferentes estágios de desenvolvimento, também estando atrelados a diferentes taxas de fluxo gênico influenciando a história evolutiva desses táxons (Hauser & Carvalho, 2008; Weersing & Toonen, 2009; Villamor et al., 2014; Santos et al., 2019).

Alpheidae Rafinesque, 1815 é uma das famílias mais diversas da ordem Decapoda, com mais de 800 espécies atualmente válidas (De Grave et al., 2023), estando entre os decápodes mais abundantes de águas rasas tropicais e subtropicais, particularmente nos recifes de coral (Rützler, 1976; Felder & Chaney, 1979; Ríos & duffy, 2007; Anker et al., 2012). *Synalpheus* Spence Bate, 1888, o segundo maior gênero da família em número de espécies, inclui camarões de vida livre ou que vivem em associação com vários grupos de invertebrados marinhos, especialmente com esponjas (Bruce, 1976; VandenSpiegel et al., 1998; Duffy & Macdonald, 1999; De Grave & Fransen, 2011; Anker et al. al., 2012; WoRMS, 2025). Ademais, devido à sua diversidade ecológica e à existência de diferentes padrões de organização social, esses

camarões têm sido utilizados como modelos para estudos de especiação, especializações com relação aos hospedeiros e evolução da socialidade (Duffy, 1992, 1996; VandenSpiegel et al., 1998; Duffy & Macdonald, 2010; Hultgren & Duffy, 2012).

Espécies Atlânticas Ocidentais de *Synalpheus* como *S. antillensis* Coutière, 1909, *S. brevicarpus* (Herrick, 1891), *S. fritzmuelleri* Coutière, 1909, *S. hoetjesi* Hultgren, Macdonald & Duffy, 2010 e *S. pandionis* Coutière, 1909, entre outras, apresentam uma distribuição disjunta (Christoffersen 1979, 1998; Bezerra & Coelho, 2006; Hultgren et al., 2010; Anker et al., 2012; 2016; Santos et al., 2012; Soledade et al., 2015; Cházaro-Olvera et al., 2017; Paixão et al., 2025), isto é, com um *gap* latitudinal nas ecorregiões da Guiana e da Amazônia (Spalding, 2007), correspondente à Plataforma Norte do Brasil. Tal tipo de distribuição pode ser explicada por artefatos de amostragem, tendo em vista que a carcinofauna dessa região é pouco conhecida, e/ou pelo fato de as espécies não apresentarem adaptações para colonizar esse ambiente devido à presença de fundos lamosos, baixa salinidade e variações na temperatura e hidrodinâmica (Isaac & Ferrari, 2017; Varona et al., 2019).

Synalpheus hoetjesi é registrada no Panamá, Curaçao (localidade-tipo), Barbados e no estado de Pernambuco, Brasil (Hultgren et al., 2010, 2011; Hultgren & Duffy, 2011; Anker et al., 2012; Paixão et al., 2025). É encontrada em recifes de corais rasos, em rochas e em associação com esponjas (e.g., *Agelas* sp., *Hyattella* sp., *Xestospongia* sp. e *Echinodictyum dendroides* Hechtel, 1983) e em profundidades de até 15 m (Hultgren et al., 2010; Anker et al., 2012; Paixão et al., 2025). A espécie faz parte do grupo *Synalpheus gambarelloides*, que incluir simbiontes obrigatórios de esponjas, caracterizados morfológicamente por apresentarem uma fileira de cerdas (cerdas gambarelloides) na superfície dorsal do dátilo da quela menor (Coutière, 1909), usadas para fragmentar o tecido da esponja hospedeira a partir de uma rápida abrasão de seus canais internos (Duffy, 2003). Paixão et al. (2025), ao reportarem a espécie para o nordeste brasileiro, observaram uma diferenciação genética no gene 16S de 0,5% entre espécimes do Brasil e do Mar do Caribe (Barbados, Curaçao e Panamá), além da separação desses dois grupos em diferentes clados, indicando a existência de uma estruturação genética sutil entre ambas populações (Kimura & Weiss, 1964; Avise, 2000).

Considerando a utilização de *Synalpheus* como modelo em estudos genéticos, sua relevância ecológica nos ambientes onde ocorre e a lacuna na distribuição encontrada em *S. hoetjesi* (Hultgren et al., 2010, 2011; Anker et al., 2012; Paixão et al., 2025), este estudo teve

como objetivo investigar a extensão da estruturação genética previamente observada em *S. hoetjesi* (Paixão et al., 2025), a partir de uma análises do gene mitocondrial COI.

Material e Métodos

Indivíduos de *S. hoetjesi* foram coletados na Praia de Carneiros, Tamandaré, e na Praia de Catuama, Goiana, ambos no estado de Pernambuco, Brasil. Para tal, foram realizados mergulhos livres e autônomos na Praia de Carneiros em profundidades de 1,5 m e de 3–5 m, respectivamente, a fim de coletar as esponjas onde esses organismos são encontrados. Após a triagem das esponjas, a partir de sua fragmentação sobre peneira com a utilização de pinças, os camarões obtidos foram separados, preservados em frascos com álcool 70% e devidamente etiquetados. Em laboratório, os camarões foram identificados com base nas chaves de identificação disponíveis (Chace, 1972; Hultgren et al., 2010; Anker et al., 2012) e na descrição original da espécie.

O processo de obtenção das sequências por meio de extração de DNA, amplificação, purificação e sequenciamento seguiu os mesmos passos descritos por Paixão et al. (2025). As diferenças foram o uso também de Chelex como método de extração, e amplificação do gene e COI mtDNA com uso dos primers COIAL2o (ACGCAACGATGATTATTTTCTAC) e COIAH2m (GACCRAAAAATCARAATAAATGTTG) (Mantelatto et al., 2016) e anelamento em 48°C. Foram obtidas sequências das duas fitas de DNA e a sequência consenso foi obtida no software Bioedit 7.2.5 (Hall, 1999) e verificadas manualmente para a correção de leituras inespecíficas quando necessária. As sequências obtidas neste estudo foram depositadas no Genbank. Sequências de espécimes de *S. hoetjesi* do Mar do Caribe, assim como de outras espécies usadas nas análises, foram retiradas do Genbank (Tabela 1).

As sequências foram alinhadas no Bioedit e a reconstrução da filogenia foi conduzida no software MEGA 11.0.11 (Tamura et al., 2021) através do método de Máxima Verossimilhança, com base no modelo de substituição GTR (General Time Reversible). A consistência das topologias foi mensurada usando o método de *bootstrap* (1000 réplicas), onde apenas os valores de confiança maiores que 50% foram evidenciados.

As análises populacionais seguiram a metodologia empregada por Vergamini et al. (2011). O número de haplótipos foi calculado no software DnaSP 6.12.03 (Rozas et al., 2017). As diversidades haplotípica e nucleotídica de cada população foram calculadas no Arlequin

3.5.2.2 (Excoffier & Lischer, 2010) e a rede haplotípica foi construída através do método Median-Joining no Network 10.2.0.0. (Bandelt et al., 1999). A variação genética foi avaliada com a Análise de Variância Molecular (AMOVA) (Excoffier et al., 1992), calculada no Arlequin. As análises foram realizadas baseadas nas frequências haplotípicas sem estrutura hierárquica (com todas as populações em um único grupo) e com subdivisão regional definida de acordo com os resultados de distância e rede haplotípicas. O grau de significância foi testado usando um processo de permutação não-paramétrica (Excoffier et al., 1992), incorporando 1000 permutações.

Tabela 1: Espécimes de *Synalpheus* Spence Bate, 1888 utilizados nas análises genéticas. Nomes de espécies destacados em **negrito** representam as sequências que foram obtidas pelo presente trabalho.

