Programa de Pós-Graduação em Biodiversidade e Evolução
Universidade Federal da Bahia

Delimitação morfológica e taxonomia do gênero *Parasmittina* Osburn, 1952 (Bryozoa: Cheilostomatida) no Atlântico Sul Ocidental

Jamile Farias Santos

Salvador
2021

Jamile Farias Santos

Delimitação morfológica e taxonomia do gênero *Parasmittina* Osburn, 1952 (Bryozoa: Cheilostomatida) no Atlântico Sul Ocidental

Dissertação apresentada ao Instituto de Biologia da Universidade Federal da Bahia para a obtenção do Título de Mestre pelo Programa de Pós-Graduação em Biodiversidade e Evolução.

Orientadora: Dra. Ana Carolina Sousa de Almeida

Coorientador: Dr. Leandro Manzoni Vieira

Salvador

2021

Santos, Jamile Farias.
Delimitação morfológica e taxonomia do gênero Parasmittina Osburn, 1952 (Bryozoa: Cheilostomatida) no Atlântico Sul Ocidental / Jamile Farias Santos. - 2021.
125 f.: il.

Orientadora: Profa. Dra. Ana Carolina Sousa de Almeida.
Coorientador: Prof. Dr. Leandro Manzoni Vieira.
Dissertação (mestrado) - Universidade Federal da Bahia, Instituto de Biologia, Salvador, 2021.

1. Biodiversidade marinha. 2. Bioinvasão. 3. Briozoário. 4. Parasmittina Osburn. I. Almeida, Ana Carolina Sousa de. II. Universidade Federal da Bahia. Instituto de Biologia. III. Título.

CDD - 593
CDU - 594.7

Programa de Pós-Graduação em
BIODIVERSIDADE E EVOLUÇÃO
UNIVERSIDADE FEDERAL DA BAHIA – INSTITUTO DE BIOLOGIA
Rua Barão de Geremoabo, s/n. Ondina – Salvador – Bahia – CEP. 40.170-000

ATA DA SESSÃO PÚBLICA DO COLEGIADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE E EVOLUÇÃO - INSTITUTO DE BIOLOGIA – UFBA

Título de Dissertação: **"Delimitação morfológica e taxonomia do gênero *Parasmittina* Osburn, 1952 (Bryozoa: Cheilostomatida) no Atlântico Sul Ocidental"**

Mestranda: **Jamile Farias Santos**
Orientadora: **Profa. Dra. Ana Carolina Sousa de Almeida**

De acordo com o regimento geral da UFBA e com o regimento interno deste programa de pós-graduação, foram iniciados os trabalhos da Comissão Examinadora, composta pela professora Dra. Ana Carolina Sousa de Almeida (Presidente), Dra. Gisele Yukimi Kawauchi e Dra. Fernanda Fernandes Cavalcanti às **9:00 h** do dia 25 de fevereiro de 2021. A mestranda fez a apresentação oral de sua dissertação durante 36 minutos. Após o encerramento das arguições, às **11:45** horas, a Comissão Examinadora pronunciou-se pela sua **Aprovação**, conforme parecer em anexo. Esta Ata será assinada pelos membros da Comissão Examinadora e deste Colegiado de curso, para compor o processo de emissão do diploma.

Salvador, 25 de fevereiro de 2021.

COMISSÃO EXAMINADORA

Ana Carolina Sousa de Almeida
Membro: Profa. Dra. Ana Carolina Sousa de Almeida
Universidade Federal da Bahia

Gisele Kawauchi
Membro: Profa. Dra. Gisele Yukimi Kawauchi
Universidade Federal de Minas Gerais

Fernanda F. Cavalcanti
Membro: Profa. Dra. Fernanda Fernandes Cavalcanti
Universidade Federal da Bahia

Agradecimentos

Agradeço primeiramente a Deus, por ter guiado meus caminhos e permitido que eu chegasse até aqui.

À Universidade Federal da Bahia (UFBA) e a todos os professores do Programa de Pós-Graduação em Biodiversidade e Evolução (PPGBioEvo), pelo conhecimento, apoio e pela estrutura para realização desse trabalho.

À Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB), pela concessão da bolsa e à Fundação Gonçalo Muniz (FIOCRUZ-BA), pelas sessões de microscopia eletrônica de varredura.

Ao Museu de História Natural da Bahia (MHNBA), pela disponibilização do acervo e estrutura para desenvolvimento dessa pesquisa e à coordenadora do MHNBA, Dra. Priscila Camelier (UFBA), por todo apoio. Aos técnicos do MHNBA por todo auxílio, amizade e companheirismo, especialmente à Laurinha, Alice, Mônica e Paulo.

À minha querida orientadora, Dra. Ana Carolina Sousa de Almeida, pela oportunidade que me deu desde a minha graduação, por ter confiado em mim desde sempre, por ter me ensinado com toda paciência e dedicação, mas também por todos os puxões de orelhas - eles foram necessários e só me incentivaram a crescer. Obrigada também por toda amizade e incentivo.

Ao meu co-orientador, Dr. Leandro Vieira (Universidade Federal de Pernambuco), pela orientação e confiança durante a realização desse trabalho.

À Dra. Facelúcia Souza, pela parceria, confiança, amizade e carinho que sempre teve por mim, durante todos os anos de convivência.

À minha mãe, por quem eu devo tudo nessa vida, obrigada por todo esforço que fez para que eu pudesse estudar e ter uma boa formação

profissional. Pelo amor incondicional, por ser o anjo sempre presente na minha vida e por ser a força que me incentiva a nunca desistir dos meus sonhos - você é e sempre sera a estrela da minha vida.

Ao meu pai, por todo apoio e incentivo para realização dos meus sonhos.

À toda minha família, em especial aos meus primos/irmãos, Geraldo, Alex e Caio, pelo amor, apoio e cumplicidade em todos os momentos.

Ao meu noivo Mauricio, por todo amor e apoio.

Aos meus amigos de trabalho, Paulinha, Alisson e Juliana, pela amizade, companheirismo e por todos os momentos de descontração.

Aos meus amigos de UFBA, Luana, Laiana, Andréia e Rodrigo, por terem sido meus melhores companheiros durante todos esses anos. Sem vocês, essa Universidade não seria a mesma.

Aos meus amigos de vida, Jacira, Elane e Vania, pela amizade, companherismo e por serem torcerem por mim.

Índice

Resumo 07

Abstract 08

Introdução geral 09

Bryozoa: caracterização geral e importância 09

Cheilostomatida: o gênero *Parasmittina* Osburn, 1952 13

Caracteres taxonômicos de *Parasmittina* Osburn, 1952 16

Objetivos 21

Objetivo geral 21

Objetivos específicos 21

Capítulo 1. Revealing the diversity of recent *Parasmittina* Osburn, 1952 (Bryozoa, Cheilostomatida) from the Southwestern Atlantic: species complexes, cryptogenic and exotic species 22

Title page 23

Abstract 24

Introduction 25

Material and methods 27

Results 28

Discussion 78

Acknowledgements 86

References 87

Considerações finais 113

Referências bibliográficas 114

Anexo 119

Resumo

Briozoários são invertebrados aquáticos, predominantemente marinhos, suspensívoros, sésseis e coloniais. Cheilostomatida Busk, 1852 constitui o grupo com maior sucesso evolutivo com mais da metade das 8.000 espécies conhecidas. Nesta, a família Smittinidae Levinsen, 1909 é considerada a mais diversa, com mais de 300 espécies amplamente relatadas em todos os mares e oceanos, colonizando substratos naturais e artificiais e com representantes relacionados com eventos de bioinvasão. Entre os gêneros de Smittinidae, *Parasmittina* Osburn, 1952 é o mais diverso, com 129 espécies descritas. No Atlântico, 30 espécies são conhecidas e 11 dessas ocorrem no Atlântico Sul Ocidental. A maioria das espécies nunca foi revisada com base em técnicas atuais para taxonomia de briozoários marinhos e muitos registros foram atribuídos a complexos de espécies. Assim, o objetivo desse trabalho foi caracterizar morfologicamente os briozoários de *Parasmittina* do Atlântico Sul Ocidental, incluindo áreas portuárias do Brasil, definir o *status* nativo/criptogênico/exótico de cada espécie; reavaliar os caracteres morfológicos tradicionais utilizados para taxonomia do gênero e, por fim, apresentar uma chave de identificação das espécies de *Parasmittina* do Atlântico. Onze espécies são descritas, incluindo uma da Argentina (*P. dubitata* Hayward, 1980), quatro previamente conhecidas para o Brasil (*P. abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018, *P. alba* Ramalho, Muricy & Taylor, 2011, *P. distincta* Ramalho, Taylor, Moraes, Moura, Amado–Filho & Bastos, 2018, *P. ligulata* (Ridley, 1881), *P. simpulata* Winston, Vieira & Woollacott, 2014), cinco originalmente descritas para o Indo-Pacífico (*P. bimucronata* (Hincks, 1884), *P. longirostrata* Liu in Liu, Yin & Ma, 2001, *P. pinctatae* Liu in Liu, Yin & Ma, 2001, *P. serrula* Soule & Soule, 1973 and *P. winstonae* Liu in Liu, Yin & Ma, 2001), e uma nova espécie. Ao menos três espécies foram atribuídas a complexos de espécies que ainda precisam ser estudados (*P. alba*, *P. distincta* and *P. simpulata*), duas são consideradas como exóticas (*P. longirostrata* and *P. serrula*) e três como criptogênicas (*P. bimucronata*, *P. pinctatae* and *P. winstonae*) para o Atlântico Sul Ocidental. Considerações taxonômicas e caracterizações de outras espécies de *Parasmittina* também são apresentadas.

Palavras-chave: Gymnolaemata; bioinvasão; complexo de espécies.

Abstract

Bryozoans are aquatic invertebrates, predominantly marine, filter-feeding, sessile and colonial. Cheilostomatida Busk, 1852 is the most successful evolutionary group with more than half of the 8,000 known species. In Cheilostomatida, the family Smittinidae Levinsen, 1909 is considered the most diverse, with more than 300 species widely reported in all seas and oceans, colonizing natural and artificial substrata and with taxa related to bioinvasion events. Among Smittinidae genera, *Parasmittina* Osburn, 1952 is the most diverse, with 129 described species. In the Atlantic, 30 species are known and 11 of these occur in the Southwestern Atlantic. Most species have never been revised based on current techniques for taxonomy of marine bryozoans and many records have been attributed to species complexes. Thus, the aims of this work were to morphologically characterize species of *Parasmittina* from the Southwestern Atlantic, including port areas of Brazil; determine the native / cryptogenic / exotic status of each species; reassess the traditional morphological characters used for taxonomy and, finally, present an identification key to the Atlantic species. Eleven species were recognized – one species from Argentina, four species previously described from Brazilian coast (*P. abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado–Filho & Bastos, 2018, *P. alba* Ramalho, Muricy & Taylor, 2011, *P. distincta* Ramalho, Taylor, Moraes, Moura, Amado–Filho & Bastos, 2018, *P. ligulata* (Ridley, 1881), *P. simpulata* Winston, Vieira & Woollacott), five species mainly known from the Indo–Pacific (*P. bimucronata* (Hincks, 1884), *P. longirostrata* Liu in Liu, Yin & Ma, 2001, *P. pinctatae* Liu in Liu, Yin & Ma, 2001, *P. serrula* Soule & Soule, 1973 and *P. winstonae* Liu in Liu, Yin & Ma, 2001) and a new species, *P. falciformis* n. sp. At least three species, *P. alba*, *P. distincta* and *P. simpulata*, are here recognized as part of species complexes that need further investigations. Among five Indo–Pacific species, two are assigned as exotic (*P. longirostrata* and *P. serrula*) in SW Atlantic, but other three are assigned as cryptogenic (*P. bimucronata*, *P. pinctatae* and *P. winstonae*). Taxonomic considerations and morphological characterization of other *Parasmittina* species are provided.

Keywords: Gymnolaemata; bioinvasion; species complex.

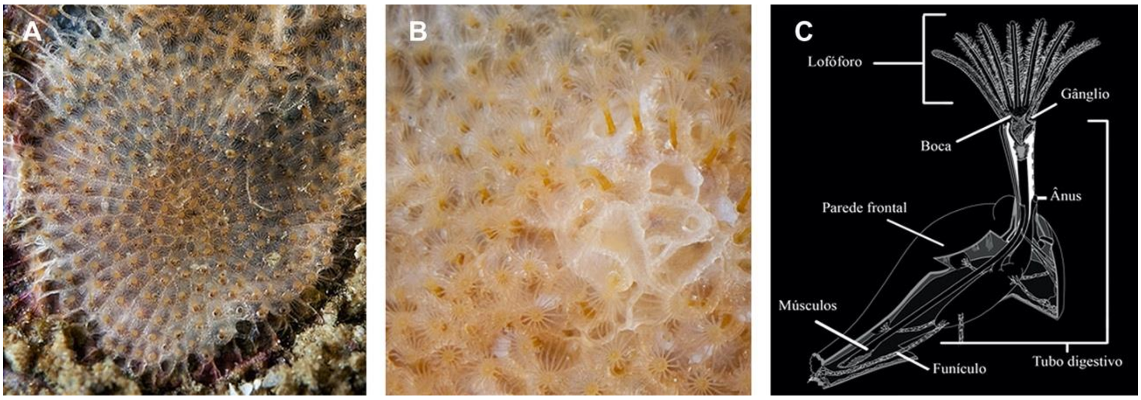
Introdução Geral

Bryozoa: caracterização geral e importância

O filo Bryozoa é composto por animais invertebrados aquáticos, predominantemente marinhos, suspensivos, sésseis, coloniais e lofoforados (COOK *et al*., 2018; MCKINNEY; JACKSON, 1989; VIEIRA *et al*., 2015). Cada colônia é formada por unidades funcionais geneticamente idênticas e chamadas de zooides, que possuem cerca de 0,5 mm de comprimento (COOK *et al*., 2018; VIEIRA *et al*., 2015). O zoóide típico com função alimentar é chamado de autozooide e representa a unidade colonial predominante. A nutrição da colônia se dá por meio do orgão retrátil (i.e., lofóforo), composto por uma coroa de tentáculos ciliados colocada em torno da boca e que auxilia na captura de partículas em suspensão presentes na água (HIROSE, 2017; MCKINNEY; JACKSON, 1989; VIEIRA *et al*., 2015).

Os autozooides dos briozoários são formados pelo polipídio (parte orgânica que compreende lofóforo, intestino em forma de U e demais órgãos e músculos) e pelo cistídio, que é a camada orgânica responsável pelo desenvolvimento do esqueleto externo que pode ser quitinoso ou calcário (GORDON, 2003; VIEIRA *et al*., 2015) (Figura 1).

Figura 1. Aspecto geral de briozoários marinhos. A, colônia incrustante em vida e B, detalhe dos autozooides mostrando lofóforos, imagens de Kåre Telnes (2020–2021) retiradas de http://www.seawater.no/fauna/bryozoa/; C, estrutura de um autozooide mostrando lofóforo, tubo digestivo, gânglio, boca, ânus, músculos, funículo (sistema interno de comunicação zooidal) e parede frontal, adaptada de Boardman *et al*., (1983).



Fonte: O autor (2021).

Apesar da grande diversidade de estratégias reprodutivas descritas para os briozoários (detalhadamente apresentada por OSTROSKY, 2013), normalmente, os zooides dos briozoários são hermafroditas, produzindo gametas masculinos e femininos. Os espermatozoides amadurecem antes dos óvulos e o crescimento colonial ocorre por brotamento (GORDON, 2003; MCKINNEY; JACKSON, 1989). Em alguns grupos, há polimorfismo e os heterozooides são os zooides encarregados de realizar outras funções que não alimentação dentro da colônia. Há diversos tipos de heterozooides, sendo os mais comuns os aviculários e vibraculários. Os aviculários atuam na defesa colonial, suporte, manutenção de corrente de água, locomoção e limpeza da colônia (CARTER, 2008, MCKINNEY; JACKSON, 1989; WINSTON, 1984). Os vibraculários, mais comuns em briozoários de vida livre e algumas formas eretas, auxiliam na locomoção entre os grãos de areia ou a limpeza da superfície da colônia. Em alguns grupos, zooides podem ser responsáveis pela incubação de embriões, sendo reconhecido como gonozooides, mas a grande maioria dos briozoários marinhos recentes apresentam estruturas denominadas ovicelos (MCKINNEY; JACKSON, 1989).

Atualmente, os briozoários são classificados em três classes: Phylactolaemata Allmann, 1856, Stenolaemata Borg, 1926 e Gymnolaemata Allmann, 1856. A classe Phylactolaemata possui representantes exclusivamente dulciaquícolas cujas colônias são monomórficas, ou seja, sem heterozoóides, e formadas por um esqueleto quitinoso flexível, com um lofóforo tipicamente em forma de ferradura. As classes Stenolaemata e Gymnolaemata compreendem grupos exclusivamente marinhos e principalmente marinhos, respectivemante, sendo a maioria formada por esqueleto calcário, um lofóforo circular e com uma ampla variedade de heterozooides, especialmente em Gymnolaemata. Dentre os Stenolaemata, a ordem Cyclostomata é a única com representantes viventes, caracterizados pelos zooides cilíndricos totalmente calcificados, sem opérculo terminal. Os Gymnolaemata por sua vez, estão divididos em duas ordens viventes: Ctenostomata, que são animais com zooides saculares formados por paredes zooidais gelatinosas ou membranosas e Cheilostomata, com zooides em forma de caixa e paredes zooidais total ou parcialmente calcificadas, com orifício cerrado por um opérculo distinto (HIROSE, 2017, MCKINNEY; JACKSON, 1989; MUKAI *et al.*, 1997; RYLAND, 2005).

O filo possui um extenso registro fóssil, facilitado pela presença de calcificação externa de muitas espécies, sendo encontrado desde o início do Ordoviciano (~ 488 e 443 milhões de anos atrás). Assim, os briozoários são potenciais bioindicadores e sua presença ou ausência no ambiente, sua diversidade, abundância e tipo de formas coloniais podem ser utilizados para interpretação ambiental em estudos paleoambientais e paleoevolutivos (AMINI *et al*., 2004; HIROSE, 2017; MCKINNEY; JACKSON, 1989; SMITH, 1995). Além disso, algumas espécies são sensíveis a variações de temperatura, salinidade e a poluentes, nesse sentido, são utilizadas em alguns estudos como bioindicadoras de impactos ambientais (BREVES–RAMOS *et al*., 2005; HEYSE, 2012; MAYER–PINTO; JUNQUEIRA, 2003).Distribuídos em todos os mares e oceanos, desde a zona entremarés até profundidades abissais, esses animais colonizam todo tipo de superfície disponível (HIROSE, 2017; MCKINNEY; JACKSON, 1989). São comuns sobre suportes naturais como conchas, rodolitos, corais, algas e esponjas e também em estruturas artificiais, como plataformas de petróleo, cascos de navios e píeres (ALMEIDA *et al*., 2015a; HIROSE, 2017). São importantes bioconstrutores ambientais e recifais que podem servir de abrigo para inúmeras espécies bentônicas e que comumente servem de alimento para moluscos, equinodermos e microcrustáceos (GORDON, 2003; RYLAND, 1970; WINSTON, 1986).