Espécie	Localidade	Número de tombo	Genbank
<i>Synalpheus brooksi</i>	Bocas del Toro, Panamá, Mar do Caribe	OUMNH.ZC.2012-07-124	KJ595048
<i>Synalpheus dardeau</i>	Panamá, Mar do Caribe	CH (U Miami)	KJ625036
<i>Synalpheus fritzmuelleri</i>	Jamaica, Mar do Caribe	VIMS JAM08-4719	KJ595081
<i>Synalpheus hoetjesi</i>	Tamandaré, Pernambuco, Brasil	DZ/UFRGS 7058	pendent (4)
<i>Synalpheus hoetjesi</i>	Goiana, Pernambuco, Brasil	DZ/UFRGS 7057	pendent (4)
<i>Synalpheus hoetjesi</i>	Barbados, Mar do Caribe	VIMS BR08-6708	KJ595101
<i>Synalpheus hoetjesi</i>	Barbados, Mar do Caribe	VIMS BR08-6701	KJ595100
<i>Synalpheus hoetjesi</i>	Bocas del Toro, Panamá, Mar do Caribe	VIMS P09-1202	KJ595098
<i>Synalpheus hoetjesi</i>	Curaçao, Mar do Caribe	VIMS CU08-4106	KJ595097
<i>Synalpheus hoetjesi</i>	Curaçao, Mar do Caribe	VIMS CU08-2901	KJ625037
<i>Synalpheus ul</i>	Barbados, Mar do Caribe	VIMS BR08-8703	KJ625044
<i>Synalpheus ul</i>	Panamá, Mar do Caribe	MNHN-IU-2010-4158	KJ595160

Resultados

O alinhamento das sequências de COI mtDNA de *S. hoetjesi* analisadas apresentou 586 loci. Não houve variação entre as sequências do gene nos indivíduos de Pernambuco, Brasil (Tabela 2); todavia, uma variação de 2,8% foi encontrada entre as sequências do Brasil e do Mar do Caribe. A variação separou os indivíduos em dois grupos: Mar do Caribe (Barbados, Bocas del Toro e Curaçao) e Brasil (Tamandaré e Goiana, Pernambuco) (Fig. 1). Adicionalmente, a distância genética estimada entre os indivíduos de *S. hoetjesi* e outras espécies de *Synalpheus* foi maior do que 2,8% (54,7 a 57,4%).

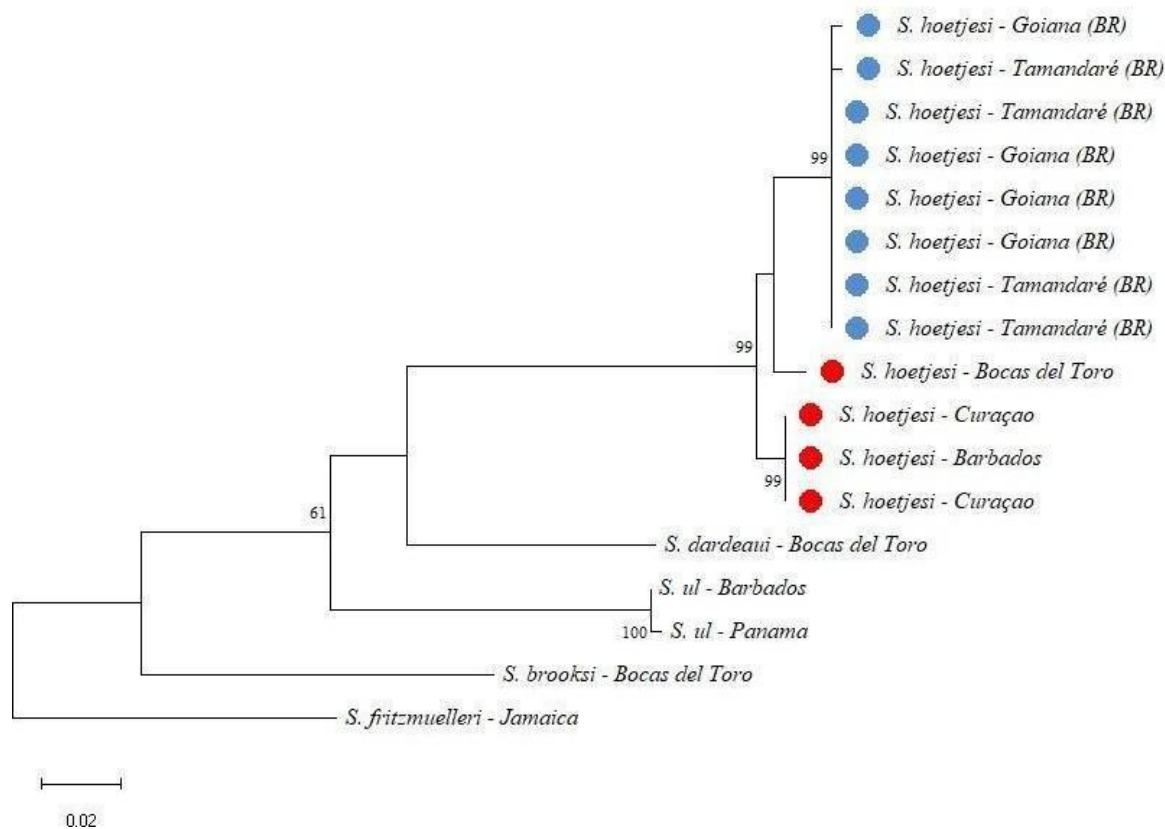


Figura 1. Árvore filogenética para os espécimes de *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010 e outras espécies de *Synalpheus* usando a análise de Máxima Verossimilhança das sequências do gene COI mtDNA. Os valores nos nós representam os valores de suporte considerando 1000 pseudo-réplicas do bootstraps. Valores <50% não são mostrados. Abreviação das localidades: BR - Brasil. Marcação em azul representam indivíduos de Pernambuco, Brasil; as vermelhas, os do Mar do Caribe.

Cinco haplótipos foram identificados com base nos fragmentos do COI mtDNA de 12 indivíduos das duas regiões (6 do Brasil e 6 do Mar do Caribe) (Fig. 2), três dos quais representaram indivíduos únicos. Além disso, a população do Mar do Caribe não compartilhou

haplótipos com a população do nordeste brasileiro. A diversidade haplotípica total foi de 0,71 e a diversidade nucleotídica foi mais elevada nos indivíduos do Brasil (Tamandaré: $4,55 \times 10^{-3}$; Goiana: $1,13 \times 10^{-3}$) do que nos do Mar do Caribe (0,00).

A Análise de Variância Molecular (Tabela 3) sem estruturação hierárquica mostrou que a maior variação (93,4%) foi encontrada entre as populações de *S. hoetjesi*. Quando as