Os briozoários também podem estabelecer relações simbióticas com outros organismos, como moluscos, esponjas e crustáceos (e.g., caranguejo eremita). Na Nova Zelândia, já é conhecida a relação entre a espécie *Akatopora circumsaepta* (Uttley, 1951) com o caranguejo eremita. Neste caso, a concha do caranguejo serve como suporte para assentamento e desenvolvimento larval, podendo induzir a colônia a crescer além dos limites da concha, assim beneficiando o caranguejo pela expansão da sua moradia e servindo de suporte e fornecendo restos de comida que podem beneficiar o briozoário (GORDON, 2003). Outro caso muito comum de simbiose e de interesse medicinal ocorrem em algumas populações de briozoários do gênero *Bugula* Oken, 1815. Bactérias simbióticas vivem na cavidade corporal dos zooides produzindo o composto *briostatina*, que têm se mostrado promissor no tratamento de diversas doenças, incluindo cânceres (CIAVATTA *et al*. 2020; GORDON, 2003; SIMA; VETVICKA, 2011)

Os briozoários constituem um dos principais componentes da comunidade incrustante de suportes artificiais (i.e., *fouling*), devido a muitas espécies serem tolerantes a variações ambientais e terem rápido crescimento (ALMEIDA *et al*., 2015b; GORDON; MAWATARI, 1992). Assim, diversos grupos são capazes de se estabelecer em qualquer tipo de suporte, seja ele natural ou artificial (GORDON; MAWATARI, 1992; HIROSE, 2017; MIRANDA *et al*., 2018).

As incrustações de briozoários em suportes artificiais podem causar impactos econômicos nas indústrias marinhas com o entupimento das tubulações, maior consumo de combustível devido ao aumento do arrasto e resistência ao atrito durante o movimento do navio e necessidade de manutenção regular envolvendo limpeza e pintura dos navios com tinta anti-incrustantes (AFFANDY *et al*., 2019). E, mesmo as indústrias marítimas utilizando tintas anti-incrustantes, as larvas de algumas espécies de briozoários são tolerantes aos metais pesados contidos nos revestimentos dessas tintas. Desse modo, os briozoários constituem um dos organismos de incrustação marinha mais problemáticos do mundo (GORDON, 2003). A bioincrustação também pode causar impactos ecológicos como a introdução de espécies exóticas, interferindo diretamente na biodiversidade local (AFFANDY *et al*., 2019; PORTER *et al*., 2015). O termo bioinvasão marinha, refere-se justamente à introdução, estabelecimento e expansão de novas espécies de uma área biogeográfica para outra, através da atividade humana de forma intencional ou não (LOPES, 2009). Atualmente, diversas espécies exóticas, criptogênicas (cuja origem exótica ou nativa não pode ser comprovada) e complexos de espécies de briozoários são reconhecidas na comunidade do *fouling* (ALMEIDA *et al*., 2015b; GORDON; MAWATARI, 1992; IGNACIO *et al*., 2010; MARQUES *et al*., 2013; MIRANDA *et al*., 2018; ROCHA *et al*., 2013).

Diversidade do gênero *Parasmittina* Osburn, 1952

A ordem Cheilostomatida Busk, 1852 (Classe Gymnolaemata) inclui mais da metade das 8.000 espécies viventes de briozoários (MARTHA *et al*., 2020; GORDON, 1993; HIROSE, 2017). Representantes dessa ordem podem ser encontrados em todos os habitats marinhos, inclusive em ambientes com salinidade baixa ou variável (COOK *et al*., 2018). Trata-se do grupo mais diverso do filo, tanto em número de espécies, quanto em formas coloniais e suportes utilizados para assentamento larval, além de apresentar um alto grau de polimorfismo zooidal, assim, representando o clado com grande sucesso adaptativo (COOK *et al*., 2018; HAYWARD; PARKER, 1994; MCKINNEY; JACKSON, 1989; SEO, 2002).

Dentro de Cheilostomatida, a família Smittinidae Levinsen, 1909 representa um dos táxons mais diversos, compreendendo 21 gêneros (20 dos quais com representantes viventes; MARTHA *et al*., 2020) e cerca de 300 espécies descritas (BOCK; GORDON, 2021; LÓPEZ GAPPA, 2002). No registro fóssil, está datada desde o Eoceno (~ 54–34 milhões de anos atrás) (TAYLOR, 1993). Sua distribuição é ampla, ocorrendo praticamente em todos os oceanos e profundidades, sendo a quarta maior família em número de espécies relatadas para o Brasil (LÓPEZ GAPPA, 2002; VIEIRA *et al*., 2008, 2021). Briozoários de Smittinidae são comuns em substratos naturais como recifes de corais, conchas e rodolitos e também ocorrem em substratos artificiais, como pilares de marinas e píeres e placas de policloreto de vinila (PVC), comumente utilizadas em experimentos (e.g., ALMEIDA *et al.,* 2018; HARMELIN *et al*., 2009; SOULE; SOULE, 1973; 2002; TAYLOR; TAN, 2015; WINSTON, 1984).

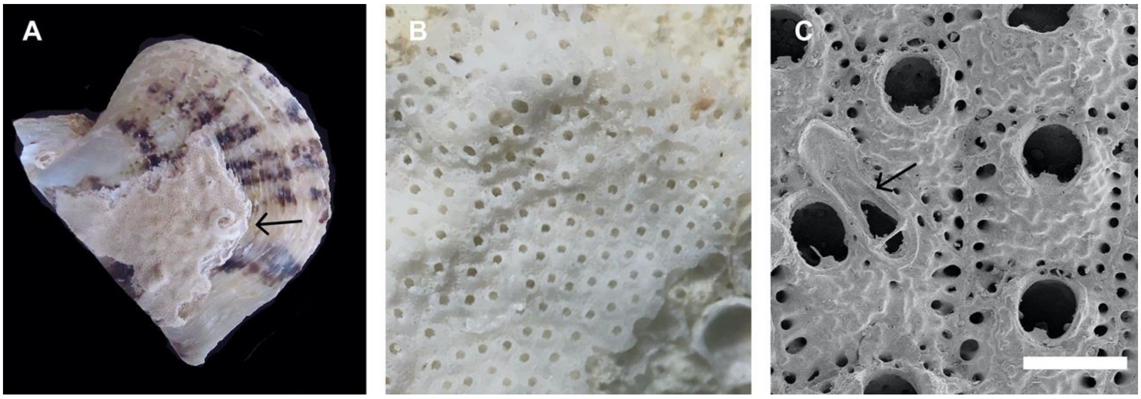
Smittinidae inclui algumas espécies conhecidas por apresentarem uma ampla distribuição que pode estar relacionada com eventos de introdução biológicas (e.g., DICK; GRISCHENKO, 2017; HARMELIN *et al*., 2009; SOUTO *et al*., 2016; TAYLOR; TAN, 2015), complexos de espécies (e.g., FARIAS *et al*., 2020; SOULE; SOULE, 1973, 2002; OSBURN, 1952; WINSTON 2005) e erros históricos de identificação (e.g., FARIAS *et al*., 2020; SOULE; SOULE, 2002; WINSTON 2005).

Dos 18 gêneros recentes de Smittinidae, três deles reúnem mais da metade da diversidade conhecida: *Smittina* Norman, 1903, *Smittoidea* Osburn, 1952 e *Parasmittina* Osburn, 1952 (BOCK; GORDON, 2021). Entretanto, até muito recentemente, a delimitação genérica entre estes e o menos diverso *Hemismittoidea*

Soule & Soule, 1973, era problemática (BARADARI *et al*., 2019; GORDON, 1984; HARMELIN *et al*., 2009; POUYET; HERRERA-ANDUAGA, 1986). Farias *et al*., (2020) estudaram a morfologia dos espécimes-tipo desses gêneros, bem como as discussões previamente levantadas a respeito dos caracteres diagnósticos utilizados, e forneceram definições morfológicas consistentes dos supracitados táxons. Assim, atualmente, espécies dos gêneros *Hemismittoidea*, *Smittina*, *Smittoidea* e *Parasmittina* são diferenciadas por caracteres da parede frontal, espinhos orais e aviculários (FARIAS *et al*., 2020).

Parasmittina (Figura 2) é considerado o gênero mais diverso de Smittinidae, com 129 espécies descritas, até o momento, em todo o mundo (BOCK; GORDON, 2021; HAYWARD, 2004; SOULE; SOULE, 1973). Entretanto, muitas espécies de *Parasmittina* de todo mundo, especialmente do Oceano Atlântico, são conhecidas apenas pelas descrições originais e muitos relatos subsequentes não fornecem descrições detalhadas dos espécimes estudados e nem utilizam microscopia eletrônica de varredura (MEV), atualmente considerada a melhor ferramenta para reconhecimento de caracteres diagnósticos para taxonomia de briozoários queilostomados (e.g., CANU; BASSLER, 1927, 1928; HAYWARD, 1980; MARCUS, 1937, 1938; O'DONOGHUE, 1957; RIDLEY, 1881).

Figura 2. Aspecto geral de colônia e zoóides de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, vista a olho nu de colônia (seta preta) incrustando concha; B, parte da colônia com detalhe de zoooides sob microscópio estereoscópico; C, autozooides e heterozooide (seta preta) vistos sob MEV. Escala: C = 200 µm.



Fonte: O autor (2021).

Espécies de *Parasmittina* são historicamente conhecidas pela acentuada variação morfológica em espécimes de diferentes localidades geográficas (FARIAS *et al*., 2020; SOULE; SOULE, 1973, 2002; SOUTO *et al*., 2016). Em alguns casos, as variações morfológicas podem ser atribuídas às diferentes espécies. Por exemplo, baseados na utilização de MEV, Soule & Soule (2002), examinaram os espécimes-tipo de *Parasmittina trispinosa* (Johnston, 1838) do Atlântico Norte Oriental e espécimes do Pacífico previamente atribuídos à este táxon. Neste trabalho, *P. trispinosa* foi redescrita e seus caracteres diagnósticos estabelecidos e os outros registros foram revistos e atribuídos a sete espécies descritas como novas para a ciência.

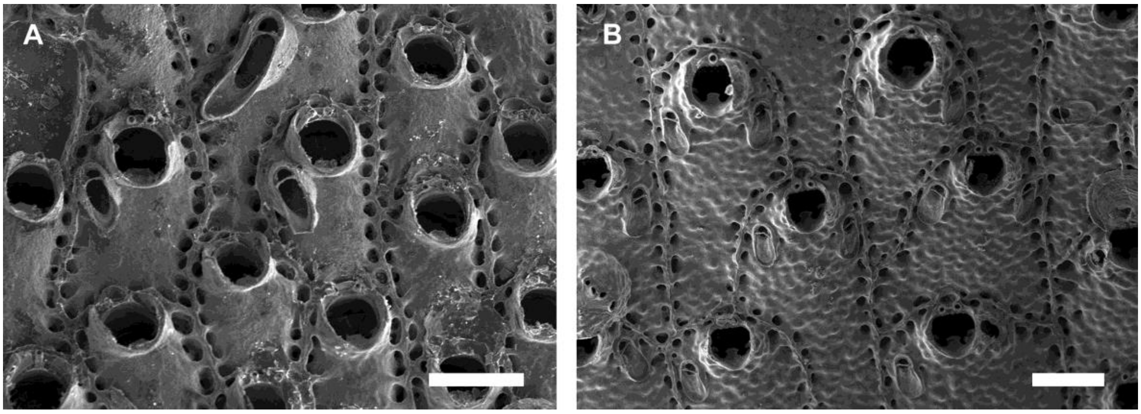
No Atlântico, ao menos 30 espécies de *Parasmittina* foram descritas, das quais 8 espécies têm localidade-tipo o Atlântico Sul Ocidental (BOCK; GORDON 2021): *P. abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018, *P. alba* Ramalho, Muricy & Taylor, 2011, *P. distincta* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018, *P. dubitata* Hayward, 1980, *P. ligulata* (Ridley, 1881), *P. loxa* (Marcus, 1938), *P. loxoides* Winston, Vieira & Woollacott, 2014 e *P. simpulata* Winston, Vieira & Woollacott, 2014. Além disso, outras 5 espécies de *Parasmittina* já foram relatadas para o Atlântico Sul Ocidental: *P. areolata* (Canu & Bassler, 1927), *P. betamorphaea* Winston, 2005, *P. munita* (Hincks, 1884), *P. spathulata* (Smitt, 1873) e *P. trispinosa* (Johnston, 1838). Contudo, muitos desses táxons são conhecidos apenas através de suas descrições ou relatos originais e, dessa forma, carecem de caracterização morfológica adequada para a delimitação das espécies. A importância ecológica do gênero *Parasmittina* (e.g. *P. alba* já foi relacionada com eventos de bioinvasões; SOUTO *et al.*, 2016), e também a presença de relatos de espécies originalmente descritas para outras localidades (e.g., *P. areolata*, originalmente descrita com base em espécimes do Havaí; CANU; BASSLER, 1927) e a presença de complexos de espécies conhecidos (e.g. *P. munita*, *P. trispinosa* e *P. spathulata*; MARCUS, 1937; OSBURN, 1952; SOULE; SOULE, 2002), tornam importante a revisão taxonômica das espécies do gênero, como já apontado por outros autores (ALMEIDA *et al.*, 2015a; FARIAS *et al.*, 2020; VIEIRA *et al.*, 2008).

Caracteres taxonômicos do gênero *Parasmittina* Osburn, 1952

Parede frontal dos autozooides

A parede frontal das espécies de *Parasmittina* é imperfurada, exceto por poros marginais (FARIAS *et al*., 2020; OSBURN, 1952; SOULE; SOULE, 1973, 2002). Os poros marginais sempre estão presentes, podendo constituir uma ou mais fileiras. Raramente pode ocorrer pseudoporos frontais junto ao desenvolvimento do aviculário sobre a parede frontal do zoóide (FARIAS *et al*., 2020) A calcificação frontal pode ser lisa (sem protuberâncias) (Figura 3A), geralmente em zooides jovens, ou nodular (com protuberâncias, como pequenos tubérculos) (Figura 3B).

Figura 3. Parede frontal de autozooides de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, parede frontal lisa em zooides jovens; B, parede frontal nodular em zooides adultos. Escalas: 200 µm.

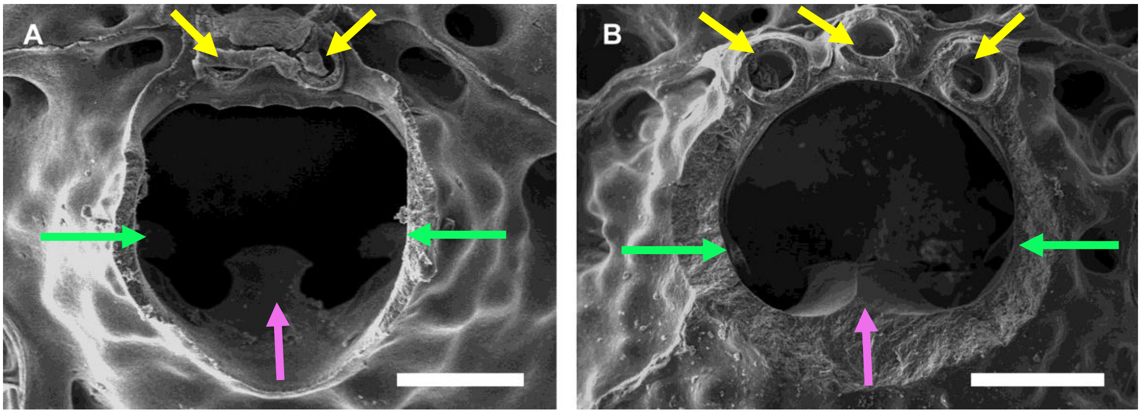


Fonte: O autor (2021).

Orifício primário dos autozooides

A abertura externa da parede corporal por onde o polipídio se projeta para alimentação, sendo fechada por um opérculo quitinoso, é denominada de orifício primário (Figura 4) (MCKINNEY; JACKSON, 1989). A forma, as ornamentações e o tamanho do orifício primário são utilizados para caracterização das espécies. A borda distal do orificio pode apresentar espinhos orais em número variável (Figura 4, seta amarela), sendo estruturas colocadas diretamente no orifício secundário (ou perístoma, que é uma elevação resultante da calcificação ao redor do orifício primário). A margem proximal do orifício primário (com ou sem denticulos) apresenta uma segunda estrutura que é colocada acima do opérculo (supraopercular), que também é formada pelo perístoma, denominada lirula (*lyrula*, em inglês) (Figura 4, seta rosa) (BERNING *et al*., 2014), que pode variar em tamanho e forma. Entre as estruturas colocadas abaixo do opérculo (suboperculares) sempre estão presentes dentículos laterais pareados, chamados de côndilos (Figura 4, seta verde), que variam em tamanho e espessura, bem como na ornamentação lisa ou serrilhada, que auxiliam a abertura e fechamento do opérculo, também podem ocorrer dentículos na margem distal do orifício primário, auxiliando a sustentação do opérculo no orifício primário (OSBURN, 1952; SOULE; SOULE, 1973, 2002) .

Figura 4. Orifício primário de autozooides de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, borda distal com dentículos suboperculares, 2 espinhos orais (peristomiais), lirula pequena (supraopercular), côndilos robustos (subopercular) e com extremidades serrilhadas; B, borda distal sem dentículos, 3 espinhos orais (peristomiais), lirula mediana (supraopercular), côndilos finos (suboperculares) e com extremidades lisas. Escalas: 50 µm.

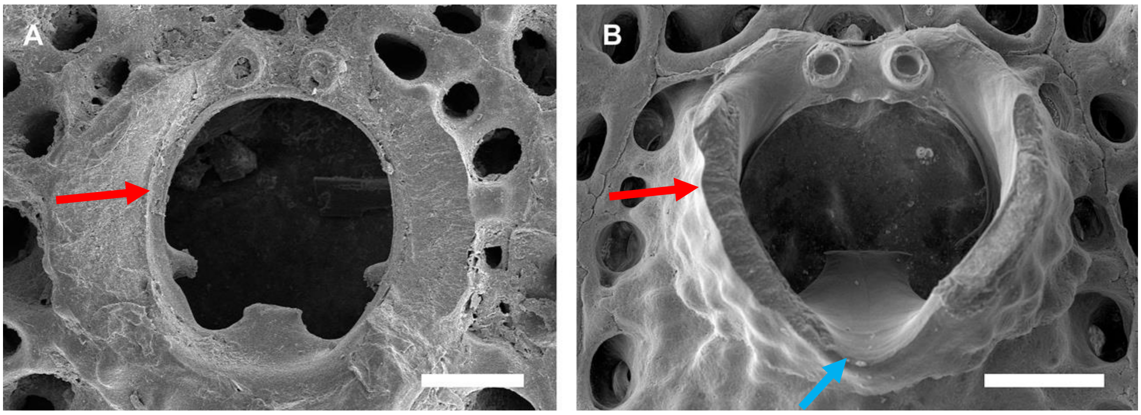


Fonte: O autor (2021).

Orifício secundário dos autozooides

O orifício secundário é a abertura da calcificação ao redor do orifício primário (MCKINNEY; JACKSON, 1989). Em *Parasmittina*, o orifício secundário varia de baixo (Figura A, seta vermelha) a fortemente desenvolvido, podendo apresentar abas e protuberâncias (Figura 5B, seta vermelha). Ocasionalmente, pode haver desenvolvimento de reentrância na borda proximal do orifício secundário, reconhecida como pseudoseio (OSBURN, 1952; SOULE; SOULE, 1973, 2002) (Figura 5B, seta azul). O orifício secundário também é responsável pela formação da lírula (BERNING *et al*., 2014).

Figura 5. Orifício secundário de autozooides de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, baixo e sem pseudoseio; B, fortemente desenvolvido e com pseudoseio. Escalas: 50 µm.

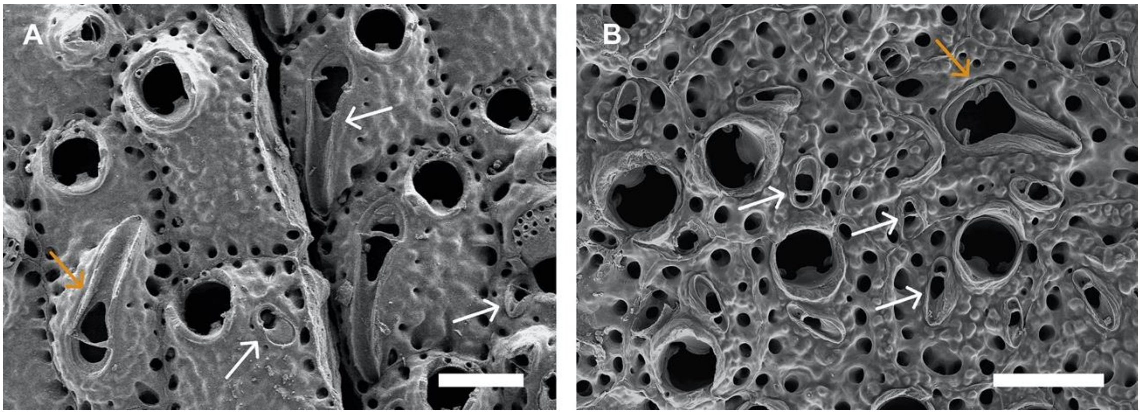


Fonte: O autor (2021).

Aviculários

Aviculários são heterozoóides com total modificação do opérculo (Figura 6), formando a estrutura denominada de mandíbula, ocorrendo comcomitantemente desenvolvimento da musculatura mandibular e redução do polipídio (CARTER *et al*., 2008). Em *Parasmittina*, podem ocorrer dois tipos de aviculários: adventícios (sobre a parede frontal dos autozoóides, mas nunca em posição mediano suboral) (seta branca) e interzooidais (entre os autozoóides) (seta laranja), sendo esse último menos comum. Em zooides ovicelados, os aviculários adventícios podem ser deslocados para a região suboral (OSBURN, 1952; FARIAS *et al*., 2020). Com relação às posições dos aviculários, estas são altamente variáveis, a depender do estágio de desenvolvimento colonial (SOULE; SOULE, 1973; HARMELIN *et al*. 2009).

Figura 6. Aviculários de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, B, aviculários adventícios (setas brancas) e aviculários interzooidais (setas laranjas). Escalas: 200 µm.

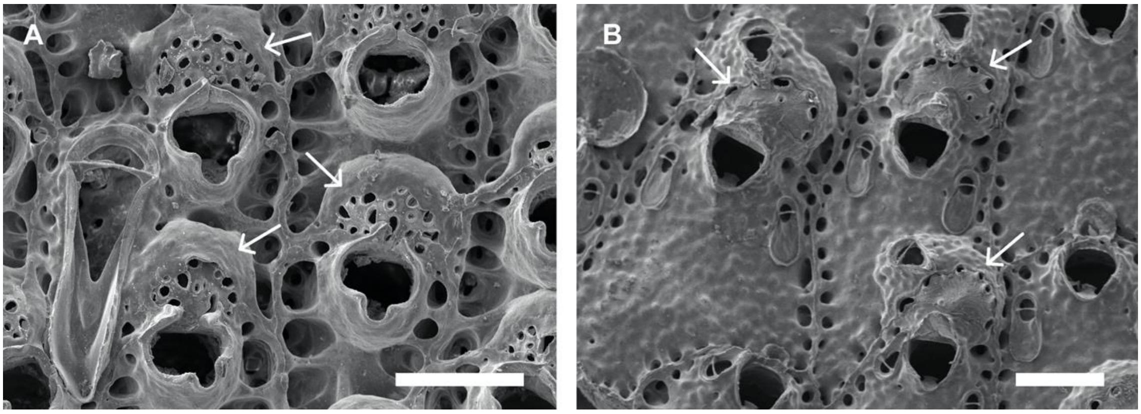


Fonte: O autor (2021).

Ovicelo

Ovicelo é toda a estrutura de incubação encontrada em alguns briozoários, compreendendo parte externa calcificada ou não, e embriões (Figura 7, seta branca). A porção calcificada externa do ovicelo é dividida em duas camadas principais: entooecio (mais interna) e ectooecio (mais externa) (OSTROVSKY, 2013). Em *Parasmittina*, o ovicelo é hiperestomial (elevado em relação a parede frontal), mas se torna imerso com o desenvolvimento colonial. O entooécio é sempre calcificado e o ectooécio é parcialmente calcificado, apresentando pseudoporos que variam em número, tamanho e forma (ALMEIDA, 2018; OSBURN, 1952; OSTROVSKY, 2013) (Figura 7). Em várias espécies de *Parasmittina*, os ovicelos podem estar cobertos por calcificação secundária.

Figura 7. Ovicelos (setas brancas) de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, ovicelos com muitos poros por toda a superfície; B, ovicelos com poucos poros distribuídos em forma de arco distal. Escalas: 200 µm.

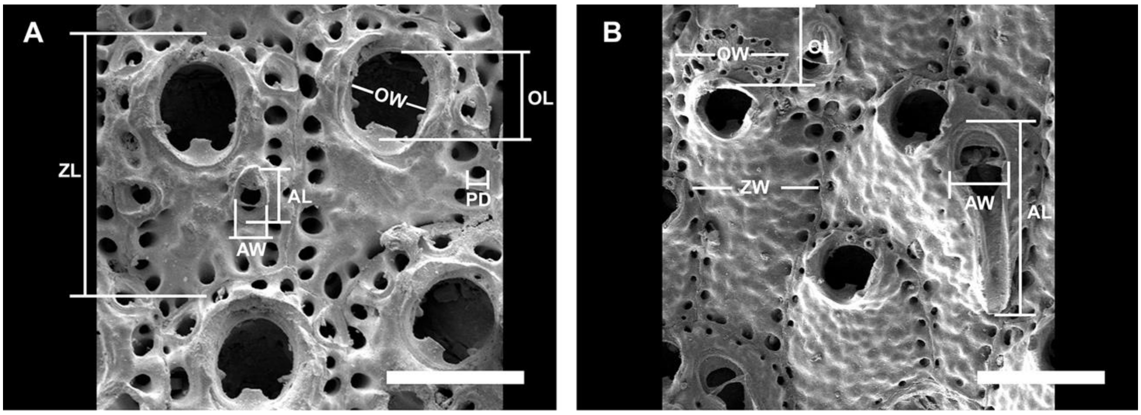


Fonte: O autor (2021).

Caracteres morfométricos

Para descrição e identificação das espécies de *Parasmittina*, são utilizados caracteres morfométricos relacionados ao comprimento do e largura do zoóide (ZL, ZW), diâmetro dos pseudoporos (Dp), comprimento e largura do orifício primário (OL, OW), comprimento e largura do aviculário (AL, AW) e comprimento e largura do ovicelo (OL, OW) (OSBURN, 1952; SOULE; SOULE, 1973, 2002) (Figura 8).

Figura 8. Caracteres morfométricos de *Parasmittina* Osburn, 1952 (Cheilostomatida). A, B, comprimento do e largura do zoóide (ZL, ZW), diâmetro dos pseudoporos (PD), comprimento e largura do orifício primário (OL, OW), comprimento e largura do aviculário (AL, AW), comprimento e largura do ovicelo (OL, OW). Escalas: 200 µm.



Fonte: O autor (2021).

Objetivos

Objetivo Geral

Realizar um estudo taxonômico dos briozoários do gênero *Parasmittina* relatados para o Atlântico Sul Ocidental.

Objetivos Específicos

(1) Caracterizar morfologicamente os briozoários do gênero *Parasmittina* do Atlântico Sul Ocidental com base em fotomicrografias obtidas em microscopia eletrônica de varredura (MEV) e morfometria;

(2) Definir o *status* nativo/criptogênico/exótico de cada espécie;

(3) Reavaliar os caracteres morfológicos tradicionais utilizados para taxonomia do gênero;

(4) Apresentar uma chave de identificação das espécies de *Parasmittina* do Atlântico.

Este capítulo contém o artigo intitulado

Revealing the diversity of recent *Parasmittina* Osburn, 1952 (Bryozoa, Cheilostomatida) from the Southwestern Atlantic: species complexes, cryptogenic and exotic species

JAMILE FARIAS, LEANDRO MANZONI VIEIRA & ANA CAROLINA SOUSA DE ALMEIDA

A ser submetido para publicação no periódico científico PLoS One.

Normas do periódico encontram-se em anexo ao final da dissertação.

Revealing the diversity of recent *Parasmittina* Osburn, 1952 (Bryozoa, Cheilostomatida) from the Southwestern Atlantic: species complexes, cryptogenic and exotic species

Jamile Farias[1,2,3*], Leandro M. Vieira[3,4], Ana C.S. Almeida[1,2,3]

[1]Programa de Pós–Graduação em Biodiversidade e Evolução, Instituto de Biologia, Universidade Federal da Bahia, Salvador, BA, Brazil.
[2]Museu de Zoologia da Universidade Federal da Bahia, Universidade Federal da Bahia, Salvador, BA, Brazil.
[3]Laboratório de Estudos de Bryozoa – LAEBry, Departamento de Zoologia, Centro de Ciências Biológicas, Universidade Federal de Pernambuco, Recife, PE, Brazil.
[4]Scientific Associate of the Department of Life Sciences, Natural History Museum, Cromwell Road, London, UK.

* Corresponding author
E–mail: jamile.farias04@gmail.com

All authors contributed equally to this work.

Abstract

Parasmittina Osburn, 1952 is the most diversified genus of the cheilostome family Smittinidae Levinsen, 1909, commonly reported among the fouling non–indigenous marine community. Here we present a review of species of *Parasmittina* from SW Atlantic based on historical specimens deposited in Museum collections and newly collected colonies. Eleven species were recognized – one species from Argentina (*P. dubitata* Hayward, 1980), nine species previously described from Brazilian coast, four of them with type locality from Brazil: (*P. abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado–Filho & Bastos, 2018, *P. alba* Ramalho, Muricy & Taylor, 2011, *P. distincta* Ramalho, Taylor, Moraes, Moura, Amado–Filho & Bastos, 2018, *P. ligulata* (Ridley, 1881), *P. simpulata* Winston, Vieira & Woollacott), and five species mainly known from the Indo-Pacific (*P. bimucronata* (Hincks, 1884), *P. longirostrata* Liu in Liu, Yin & Ma, 2001, *P. pinctatae* Liu in Liu, Yin & Ma, 2001, *P. serrula* Soule & Soule, 1973 and *P. winstonae* Liu in Liu, Yin & Ma, 2001), and a new species, *P. falciformis* n. sp. At least three species from Brazil, *P. alba*, *P. distincta* and *P. simpulata*, are here recognized as part of species complexes that need further investigations. Among five Indo–Pacific species, two are assigned as exotic (*P. longirostrata* and *P. serrula*) in SW Atlantic, but the other three are assigned as cryptogenic (*P. bimucronata*, *P. pinctatae* and *P. winstonae*). The cryptogenic species are widespread along Brazil and found on both natural and artificial substrata. The exotic species were typically found on artificial substrata near harbors areas. Records previously attributed to *P. munita* (Hincks, 1884), *P. nitida* (Verrill, 1875) and *P. trispinosa* (Johnston, 1838), truly belong to *P. falciformis* n. sp., *P. pinctatae* and *P. bimucronata*, respectively. Other recently described species from Brazil (*P. loxoides* Winston, Vieira & Woollacott, 2014) is here synonymized under *P. winstonae*. To the species complexes, cryptogenic and exotic species, integrative studies using molecular tools and ecological approaches are recommend to reveal the identity, origin and possible impacts of these species in the environment.

Key words: Atlantic Ocean, non–native species, Smittinidae, redescription, taxonomy.

Introduction

Smittinidae Levinsen, 1909 [1] is among the most diverse families of cheilostome bryozoans in Southwestern Atlantic, especially in Brazil, comprising more than 15 taxa [2]. Among the 20 genera currently recognized worldwide belonging to Smittinidae, *Hemismittoidea* Soule & Soule, 1973 [3], *Parasmittina* Osburn, 1952 [4], *Pleurocodonellina* Soule & Soule, 1973 [3], *Smittina* Norman, 1903 [5] and *Smittoidea* Osburn, 1952 [3], are reported from the Brazilian coast [6]. Most of the species belong to *Parasmittina*, the most diversified genus of the family, constituting the most successful group both in number of individuals and species [3]. Currently, the Pacific Ocean is considered the most diverse area, with more than 50 species of *Parasmittina* reported [7]. Besides some recent studies including some new *Parasmittina* species in last two decades (e.g., [8–11]), one of the most significant contributions to the knowledge of *Parasmittina* diversity was published by Soule & Soule [3], that described 23 Hawaiian species, 15 of which new to science.

Smittinidae species, including *Parasmittina* were already related with bioinvasion events and non–indigenous species were reported far from their expected natural geographic distribution (e.g., [6, 11–13]). Therefore, an accurate taxonomic identification is needed for detection and tracking invasions. The generic placement of *Parasmittina* species is historically confusing and specimens of *Smittoidea* and

Hemismittoidea are commonly misassigned as *Parasmittina* (e.g., [14–16]). However, Farias *et al.* [6] redefined the morphological characters of some Smittinidae genera, including *Hemismittoidea*, *Smittoidea* and *Parasmittina*, mainly based in the number of oral spines and position of the oral avicularium. Use of specimens based on early and later astogeny for confident taxonomic identification was highlighted due colonies have highly variable development that can hide the characters of the spines and oral avicularium [3, 6, 11, 17].

Until now, eleven species of *Parasmittina* are reported from Southwestern Atlantic: *P. abrolhosensis* Ramalho, Taylor & Moraes, 2018 [18], *P. alba* Ramalho, Muricy & Taylor, 2011 [19], *P. betamorphaea* Winston, 2005 [9], *P. distincta* Ramalho, Taylor & Moraes, 2018 [18], *P. dubitata* Hayward, 1980 [20], *P. ligulata* (Ridley, 1881) [21], *P. loxoides* Winston, Vieira & Woollacott, 2014 [22], *P. munita* (Hincks, 1884) [23], *P. simpulata* Winston, Vieira & Woollacott, 2014 [22], *P. spathulata* (Smitt, 1873) [24] and *P. trispinosa* (Johnston, 1838) [25]. Among these, *P. munita*, *P. spathulata* and *P. trispinosa* are assigned to be part of the *P. trispinosa* complex [4, 8, 27]. Although originally described to the North Eastern Atlantic Ocean, *P. trispinosa* and many variations attributed to it (e.g., *P. trispinosa* var. *loxa* and *P. trispinosa* var. *spathulata*) have been reported in different oceans. Soule & Soule [11], however, used morphological differences to reassign specimens reported as *P. trispinosa* to fourteen species, eight of those described as new species. Also, the need of taxonomic reviews in these taxa was already indicated by Vieira *et al.* [27], Almeida *et al.* [28] and Farias *et al.* [6]. In this sense, here we reexamined specimens assigned to the genus *Parasmittina* from the Southwestern Atlantic, presenting morphological characterization of twelve species, including a new species. The assessment of the exotic status of five species and a tabular identification key to Atlantic taxa is also provided.

Material and methods

Type and non–type specimens from Brazil are deposited at the Bryozoa collection in the Museu de Zoologia da Universidade Federal da Bahia, Salvador, Brazil (UFBA), Coleção de Bryozoa da Universidade Federal de Pernambuco, Recife, Brazil (UFPE), Museu de Zoologia da Universidade de São Paulo (MZUSP), Smithsonian Institution National Museum of Natural History, Washington D.C., USA (USNM), Natural History Museum, London, United Kingdom (NHMUK) and Museum für Naturkunde, Berlin, Germany (MFN). Additional material from Brazil was collected manually, by scuba diving or by dredging along the coast of Espírito Santo, Bahia, Alagoas, Pernambuco, Paraíba and Rio Grande do Norte. The specimen from Argentina was analyzed base on images (SEM) provided by Juan López Gappa.

In the newly collected specimens, whole colonies and/or fragments of colonies were initially washed in sodium hypochlorite. Then, the specimens were immersed in water and the surface was carefully cleaned with a thin brush until the external film was totally dissolved. These specimens were naturally dried before being examined under a stereoscopic microscope for description of the external morphology and delimitation of morphotypes. Selected specimens of each morphotype were fixed on stubs, coated with gold and examined by scanning electron microscopy (SEM) at the Centro de Pesquisa Gonçalo Moniz, FIOCRUZ, Bahia, Brazil (JEOL JSM–6390LV). Other specimens were imaged at the NHMUK by Mary Spencer Jones (LEO 1455–VP) and at the USNM by JoAnn Sanner (PhilipsXL30), equipped with a low–vacuum chamber and back-scattered electron detector.

Measurements were made from digital SEM images using ImageJ® software and include the following characters: autozooid’s length and width (ZL, ZW), primary orifice length and width (OL, OW), lyrula width (LW), adventitious latero-oral avicularium length and width (A1L, A1W), adventitious large avicularium length and width (A2L, A2W), adventitious frontal and marginal avicularium length and width (A3L, A3W), and ovicell length and width (OvL, OvW). Measurements are represented in the descriptions as minimum–median–maximum, number of measurements (n) and standard deviation (SD), all in millimeters (mm). The taxonomy follows Martha *et al.* [29].