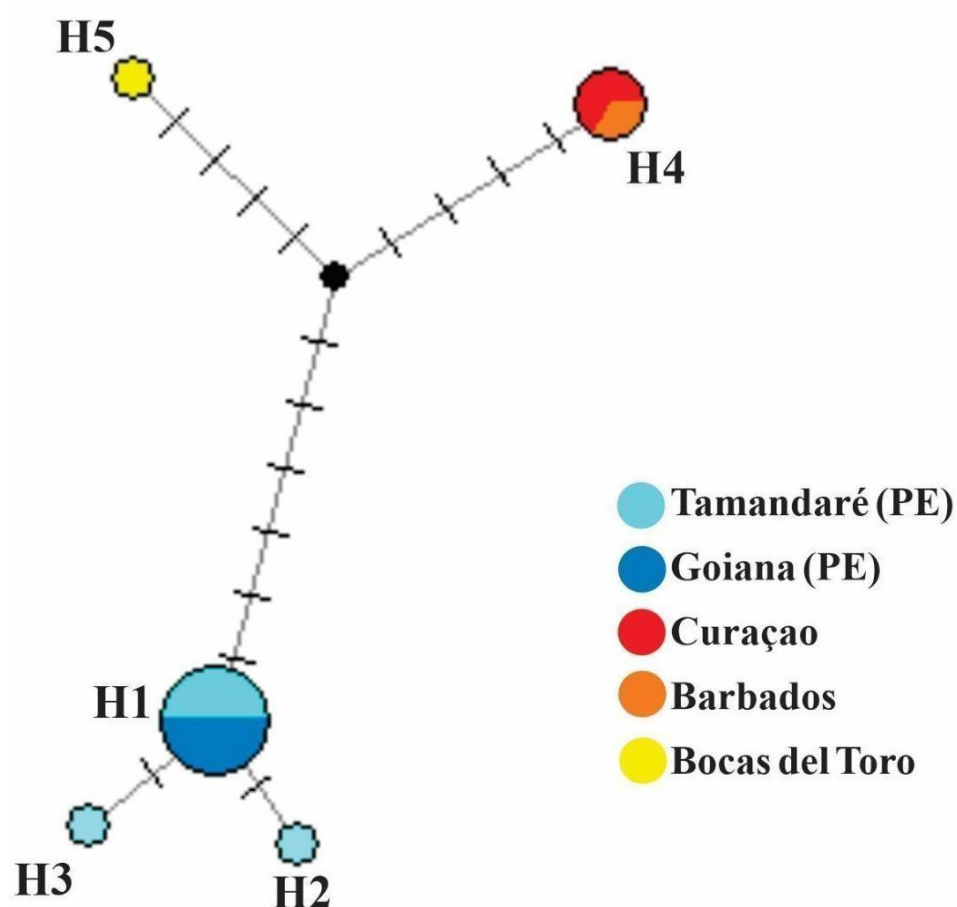


Figura 2: *Synalpheus hoetjesi*. Rede de haplótipos baseada na análise de Median-Joining do gene COI mtDNA, indicando a presença de cada haplótipo (H) encontrado na população (5 haplótipos em 12 espécimes). O tamanho do círculo é proporcional à frequência do haplótipo. Círculo preto representam os vetores médios. Diferentes cores representam diferentes localidades. Cada traço representa um passo mutacional

populações foram estruturadas com base nos resultados das análises filogenética, de distância genética e de rede haplotípica, separando as populações entre Mar do Caribe e Brasil a maior

variação foi encontrada entre os grupos (73,6%, $p = 0,000$), enquanto que a variação entre as populações foi de 17,7% ($p = 0,000$).

Tabela 2: Matriz de distância genética do gene COI mtDNA entre espécimes de *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010 e outras espécies de *Synalpheus*.

Espécimes	1	2	3	4	5	6
1. <i>S. hoetjesi</i> – Brasil (6 espécimes)						
2. <i>S. hoetjesi</i> – Mar do Caribe (6 espécimes)	0,028					
3. <i>S. dardeui</i> – Panamá	0,553	0,557				
4. <i>S. ul</i> – Mar do Caribe (2 espécimes)	0,564	0,574	0,142			
5. <i>S. brooksi</i> – Bocas del Toro, Panamá	0,547	0,548	0,188	0,180		
6. <i>S. fritzmuelleri</i> - Jamaica	0,552	0,560	0,147	0,179	0,196	

Tabela 3: *Synalpheus hoetjesi* Hultgren, Macdonald & Duffy, 2010. Análise de Variância Molecular (AMOVA). *Valores significantes, $p < 0,05$.

Estrutura da AMOVA	Fonte da Variação	da	%	Fst/Fct	p
Sem estrutura	entre populações		93,39	0,934	0,000*
	dentro das populações		6,61		
Mar do Caribe (Bocas del Toro/Panamá, Barbados e Curaçao)	entre grupos		77,63	FSC 0,793	0,000*
Brasil (Tamandaré e Goiana, Pernambuco)	entre populações		17,74	FST 0,954	0,000*
	dentro das populações		4,64	FCT 0,776	0,000*

Discussão

A análise de Máxima Verossimilhança da região barcode COI mostrou uma separação entre as populações de *S. hoetjesi* do Brasil e do Mar do Caribe (Fig 1)., com uma diferenciação genética de 2,8% (Tabela 2). Adicionalmente, a construção da rede de haplótipos resultou em haplótipos não compartilhados entre as populações do Brasil e Mar do Caribe e a variância molecular (Tabela 3), enquanto populações estruturadas, foi maior entre os grupos (73,6%) do que entre as populações (17,7%).

Hultgren et al. (2014), ao realizarem uma análise genética do gene COI entre indivíduos de 93 espécies de *Synalpheus*, estipularam, dentro do grupo *S. gambarelloides*, valores de

divergência genética intraespecífica ($1,02 \pm 0.92\%$), divergência média entre espécies irmãs ($8,14 \pm 1.41\%$), divergência média interespecífica ($19,57 \pm 0.21\%$), e um valor de *threshold* para espécies crípticas (10,2%). Baseado nessas informações, é possível dizer que, apesar da variação encontrada entre as populações de *S. hoetjesi* ser maior do que a divergência genética intraespecífica esperada, ela ainda é menor do que a divergência projetada para espécies diferentes, inferindo que as duas populações pertencem à mesma espécie. Paixão et al. (2025), ao analisarem sequências do gene 16S de *S. hoetjesi* do Brasil (Pernambuco) e do Mar do Caribe (Barbados, Curaçao e Panamá), verificaram que as duas populações, apesar de formarem um clado bem suportado, estavam subdivididas em duas linhagens correspondentes (Brasil e Mar do Caribe). Ademais, o estudo também evidenciou uma pequena variação genética de 0,5% entre as linhagens analisadas. Os resultados obtidos no presente estudo, suportam, portanto, àqueles obtidos por Paixão et al. (2025).

Hultgren et al. (2014), ao realizarem uma análise genética do gene COI entre indivíduos de 93 espécies de *Synalpheus*, estipularam, dentro do grupo *S. gambarelloides*, valores de divergência genética intraespecífica ($1,02 \pm 0.92\%$), divergência média entre espécies irmãs ($8,14 \pm 1.41\%$), divergência média interespecífica ($19,57 \pm 0.21\%$), e um valor de *threshold* para espécies crípticas (10,2%). Baseado nessas informações, é possível dizer que, apesar da variação encontrada entre as populações de *S. hoetjesi* ser maior do que a divergência genética intraespecífica esperada, ela ainda é menor do que a divergência projetada para espécies diferentes, inferindo que as duas populações pertencem à mesma espécie. As análises filogenéticas do gene 16S de *S. hoetjesi* apresentadas por Paixão et al. (2025) já indicavam divergência genética entre indivíduos provenientes do Mar do Caribe e no Brasil. Os resultados obtidos no presente estudo, utilizando o gene COI, corroboram, portanto, àqueles obtidos por Paixão et al. (2025).

A lacuna na distribuição de *S. hoetjesi* pode estar relacionada a uma série de fatores, como a falta de amostragens na região, a capacidade de dispersão da espécie e a existência de barreiras a essa dispersão (Hellberg et al., 2002; Palumbi, 2003; Shanks et al., 2003). Uma barreira geográfica conhecida nessa região é a formada pelos rios Orinoco, na Venezuela, e Amazonas, no Brasil (Curtin, 1986). A pluma do Amazonas-Orinoco foi apontada como possível fator de diferenciação genética em outras espécies marinhas, incluindo crustáceos (Lessios et al., 2003; Hollatz et al., 2011; Terossi & Mantelatto, 2012; Araujo et al., 2022; Peres et al., 2022). A descarga massiva de água doce e sedimentos no oceano pelo deságue combinado de ambos os rios promove alterações na salinidade, pH, sedimentação e turbidez do ambiente,

sendo responsável pela descontinuidade da fauna entre as Províncias Biogeográficas Brasileira e Caribenha (Rocha, 2003; Robertson et al., 2006; Moura et al., 2016 Araujo et al., 2022).

Apesar de essas barreiras, Moura et al. (2016) comprovaram a existência de um sistema recifal sob a pluma do rio Amazonas, que se estende da Guiana Francesa até o Parcel de Manuel Luís, Maranhão, o recife emergente mais ao norte da Província Biogeográfica Brasileira. Tais formações poderiam servir de *stepping stones* entre a população de *S. hoetjesi* do Mar do Caribe e do Brasil; todavia, a ausência de indicativos de fluxo gênico entre elas, evidenciada pela ausência de haplótipos compartilhados (Fig. 2), não suporta tal hipótese.

Como observado em outros alfeídeos, espécies de *Synalpheus* que formam pares heterossexuais apresentam desenvolvimento estendido, com larvas livre-natantes que se desenvolvem na coluna d'água após a eclosão (Dobkin, 1965; Duffy & Macdonald, 2010). Tal forma de desenvolvimento também foi observada em espécies que formam grupos comuns em esponjas, onde há vários pares de indivíduos adultos se reproduzindo igualmente (Hultgren et al., 2017). *Synalpheus hoetjesi* tem sido observada em pares heterossexuais, mas também em agregações (Hultgren et al., 2010; Anker et al., 2012; Paixão et al., 2025). Pelo fato de as larvas serem liberadas para fora das esponjas hospedeiras, é esperado que o potencial de dispersão da espécie seja elevado, propiciando a conectividade entre suas populações (Mazzei & Rubenstein, 2021). Todavia, por se tratar de uma espécie que vive, principalmente, em simbiose com esponjas em fundos rochosos recifais rasos (Hultgren et al., 2010; Anker et al., 2012; Paixão et al., 2025), o assentamento dos indivíduos após o período de dispersão larval é dependente da presença de seus hospedeiros. Consequentemente, a ausência desses hospedeiros acarretaria na ausência da espécie nessas localidades. Infelizmente, o desenvolvimento larval e o potencial de dispersão ainda não são conhecidos em *S. hoetjesi*, havendo a necessidade de estudos com esse enfoque para inferências sobre a distribuição da espécie.

É interessante considerar que, enquanto em alguns casos, essa separação acarreta na especiação, como ocorre em *Alpheus coralvivo* Santos, Terossi, Mantelatto, Torres & Almeida, 2024, cujo processo de separação se deu a partir do isolamento de *A. simus* Guérin-Méneville, 1856 durante os fenômenos vicariantes ocorridos na região do Mar do Caribe, o presente trabalho aponta essa separação como provocadora de estruturação genética entre populações geograficamente separadas. Apesar das condições desfavoráveis para sua dispersão e homogeneização populacional, os resultados do presente estudo suportam a separação das

populações em dois grupos distintos, proporcionando mais um caso de diferenciação genética entre espécies com distribuição disjunta entre o Mar do Caribe e o Brasil.

Agradecimentos

Ao CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) pelos auxílios financeiros concedidos à MT (Universal 421193/2018-2, PQ 311340/2021-0) e AOA (PQ 311217/2022-2). À FACEPE (Fundação de Amparo à Ciência e Tecnologia de Pernambuco) e a CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) pelos auxílios concedidos a PHP (bolsa de mestrado Processo IBPG-1407-2.04/18 e bolsa de doutorado Proc. 88887.611870/2021-00, respectivamente). Ao ICMBIO pelas autorizações para as coletas nos arquipélagos (66478) concedida a MT e nas áreas litorâneas de Pernambuco (58697-1) ao Dr. Gabriel Lucas Bochini, a quem agradecemos pela coleta dos exemplares. À Karmine Pasinatto pelo auxílio nas coletas e triagem dos animais.

Referências

- Anker, A., Ahyong, S.T., Noel, P.Y. & Palmer, A.R. (2006) Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. *Evolution*, 60, 2507 – 2528.
- Anker, A., Pachelle, G., De Grave, S. & Hultgren, K.M. (2012) Taxonomic and biological notes on some Atlantic species of the snapping shrimp genus *Synalpheus* Spence Bate, 1888 (Decapoda, Alpheidae). *Zootaxa*, 3598, 1 - 96.
- Anker, A., Tavares, M. & Mendonça, J.B. (2016) Alpheid shrimps (Decapoda: Caridea) of the Trindade & Martin Vaz Archipelago, off Brazil, with new records, description of a new species of *Synalpheus* and remarks on zoogeographical patterns in the oceanic islands of the tropical southern Atlantic. *Zootaxa*, 4138 (1), 1 – 58.
- Araujo, G.S., Rocha, L.A., Lastrucci, N.S., Luiz, O.J., Di Dario, F., & Floeter, S.R. (2022) The Amazon-Orinoco Barrier as a driver of reef-fish speciation in the Western Atlantic through time. *Journal of Biogeography*, 49 (8), 1407 - 1419.

- Arnaud-Haond S., Vonau V., Rouxel C., Bonhomme F., Prou J., Goyard E. & Boudry P. (2008) Genetic structure at different spatial scales in the pearl oyster (*Pinctada margaritifera cumingii*) in French Polynesian lagoons: beware of sampling strategy and genetic patchiness. *Marine Biology*, 155, 147 – 157.
- Avisa J.C. (2000) Phylogeography: the History and Formation of Species. *Harvard University Press, Cambridge*: 1 – 279.
- Baeza, J. A., & Fuentes, M. S. (2013) Phylogeography of the shrimp *Palaemon floridanus* (Crustacea: Caridea: Palaemonidae): A partial test of meta-population genetic structure in the wider Caribbean. *Marine Ecology*, 34 (4), 381 - 393.
- Bandelt, H.J., Forster, P. & Röhl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. *Mol Biol Evol*, 16, 37 - 48
- Baums, I.B., Miller, M.W. & Hellberg M.E. (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology*, 14, 1377–1390.
- Bezerra, L.E.A. & Coelho, A. (2006) Crustáceos associados a esponjas no litoral do Estado do Ceará, Brazil. *Revista Brasileira de Zoologia*, 23 (3), 699 - 702.
- Bruce, A.J. (1976) Coral Reef Caridea and “Commensalism”. *Micronesica*, 12 (1), 83 - 98.
- Buranelli, R.C. & Mantelatto, F.L. (2019) Comparative genetic differentiation study of three coexisting mangrove crabs in western Atlantic. *Journal of Natural History*, 53, 2883–2903.
- Coelho, P.A. & Ramos, M.A. (1972). A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes de 5°N e 39°S. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco*, 13, 133–236.
<https://doi.org/10.5914/tropocean.v13i1.2555>
- Coutière, H. (1909) The American species of snapping shrimps of the genus *Synalpheus*. *Proceedings of the United States National Museum*, 36, 1–93.
- Cowen R.K., Kamazima M.M.L., Sponaugle S., Paris C.B. & Olson D.B. (2000) Connectivity of marine populations: open or closed? *Science*, 287, 857–859.

Chace Jr., F.A. (1972) The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). *Smithsonian Contributions to Zoology*, 98, 1 - 179.

Cházaro-Olvera, S., Hernández-Vidal, G.A., Ortiz, M. & Winfield, I. (2017) Primer registro de la asociación de *Synalpheus herricki* y *S. pandionis* con *Aiolochroia crassa* en el parque nacional arrecife Puerto Morelos, Quintana Roo, México. *Revista de Biología Marina y Oceanografía*, 52 (3), 617 - 620.

Christoffersen, M.L. (1979) Decapod Crustacea: Alpheoidea. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962). I. 36, *Annales de l'Institut Océanographique, Monaco*, (Suppl.), 55, 297 - 377.

Christoffersen, M.L. (1998) Malacostraca. Eucarida. Caridea. Crangonoidea and Alpheoidea (Except Glyphocrangonidae and Crangonidae). In: Young, S. (Ed.), *Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro*, 351 - 372.

Coelho-Filho, P.A. (2006) Checklist of the decapods (Crustacea) from the outer continental shelf and seamounts from Northeast of Brazil—REVIZEE Program (NE III). *Zootaxa*, 1184, 1–27.

Coutière, H. (1909) The American species of snapping shrimps of the genus *Synalpheus*. *Proceedings of the United States National Museum*, 36, 1 - 93.

Cowen R.K., Paris C.B., Srinivasan A. (2006) Scaling of connectivity in marine populations. *Science*, 311, 522–527.