The assessment of the native/exotic status of the studied species was made based on local and global criteria of Chapman & Carlton [30, 31], following Almeida *et al*. [32] and Miranda *et al*. [33].

Results

Systematic account

Order Cheilostomata Busk, 1852 [34]

Suborder Neocheilostomina d’Hondt, 1985 [35]

Family Smittinidae Levinsen, 1909 [1]

Type genus. *Smittina* Norman, 1903 [5] (type species *Lepralia landsborovii* Johnston, 1847 [36], by original designation).

Remarks. Characteristics of the primary orifice, such as the presence of lyrula and avicularium, and presence of pseudopores on the frontal wall and ectooecium represent the main taxonomic criteria to distinguish Smittinidae genera [3, 4, 8, 11, 37, 38]. Most genera are represented by less than 10 species and *Parasmittina*, *Smittina* and *Smittoidea* are the most diverse, the first two with more than 100 known species [38]. Among these, *Parasmittina* and *Smittoidea* share morphological similarities that led misinterpretations regarding diagnostic features and generic placement of several taxa [6, 14–17]. Thus, the taxonomic review of both *Parasmittina* and *Smittoidea* is strongly recommended [6, 11, 13].

Genus *Parasmittina* Osburn, 1952 [4]

Type species. *Lepralia jeffreysi* Norman, 1876 [39], by original designation.

Remarks. Among Smittinidae genera, *Parasmittina* most resembles *Smittoidea* in having imperforate frontal wall with marginal pores, primary orifice with spines, condyles and lyrula, adventitious avicularia originated from frontal or marginal pseudopores and pseudoporous ectooecium. However, these genera are distinguished by the position of the adventitious avicularium. In *Parasmittina*, adventitious avicularium is lateral and/or marginal and only occupy a suboral position in ovicelled or adjacent zooids. In *Smittoidea*, however, adventitious avicularium is medial, intra or suboral (it is never lateral or marginal), even in ovicelled zooids. Also, *Parasmittina* species may have interzooidal avicularium (i.e., originated from pores in the lateral wall), which is absent in *Smittoidea* [3–4, 6].

Historically, the taxonomic identification of *Parasmittina* was mainly based on the morphology and position of the adventitious avicularia [4, 9, 26, 40–46]. Soule & Soule [3, 8] made extensive taxonomic studies with genera of Smittinidae, especially *Parasmittina*, showing that a combination of morphological characters is needed to a confident identification. However, to date, some descriptions of new species and new records remain essentially based only in avicularia characteristics (e.g., [9, 19]). Also, some *Parasmittina* species were described based on colonies fragments (i.e., [18, 22, 45]) that may not represent a good characterization of the intraspecific morphological variation of the taxa, especially regarding the avicularia development [3, 6, 8, 11, 13, 17, 47].

Thus, here we attempt to analyze colonies in different astogenetic stages, comparing with all congeners reported worldwide and using a combination of morphological and morphometric characters. Diagnostic features were based mainly on the primary orifice (distal margin ornamentation, number of spines, lyrula width and condyles morphology), avicularia (if adventitious and/or interzooidal, placement, orientation, size and morphologies) and ovicells (number of pseudopores and secondary calcification).

Parasmittina abrolhosensis **Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018 [18]**

(Figs 1, 2; Tables 1, 12)

Parasmittina abrolhosensis Ramalho *et al.* [18]: 165; *Smittina areolata*: Canu & Bassler [40]: 87; NOT *Smittina areolata* Canu & Bassler [46]: 23; *Smittina trispinosa spathulata*: Canu & Bassler [40]: 87; *Parasmittina spathulata*: Vieira *et al*. [27]: 27. (in part); *Parasmittina spathulata*: Almeida *et al.* [28]: 4 (in part); NOT *Escharella jacotini* var. *spathulata* Smitt, [24]

Material examined. UFPE 813–815, UFBA 2414– 2416, UFBA 2877–2883, UFBA 2885–2887, UFBA 3125, UFBA 3292.5 Recife dos Cascos, Todos os Santos Bay, Bahia, Brazil, 13°7’ S, 38°38’ W, 13–21 m, coll. 2016–2017; UFBA 696, UFBA 3117, UFBA 3123, Costa do Dendê, Bahia, Brazil, 13°33’ S, 38°44’ W, coll. 2002; UFPE 652–661, Bacia Potiguar, Rio Grande do Norte, 4º30’00” to 5º10’00” S, 36º10’00” to 36º50’00” W, coll. 2009–2010; USNM 8558, USNM 8559, *Smittina trispinosa spathulata* and *Smittina areolata*, respectively, F. Canu & R. Bassler det., Bahia, Brazil, 49 m, coll. 1876. *Comparative material examined*: USNM 8443, *Smittina areolata*, holotype, F. Canu & R. Bassler det., Molokai, Hawaii, 142–406 m, coll. 1902.

Description. Colony encrusting. Autozooids (Fig 1A) polygonal, almost rhombic, limited by slightly raised lateral walls, surrounded by a single row of 19–23 marginal pores (0.009–0.025–0.042 mm in diameter; n = 30; SD = 0.008 mm). Frontal wall initially smooth in very young zooids (Figs 1A, top; 1B), with rough, rugose and nodular calcification in older zooids (Figs 1C and 1D). Primary orifice (Fig 1B) elliptical, distal margin smooth, with 2–3 oral spines, lyrula narrow (0.012–0.021–0025 mm wide; n = 30; SD = 0.004 mm); a pair of robust and down–curved hooked condyles with serrated margins. Secondary orifice (Figs 1B and 1C) pear–shaped, forming 2–4 lateral flaps in autozooids, often with in a shallow U–shaped pseudosinus, more pronounced in old zooids or ovicelled zooids (Figs 1D and 1E). Adventitious avicularia variable in shapes and sizes (Figs 1A and 1D), with four morphologies: (1) small, narrow and elongate avicularia (Figs 1C and 1E, 2B and 2E, orange arrow) present at one or both side of the orifice, unequal in size if paired, placed below to the secondary orifice, proximally oriented, rostrum narrow and slightly curved, smooth to slightly corrugated at its lateral margins, rounded tip, palate occupying about half of the rostrum length and oblong foramen; (2) small, subtriangular, bulbous avicularia (Figs 1A and

1D, blue arrow), more common in younger zooids, placed laterally at one side of the orifice, proximally oriented, rostrum subtriangular, corrugated at its lateral margins, pointed tip, palate narrow and subtriangular foramen; (3) small, narrow and subtriangular avicularia (Figs 1C and 1E–1F, 2B and 2E, green arrow), placed in zooidal margins and/or in the frontal wall, with smooth lateral margins, rounded tip, palate narrow and elliptical foramen; (4) large spatulate avicularia (Figs 1F and 2E), more common in older zooids, placed proximolaterally below the orifice, oriented proximally, with rounded distal edge, palate broad, foramen subtriangular, elongate rostrum, with smooth margins and crossbar complete, with 2–3 pseudopores adjacent to the avicularia. Interzooidal avicularia (Figs 1F and 2D) occasionally present, with same morphology as the large spatulate adventitious avicularia. Ovicells (Figs 1D and 2E, red arrow) globose, initially prominent (Fig 1D) and densely surrounded by adjacent frontal wall in older colonies (Figs 1F and 2F, yellow arrow); ectooecium perforated by 18–25 small pseudopores (0.003–0.005–0.008 mm in diameter; n = 30; SD = 0.001 mm), mainly placed at the distal region of the ectooecium surface.

Remarks. Canu & Bassler [40]) studied specimens from northeastern Brazil (Bahia) and attributed them to two species, *Smittina areolata* Canu & Bassler, 1927 and *Smittina trispinosa spathulata* Smitt, 1873 based on differences of avicularia in that specimens. Following Canu & Bassler [40], Vieira *et al.* [27] and Almeida *et al.* [28] also attributed specimens from Espírito Santo and Bahia to *P. spathulata* (Smitt, 1873) [24]. Part of these specimens belong to *P. abrolhosensis* and part are *P. ligulata* (see below).

Parasmittina areolata was originally described by Canu & Bassler [46] based on specimens from Hawaii, Pacific Ocean. However, this species was subsequently reported from Brazil and in the Caribbean [40, 43– 44]. Here we analyzed the type material of *P. areolata* (USNM 8443; Figs 3A– 3D), that allow us to differentiate this species from specimens from Brazil, here referred as *P. abrolhosensis*. *Parasmittina areolata* differs from *P. abrolhosensis* in having a double row of areolar pores (single in *P abrolhosensis*), 2 oral spines, low secondary orifice and ectooecium centrally perforated. These species also resemble *P. spathulata*, but it is distinct in having shorter lyrula (larger in *P. spathulata*) and in having only 2 oral spines (2–4 oral spines in *P. spathulata*) [acc. 6]. Specimens from Caribbean previously attributed to *P. areolata* by Winston [43] requires reexamination and it may comprise a distinct species rather than *P. areolata* or *P abrolhosensis*.

Among *Parasmittina* species, *P. abrolhosensis* most resembles *P. ligulata*, originally described based on specimens from southeastern Brazil, due having primary orifice with narrow lyrula and small, narrow and elongate adventitious avicularia present at one or both sides below the orifice. Here we examined the syntype of *P. ligulata* studied by Ridley [21] (*Smittia trispinosa* var. *ligulata*, NHMUK Uncatalogued specimen, syntype; Figs 8A–8D; see description and remarks below) and were able to see that most features of the primary orifice (smooth distal margin, narrow lyrula and robust and down-curved hooked condyles with serrated margins) are the same as *P. abrolhosensis*. However, oral spines are lacking. Also, only two morphologies of small adventitious avicularia are seen in the type specimen of *P. ligulata*, thus differing from the four adventitious avicularia of *P. abrolhosensis*. Finally, the small, narrow and elongate adventitious avicularia of *P. ligulata* have a slight curved rostrum differing from the almost straight rostrum of the narrow avicularia of *P. abrolhosensis*.

Table 1. Morphometric data of specimens here assigned to *P. abrolhosensis*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	Taxa / reference			
	P. abrolhosensis / holotype in Ramalho *et al.* (2018)	*P. spathulata /* Canu & Bassler (1928), USNM 8558, measured here	*P. areolata* Canu & Bassler (1928), USNM 8559, measured here	*P. ligulata* / present study
ZL	0.312–0.396–0.471 (?)	0.475–0.531–0.635 (7)	0.409–0.567–0.811 (12)	0.311–0.356–0.458 (15)
ZW	0.280–0.308–0.360 (?)	0.344–0.421–0.532 (7)	0.290–0.411–0.640 (12)	0.237–0.310–0.418 (15)
OL	0.093–0.106–0.113	0.101–0.122–0.142 (5)	0.120–0.129–0.138 (2)	0.089–0.100–0.109 (12)
OW	0.075–0.084–0.099	0.097–0.106–0.119 (5)	0.096–0.096–0.097 (2)	0.076–0.091–0.101 (12)
AvZ1 (elongate)	0.121–0.142–0.178	0.101–0.132–0.163 (5)	0.118–0.169–0.237 (15)	0.065–0.113–0.207 (15)
AvW1 (elongate)	–	0.007–0.012–0.014 (5)	0.011–0.019–0.033 (15)	0.011–0.018–0.029 (15)
AvZ2 (spatulate)	–	0.167–0.254–0.389 (7)	0.204–0.278–0.400 (3)	0.226–0.293–0.339 (6)
AvW2 (spatulate)	–	0.043–0.052–0.065 (7)	0.070–0.076–0.082 (3)	0.043–0.064–0.084 (6)
AvZ3 (subtriangular)	0.079–0.090–0.106	0.075–0.101–0.124	0.097–0.116–0.139 (15)	0.062–0.078–0.098 (15)
AvW3 (subtriangular)	–	0.008–0.017–0.024 (13)	0.006–0.013–0.023 (15)	0.021–0.027–0.042 (15
OvL	–	0.176–0.191–0.207 (2)	0.177–0.187–0.212 (4)	0.142–0.170–0.191 (15)
OvW	–	0.176–0.205–0.234 (2)	0.206–0.230–0.246 (4)	0.197–0.211–0.242 (15)

Fig 1. *Parasmittina abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018, UFBA 2416 (A–B); UFBA 2877 (C–D); UFBA 714.2 (E–F). (A) autozooids of the growing edge of the colony with small bulbous subtriangular adventitious avicularium (blue arrow). (B) detail of primary orifice and small elongate avicularia. (C) autozooids with secondary calcification showing small elongate (orange arrow) and subtriangular (green arrow) adventitious avicularia. (D) group of ovicelled zooids with small bulbous subtriangular adventitious avicularium (blue arrow). (E) detail of autozooids with small elongate (orange arrow) and subtriangular adventitious

avicularia (green arrow). (F) ovicelled zooids showing ovicell (yellow arrow) densely surrounded by adjacent frontal wall and with small subtriangular (green arrow) and large spatulate (pink arrow) adventitious avicularia. Scale bars: A, D = 500 µm; B = 100 µm; C, E = 200 µm; F = 300 µm.

Fig 2. *Parasmittina abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018, USNM 8558 (A–D), *Smittina trispinosa spathulata*. USNM 8559 (E–F) *Smittina areolata*, Canu & R. Bassler det., Bahia, Brasil, 49 m, coll. 1876. (A) group of autozooids. B. detail of an autozooid showing small elongate (orange arrow), small subtriangular (green arrow) and large spatulate (pink arrow) adventitious avicularia. (C) detail of primary orifice. (D) detail of interzooidal avicularia (purple arrow). (E) group of young autozooids showing small elongate (orange arrow), small subtriangular (green arrow) and large spatulate (pink arrow) adventitious avicularia. (F) detail of ovicelled (yellow arrow) zooids. Scale bars: A, E = 400 µm; B, D, F = 200 µm; C = 50 µm.

Fig 3. *Parasmittina areolata* (Canu & Bassler, 1927), USNM 8443 (holotype, A–D). (A) group of zooids showing small elongate (orange arrow) and small subtriangular adventitious avicularia (green arrow). B. detail of autozooid. (C) detail of primary orifice. (D) detail of ovicelled (yellow arrow) zooids and large spatulate adventitious avicularium (pink arrow). Scale bars: (A) D = 200 µm; B = 100 µm; C = 50 µm.

Parasmittina alba Ramalho, Muricy & Taylor, 2011 [19]

(Fig 4; Tables 2, 12)

Parasmittina alba Ramalho *et al.* [19]: 769; *Parasmittina alba:* Souto *et al.* [13]: 3; ?

Parasmittina lavela Soule & Soule [8]: 36; ? *Parasmittina betamorphaea* Winston [9]: 58.

Material examined. UFPE 785, Ilhas Rasas, Guarapari, Espírito Santo, Brazil, 20°40’ S, 40°21’ W, 11–15 m, coll. 27/03/2017; UFPE 786 –795; UFBA 3445–3446, UFBA 3448–3449.1, UFBA 3454–3464, UFBA 3467–3471, UFBA 3473.1, UFBA 3479.5, UFBA 3481.1, UFBA 3494.1, UFBA 3502.1, UFBA 3506.6, UFBA 3510–3511, UFBA 3513.1, UFBA 3637, UFBA 3806–3809, UFBA 3911.1, UFBA 3942– 3944, UFBA 3946.1, 3948.2, 3950.3, UFBA 3956.1, UFBA 3958.3960, UFBA 3964.4, UFBA 3966.1, UFBA 3972.3, UFBA 3975–3976, UFBA 3981.1, Todos os Santos Bay, Salvador, Bahia, Brazil, 12°99’S, 38°53’W, 3–5 m, coll. 2012.

Description. Colony encrusting. Ancestrula (Fig 4A) tatiform, without marginal cryptocyst, 8 marginal spines; 5 orificial spines in first daughter zooid. Autozooids (Fig 4B) subrectangular, limited by slightly raised lateral walls, surrounded by a single row of 20–27 marginal pores (0.012–0.021–0.033 mm in diameter; n = 30; SD = 0.004 mm). Frontal wall rugose, with small, rounded tubercles. Primary orifice (Fig 4C) elliptical, distal margin smooth, with 1–3 oral spines; lyrula broad (0.030–0.043–0.058 mm wide; n = 15; SD = 0.007 mm), but shallow and often with median keel; condyles paired, thin, with smooth margins and down-curved hooked tips. Secondary orifice (Figs 4E and 4F) raised around proximal border of primary orifice, formed from lateral flaps, resulting in a shallow V-shaped pseudosinus. Adventitious avicularia variable shapes and sizes (Figs 4B–4F). Adventitious avicularia variable in shapes and sizes (Figs 4B, and 4D–4F), with three morphologies: (1) small, narrow and subtriangular (Fig 4B and 4F, orange arrow) avicularia rare in very young zooids, placed laterally at one side of the orifice, commonly proximally oriented, rostrum subtriangular, finely serrated at its lateral margins, pointed tip, palate narrow and subtriangular foramen; (2) small, spatulate with wide rostrum (Figs 4F, blue arrow) avicularia, rare in young zooids, placed laterally at one side of the orifice, proximally oriented, rostrum subspatulate, rounded distal edge, palate narrow and elliptical foramen; (3) large spatulate avicularia (Fig 4D, red arrow), more common in older zooids, placed laterally at one side of the orifice, oriented proximally, with rounded distal edge, palate broad, foramen elliptical, with smooth margins and crossbar complete, with 2–3 pseudopores adjacent to the avicularia. Ovicells (Figs 4E and 4F) densely surrounded by adjacent frontal wall, immersed in older colonies; ooecium almost globular with flattened frontal surface (0.006–0.017–0.034 mm in diameter; n = 30; SD = 0.006 mm), ectooecium with 20–22 funnel-shaped rounded pseudopores, that become merged and polygonal.

Remarks. Originally described based on specimens from southeastern Brazil, *P. alba* was characterized by having granular frontal wall, condyles with hooked tips, large lyrula, 1–2 oral spines, secondary orifice with lateral projections and pseudosinus, avicularia latero-oral (small subtriangular or rounded), large (spatulate) and interzooidal (subtriangular) with only one avicularium occurring per zooid, and ectooecium with pseudopores (misassigned as pores) Ramalho *et al.* [19]. Most of these morphological characters are also seen in colonies from southeastern and northeastern Brazil examined here, but the orificial spines ranged from 1–3 and no interzooidal avicularia were observed. Most of our colonies are small patches growing on ceramic experimental tile plates from northeastern Brazil (Fig 4A) and larger specimens were only found on rhodoliths from southeastern Brazil (Fig 4F). Interestingly, avicularia were more common in older regions of the colonies (Fig 4F) than in growing zone with new zooids (Fig 4B), suggesting presence of avicularia in later colony astogeny. Moreover, zooidal measurements are in agreement among *P. alba* and specimens examined here (Table 2), indicating that examined specimens with and without avicularia are conspecific.

Parasmittina alba was reported as a non-indigenous species in Portugal, Northeastern Atlantic [13]. Souto *et al*. [13] noted small variations between specimens from Rio de Janeiro (acc. [19]) and those from Portugal, including smaller ectooecial pseudopores related with greater calcification, the occurrence of two avicularia in ovicelled zooids and absence of interzooidal avicularia. Additionally, Souto *et al*. [13] suggested that *P. alba* could be assigned as junior synonym of *P. betamorphaea* Winston, 2005 [9] described from Florida, USA, since characters used to distinguish these taxa are very variable among colonies and zooids (i.e., number of avicularia, calcification of margins and rostrum of the avicularia) and both species were described based on only colonies fragments that may not represent intraspecific variations, which seems to be necessary to characterize Smitiinidae species [3, 6, 11, 13,17].

Another Caribbean taxon, *P. lavela* Soule & Soule, 2002 [8], share most morphological diagnostic features of *P. alba*, including the granular frontal calcification, primary orifice without distal denticles, with large lyrula and thin down-curved hooked condyles, secondary orifice with a short pseudosinus and ooecium with merged pseudopores [8]. The only difference between *P. alba* and *P. lavela* is the presence of a single kind of avicularia of *P. lavela* (i.e., small subtriangular latero-oral avicularia), lacking all others of avicularia described to *P. alba*. Indeed, Soule & Soule [8] stated that avicularia are not common in *P. lavela*, but only a small single specimen growing on algae on anchor chain was examined by Soule & Soule [8], somewhat corroborating morphological variation and biological association already reported [13,19] and also described here to *P. alba*.

Avicularia development is known to be very variable in Smittinidae between colonies and habitats (e.g., [3, 6, 8, 11, 17, 47]), and these characteristics are also seen in specimens of *P. alba* here examined. We suspect that *P. alba* and *P. betamorphea* may represent different astogenetic variation of *P. lavela* – specimens of *P. alba* represent an adult stage with all type of avicularia, ovicells and secondary calcification [19], whereas *P. betamorphea* could represent young colony that lacks ovicells and have few avicularia [9]. Additionally, zooidal measurements of specimens attributed to *P. alba* and *P. betamorphea* are also similar to those of *P. lavela* (Table 2). Thus, here we consider that at least a species complex involving *P. alba*, *P. betamorphea* and *P. lavela* can be recognized (Table 2).

Distribution. Northeastern Atlantic: Portugal [13]; Southwestern Atlantic: Brazil (Bahia, Espírito Santo and Rio de Janeiro) [19]; present study).

Table 2. Morphometric data of specimens here assigned to *P. alba*, *P. lavela* and *P. betamorphea*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**				
	P. alba / holotype in Ramalho *et al.* 2011	*P. alba /* Souto *et al.* (2016)	*P. alba* / present study	*P. lavela* / holotype in Soule & Soule (2002)	*P. betamorphea* / holotype in Winston (2005)
ZL	0.392–0.451–0.490 (?)	0.390–0.488–0.670 (24)	0.325–0.408–0.582 (15)	0.350–0.400 (?)	0.378–0.470–0.576 (6)
ZW	0.265–0.305–0.383 (?)	0.240–0.340–0.460 (24)	0.249–0.317–0.424 (15)	0.243–0.320 (?)	0.252–0.290–0.324 (6)
OL	–	0.076–0.082–0.101 (20)	0.090–0.129–0.150 (15)	?	0.072–0.080–0.090 (?)
OW	–	0.103–0.125–0.143 (20)	0.097–0.111–0.126 (15)	0.100–0.120 (?)	0.090–0.100–0.108 (?)
AvZ1 (subtriangular)	0.098–0.109–0.118 (?)	0.068–0.078–0.089 (10)	0.098 (1)	0.120–0.150 (?)	0.72–0.090–0.162 (6)
AvW1 (subtriangular)	0.069–0.083–0.098 (?)	0.037–0.047–0.054 (10)	0.046 (1)	–	0.045–0.050–0.054 (6)
AvZ1 (oblong)	–	0.074–0.092–0.104 (9)	–	–	–
AvW1 (oblong)	–	0.051–0.056–0.063 (9)	–	–	–
AvZ2 (spatulate)	0.353 (?)	–	0.300–0.337–0.375 (2)	–	0.324–0.360–0.396 (6)
AvW2 (spatulate)	0.137 (?)	–	0.086–0.097–0.107 (2)	–	0.180–0.190–0.198 (6)
OvL	0.274 (?)	0.235–0.265–0.297 (20)	0.218–0.244–0.268 (15)	0.200–0.260 (?)	0.180–0.200–0.216 (2)
OvW	0.323 (?)	0.233–0.267–0.300	0.253–0.275–0.294	0.225–0.260 (?)	0.180–0.200–0.216

	(20)	(15)	(2)

Fig 4. *Parasmittina alba* Ramalho, Muricy & Taylor, 2011, UFBA 3637 (A–F). (A) ancestrula and first zooids of the colony. (B) young autozooids showing small subtriangular adventitious avicularium (orange arrow). (C) detail of primary orifice. (D) young autozooid with large adventitious avicularium (pink arrow). (E) colony with secondary calcification showing autozooids and ovicelled zooids. UFPE 785 (F). detail of ovicelled zooids with small subtriangular (orange arrow) and spatulate (blue arrow) adventitious avicularia. Scale bars: A, B, D, E, F = 200 μm; C = 50 μm.

***Parasmittina bimucronata* (Hincks, 1884) [48]**

(Fig 5; Tables 3, 12)

Smittia trispinosa form *bimucronata* Hincks, [48]: 118; *Parasmittina bimucronata*: Hayward & Parker [49]: 70 [under remarks of *P. pectinata*]; ? *Parasmittina glomerata*: Liu [50]: 618; NOT *Smittia glomerata* Thornely, [51]: 152.

Material examined. UFBA 946, Todos os Santos Bay, Bahia, Brazil, 12°46’ S, 38°33’ W, coll. 22/05/1997; UFBA 3113, Costa do Dendê, Bahia, Brazil, 38°80’ S, 13°74’ W, coll. 2002.

Description. Colony encrusting. Autozooids (Fig 5A) subrectangular to polygonal, limited by slightly raised lateral walls, with a single row of 18–24 marginal pores (0.009–0.019–0.033 mm wide; n = 30; SD = 0.005 mm). Frontal wall rugose, with large, rounded tubercles. Primary orifice (Fig 5C) transversely elliptical, distal margin smooth, with 1–2 oral spines; lyrula narrow (0.019–0.025–0.032 mm wide; n = 15; SD = 0.004 mm), latero-proximal condyles triangular and thin. Secondary orifice initially low, becoming raised and forming lateral flap-shaped projections with increasing calcification, often with a shallow U-shaped pseudosinus (Fig 5D), but may partially obscuring primary orifice in latter astogeny, especially in ovicelled zooids, resulting in a deep U-shaped pseudosinus, but often not obscuring the lyrula (Fig 5E). Adventitious avicularia variable in shapes and sizes (Figs 5A–5E), with three morphologies: (1) small, subtriangular, bulbous avicularia (Figs 5A and 5B, orange arrow), placed laterally at one side of the orifice, proximally oriented, rostrum subtriangular, corrugated at its lateral margins, pointed tip, palate narrow and subtriangular foramen; (2) small, oblong avicularia (Fig 5A and 5B, blue arrow) single, common in younger zooids, placed below the secondary orifice, proximally oriented, rostrum subspatulate and straight, smooth at its lateral margins, rounded tip, palate occupying about half of the rostrum length and elliptical foramen; (3) large, sublanceolate avicularia (Fig 5A, red arrow), placed laterally at one side of the orifice, oriented proximally, with acute rostrum, palate broad, foramen subtriangular, with finely serrated margins and crossbar complete, with 2–3 pseudopores adjacent to the avicularia. Interzooidal avicularia (Figs 5A and 5B, purple arrow) occasionally present, with same morphology as the large spatulate adventitious avicularia. Ovicells (Figs 5E–5F) wider than long, ooecium globular, becoming immersed in the frontal calcification with increasing calcification (Fig 5F); ectooecium perforated by 20–27 pseudopores with slightly raised rim (0.004–0.011–0.020 mm wide; n = 30; SD = 0.004 mm).

Remarks. *Parasmittina bimucronata* is characterized by having primary orifice smooth distally, 1–2 oral spines, thin and smooth condyles and lyrula occupying one-quarter of the orificial width; adventitious latero-oral avicularia with three morphologies: small, with subtriangular or oblong profile, and large, with sublanceolate profile; and ovicell with more than 18 pseudopores [48–49]. Moreover, zooidal measurements of specimens studied here and with the lectotype of *P. bimucronata* (BMNH 1899.5.1.920; see Hayward & Parker [49] are within the same range value (Table 3).

Parasmittina bimucronata was originally described based on specimens from Indian Ocean as a variation of *P. trispinosa* [48], and the lectotype of that species was selected by Hayward & Parker [49]. Several differences can be observed between these two species, including the number of oral spines (1–2 in *P. bimucronata* and 2–3 in *P. trispinosa*), the orientation of the large avicularium (proximolateral in *P. bimucronata* and distolateral in *P. trispinosa*), and the number of ectooecial pseudopores (20–37 in *P. bimucronata* and 2–4 in *P. trispinosa*) [8, 47]. Hincks [48] referred to specimens from the Pacific Ocean as belonging to *P. bimucronata*, but later, however, Harmer [42] relocated specimens from Indian and Pacific Oceans studied by Hincks [23, 48] to *P. raigii* (Audouin, 1826) [52], originally described from the Red Sea (Gulf of Suez as type locality). Hayward & Parker [49] reexamined Hincks' (23, 48) original specimens and stated that none of them belong to *P. raigii*—specimens from Indian Ocean belong to *P. bimucronata* and those from the Pacific were renamed as a new species, *Parasmittina pectinata* Hayward & Parker [49]. Although *P. bimucronata, P. raigii* and *P. pectinata* have adventitious avicularia placed laterally to the orifice with similar morphologies, these species can be distinguished mainly by features of the primary orifice, including the distal margin (smooth in *P. bimucronata*; beaded in *P. raigii* and *P. pectinata*), oral spines (1–2 in *P. bimucronata* and *P. raigii*; 2–3 in *P. pectinata*), condyles (thin and smooth in *P. bimucronata* and *P. raigii*; robust and serrated in *P. pectinata*) and lyrula size (narrow in *P. bimucronata*; broad *in P. raigii* and *P. pectinata*). Liu [50] assigned specimens of *P. bimucronata* from China as *P. glomerata* also due having avicularia with similar morphologies. However, these specimens differ from *P. glomerata* by having a primary orifice with smooth distal margin (beaded in *P. glomerata*) and narrow lyrula (medium-sized in *P. glomerata*), and probably belong to *P. bimucronata*.

Distribution. Indo-Pacific: Myanmar and China [48]; Southwestern Atlantic: Brazil (Bahia) (present study).

Table 3. Morphometric data of specimens here assigned to *P. bimucronata*. Values represented as median (number of zooidal measures) or minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**	
	P. bimucronata / lectotype in Hayward & Parker (1994)	*P. bimucronata* / present study
ZL	0.360 (20)	0.330–0.459–0.663 (15)
ZW	0.230 (20)	0.268–0.311–0.463 (15)
OL	0.080 (20)	0.100–0.115–0.141 (15)
OW	0.090 (20)	0.079–0.095–0.110 (15)
AvZ1 (subtriangular)	–	0.089–0.117–0.144 (15)
AvW1 (subtriangular)	–	0.033–0.052–0.069 (15)
AvZ1 (oblong)	–	0.100–0.105–0.111 (6)
AvW1 (oblong)	–	0.037–0.047–0.053 (6)
AvZ2 (sublanceolate)	–	0.217–0.363–0.472 (15)
AvW2 (sublanceolate)	–	0.034–0.054–0.076 (15)
OvL	–	0.150–0.194–0.210 (15)
OvW	–	0.216–0.255–0.293 (15)

Fig 5. *Parasmittina bimucronata* (Hincks, 1884b), UFBA 946 (A–D). (A) group of autozooids with small subtriangular (orange arrow), small spatulate (blue arrow) and large (pink arrow) adventitious avicularia and interzooidal (purple arrow) avicularium. (B) detail of autozooids showing small subtriangular (orange arrow) and small spatulate (blue arrow) adventitious avicularia and interzooidal (purple arrow) avicularium. (C) detail of primary orifice. (D) autozooids with secondary calcification. (E) ovicelled zooids with secondary calcification. (F) detail of ovicells. Scale bars: A, B, D, E = 500 µm; C, F = 200 µm.

Parasmittina distincta Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018 [18]

(Fig 6; Tables 4, 12)

Parasmittina distincta Ramalho *et al.* [18]: 164.

Material examined. UFPE 796–812, UFBA 1928.4, UFBA 3446.5, UFBA 3448.5, UFBA 3450–3451, UFBA 3453.6, UFBA 3455.2, UFBA 3459.5, UFBA 3462.4, UFBA 3465.1, UFBA 3467.6, UFBA 3467–3468, UFBA 3470.3, 3472.4, UFBA 3474–3476, UFBA 3478–3480, UFBA 3484.7, UFBA 3486.5, UFBA 3489–3492, UFBA 3494–3495, UFBA 3498–3500, UFBA 3502–3503, UFBA 3505–3508, 3511.5, UFBA 3919–3920, UFBA 3923–3926, UFBA 3928.3, UFBA 3930.5, UFBA 3940–3941, UFBA 3943–3946, UFBA 3950.1, UFBA 3952.1, UFBA 3954 –3957, UFBA 3960–3964, UFBA 3968.4, UFBA 3970.2, UFBA 3975–3976, UFBA 3978–3979, UFBA 3981.3, UFBA 3983–3984, Todos os Santos Bay, Salvador, Bahia, Brazil, 12°99'S, 38°53'W, 3–5 m, coll. 2012. *Comparative material examined*: MFN Uncatalogued, *Smittina egyptiaca*, holotype, Waters det., Red Sea.

Description. Colony encrusting. Ancestrula (Fig 6A) tatiform, marginal cryptocyst short, 6 marginal spines; first daughter zooid has 3 orificial spines. Autozooids (Fig 6B) subrectangular, limited by slightly raised lateral walls, surrounded by a single row of 16–22 marginal pores (0.010–0.016–0.025 mm wide; n = 30; SD = 0.003 mm). Frontal wall rugose, with several nodules. Primary orifice (Fig 6C) transversely elliptical, longer than wide, distal margin initially smooth in very young zooids (Fig 6B), slightly beaded with 4–6 spaced and low denticles in older zooids (Figs

6C and 6D), 1–2 oral spines in younger zooids (up to 3 in zooids close to ancestrula) and up to 4 in older zooids, lyrula medium-sized in width (0.0024–0.032–0.045 mm wide; n = 15; SD = 0.007 mm), a pair of rounded condyles with serrated margins. Secondary orifice in young zooids (Fig 6D and 6F) initially low and soon forming lateral flaps resulting in a two-pointed U-shaped pseudosinus (Fig 6D). Adventitious avicularia variable in shapes and sizes (Figs 6B and 6D–F), with two morphologies: (1) small, oblong avicularia (Fig 6B, orange arrow) single, laterally at one side of the orifice and oriented proximally in young zooids, placed near margins in older zooid (Fig 6F, orange arrow), rostrum subspatulate and straight, smooth at its lateral margins, rounded tip, palate occupying about half of the rostrum length and elliptical foramen; (2) large, sublanceolate avicularia (Fig 6D, red arrow), placed laterally at one side of the orifice, oriented proximally, with acute rostrum, palate broad, foramen elliptical, with slightly corrugated margins and crossbar complete, with 1–3 pseudopores adjacent to the avicularia. Interzooidal avicularia (Fig 6E, purple arrow) shorter than autozooids, subtriangular, common in older regions of the colony, randomly oriented, with rounded distal edge, narrow palate, occupying about half of the rostrum length, foramen elliptical and acute rostrum, with smooth margins and crossbar complete. Ovicells (Figs 6E and 6F) densely surrounded by adjacent frontal wall; ectooecium perforated by 20–37 (0.003–0.006–0.012 mm in diameter; n = 30; SD = 0.001 mm) pseudopores, regularly distributed through the ectooecial surface.

Remarks. Ramalho *et al.* [18] stated that the diagnostic features of *P. distincta* include the primary orifice with beaded distal margin, medium-sized lyrula, adventitious latero-oral avicularia with three morphologies (i.e., small subtriangular and oblong – described as shoe-shaped in the original description and large sublanceolate and ovicell globose with ectooecium perforated by large pseudopores. Here we analyzed several specimens from northeastern Brazil that have most of these diagnostic characters, except to the small subtriangular adventitious avicularia. The holotype of *P. distincta* and specimens studied here also have frontal wall with several nodules, primary orifice transversally elliptical, prominent condyles, 2–4 oral spines, lyrula occupying half of the orifice width, and secondary orifice forming lateral flaps [26]. Indeed, morphometric data are in agreement (Table 4).

Parasmittina distincta was described based on specimens from northeastern Brazil [18]. The authors compared the specimens studied with congeners already reported in Brazil and with species that have latero-oral avicularia with an oblong profile [18]. Most congeners with the same morphologies of adventitious avicularia as *P. distincta* differ from this species mainly in characters of the orifice: *P. bimucronata* (no distal denticles and narrow lyrula); *P. dubitata* Hayward, 1980 [20] (no distal denticles, wide lyrula, short secondary orifice, large avicularia with smooth margins), *P. margaritata* Hayward, 1988 [15] (no distal denticles and thin condyles), *P. munita* (Hincks, 1884) [23] (tubular secondary orifice), *P. parsloeparsloei* Hayward & Parker [49] (tubular secondary orifice and large avicularia with smooth margins), *P. pectinata* Hayward & Parker [49] (wide lyrula), *P. raigii* (Audouin, 1826) [52] (wide lyrula, thin condyles, broad lyrula, tubular secondary orifice, large avicularia with smooth margins) and *P. variabilis* Liu, [50] (no distal denticles, broad lyrula and thin condyles).

However, among all *Parasmittina* and considering the combination of characters of the orifice and avicularia, *P. distincta* is more similar to *P. egyptiaca* Waters, 1909 and *P. floridana* Winston, 2005 [9, 53].