Curtin, T.B. (1986) Physical observations in the plume region of the Amazon River during peak discharge—II. Water masses. *Cont. Shelf. Res.*, 6, 53 – 71.

De Grave, S., Decock, W., Dekeyser, S., Davie, P.J., Franssen, C.H., Boyko, C.B., Poore, G.C.B., Macpherson, E., Ahyong, S.T., Crandall, K.A., Mazancourt, V., Osawa, M., Chan, T.Y., Ng, P.K.L., Lemaitre, R., van der Merj, S.E.T. & Santos, S. (2023). Benchmarking global biodiversity of decapod crustaceans (Crustacea: Decapoda). *Journal of Crustacean Biology*, 43 (3), ruad042.

Dobkin, S. (1965) The first post-embryonic stage of *Synalpheus brooksi* Coutière. *Bulletin of Marine Science*, 15, 450 - 462.

- Duffy, J. (1992) Host use patterns and demography in a guild of tropical spongedwelling shrimps. *Mar. Ecol. Prog. Ser.* 90, 127 – 138.
- Duffy, J. (1996) Species boundaries, specialization, and the radiation of spongedwelling alpheid shrimp. *Biol. J. Linn. Soc.* 58, 307 – 324.
- Duffy, J.E. & Macdonald, K.S. (1999) Colony structure of the social snapping shrimp *Synalpheus filidigitus* in Belize. *Journal of Crustacean Biology*, 19 (2), 283 - 292.
- Duffy, J.E. (2003) The ecology and evolution of eusociality in sponge-dwelling shrimp. In: Genes, Behavior and Evolution in Social Insects. *University of Hokkaido Press, Sapporo*, pp. 1–38.
- Duffy, J.E. & Macdonald, K.S. (2010) Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proc. R. Soc. Lond. B Biol. Sci.*, 277, 1 – 13.
- Excoffier, L. & Lischer, H.E. L. (2010) Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, 10, 564 - 567.
- Excoffier, L., Smouse, P. E., & Quattro, J. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, 131 (2), 479 - 491.
- Felder, D.L. & Chaney, A.H. (1979) Decapod crustacean fauna of Seven and One-Half Fathom Reef, Texas: species composition, abundance, and species diversity. *Contrib. Mar. Sci.*, 22, 1 – 29.
- Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser.*, 41, 95 - 98.
- Hauser, L. & Carvalho, G.R. (2008) Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. *Fish and Fisheries*, 9, 333 – 362.
- Hellberg, M.E. (1994) Relationships between inferred levels of gene flow and geographic distance in a philopatric coral, *Balanophyllia elegans*. *Evolution*, 48(6), 1829-1854.
- Herrick, F.H. (1891) *Alpheus*: a study in the development of Crustacea. In: Brooks, W.K. & F.H. Herrick, The embryology and metamorphosis of the Macroura: *Memoirs of the National Academy of Sciences*, Washington, 5, 370 - 463.

- Hechtel, G.J. (1983) New species of marine Demospongiae from Brazil. *Iheringia (Zoologia)*, 63, 58–89.
- Hollatz, C., Vilaca, S.T., Redondo, R.A., Marmontel, M., Baker, C.S. & Santos, F.R. (2011) The Amazon River system as an ecological barrier driving genetic differentiation of the pink dolphin (*Inia geoffrensis*). *Biological Journal of the Linnean Society*, 102 (4), 812 - 827.
- Hultgren, K.M. & Duffy, J.E. (2011) Multi-locus phylogeny of sponge-dwelling snapping shrimp (Caridea: Alpheidae: *Synalpheus*) supports morphology-based species concepts. *Journal of Crustacean Biology*, 31, 352 - 360.
- Hultgren, K.M. & Duffy, J.E. (2012) Phylogenetic community ecology and the role of social dominance in sponge-dwelling shrimp. *Ecol. Lett.*, 15, 704 – 713.
- Hultgren, K.M., Macdonald, K.S.III. & Duffy, J.E. (2010) Sponge-dwelling snapping shrimps of Curaçao, with descriptions of three new species. In: De Grave, S. & C.H.J.M. Fransen (eds.), Contributions to shrimp taxonomy. *Zootaxa*, 2372, 221 - 262.
- Hultgren, K.M., Macdonald, K.S.III. & Duffy, J.E. (2011) Sponge-dwelling snapping shrimps (Alpheidae: *Synalpheus*) of Barbados, West Indies, with a description of a new eusocial species. *Zootaxa*, 2834, 1 - 16.
- Hultgren, K.M., Hurt, C., & Anker, A. (2014) Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). *Molecular Phylogenetics and Evolution*, 77, 116 - 125.
- Hultgren, K., Duffy, J.E. & Rubenstein, D.R. (2017) Sociality in shrimps. *Comparative social evolution*, 224 - 250.
- Isaac, V.J. & Ferrari, S.F. (2017) Assessment and management of the North Brazil Shelf Large Marine Ecosystem. *Environmental Development*, 22, 97 – 110.
- Lessios, H.A., Kane, J., & Robertson, D.R. (2003) Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. *Evolution*, 57 (9), 2026-2036.
- Kimura, M. & Weiss, G.H. (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics*, 49, 561 - 576.

- Mantelatto, F.L., Carvalho, F.L., Simões, S.M., Negri, M., Souza-Carvalho, E.A. & Terossi, M. (2016) New primers for amplification of cytochrome c oxidase subunit I barcode region designed for species of Decapoda (Crustacea). *Nauplius*, 24, 1 – 4.
- Mazzei, R., & Rubenstein, D. R. (2021). Larval ecology, dispersal, and the evolution of sociality in the sea. *Ethology*, 127 (10), 808 - 820.
- Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva Jr., J.M., Araujo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C.V., Bahia, R.G., Paranhos, R.P., Dias, R.J.S., Siegle, E., Figueiredo Jr., A.G., Pereira, R.C., Leal, C.V., Hajdu, E., Asp, N.E., Gregoracci, G.B., Neumann-Leitão, S., Yager, P.L., Francini-Filho, R.B., Fróes, A., Campeão, M., Silva, B.S., Moreira, A.P.B., Oliveira, L., Soares, A.C., Araujo, L., Oliveira, N.L., Teixeira, J.B., Valle, R.A.B., Thompson, C.C., Rezende, C.E. & Thompson, F. L. (2016). An extensive reef system at the Amazon River mouth. *Science advances*, 2 (4), e1501252.
- Palumbi, S.R. (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological applications*, 13, 146-158.
- Peres, P.A. & Mantelatto, F.L. (2023) Demographic changes and life-history strategies predict the genetic diversity in crabs. *Journal of Evolutionary Biology*, 36 (2), 432–443.
- Peres, P. A., Bracken-Grissom, H., Timm, L. E., & Mantelatto, F. L. (2022). Genomic analyses implicate the Amazon–Orinoco Plume as the driver of cryptic speciation in a swimming crab. *Genes*, 13 12, 2263.
- Planes S. & Fauvelot C. (2002) Isolation by distance and vicariance drive genetic structure of a coral reef fish in the Pacific Ocean. *Evolution*, 56, 378 – 399.
- Rafinesque, C.S. (1815) Analyse de la Nature ou Tableau de l’Univers et des corps organisés. *Palerme*, 1 - 224.
- Riginos C. & Nachman M.W. (2001) Population subdivision in marine environments: the contributions of isolation by distance, discontinuous habitat, and biogeography to genetic differentiation in a blennioid fish, *Axoclinus nigricaudus*. *Molecular Ecology*, 10, 1439 – 1453.
- Ríos, R. & Duffy, J.E. (2007) A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of *Zuzalpheus*, new genus, and six new species. *Zootaxa*, 1602, 1 - 89.