These species have a medium-sized lyrula, occupying about half the width of the orifice and avicularia placed latero-proximal to the orifice with profile oblong. Few differences are seen between these taxa, including the number of oral spines (2–4 in *P.*

distincta, 2 in *P. egyptiaca*, and 2–3 in *P. floridana*); denticles on the distal edge of the primary orifice (present in *P. distincta* and *P. floridana* and absent in *P. egyptiaca*); avicularia with subtriangular profile (present in *P. distincta* and *P. floridana* and absent and *P. egyptiaca*), and avicularia large with sublanceolate profile (present in *P. distincta* and *P. egyptiaca* and absent in *P. floridana*) [9, 18, 53]. Both *P. egyptiaca* and *P. floridana* were described based on single colony fragments [9, 53], thus is not unlikely that they may represent same species despite of the differences in number of oral spines, absence of distal orificial denticles and avicularia. Also, zooidal measurements of these three taxa are within the same range, including specimens studied here (Table 4).

Parasmittina distincta is also very similar to *P. glomerata* (Thornely, 1912) [51] that was originally described from the Indian Ocean and also reported in localities from the Pacific and Mediterranean regions [42]. Both species have two types of avicularia with similar morphologies and primary orifice with distal denticles. However, data of other features of the primary orifice, including the morphologies of the lyrula and condyles are lacking, preventing us to better compare these taxa. Analysis of type specimens would be useful but apparently original colonies studied by Thornely [51] was not located and it was supposedly deposited at the Liverpool University Zoology Museum (Mary Spencer Jones, per. comm. 2020), which part of bryozoan collection was lost [54].

Thus, due to the morphological and morphometric similarities of these species, it is likely that *P. distincta*, *P. egyptiaca*, *P. floridana* and *P. glomerata* represent a species complex and more studies is needed based on specimens from other localities, including topotypes.

Distribution. Southwestern Atlantic: Brazil (Ceará, Alagoas, Bahia, and São Paulo) [18]; present study).

Table 4. Morphometric data of specimens assigned to *P. distincta*, *P. egyptiaca* and *P. floridana*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**			
	P. distincta / holotype in Ramalho *et al*. (2018)	*P. distincta* / present study	*P. egyptiaca* / holotype in Waters (1909)	*P. floridana* / holotype in Winston (2005)
ZL	0.327–0.455–0.596 (?)	0.279–0.378–0.654 (15)	0.301–0.375–0.499 (12)	0.450–0.570–0.612 (6)
ZW	0.252–324–0.465 (?)	0.222–0.308–0.501 (15)	0.155–0.253–0.314 (12)	0.378–0.420–0.450 (6)
OL	0.084–0.103–0.129 (?)	0.106–0.120–0.132 (15)	0.115–0.120–0.127 (3)	0.108–0.120–0.126 (6)
OW	0.093–0.104– 0.116 (?)	0.092–0.101–0.118 (15)	0.074–0.085–0.097 (3)	0.108–0.120–0.126 (6)
A1L (subtriangular)	0.076–0.182 (?)	0.065–0.079–0.089 (5)	–	0.162–0.190–0.198 (6)
A1W (subtriangular)	–	0.031–0.036–0.046 (5)	–	0.090–0.090– 0.108 (6)
A1L (oblong)	0.087–0.104–0.115 (?)	0.087–0.119–0.139 (9)	0.088–0.109–0.126 (12)	–
A1W (oblong)	–	0.035–0.041–0.046 (9)	0.030–0.038–0.051 (12)	–
A2L (sublanceolate)	225 (?)	0.183–0.257–0.315 (6)	0.244 (1)	–
A2W (sublanceolate)	–	0.059–0.076–0.094 (6)	0.072 (1)	–
OvL	–	0.142–0.161–0.175 (15)	0.196 (1)	0.324–0.370–0.414 (6)
OvW	–	0.183–0.208–0.226 (15)	0.250 (1)	0.198–0.220–0.234 (6)

Fig 6. *Parasmittina distincta* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018, UFBA 3486.5 (A–D, F), UFPE 833 (E). (A) ancestrula and first zooids of the colony. (B) detail of young autozooids showing small oblong (orange arrow) adventitious avicularia. (C) detail of primary orifice. (D) adult autozooid with large (pink arrow) adventitious avicularium. (E) colony with secondary calcification showing interzooidal (purple arrow) avicularia. (F) detail of ovicelled zooids with small oblong

(orange arrow) adventitious avicularium. Scale bars: A, B, E, F = 200 µm; C = 50 µm; D = 100 µm.

Parasmittina dubitata **Hayward, 1980 [20]**

(Fig 7; Table 12)

Parasmittina dubitata Hayward [20]: 701.

Material examined. Uncatalogued, Tierra del Fuego, Argentina, 90 m.

Description. Colony encrusting. Autozooids (Fig 7A), (0.291–0.367–0.481 mm length; n= 5; SD= 0.081 mm; 0.246–0.306–0.455 mm wide; n= 5; SD= 0.087 mm), subrectangular to polygonal, limited by slightly raised lateral walls, with a single row of 11–16 marginal pores (0.013–0.029–0.059 mm wide; n = 30; SD = 0.010 mm). Frontal wall rugose, with large, rounded tubercles. Primary orifice (Fig 7C), (0.115–0.119–0.122 mm length; n= 4; SD=0.002 mm; 0.112–0.123–0.133 mm wide; n=4), subcircular, distal margin smooth, with single oral spine; lyrula large, varying in size, occupy about half width of the orifice (0.034–0.041–0.049 mm wide; n = 7; SD = 0.005 mm), robust, with concave distal margin; a pair of prominent condyles with rounded and coarsely serrated margins. Secondary orifice cormidial, low, forming slightly raised side flaps and a hood distal to the orifice (Fig 7B). Adventitious avicularia variable in shapes and sizes (Figs 7B and 7D), with three morphologies: (1) small (0.059–0.099–0.131 mm length; n = 15; SD = 0.022; 0.017–0.031–0.046 mm wide; n = 15; SD = 0.008 mm), oblong avicularia (Figs 7A and 7B, orange arrow) single or paired, laterally at one side of the orifice and oriented proximally or placed near zooidal margins, smooth at its lateral margins, rounded tip, palate occupying one quarter of the rostrum length and elliptical foramen; (2) small, spatulate avicularia (Figs 7A and 7D, green arrow), placed in zooidal margins, commonly replacing a marginal pore; (3) large (0.241mm in length; n = 1; 0.123 mm in wide; n = 1), subtriangular to sublanceolate avicularia (Fig 7B, red arrow), placed laterally at one side of the orifice, oriented proximally, with acute rostrum, palate broad, foramen elliptical, with smooth margins and crossbar complete. Interzooidal avicularia (Fig 7D, purple arrow) shorter than autozooids (0.266 mm in length; n = 1; 0.110 mm in wide; n = 1), with same morphology as the large adventitious avicularium, randomly oriented. Ovicells not observed.

Remarks. *Parasmittina dubitata* was originally described based on specimens from Burdwood Bank, an underwater platform, located 150 km to the east of the Island of the South Atlantic States (Argentina). Here, we provide description of a single specimen from Tierra del Fuego, also in Argentina, kindly send by Juan Lopez Gappa (pers. comm., 2021), that shares all the diagnostic characters of the original description of *P. dubitata*. This species is readily distinguished from other congeners by the morphology of the primary orifice that include a lyrula with a concave distal margin and rounded condyles unlike the straight lyrula and triangular to hooked condyles of most *Parasmittina*.

Distribution. Southwestern Atlantic: Argentina (Burdwood Bank and Tierra del Fuego) [20].

Fig 7. *Parasmittina dubitata* Hayward, 1980, Uncatalogued specimen (A) group of autozooids showing small oblong (orange arrow) and small spatulate (green arrow) adventitious avicularia. (B) detail of autozooids with small oblong (orange arrow) and large subtriangular (pink arrow) adventitious avicularium. (C) detail of primary orififce.

(D) detail of interzooidal (purple arrow) avicularium and small spatulate (green arrow) adventitious avicularium. Scale bars: A= 200 µm; B, D = 100 µm; C = 50 µm.

Parasmittina ligulata **(Ridley, 1881) [21]**

(Fig 8)

Smittia trispinosa var. *ligulata* Ridley [21]: 53.

Material examined. *Syntype*: NHMUK Uncatalogued, *Smittia trispinosa* var. *ligulata*, S.O. Ridley det., Victoria Bank, Espírito Santo, Brazil, 60 m.

Redescription. Colony encrusting. Autozooids (0.326–0.430–0.524 mm length; n= 15; SD= 0.060 mm; 0.212–0.326–0.476 mm wide; n = 15; SD= 0.065 mm), (Fig 8A) polygonal, almost rhombic, limited by slightly raised lateral walls, surrounded by a single row of 19–27 marginal pores (0.010–0.019–0.032 mm in diameter; n = 30; SD = 0.004 mm). Frontal wall with rugose and nodular calcification (Fig 8A). Primary orifice (0.094–0.108–0.120 mm length; n= 4; SD= 0.011 mm; 0.092–0.099–0.107 mm wide; n= 4; SD= 0.006 mm) (Fig 8C) elliptical, distal margin smooth, oral spines not observed, lyrula narrow (0.015–0.021–0027 mm wide; n = 4; SD = 0.005 mm); a pair of robust and down-curved hooked condyles with coarsely serrated margins (Fig 8B). Secondary orifice (Figs 8C and 8D) pear-shaped, forming lateral flaps, and resulting a shallow U-shaped pseudosinus (Fig 8D). Adventitious avicularia variable in shapes and sizes (Figs 8B and 8D), with two morphologies: (1) small (0.108–0.163–0.210 mm in length; n = 10; SD = 0.034 mm; 0.015–0.022–0.032 mm in wide; n = 10; SD = 0.005 mm), narrow and elongate avicularia (Fig 8A–8B and 8D, orange arrow) present at one or both side of the orifice, unequal in size if paired, placed below to the secondary orifice, proximally oriented, rostrum narrow and slightly curved, smooth to slightly corrugated at its lateral margins, rounded tip, palate occupying about half of the rostrum length and oblong foramen; (2) small (0.060–<u>0.083</u>–0.116 mm in length; n = 10; SD = 0.014 mm; 0.013–<u>0.017</u>–0.025 mm in wide; n = 10; SD = 0.003 mm), narrow and subtriangular avicularia (Figs 8A–8B and 8D, blue arrow), placed in zooidal margins and/or in the frontal wall, with smooth lateral margins, rounded tip, palate narrow and elliptical foramen. Ovicells (0.171–<u>0.185</u>–0.211mm length; n= 5; SD= 0.017 mm; 0.163–<u>0.188</u>–0.212 mm wide; n= 5; SD= 0.022 mm) globose, densely surrounded by adjacent frontal wall, ectooecium perforated by 6–10 medium–sized pores (Fig 8D, yellow arrow).

Remarks. Originally described based on specimens from southeastern Brazil (Espírito Santo), the usage of the name *P. ligulata* is historically confused. *Parasmittina ligulata* belong to the complex *P. spathulata*–*P. areolata*, reported from Atlantic and Pacific Ocean, respectively, that comprise species with adventitious latero-oral avicularia single or paired and with narrow and elongate profile, and large spatulate avicularium sometimes replacing the small ones (e.g., [9, 43–44]). In 2008, *P. ligulata* was synonymized by Vieira *et al.* under *P. spathulata*, also including the specimen of Canu & Bassler [40] attributed to *Smittina trispinosa spathulata* (USNM 8558). As previous stated, the specimen studied by Canu & Bassler [40] is here assigned to *P. abrolhosensis.* However, the analysis of the syntype of *P. ligulata* showed no large avicularia and the oral spines are lacking, thus preventing us to compare these species. Also, features of the primary orifice and ovicells (Table 12), that are the main differences among these species, however, were not discussed. Thus, here we choose to keep these taxa separated until more specimens from the topotype locality of *P. ligulata* are analyzed.

Distribution. Southwestern Atlantic: Brazil (Espírito Santo) Ridley, 1881[21].

Fig 8. *Parasmittina ligulata* (Ridley, 1881), NHMUK Uncatalogued specimen (syntype, A–D). (A) group of autozooids showing small elongate (orange arrow) and small subtriangular (blue arrow) adventitious avicularia. (B) detail of autozooid showing small elongate (orange arrow) and small subtriangular (blue arrow) adventitious avicularia. (C) detail of primary orifice. (D) detail of ovicelled (yellow arrow) zooids and small elongate (orange arrow) and small subtriangular (blue arrow) adventitious avicularia. Scale bars: A = 200 μm; B, D = 100 μm; C = 40 μm.

***Parasmitina longirostrata* Liu in Liu, Yin & Ma, 2001 [50]**

(Fig 9; Table 5)

Parasmittina longirostrata Liu *et al.* [50]: 800; ? *Parasmittina serruloides* Harmelin *et al.* [11]: 174.

Material examined. UFPE 816–821, UFBA 3492.5, UFBA 3496.4, UFBA 3508.2, UFBA 3634, UFBA 3638, UFBA 3805.1, UFBA 3886.2, UFBA 3893.10, UFBA 3895.6, UFBA 3899.4, UFBA 3904.4, UFBA 3908–3909, UFBA 3911–3913, UFBA 3922.2, UFBA 3924–3925, UFBA 3948.4, UFBA 3951.3, UFBA 3977.2, UFBA 3979.4, UFBA 3981.8, UFBA 3983.2, Todos os Santos Bay, Salvador, Bahia, Brazil, 12°99’S, 38°53’W, 3–5 m, coll. 2012.

Description. Colony encrusting (Fig 9A). Autozooids (Fig 9B) subretangular to polygonal, limited by slightly raised lateral walls, surrounded by a single row of 12–18 small marginal pores (0.004–0.013–0.025 mm in diameter; n =30; SD = 0.004 mm).

Frontal wall rugose and nodular. Primary orifice elliptical (Fig 9C), wider than long, distal margin smooth, with 3–4 oral spines, lyrula median-sized (0.025–0.030–0.036 mm wide; n = 15; SD = 0.003 mm), a pair of robust, hooked, condyles with serrated margins. Secondary orifice (Figs 9D and 9F) moderate to well-developed, pear-shaped, forming 2–4 lateral flaps in autozooids, commonly resulting in a shallow U-shaped pseudosinus in ovicelled zooids, only partly obscuring the lyrula. Adventitious avicularia variable in shapes and sizes (Figs 9B–9D), with three morphologies: (1) small, narrow and elongate avicularia (Figs 9B and 9D, orange arrow) present at one side below to the secondary orifice, proximally oriented, rostrum narrow and slightly curved, slightly corrugated at its lateral margins, rounded tip, palate occupying about half of the rostrum length, oblong foramen and crossbar complete; (2) small, oblong avicularia (Fig 9E, blue arrow) single, more common in adult zooids, laterally at one side of the orifice and oriented proximally, smooth at its lateral margins, rounded tip, palate occupying half of the rostrum length, elliptical foramen and crossbar complete; (3) large, sublanceolate avicularia (Figs 9C and 9E, red arrow), placed laterally at one side of the orifice, oriented proximally, rostrum slightly curved with coarsely serrated margins and rounded distal edge, palate narrow, occupying about half the rostrum length, foramen subtriangular with 2–3 pseudopores adjacent to the avicularia. Ovicells globose, initially prominent (Figs 9D, and 9F) and densely surrounded by adjacent frontal wall (Fig 9F, black arrow) in older zooids; ectooecium perforated by 18–24 medium-sized pseudopores (0.003–0.006–0.009 in diameter; n = 30; SD = 0.001 mm), regularly distributed through the ectooecial surface.

Remarks. *Parasmittina longirostrata* is characterized by having a unique combination of characters that include a primary orifice with smooth distal margin, with 3–4 oral spines, lyrula median-sized, secondary orifice forming a U-shaped pseudosinus, and two types of proximolateral avicularia: small, elongate and thin and large, sublanceolate with crenulated margins [50].

Liu *et al*. [50] considered that *P. serrula* Soule & Soule (1973) [3] was the most similar congener to *P. longirostrata* probably due having two types of avicularia with the smaller proximolateral being thin and narrow. However, several differences are observed between these species, including the primary orifice (with smooth distal margin and lyrula occupying half of the orificial width in *P. longirostrata* and with distal denticles and lyrula occupying one-quarter of the orificial width in *P. serrula*), placement of the smaller avicularia (typically straightly placed proximolateral to the orifice in *P. longirostrata* and transversally below the orifice in *P. serrula*) and profile of the large avicularium (sublanceolate in *P. longirostrata* and spatulate in *P. serrula*) [3].

Harmelin *et al.* [11] described the species *P. serruloides*, based on specimens from Lebanon. These specimens also fit morphological characters of *P. longirostrata*, except, for the profile of the condyles that are thin. Considering that only the condyles profile differs between species, more studies are needed, to compare these species and validate whether they are in fact different species or not.

Despite the type locality of *P. longirostrata* being in the North Pacific, all Brazilian specimens studied here are morphologic and morphometric (Table 5) indistinguishable from those from China [50].

Distribution. Northeastern Pacific: China [50]. Southwestern Atlantic: Brazil (Bahia) (present study).

Table 5. Morphometric data of specimens here assigned to *Parasmittina longirostrata*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	Taxa / reference	
	P. longirostrata / holotype in Liu *et al.* (2001)	*P. longirostrata* / present study
ZL	0.480–0.600–0.744 (10)	0.229–0.300–0.353 (15)
ZW	0.314–0.342–0.358 (10)	0.189–0.206–0.247 (15)
OL	0.098–0.100–0.106 (10)	0.079–0.092–0.103 (15)
OW	–	0.066–0.080–0.095 (15)
AvZ1 (elongate)	0.072–0.120–0.144	0.080–0.098–0.122 (7)
AvW1 (elongate)	0.028–0.042–0.056 (10)	0.019–0.023–0.027 (7)
AvZ2 (sublanceolate)	0.330–0.369–0.414 (10)	0.205–0.234–0.280 (8)
AvW2 (sublanceolate)	0.174–0.218–0.258 (10)	0.036–0.041–0.050 (8)
OvL	0.142–0.158–0.172 (10)	0.113–0.127–0.150 (15)
OvW	0.186–0.204–0.214 (10)	0.128–0.150–0.176 (15)

Fig 9. *Parasmittina longirostrata* Liu in Liu, Yin & Ma, 2001, UFBA 3805.1 (A–D); UFBA 3886.2 (E–F). (A) general view of a colony. (B) autozooids at the growing edge of the colony showing small elongate (orange arrow) adventitious avicularia. (C) autozooid with details of the primary orifice and showing large sublanceolate (pink arrow) adventitious avicularia. (D) group of autozooids with small elongate (orange arrow) and large sublanceolate (pink arrow) adventitious avicularia. (E) detail of autozooids with small oblong (blue arrow) and large sublanceolate (pink arrow) adventitious avicularia. (F) group of ovicelled zooids. Scale bars: A = 500 μm; B, D = 200 μm; C, E, F = 100 μm.

Parasmittina pinctatae Liu in Liu, Yin & Ma, 2001 [50]

(Fig 10; Table 6)

Parasmittina pinctatae Liu *et al.* [50] 805; *Smittina trispinosa*: Luederwaldt, [55]: 65; *Smittina trispinosa* var. *nitida*: Marcus [26]: 104; *Parasmittina betamorphaea*: Vieira *et* *al*. [27]: 27; *Parasmittina parsevalii*: Liu *et al*. [50]: 621; *Parasmittina egyptiaca*: Harmelin *et al.* [11]: 166; *Parasmittina egyptiaca*: Baradari *et al*. [14]: 474; NOT *Discopora trispinosa* Johnston, [25]: 280; NOT *Discopora nitida* Verril, [56]: 415; NOT *Cellepora parsevalii* Audouin [52]: 238; NOT *Parasmittina betamorphaea* Winston, [9]: 58; NOT *Smittia egyptiaca* Waters, [53]: 157.

Material examined. UFBA 301, Salvador, Bahia, Brazil, 12°58’ S, 38°44’ W, 37 m, coll. 17/04/1997; UFBA 644, Baía de Todos os Santos, Bahia, Brazil, 12°46’ S, 38°33’ W, coll. 20/03/1997; UFPE 650, UFBA 3310, UFBA 3312.2, Praia Araçá, São Sebastião, São Paulo, Brazil,23°48' S, 45°24' W, coll. 07/07/2009; USNM Uncatalogued, H. Luederwaldt det. 1926, Ilha de São Sebastião, São Paulo, Brazil; UFPE 822–830, UFBA 1928.1, UFBA 2995.1, UFBA 3034.5, UFBA 3444.1 UFBA 3446–3451, UFBA 3453.1, UFBA 3455.4, UFBA 3457.2, UFBA 3459–3470, UFBA 3472–3476, UFBA 3478–3480, UFBA 3482–3484, UFBA 3486–3488, UFBA 3490–3496, UFBA 3498–3500, UFBA 3502–3509, UFBA 3511–3514, UFBA 3516–3521, UFBA 3670.1, UFBA 3802–3806, UFBA 3808–3810, UFBA 3812–3814, UFBA 3884–3886, UFBA 3889, UFBA 3891–3894, UFBA 3896–3897, UFBA 3899–3900, UFBA 3902, UFBA 3904–3906, UFBA 3910.1 UFBA 3917.4, UFBA 3919.5, UFBA 3921–3923, UFBA 3926–3927, UFBA 3929–3930, UFBA 3940–3951, UFBA 3953.1, UFBA 3955–3968, Todos os Santos Bay, Salvador, Bahia, Brazil, 12°99’S, 38°53’W, 3–5 m, coll. 2012; MZUSP 921, *Smittina trispinosa* var. *nitida*, det. Marcus, 1937, Santos, São Paulo, Brazil, MZUSP 1160, Yatch Club de Ilhabela, Ilhabela, São Paulo, Brazil, 23°75’S, 45°41’W, 2 m, coll. 05/03/2010; MZUSP Uncatalogued CE59, Porto do Mucuripe, Fortaleza, Ceará, Brazil, 3°32’S, 38°48’W, coll. 27/08/2009; MZUSP Uncatalogued CE65, Porto do Mucuripe, Fortaleza, Ceará, Brazil, 3°32’S, 38°48’W, coll. 27/08/2009; MZUSP Uncatalogued CE69, Porto do Mucuripe, Fortaleza, Ceará, Brazil, 3°32’S, 38°48’W, coll. 27/08/2009, MZUSP 1015, São Paulo, Brazil. USNM Uncatalogued, *Smittina trispinosa*, det. H. Luederwaldt, São Sebastião, São Paulo, Brazil, coll. Jul 1925.

Description. Colony encrusting, uni to multilaminar (Fig 10A). Autozooids (Fig 10B) subquadrangular to polygonal, limited by slightly raised lateral walls, surrounded by a single row of 16–22 marginal pores (0.011–<u>0.022</u>–0.032 mm in diameter; n= 30; SD = 0.004 mm). Frontal wall rugose and nodular. Primary orifice (Fig 10C) subcircular, as long as wide, smooth distally, 1–2 oral spines, lyrula relatively wide but low, occupying about half of the orifice length (0.025–<u>0.038</u>–0.047 mm wide; n = 15; SD = 0.006 mm), a pair of almost straight and robust condyles with margins finely. Secondary orifice low, forming short lateral flaps (Fig 10C), larger in ovicelled zooids (arrow, Fig 10F). Adventitious avicularia variable in shapes and sizes (Figs 10B–10D), with three morphologies: (1) small subtriangular avicularia (Figs 10B and 10E, orange arrow), placed distolaterally to the orifice in younger zooids and randomly scattered on the frontal wall (i.e., around the orifice, in a suboral position and on the ovicell) in older zooids (Fig 10F); (2) small, profile elongate (Figs 10D and 10E, green arrow), sublanceolate, narrow and with a pointed rostrum, placed in zooidal margins, more common in older zooids; (3) large, profile spatulate (Fig 10E, red arrow), placed distolaterally to the orifice, oriented proximolaterally, palate narrow, occupying about 3/4 of the rostrum length, with smooth margins and crossbar complete; 3–5 pseudopores adjacent to the avicularia, foramen elliptical. Ovicells globose (Fig 10F), densely surrounded by adjacent frontal wall (Fig 10F, black arrow); ectooecium perforated by more than 20 smalls to medium-sized pseudopores (0.002–<u>0.007</u>–0.011 in diameter; n = 30; SD = 0.002 mm) distributed through the entire ovicell surface.

Remarks. Despite *P. pinctatae* occurs in Brazil since at least 1929, due to misleading identifications [26, 28,55], here we present the first formal record of this species to the Western Atlantic. Most records were previously attributed to *P. trispinosa* [26, 55] and to *P. nitida* (Verrill, 1875) [56] but Vieira *et al*. [27] assigned Marcus's *P. nitida* to *P. betamorphaea*. Here we examined specimens studied by these authors (Luederwaldt 1929 [55], USNM Uncatalogued; Marcus 1937 [26], MZUSP 921; Almeida *et al*. 2015 [27], UFBA 301, UFBA 644) and all share diagnostic features of *P. pinctatae*, including the subcircular primary orifice, secondary orifice with lateral flaps, short lyrula, nodular frontal calcification and three types of avicularia.

Parasmittina pinctatae differs from *P. trispinosa* in the profile of the primary orifice (as long as wide in *P. pinctatae* and longer than wide in *P. trispinosa*), number of oral spines (1–2 in *Parasmittina pinctatae* and 2–3 in *P. trispinosa*), profile of avicularia (the proximolateral is subtriangular in *P. pinctatae* and oblong in *P. trispinosa*; the large is spatulate in *P. pinctatae* and subtriangular in *P. trispinosa*), and number of ovicell pseudopores (more than 20 in *P. pinctatae* and 2–4 in *P. trispinosa*) [11]. Differences between *P. pinctatae* and *P. nitida* include the profile of the primary orifice (subcircular in *P. pinctatae* and rounded in *P. nitida*), lyrula (median in *P. pinctatae* and narrow in *P. nitida*), types of avicularia (three types in *P. pinctatae*: proximolateral, marginal and large; two types in *P. nitida*: proximolateral and marginal) and orientation of the proximolateral avicularia (distolateral in *P. pinctatae* and proximolateral in *P. nitida*) [67]. Finally, *P. pinctatae* is distinguished from *P. betamorphea* in having a narrower lyrula (the lyrula of *P. betamorphaea* is twice the length of that from *P. pinctatae*) and condyles thin and almost straight (robust and curved in *P. betamorphaea*) [9].

The taxonomic history of *P. pinctatae* is puzzle. In the same paper of its original description [50], other specimens from China were misidentified as *P. parsevalii* (Audouin, 1826) [52]. However, specimens studied by Liu *et al.* (2001) [50] differ from *P. parsevalii* by having primary orifice with smooth distal margin (beaded in *P. parsevalii*), relatively wide and low lyrula (narrow and high in *P. parsevalii*), almost straight and thin condyles (robust and hooked in *P. parsevalii*) and large spatulate avicularia (subtriangular in *P. parsevalii*) [49], this combination of characters belongs *to P. pinctatae*. Additionally, at least records of *Parasmittina egyptiaca* (Waters, 1909) [53] made by Harmelin *et al.* [11, 57] and Baradari *et al*. [14] belong to *P. pinctatae*. Here we analyzed type specimens of *P. egyptiaca* (MFN Uncatalogued; Fig 11) and several differences are seen between descriptions and figures provided by these authors, including a short secondary orifice (raised in *P. egyptiaca*; Figs 11B and 11C), low lyrula (higher in *P. egyptiaca*; Figs 11D and 11E), large avicularia with spatulate profile and smooth margins (subtriangular with serrated margins in *P. egyptiaca*; Fig 11C) and latero-oral avicularia oriented distally (proximally in *P. egyptiaca*; Fig 11B). In this sense, as all the morphological characters of the mentioned specimens are the same of *P. pinctatae* and morphometric data are generally within the same range (Table 6), a review of specimens already attributed to both *P. parsevalii* and *P. egyptiaca* are strongly recommended.

Distribution. Pacific: China [50]); Red Sea [53]; Mediterranean ([11, 57]; Southwestern Atlantic: Brazil (Ceará, Bahia and São Paulo) [26, 28, 55]; present study).

Table 6. Morphometric data of *P. pinctatae, P. parsevalii* and *P. egyptiaca*. Values represented as minimum–<u>median</u>–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**				
	P. pinctatae / holotype in Liu *et al*. (2001)	*P. parsevalii* / Liu *et al*. (2001)	*P. pinctatae* / present study	*P. egyptiaca* / Harmelin *et al.* (2009)	*P. egyptiaca* / Baradari *et al.* (2019)
ZL	0.483–0.522–0.655 (10)	0.366–0.498–0.670	0.260–0.433–0.833 (15)	0.365–0.492–0.730 (33)	0.270–0.397–0.531 (13)
ZW	0.277–0.320–0.350 (10)	0.280–0.302–0.340	0.207–0.298–0.392 (15)	0.265–0.338–0.605 (33)	0.230–0.266–0.320 (13)
OL	0.112–0.122–0.135 (10)	0.098–0.106–0.110 (10)	0.090–0.110–0.153 (15)	0.085–0.107–0.130 (28)	–
OW	0.088–0.098–0.102 (10)	0.084–0.092–0.098 (10)	0.074–0.100–0.115 (15)	0.105–0.113–0.135 (28)	–
AvZ1 (subtriangular)	0.064–0.084–0.098 (10)	0.084–0.090 (10)	0.057–0.064–0.075 (3)	–	–
AvW1 (subtriangular)	0.036–0.040–0.064 (10)	0.050–0.062–0.072 (10)	0.034–0.037–0.040 (3)	–	–
AvZ2 (spatulate)	0.292–0.304–0.316 (10)	0.240–0.254–0.268 (10)	0.307–0.317–0.327 (2)	0.315–0.371–0.435 (10)	–
AvW2 (spatulate)	0.074–0.080–0.088 (10)	0.098–0.098–0.114 (10)	0.062–0.062–0.063 (2)	0.085–0.108–0.120 (10)	–
AvZ23 (sublanceolate)	0.088–0.102–0.110 (10)	0.072–0.080–0.086 (10)	0.090 (1)	–	–
AvW3 (sublanceolate)	0.038–0.048–0.056 (10)	0.048–0.054–0.072	0.020 (1)	–	–
OvL	0.180–0.200–0.216 (10)	0.184–0.198–0.220 (10)	0.129–0.173–0.192 (15)	0.195–0.205–0.230 (16)	–
OvW	0.208–0.240–0.245 (10)	0.224–0.236–0.256 (10)	0.163–0.221–0.243 (15)	0.205–0.236–0.265 (16)	–

Fig 10. *Parasmittina pinctatae* Liu in Liu, Yin & Ma, 2001, UFBA 3885.1 (A–D, F); UFBA 3884 (E). (A) general view of a colony. (B) autozooids at the growing edge of the colony showing small subtriangular (orange arrow) adventitious avicularia. (C) detail of primary orifice. (D) detail of primary orifice and small elongate (green arrow) adventitious avicularia. (E) group of autozooids with small subtriangular (orange arrow) and small elongate (green arrow) adventitious avicularia and large spatulate (pink arrow) adventitious avicularia. (F) group of ovicelled zooids with secondary calcification. Scale bars: A, F = 500 µm; B, E = 200 µm; C, D = 100 µm.

Fig 11. *Parasmittina egyptiaca* (Waters, 1909), MFN Uncatalogued, type (A–F). (A) general view of a colony fragment showing small oblong (orange arrow) and large subtriangular (pink arrow) adventitious avicularia. (B) autozooid showing small oblong (orange arrow) adventitous avicularia. (C) autozooid showing large subtriangular (pink arrow) adventitious avicularia. (D) detail of primary orifice showing condyles and lyrula. (E) detail of primary orifice showing slightly denticulate distal margin. (F) detail of ovicell. Scale bars: A = 300 μm; B, C, F = 100 μm; D, E = 20 μm.

Parasmittina serrula Soule & Soule, 1973 [3]

(Fig 12; Tables 7, 8)

Parasmittina serrula Soule & Soule [3]:386; *Parasmittina serrula*: Winston [43]: 23; *Parasmittina serrula*: Winston [44]: 22; ? *Parasmittina serrula*: Gordon [17]: 96; ? *Parasmittina serrula*: Ryland & Hayward [58]: 272; ? *Parasmittina serrula*: Gordon & D'Hondt [59]: 21; ? *Parasmittina serrula*: Tilbrook *et al.* [60]: 76; ? *Parasmittina serrula*: Tilbrook *et al.* [10]: 154; ? *Parasmittina serrula*: Dick *et al.* [61]: 2221; ? *Parasmittina serrula*: Dick & Grischenko [12]: 188.

Material examined. UFBA 2850, Guarajuba, Camaçari, Bahia, Brazil, 12°45’ S, 38°06’ W, 25–27 m, coll. 1997; UFBA 2859, Recife dos Cascos, Todos os Santos Bay, Bahia, Brazil, 13°7’ S, 38°38’ W, 13–21 m, coll. 2016–2017.

Description. Colony encrusting, uni to multilaminar (Fig 12A). Autozooids (Fig 12B) rhombic-polygonal, limited by slightly raised lateral walls, surrounded by a single row of 14–22 marginal pores (0.009–$\underline{0.019}$–0.036 mm wide; n = 30; SD = 0.005 mm). Frontal wall rugose and nodular. Primary orifice (Fig 12C) elliptical, wider than long, distal margin with several well-spaced minute denticles, 3–5 oral spines, lyrula narrow, occupying about half of the orifice length (0.020–0.023–0.028 mm wide; n = 10; SD = 0.002 mm), a pair of hooked condyles with coarsely serrated margins. Secondary orifice pear-shaped, forming 2 proximolateral flaps and resulting in a pseudosinus (Figs 12B and 12D), larger in ovicelled zooids (arrow, Fig 12D). Adventitious avicularia variable in shapes and sizes (Figs 12A–B and 12D), with two morphologies: (1) small, narrow and elongate avicularia (Fig 12B, orange arrow) present at one or both sides below to the secondary orifice, proximally oriented, rostrum narrow and slightly curved, slightly corrugated at its lateral margins, rounded tip, palate occupying about half of the rostrum length, oblong foramen and crossbar complete; (2) large avicularia with profile spatulate (Figs 12B and 12D, red arrow), placed distolaterally to the orifice and oriented proximally, palate broad, occupying about 3/4 of the rostrum length, foramen oval, rostrum spatulate, with strongly serrated margins and crossbar complete; 1–2 pseudopores adjacent to the avicularia. Ovicells globose (Fig 12D, yellow arrow), surrounded by adjacent frontal wall; ectooecium perforated by 12–27 medium-sized pseudopores (0.005–0.007–0.0013 mm wide; n = 30; SD = 0.001 mm) distributed through the entire ovicell surface. Secondary calcification around the primary orifice in ovicelled zooids forming a hood in the distal margin of the ovicell (Fig 12D).

Remarks. As *P. ligulata*, *P. serrula* belong to the *P. spathulata*–*P. areolata* complex that comprise Atlantic species with avicularia types one and two but that are easily distinguished based on features of the primary orifice, avicularia and ovicells (Table 12). *Parasmittina serrula* differs from all these congeners by having up to 6 oral spines (up to 4 in all other species) and large spatulate avicularium with strongly serrated margins (with smoother margins in all other species).

First described based on specimens from Hawaii (Soule & Soule 1973) [3], *P. serrula* was already recorded from coral reefs of Belize, Gulf of Mexico, and experimental panels from Jamaica [43, 44]. Winston (1984) [43] attributed an opportunistic behavior to these species indicating that it could be more widely distributed in tropical waters than it is known. It was also recorded from several localities from the Western and Central Pacific (Table 7 and see Dick & Grischenko 2017 [12] for more information) but most of these differ in characters of the primary orifice and can represent distinct species [12]. However, specimens studied here fit all morphological and morphometric characters of the original description provided by Soule & Soule [3] (Tables 7 and 8), thus being considered the same morphospecies as *P. serrula*.

Morphological variations already attributed to *P. serrula* can truly represent intraspecific variations [9] and its geographical unusual distribution including records in the Pacific and Caribbean were already related with hull shipping through the Panama Canal [12]. Interestingly, colonies studied here were also found encrusting artificial substrata, indicating the potential of this taxa to colonize man-made structures with passive dispersal ability. Thus, as already as *P. alba* and *P. distincta*, it is clear that more integrative studies are needed to better understand the taxonomy and distribution of *P. serrula*.

Distribution. Central Pacific: Hawaii [3], Caribbean: Belize, Gulf of Mexico and Jamaica [43, 44]; Southwestern Atlantic: Brazil (Bahia) (present study).

Table 7. Morphological variations in specimens from different localities assigned to *Parasmittina serrula*. Number, (N), unknown states (?). The lyrula information correspond to the lyrula width in relation to the orifice width.