- Robertson, D.R., Karg, F., Moura, R.L., Victor, B.C. & Bernardi, G. (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Molecular Phylogenetics and Evolution*, 40 (3), 795 – 807.
- Rocha, L.A. (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography*, 30 (8), 1161 – 1171.
- Rodríguez, P., Lira, C., Muñoz, N., & Morales, D. (2020) Crustáceos decápodos de la playa El Amparo, isla de Coche, Venezuela. I. Suborden Dendrobranchiata e Infraordenes Stenopodidea y Caridea. *Acta Biológica Venezuelica*, 40 (2), 171 - 209.
- Rolan-Alvarez E., Zapata C. & Alvarez G. (1995) Distinct genetic subdivision in sympatric and sibling species of the genus *Littorina* (Gastropoda: Littorinidae). *Heredity*, 74, 1 – 9.
- Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J.C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S.E. & Sánchez-Gracia, A. (2017) DnaSP 6: DNA Sequence Polymorphism Analysis of Large Datasets. *Mol. Biol. Evol.* 34, 3299 - 3302.
- Rützler, K. (1976). Ecology of Tunisian commercial sponges. *Tethys*, 7, 249 – 264.
- Santos, S., Soledade, G.O. & Almeida, A.O. (2012) Decapod crustaceans on dead coral from reef areas on the coast of Bahia, Brazil. *Nauplius*, 20 (2), 145 - 169.
- Santos, P.S., Terossi, M., Mantelatto, F.L., & Almeida, A.O. (2019) Using integrative taxonomy to establish the status of *Alpheus peasei* (Armstrong, 1940)(Decapoda: Alpheidae) as a single species throughout its distribution. *Zootaxa*, 4629 (1), 51 - 68.
- Santos, P.S., Terossi, M., Mantelatto, F.L., Torres, R.A., & Almeida, A.O. (2024). Morphology and molecular evidence reveal hidden diversity among snapping shrimp of the *Alpheus obesomanus* group (Decapoda: Alpheidae) with the description of a new species from Brazil. *Zootaxa*, 5474(3), 225-242.
- Shanks, A.L., Grantham, B.A., Carr, M.H. (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological applications*, 13, 159-169.
- Soledade, G.O., Fonseca, M.S. & Almeida, A.O. (2015) Shallow-water stenopodidean and caridean shrimps from Abrolhos Archipelago, Brazil: new records and updated checklist. *Zootaxa*, 3905 (1), 52 - 68.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson J. (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *Bioscience*, 57, 573 – 583.

Spence Bate, C. (1888) Report on the Crustacea Macrura collected by the Challenger during the years 1873-76. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873-76. *Zoology*, 24 (52), i-xc, 1-942, pl. 1-150.

Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: molecular evolutionary genetics analysis version 11. *Molecular biology and evolution*, 38 (7), 3022 - 3027.

Taylor, M.S. & Hellberg, M.E. (2003) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science*, 299, 107 – 109.

Teske, P.R., Papadopoulos, I., Zardi, G.I., McQuaid, C.D., Griffiths, C.L., Edkins, M.T. & Barker N.P. (2007) Implications of life history for genetic structure and migration rates of five southern African coastal invertebrates: planktonic, abbreviated and direct development. *Marine Biology*, 152, 697 – 711.

Terossi, M., & Mantelatto, F. L. (2012). Morphological and genetic variability in *Hippolyte obliquimanus* Dana, 1852 (Decapoda, Caridea, Hippolytidae) from Brazil and the Caribbean Sea. *Crustaceana*, 685 - 712.

Vandenspiegel, D., Eeckhaut, I. & Jangoux, M. (1998) Host selection by *Synalpheus stimpsoni* (De Man), an ectosymbiotic shrimp of comatulid crinoids, inferred by a field survey and laboratory experiments. *Journal of Experimental Marine Biology and Ecology*, 225 (2), 185 - 196.

Varona, H.L., Veleza, D., Silva, M., Cintra, M. & Araujo, M. (2019) Amazon River plume influence on Western Tropical Atlantic dynamic variability. *Dynamics of Atmospheres and Oceans*, 85, 1 – 15.

Vergamini, F.G., Pileggi L.G. & F. L. Mantelatto, 2011. Genetic variability of the Amazon River prawn *Macrobrachium amazonicum* (Decapoda, Caridea, Palaemonidae). *Contributions to Zoology, Amsterdam*, 80 (1), 67 - 83.

- Verrill, A.E. (1922) Decapod Crustacea of Bermuda. Part II. Macrura. *Transactions of the Connecticut Academy of Arts and Sciences*, 26, 1–179.
- Villamor, A., Costantini, F. & Abbiati, M. (2014) Genetic structuring across marine biogeographic boundaries in rocky shore invertebrates. *PLoS ONE*, 9, e101135.
- Weersing, K. & Toonen, R.J. (2009) Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series*, 393, 1 – 12.
- White, C., Selkoe, K.A., Watson, J., Siegel, D.A., Zacher, D.C. & Toonen R.J. (2010) Ocean currents help explain population genetic structure. *Proceedings of the Royal Society of London Series B*, 277, 1685 – 1694.
- WoRMS (2023). *Synalpheus* Spence Bate, 1888. Disponível em: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106982>. Acesso em: 19 de julho de 2023.

CONSIDERAÇÕES FINAIS

Por se tratar de um gênero que reúne diversos complexos de espécies crípticas, como *S. apioceros*, *S. brevicarpus*, *S. brooksi* e *S. paraneptunus*, é de se esperar que *Synalpheus* abrigue uma diversidade ainda não formalmente reconhecida. A presente tese revisa de forma abrangente a diversidade e a taxonomia dos camarões-de-estalo desse grupo no litoral do Nordeste do Brasil, a partir de uma abordagem integrativa. Com as descobertas obtidas, foi possível ampliar o conhecimento sobre a fauna local por meio do registro de seis novas ocorrências, extensões de distribuição de 19 espécies, exclusão dos registros de *S. filidigitus*, *S. longicarpus*, *S. paraneptunus*, e *S. rathbunae*, considerados duvidosos, e também da descrição de duas novas espécies de *Synalpheus*. Esses achados reforçam o potencial ainda pouco explorado de regiões costeiras e de áreas protegidas ao longo do Nordeste brasileiro, especialmente no que tange ao estudo de grupos taxonomicamente problemáticos. Além disso, quando analisada a estruturação genética de *S. hoetjesi*, foi revelada uma diferenciação entre as populações do Mar do Caribe e do Brasil, possivelmente ocasionada por barreiras oceanográficas, como a pluma dos rios Amazonas e Orinoco, que atuam como limitantes ao fluxo gênico, ou até mesmo pela ausência de substratos adequados para o assentamento larval desses camarões, uma vez que ele é encontrado, geralmente, em associação com esponjas. Tais resultados demonstram como fatores ecológicos e físicos desempenham um papel crucial na conectividade entre populações marinhas. Com isso, evidencia-se a necessidade de aprofundamento nos estudos sobre o desenvolvimento larval e comportamento reprodutivo em *Synalpheus* para auxiliar no entendimento das problemáticas presentes no grupo, solucionando conflitos taxonômicos e preenchendo lacunas de conhecimento presentes no grupo. Os resultados aqui apresentados reiteram a importância de estudos taxonômicos voltados ao gênero *Synalpheus*, contribuindo de forma significativa para a ampliação do conhecimento sobre a biodiversidade de crustáceos no Brasil.

REFERÊNCIAS

- ALMEIDA, A.O.; SANTOS, P.S.; SOLEDADE, G.O.; SANTOS, J.P.; PÉREZ, C.D. New invertebrate host records (Porifera and Cnidaria) for some caridean shrimps in estuaries of north-eastern Brazil. **Marine Biodiversity Records**, v. 8, p. 1 - 6, 2015.
- ANGER, K. **The biology of decapod crustacean larvae**. Lisse: AA Balkema Publishers, 2001.
- ANKER, A. & DE GRAVE, S. *Zuzalpheus*: a junior synonym of *Synalpheus* (Decapoda: Alpheidae). **Journal of Crustacean Biology**, v. 28, n. 4, p. 735 - 740, 2008.
- ANKER, A. & PACHELLE, P.P. Taxonomic notes on some Brazilian species of *Synalpheus* Spence Bate, 1888, with new records and description of a new species (Decapoda, Alpheidae). **Zootaxa**, v. 3815, n. 2, p. 215 - 232, 2014.
- ANKER, A.; PACHELLE, P.P.G.; DE GRAVE, S.; HULTGREN, K.M. Taxonomic and biological notes on some Atlantic species of the snapping shrimp genus *Synalpheus* Spence Bate, 1888 (Decapoda, Alpheidae). **Zootaxa**, v. 3598, p. 1 - 96, 2012.
- BANNER, D.M. & BANNER, A.H. The alpheid shrimp of Australia. Part 2: the genus *Synalpheus*. **Rec. Aust. Mus.**, v. 29, p. 267 - 389, 1975.
- BANNER, D.M. & BANNER, A.H. Annotated checklist of the alpheid shrimp of the Red Sea and Gulf of Aden. **Zoologische Verhandelingen**, v. 190, p. 1 - 99, 1981.
- BANNER, D.M. & BANNER, A.H. An annotated checklist of the alpheid shrimp from the Western Indian Ocean. **Travaux et Documents de l'ORSTOM**, v. 158, p 2 - 164, 1983.
- BAUER, R.T. Remarkable shrimps: adaptations and natural history of the carideans. **University of Oklahoma Press, Norman**, 282 pp, 2004.
- BARBER, P.H.; PALUMBI, S.R.; ERDMANN, M.V.; MOOSA, M.K. A marine Wallace's line?. **Nature**, v. 406, n. 6797, p. 692-693, 2000.
- BOURKE, A. Colony size, social complexity and reproductive conflict in social insects. **Journal of Evolutionary Biology**, v. 12, p. 245 - 257, 1999.
- BOWEN, B.W.; BASS, A.L.; MUSS, A.; CARLIN, J.; ROBERTSON, D.R. Phylogeography of two Atlantic squirrelfishes (Family Holocentridae): exploring links between pelagic larval duration and population connectivity. **Marine Biology**, v. 149, n. 4, p. 899-913, 2006.
- BRUCE, A.J. Coral Reef Caridea and "Commensalism". **Micronesica**, v. 12, n. 1, p. 83 - 98, 1976.
- BRUSCA, R.C.; MOORE, W.; SHUSTER, S.M. Invertebrados. 3ª Edição. Brasil: Guanabara koogan, 1032p, 2018.

BURTON, R.S. Protein polymorphisms and genetic differentiation of marine invertebrate populations. **Mar. Biol. Lett**, v. 4, p. 193-206, 1983.

BURTON, R.S.; FELDMAN, M.W. Population genetics of coastal and estuarine invertebrates: does larval behavior influence population structure?. In: **Estuarine comparisons**. Academic Press, 1982. p. 537-551.

CHACE JR., F.A. The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). **Smithsonian Contributions to Zoology**, v. 98, p. 1 - 179, 1972.

CHACE JR., F.A. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907-1910, part 5: family Alpheidae. **Smithsonian Contributions to Zoology**, v. 466, p. 1 - 99, 1988.

COUTIÈRE, H. Sur les *Synalphees américaines*. **Comptes rendus hebdomadaires des séances de l'Académie des sciences**, v. 146, p. 710 - 712, 1908.

COUTIÈRE, H. The American species of snapping shrimps of the genus *Synalpheus*. **Proceedings of the United States National Museum**, v. 36, p. 1 - 93, 1909.

COWEN, R.K.; PARIS, C.B.; SRINIVASAN, A. Scaling of connectivity in marine populations. **Science**, v. 311, n. 5760, p. 522-527, 2006.

DE GRAVE, S. & ANKER, A. An annotated checklist of marine caridean and stenopodidean shrimps (Malacostraca: Decapoda) of the Caribbean coast of Panama. **Nauplius**, v. 25, p. 1 - 40, 2017.

DE GRAVE, S.; DECOCK, W.; DEKEYZER, S.; DAVIE, P.J.F.; FRANSEN, C.H.J.M.; BOY KO, C.B.; POORE, G.C.B.; MACPHERSON, E.; AHYONG, S.T.; CRANDALL, K.A.; DE M AZANCOURT, V.; OSAWA, M.; CHAN, T.Y.; Ng, P.K.L.; LEMAITRE, R.; VAN DER MEI J, S.E.T.; & SANTOS, S. Benchmarking global biodiversity of decapod crustaceans (Crustacea: Decapoda). **Journal of Crustacean Biology**, v. 43, n. 3, p. 1-9, 2023.

DIDDEREN, K.; FRANSEN, C.; DEVOOGD, N. Observations on sponge-dwelling colonies of *Synalpheus* (Decapoda, Alpheidae) of Sulawesi, Indonesia. **Crustaceana**, v. 79, p. 961 - 975, 2006.

DOBKIN, S. The first post-embryonic stage of *Synalpheus brooksi* Coutière. **Bulletin of Marine Science**, v. 15, p. 450 - 462, 1965.

DUFFY, J.E. *Synalpheus regalis*, new species, a sponge-dwelling shrimp from the Belize Barrier Reef, with comments on host specificity in *Synalpheus*. **Journal of Crustacean Biology**, v. 16, p. 564 - 573, 1996a.

DUFFY, J. E. Eusociality in a coral-reef shrimp. **Nature**, v. 381, p. 512 - 514, 1996b.

DUFFY, J.E. Eusociality in sponge-dwelling shrimp. In: T. KIKUCHI, **Genes, behaviour, and evolution in social insects**, p. 1 - 38, 2002.

DUFFY, J.E. The ecology and evolution of eusociality in sponge-dwelling shrimp. In: **Genes, Behavior and Evolution in Social Insects**. University of Hokkaido Press, Sapporo, pp. 1–38, 2003.

DUFFY, J.E. Ecology and evolution of eusociality in sponge-dwelling shrimp. In: Duffy, J. E. & Thiel, M. (eds.) *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms*. **New York: Oxford University Press**, p. 387 - 409, 2007.

DUFFY, J.E. & MACDONALD, K.S. Kin structure, ecology and the evolution of social organization in shrimp: A comparative analysis. **Proceedings of the Royal Society of London B**, v. 277, p. 1 - 13, 2010.

FABRICIUS, J.C. *Entomologia Systematica emendata et aucta, secundum classes, ordines, genera, species adjectis synonymis locis observationibus descriptionibus. Hafniae. I-IV. Supplementum Entomologiae Systematicae Copenhagen*, p. 1 - 572, 1798.

GIBSON, R.N. Go with the flow: tidal migration in marine animals. **Hydrobiologia**, v. 503, n. 1, p. 153-161, 2003.

HAMASAKI, K. Iizuka, C.; Ojima, A.; Sugizaki, M.; Sugimoto, A.; Shigeki, D.; Kitada, S. Genetic diversity and demographic history of the terrestrial hermit crabs *Birgus latro* and *Coenobita brevimanus* in the North-Western Pacific Region. **Journal of Crustacean Biology**, v. 35, n. 6, p. 793-803, 2015.

HELLBERG, M.E. Relationships between inferred levels of gene flow and geographic distance in a philopatric coral, *Balanophyllia elegans*. **Evolution**, v. 48, n. 6, p. 1829-1854, 1994.

HELLBERG, M.E.; BURTON, R.S.; NEIGEL, J.E. & S.R. PALUMBI. Genetic assessment of connectivity among marine populations. **Bulletin of Marine Science**, v. 70, n. 1, p. 273-290, 2002.

HERRICK, F.H. *Alpheus*: a study in the development of Crustacea. In: Brooks, W.K. & F.H. Herrick, The embryology and metamorphosis of the Macroura: **Memoirs of the National Academy of Sciences**, Washington, v. 5, p. 370 - 463, 1891.

HULTGREN, K.M. & DUFFY, J.E. Sponge host characteristics shape the community structure of their shrimp associates. **Marine Ecology Progress Series**, v. 407, p. 1 - 12, 2010.

HULTGREN, K.M.; MACDONALD, K.S.; DUFFY, J.E. Sponge-dwelling snapping shrimps of Curaçao, with descriptions of three new species. In: De Grave, S. & C.H.J.M. Fransen (eds.), *Contributions to shrimp taxonomy*. **Zootaxa**, v. 2372, p. 221 - 262, 2010.

HULTGREN, K.M.; MACDONALD, K.S.; DUFFY, J.E. Sponge-dwelling snapping shrimps (Alpheidae: *Synalpheus*) of Barbados, West Indies, with a description of a new eusocial species. **Zootaxa**, v. 2834, p. 1 - 16, 2011.

HULTGREN, K. M.; HURT, C.; ANKER, A. Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). **Molecular Phylogenetics and Evolution**, v. 77, p. 116 – 125, 2014.

HULTGREN, K.; DUFFY, J.E.; RUBENSTEIN, D. R. Sociality in shrimps. **Comparative social evolution**, p. 224 - 250, 2017.

ITUARTE, R.B.; D'ANATRO, A.; LUPPI, T.A.; RIBEIRO, P.D.; SPIVAK, E.D.; IRIBARNE, O.O.; LESSA, E.P. Population structure of the SW Atlantic estuarine crab *Neohelice granulata* throughout its range: a genetic and morphometric study. **Estuarine and Coasts**, v. 35, p. 1249-1260, 2012.

KELLY, R.P.; PALUMBI, S.R. Genetic structure among 50 species of the northeastern Pacific rocky intertidal community. **PloS one**, v. 5, n. 1, p. e8594, 2010.

KNOWLTON, N. Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp, **Evolution**, v. 34, p. 161 - 173, 1980.

LANDEIRA, J.M.; LOZANO-SOLDEVILLA, F.; HERNÁNDEZ-LEÓN, S.; BARTON, E.D. Spatial variability of planktonic invertebrate larvae in the Canary Islands area. **Journal of the marine biological association of the United Kingdom**, v. 90, n. 6, p. 1217-1225, 2010.

MACDONALD, K.S.; HULTGREN, K.; DUFFY, J.E. The sponge-dwelling snapping shrimps (Crustacea, Decapoda, Alpheidae, *Synalpheus*) of Discovery Bay, Jamaica, with descriptions of four new species. **Zootaxa**, v. 2199, p. 1 - 57, 2009.

Mantelatto, F.L.; FRANÇA, N.F.; CUNHA, A.M.; ALMEIDA, A.O. Molecular data highlight cryptic diversity and reveal a new species in the *Synalpheus brevicarpus* (Herrick 1891) complex (Decapoda: Caridea: Alpheidae) in the Western Atlantic. **Journal of Crustacean Biology**, v. 43, 2023.

MATHEWS, L. Tests of the mate-guarding hypothesis for social monogamy: Does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)? **Behavioral Ecology and Sociobiology**, v. 51, p. 426 - 432, 2002.

MACDONALD, K.S. & DUFFY, J.E. Two new species of sponge-dwelling snapping shrimp from the Belizean Barrier Reef, with a synopsis of the *Synalpheus brooksi* species complex. **American Museum Novitates**, v. 3543, 1 - 22, 2006.

MORRISON, C.L.; RÍOS, R.; DUFFY, J.E. Phylogenetic evidence for an ancient rapid radiation of Caribbean sponge-dwelling snapping shrimps (*Synalpheus*). **Molecular Phylogenetics and Evolution**, v. 30, p. 563 - 581, 2004.

PALUMBI, S.R. Marine speciation on a small planet. **Tree**, v. 7, n. 4, p. 114-118, 1992.

PALUMBI, S.R. Population genetics, demographic connectivity, and the design of marine reserves. **Ecological applications**, v. 13, n. sp1, p. 146-158, 2003.

- RAFINESQUE, C.S. Analyse de la Nature ou Tableau de l'Univers et des corps organisés. **Palerme**, p. 1 - 224, 1815.
- REED, J.K.; GORE, R.H.; SCOTTO, L.E.; WILSON, K.A. Studies on decapod Crustacea from the Indian River region of Florida, XXIV. Community composition, structure, areal and trophic relationships of decapods associated with shallow-and deep-water *Oculina varicosa* coral reefs. **Bulletin of Marine Science**, v. 32, p. 761 - 786, 1982.
- RÍOS, R. & DUFFY, J.E. A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of *Zuzalpheus*, new genus, and six new species. **Zootaxa**, v. 1602, p. 1 - 89, 2007.
- RUBENSTEIN, D.R. Sexual and social competition: Broadening perspectives by defining female roles. **Philosophical Transactions of the Royal Society B-Biological Sciences**, v. 367, p. 2248 - 2252, 2012.
- RUBENSTEIN, D.R.; MCCLEERY, B.; DUFFY, J. E. Microsatellite development suggests evidence of polyploidy in the social sponge-dwelling snapping shrimp *Zuzalpheus brooksi*. **Molecular Ecology Resources**, v. 8, p. 890 - 894, 2008.
- SANTANA, C.S; Schwamborn, R.; NEUMANN-LEITÃO, S.; MONTES, M. D. J. F.; LIRA, S.M.D.A. Spatio-temporal variation of planktonic decapods along the leeward coast of the Fernando de Noronha archipelago, Brazil. **Brazilian Journal of Oceanography**, v. 66, p. 1-14, 2018.
- SANTOS, P.S.; TEROSSI, M.; MANTELATTO, F.L.; TORRES, R.A.; ALMEIDA, A.O. Morphology and molecular evidence reveal hidden diversity among snapping shrimp of the *Alpheus obesomanus* group (Decapoda: Alpheidae) with the description of a new species from Brazil. **Zootaxa**, v. 5474, n. 3, p. 225–242, 2024.
- SAY, T. An account of the Crustacea of the United States, part 5. **Journal of the Academy of Natural Sciences at Philadelphia**, v. 1, p. 235 - 253, 1818.
- SCHELTEMA, R.S. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. **Biological Bulletin**, v. 140, n. 2, p. 284-322, 1971.
- SHANKS, A.L.; GRANTHAM, B.A.; CARR, M.H. Propagule dispersal distance and the size and spacing of marine reserves. **Ecological applications**, v. 13, n. sp1, p. 159-169, 2003.
- SHERMAN, P.W.; LACEY, E.A.; REEVE, H.K.; KELLER, L. The eusociality continuum. **Behavioral Ecology**, v. 6, p. 102 - 108, 1995.
- SNELGROVE, P.V.R. & LEWIS, J.B. Response of a coral-associated crustacean community to eutrophication. **Mar. Biol.**, v. 101, p. 249 - 257, 1989.

SPENCE BATE, C. Report on the Crustacea Macrura collected by the Challenger during the years 1873-76. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873-76. **Zoology**, v. 24, n. 52, i-xc, 1-942, pl. 1-150, 1888.

STRATHMANN, R.R.; HUGHES, T.P.; KURIS, A.M.; LINDEMAN, K.C.; MORGAN, S.G.; PANDOLFI, J.M.; WARNER, R.R. Evolution of local recruitment and its consequences for marine populations. **Bulletin of Marine Science**, v. 70, p. 377-396, 2002.

VEHRENCAMP, S. Optimal degree of skew in cooperative societies. **American Zoologist**, v. 23, p. 327 - 335, 1983.

WILSON, E. The Insect Societies. **Cambridge, MA**: Belknap Press of Harvard University, 548 pp, 1971.

WORMS. *Alpheus* Fabricius, 1798. Disponível em: <<https://www.marinespecies.org/aphia.php?p=taxdetails&id=106978>>. Acesso em: 16 de julho de 2025, 2025a.

WORMS. *Synalpheus* Spence Bate, 1888. Disponível em: <<https://www.marinespecies.org/aphia.php?p=taxdetails&id=106982>>. Acesso em: 16 de julho de 2025, 2025b.