Localities	**Reference**	**Oral spines (N)**	**Lyrula**	**Condyles**	**Large avicularium**
Hawaii (EUA)	Soule & Soule (1973)	3–6	one quarter	robust	spatulate
Hawaii (EUA)	Gordon (1984)	4	one quarter	?	–
Bow Cay Belize	Winston (1984)	4	one quarter	robust	–
Heron Island (Australia)	Ryland & Hayward (1992)	2–4	half	robust	spatulate
Philippines	Gordon & D'Hondt (1997)	3	?	?	–
Vanuatu	Tilbrook *et al.* (2001)	2–4	half	robust	spatulate
Vanuatu	Tilbrook *et al.* (2006)	3–4	one quarter	thin	spatulate
Hawaii (EUA)	Dick *et al.* (2006)	2–4	one quarter	robust	–
Okinawa (Japan)	Dick & Grischenko (2017)	3–4	half	robust	–
Brazil	Present study	3–5	one quarter	robust	spatulate

Table 8. Morphometric data of specimens assigned to *Parasmittina serrula*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**			
	P. serrula / holotype in Soule & Soule (1973)	*P. serrula* / Winston (1984)	*P. serrula /* Dick et al. (2006)	*P. serrula* / present study
ZL	0.320–0.368–0.400 (10)	0.319–0.434–0.592 (15)	0.280–0.374–0.470 (20)	0.302–0.392–0.602 (15)
ZW	0.260–0.284–0.310 (10)	0.182–0.274–0.328 (15)	0.190–0.239–0.290 (20)	0.193–0.261–0.332 (15)
OL	0.080–0.084–0.090 (10)	0.082–0.103–0.137 (15)	–	0.083–0.108–0.120 (10)
OW	0.060–0.066–0.075 (10)	0.091–0.103–0.127 (15)	–	0.0065–0.088–0.116 (10)
AvZ1 (elongate)	0.075–0.079–0.080 (6)	0.036–0.093–0.127 (15)	0.080–0.096–0.120 (20)	0.069–0.102–0.137 (10)
AvW1 (elongate)	0.030–0.031–0.035 (6)	0.018–0.024–0.027 (15)	–	0.010–0.014–0.019 (10)
AvZ2 (spatulate)	0.240–0.252–0.260 (5)		–	0.246–0.305–0.357 (9)
AvW2 (spatulate)	0.060–0.063–0.065 (5)		–	0.048–0.060–0.075 (9)
OvL	0.220 (1)	0.109–0.118–0.137 (3)	0.160–0.167–0.180 (13)	0.116–0.152–0.184 (15)
OvW	0.240 (1)	0.191–0.200–0.209 (3)	0.180–0.198–0.220 (13)	0.170–0.187–0.199 (15)

Fig 12. *Parasmittina serrula* Soule & Soule, 1973, UFBA 2850 (A–D). (A) general view of a colony. (B) autozooids at the growing edge of the colony showing small elongate (orange arrow) and large spatulate (pink arrow) adventitious avicularia. (C) detail of primary orifice. (D) group of ovicelled (yellow arrow) zooids with large spatulate (pink arrow) adventitous avicularia. Scale bars: A = 500 µm; (B) D = 200 µm; C = 50 µm.

Parasmittina simpulata **Winston, Vieira & Woollacott, 2014 [22]**

(Fig 13; Tables 9)

Parasmittina simpulata Winston *et al*. [22]: 200; *Parasmittina spathulata*: Almeida *et al.* [28]: 4 (in part); ? *Parasmittina parsevaliformis* Soule & Soule [3]: 412; ? *Parasmittina barbadensis* Winston & Woollacott [45]: 262; NOT *Escharella jacotini* var. *spathulata* Smitt, [24]: 60.

Material examined. UFBA 209, UFBA 646, UFBA 716, UFBA 1112, UFBA 3266, UFBA 3619.2, UFPE 831–832, Costa dos Coqueiros, Camaçari, Bahia, Brazil, 12°48'–12°58' S, 38°06'–38°20' W, 25–30 m, coll. 1993–2004; UFBA 365, Salvador, Bahia, Brazil, 12°57'–12°59' S, 38°21'–38°23' W, 0–25 m, coll. 05/04/2012; UFBA 952, UFBA 959, UFBA 2268.3, Todos os Santos Bay, Bahia, Brazil, 12°46'–13º00' S, 38°35'–38°39' W, 0–48 m, coll. 1997–2006; UFBA 3110, UFBA 3112, UFBA 3116, Costa do Dendê, Bahia, Brazil, 13°27'–14º11' S, 38°46'–38°55' W, coll. 2012; UFBA 947, Banco Charlotte, Bahia, Brazil, 16°07' S, 38°29' W, 35 m, coll. 03/1996.

Description. Colony encrusting, initially unilaminar (Fig 13A). Autozooids (Fig 13A) subrectangular to subquadrangular, limited by slightly raised lateral walls, with a single row of 20–31 marginal pores (0.007–<u>0.019</u>–0.0040 mm in diameter; n = 30; SD = 0.007 mm). Frontal wall rugose and nodular. Primary orifice (Fig 13D) elliptical, slightly longer than wide, distal with 4–6 well-spaced minute denticles, up to 3 oral spines, lyrula narrow (0.017–<u>0.031</u>–0.038 mm wide; n = 15; SD = 0.005 mm), a pair of hooked condyles with coarsely serrated margins. Secondary orifice initially developed as two lateral short projections (Fig 13B), sometimes forming a broad U-shaped pseudosinus (Fig 13F). Adventitious avicularia variable in shapes and sizes (Figs 13B and 13F), with three morphologies: (1) small, subtriangular, avicularia (Figs 13B–13D, orange arrow), placed laterally at one side of the orifice, distally oriented, rostrum subtriangular, smooth at its lateral margins, pointed tip, palate narrow, subtriangular foramen and crossbar complete; (2) small, oblong avicularia (Figs 13B–13D, blue arrow) single or paired, placed below the secondary orifice, proximally oriented, smooth at its lateral margins, rounded tip, palate occupying about three-quarters of the rostrum length, oval foramen and crossbar complete; (3) large, spatulate avicularia (Figs 13B and 13C, red arrow), placed laterally at one side of the orifice, oriented proximally, with rostrum oblong to spoon-shaped arched upwards, palate broad occupying three-quarters of the rostrum length, foramen subtriangular to elliptical, with smooth margins and crossbar complete, with 2–3 pseudopores adjacent to the avicularia. Secondary calcification of the frontal wall can place avicularia randomly scattered on the frontal wall (i.e., around the orifice, in a suboral position and on the ovicell, Figs 13E–13F). Ovicells globose, densely surrounded by adjacent frontal wall (Figs 13E, yellow arrow); ectooecium perforated by 8–10 large pseudopores (0.007–<u>0.013</u>–0.026 in diameter; n = 30; SD = 0.004 mm). Secondary calcification around the primary orifice in ovicelled zooids forming a hood in the distal margin of the ovicell (Fig 13F, arrow).

Remarks. *Parasmittina simpulata* was originally described based on a single specimen from southeastern Brazil, being diagnosed by having primary orifice with distal denticles, serrated condyles, proximolateral small avicularia oval and subtriangular and large avicularia spatulate [22]. All these characters are observed in specimens from coral reefs and experimental plates of tiles from northeastern Brazil analyzed in this study, adding that our colonies have ovicell with large pseudopores (Figs 13E and 13F). Also, we observed that avicularia development and ovicell calcification vary between younger (Figs 13A and 13B) and older (Figs 13C and 13E) colonies.

Winston *et al*. [22] distinguished its specimen from previous Brazilian records of *P. areolata* and *P. spathulata*, as already discussed under *P. ligulata* (see above). Also, *P. simpulata* was considered very similar to the Caribbean *P. barbadensis* Winston & Woollacott [45], differing only in the large avicularia (absent in *P. barbadensis*), larger zooids of *P. barbadensis* [45] and ovicell (absent in *P. simpulata*). In turn, the original description only compared *P. barbadensis* with *P. inalienata* Tilbrook, 2006 [10] from the Pacific, based on similarities on the profile of the proximolateral avicularia, oral spines, condyles and secondary orifice, but differing in having one type of avicularium (two types in *P. barbadensis*) and distal margin of the orifice smooth (with denticles in *P. barbadensis*) [45]. Interestingly, *P. barbadensis* was also described base on a single colony fragment.

However, among all congeners, *P. simpulata* and *P. barbadensis* share all diagnostic features of frontal calcification, primary and secondary orifices and avicularia of *P. parsevaliformis* Soule & Soule, 1973 [3] from the Hawaii, with the exception of the large avicularium (absent in *P. barbadensis*) and ovicell (absent in *P. simpulata*) (Table 9). Soule & Soule [3] described differences in avicularia morphology and secondary calcification in the orifice and ovicell pending on the colonial ontogenetic development of *P. parsevaliformis*. Here we studied more than 20 specimens from northeastern Brazil and were able to see that that the avicularia development and ovicell calcification truly vary between younger (Figs 13A and 13B) and older (Figs 13E and 13F) colonies. Also, our values comprise morphometric variations seen in the three taxa – *P. simpulata*, *P. barbadensis* and *P. parsevaliformis* (Table 9). Thus, we have some evidence that the absence of ovicells and avicularia in specimens originally attributed to *P. simpulata* and *P. barbadensis*, respectively, as well as the morphometric variations, can be related to the ontogenetic stage of the studied specimens.

If *P. simpulata*, *P. barbadensis* and *P. parsevaliformis* represent a single species, an unlikely geographical distribution will be attributed, with records from Central Pacific (Hawaii) [3] and Western Atlantic (Caribbean and Brazil) [22, 45]. Not surprising, *P. parsevaliformis* was described based on specimens that were encrusting a variety of substrata including rocks, corals, shells and cement [3] and material studied here include colonies from coral reefs and experimental plates of tiles. At least the association with artificial substrata could be related with these somewhat isolated geographical records. However, until more data on these taxa are known, we choose to keep them as distinct species.

Distribution. Southwestern Atlantic: Brazil (Bahia and Rio de Janeiro) [22]; present study).

Table 9. Morphometric data of *P. simpulata*, *P. parsevaliformi*s and *P. barbadensis*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**			
	P. simpulata / holotype Winston *et al.* (2014)	*P. simpulata* / present study	*P. parsevaliformi*s / holotype in Soule & Soule (1973)	*P. barbadensis* / holotype in Winston & Woollacatt (2009)
ZL	0.450–0.585–0.684 (6)	0.396–0.618–0.867 (15)	0.500–0.600–0.700 (10)	0.655–0.804–0.892 (6)
ZW	0.324–0.360–0.396 (6)	0.218–0.413–0.560 (15)	0.320–0.385–0.480 (10)	0.400–0.510–0.637 (6)
OL	0.090–0.111–0.126 (6)	0.119–0.136–0.164 (14)	0.110–0.127–0.160 (10)	0.127–0.141–0.155 (6)
OW	0.090–0.099–0.108 (6)	0.092–0.104–0.114 (14)	0.100–0.106–0.110 (10)	0.127–0.133–0.146 (6)
AvZ1 (subtriangular)	0.162–0.447–0.612 (6)	0.086–0.131–0.188 (15)	0.140–0.168–0.200 (10)	0.127–0.133–0.146 (6)

AvW1 (subtriangular)	0.108–0.129–0.144 (6)	0.033–0.057–0.069 (15)	0.080–0.092–0.100 (10)	0.055–0.074–0.091 (6)
AvZ1 (oblong)	0.126–0.180–0.270 (6)	0.097–0.124–0.160 (15	0.080–0.111–0.140 (10)	0.127–0.176–328 (6)
AvW1 (oblong)	0.054–0.081–0.144 (6)	0.039–0.046–0.056 (15)	0.040–0.053–0.060 (10)	0.055–0.086–0.200 (6)
AvZ2 (spatulate)	–	0.302–0.451–0.553 (8)	0.310–0.360–0.390 (10)	–
AvW2 (spatulate)	–	0.100–0.126–0.156	0.120–0.174–0.200 (10)	–
OvL	–	0.199–0.226–0.254 (14)	0.200–0.215–0.240 (4)	0.237–0.267–0.291 (6)
OvW	–	0.225–0.270–0.346 (14)	0.240–0.245–0.260 (4)	0.291–0.340–0.382 (6)

Fig 13. *Parasmittina simpulata* Winston, Vieira & Woollacott, 2014, UFBA 365 (A), UFBA 1112 (B–D). A, autozooids at the growing edge of the colony showing small adventitous avicularia origin. (B) group of autozooids with small subtriangular (orange arrow), small oblong (blue arrow) and large spatulate (pink arrow) adventitious avicularia. (C) detail of autozooid showing small subtriangular (orange arrow), small oblong (blue arrow) and large spatulate (pink arrow) adventitious avicularia. (D) detail of primary orifice showing small subtriangular (orange arrow) and small oblong (blue arrow) adventitious avicularia. (E) group of ovicelled (yellow arrow) zooids. (F) detail of ovicelled zooids and secondary calcification around the ovicells. Scale bars: A = 500 µm; B, D = 100 µm; C, F = 200 µm; E = 250 µm.

Parasmittina winstonae **Liu in Liu, Yin & Ma, 2001 [50]**

(Fig 14; Table 10)

Parasmittina winstonae Liu *et al.* [50]: 801; *Parasmittina winstonae*: Tilbrook, [10]: 156; *Parasmittina winstonae*: Taylor & Tan [62] 19; *Parasmittina loxoides* Winston *et al*. [22]: 202; *Parasmittina loxoides*: Almeida *et al*. [63]: 409.

Material examined. UFPE 545–554, UFBA 2159, UFBA 1619, UFBA 1621, UFBA 1622, UFBA 1627, UFBA 1628, UFBA 1652, UFBA 1661, UFBA 2846, UFBA 3316–3344, Todos os Santos Bay, Ilha de Itaparica, Itaparica, Bahia, Brazil, 12º52'–12º53' S, 38°41' W, 38°40'–38°41' W, intertidal, coll. 2012–2015; UFBA 2852, Todos os Santos Bay, Porto da Barra, Salvador, Bahia, Brazil, 13°00' S, 38°32' W, 24 m, coll. 07/2017, UFBA 575, UFBA 2847–2849, Costa dos Coqueiros, Camaçari, Bahia, Brazil, 12°45–'12°49' S, 38°06–'38°10' W, 22–27 m, coll. 1997–2002, UFBA 697, UFBA 2863, Costa do Dendê, Bahia, Brazil, 13°56' 'S, 38°59' W, 30 m, coll. 2002; UFPE 641–644, UFBA 3028, Praia do Francês, Marechal Deodoro, Alagoas, Brazil, 9º46' S, 35º50' W, coll. 03/02/2003– 22/02/2019; UFPE 651, Jatiuca, Maceio, Alagoas, Brazil, 9º39'10"S, 35º41'40"W, coll. 15/10/2005; MZUSP Uncatalogued PE26, UFPE 579, Porto de Suape, Cabo de Santo Agostinho, Pernambuco, Brazil, 8°23'04"–8°24'04" S, 34°57'45" W, coll. 01/08/2020; UFPE 621, UFPE 649 Barra de Catuama, Goiana, Pernambuco, Brazil, 7°39'18" S, 34°49'27" W; UFBA 3072, Pontas de Pedra, Goiana, Pernambuco, Brazil, 07°37' S, 38°48' W, intertidal, coll. 20/02/2015, UFPE 343, UFPE 645–646, Porto do Cabedelo, Cabedelo, Paraíba, Brazil, 6º58' S, 34º50'W, intertidal, coll. 27/09/2009; UFPE 274, Saco da Pedra, coll. 16/09/2004; UFPE 340, Amores, 22/09/ 2006; UFBA 3034.2, UFBA 3453.5, UFBA 3485.1, UFBA 3806–3808, UFBA 3810.4 UFBA 3813–3814, UFBA 3817.5, UFBA 3921, UFBA 3924–3925, UFBA 3928–3929, UFBA 3955.3, UFBA 3959.3, UFBA 3964.7, UFBA 3966.3, UFBA 3981.4, Todos os

Santos Bay, Salvador, Bahia, Brazil, 12°99’S, 38°53’W, 3–5 m, coll. 2012, MZUSP 887, Santos, São Paulo, Brazil.

Description. Colony encrusting, unilaminar, autozooids (Fig 14A) subrectangular to polygonal, limited by slightly raised lateral walls, with a single row of 25–30 large marginal pores. Frontal wall slightly rugose and nodular. Primary orifice (Fig 14B) elliptical, slightly longer than wide, anter smooth, 1–2 oral spines, lyrula narrow (0.020–0.041 mm wide), and a pair of hook-shaped condyles with coarsely serrated tips. Secondary orifice low (Fig 14D), forming two lateral short projections. Adventitious avicularia variable in shapes and sizes (Figs 14B and 14F), with three morphologies: (1) small, subtriangular avicularia (Figs 14C and 14D, orange arrow), placed laterally to the orifice and distally oriented in autozooids, with a suboral or randomly arranged in ovicelled and adjacent zooids (Figs 14E–14F), rostrum subtriangular, smooth at its lateral margins, pointed tip, palate narrow, elliptical foramen and crossbar complete; (2) small, spatulate avicularia (Figs 14B and 14C, green arrow), placed in zooidal margins, commonly replacing a marginal pore; (3) large, spatulate avicularia (Figs 14B and 14C, red arrow), placed laterally at one side of the orifice, oriented distally, palate broad occupying half of the rostrum length, foramen subtriangular to elliptical, with smooth margins and crossbar complete, with 2–3 pseudopores adjacent to the avicularia. Ovicell (Figs 14E–14F) densely surrounded by adjacent frontal wall, soon becoming immersed in the frontal calcification; ectooecium perforated by 20–32 medium-sized pores, (0.004–0.016 mm in diameter).

Remarks. Almeida *et al.* [63] redescribed *P. loxoides* Winston, Vieira & Woollacott, 2014 [22] based on specimens from Bahia, characterized by having subrectangular to polygonal autozooids with large marginal pores (Fig 14A), 1–2 oral spines (Figs 14B and 14D), narrow and short lyrula, condyles with serrated margins.

The latero-oral and marginal adventitious avicularia were characterized by Almeida *et al.* [63], as three types of avicularia (Figs 14B–14D): small, subtriangular; small, obovate; large, spatulate (Fig 14C), and ooecium with small ectooecial pseudopores (Figs 14E and 14F). A diagnostic feature of this species was the large avicularia distally directed [63]. We noted, however, morphological similarities between specimens assigned to *P. loxoides* from Brazil and *P. winstonae,* originally described from China by Liu *et al.* [50], including the large spatulate distolateral avicularia and the morphometric characteristics of the specimens (Table 10) (see also [10, 62], that allow us to synonymize *P. loxoides* under *P. winstonae*.

Among all congeners, *P. winstonae* most resembles *Parasmittina californica* (Robertson, 1908) [64], *Parasmittina collifera* (Robertson, 1908) [64] and *Parasmittina regularis* Soule & Soule, 2002 [8] in having three types of avicularia - lateral, marginal and large, the large being distally directed. However, these species are readily distinguished from *P. winstonae* by having large avicularium with subtriangular profile and an acute rostrum (large avicularium of *P. winstonae* is spatulate with a rounded tip).

As other species described here, *P. winstonae* have an unexpected geographic distribution in the Indo-Pacific and Southwestern Atlantic [10, 22, 50, 62–63]. Colonies studied here are from natural and artificial substrata from northeastern to southeastern Brazil, which include common association with bivalve shells of *Plicatula gibbosa* Lamarck, 1801 and *Pinctada imbricata* Roding, 1798 [50, 62–63]. Specimens from Malaysia were encrusting shells on a rope hanging from jetty [58], indicating that a passive dispersal (phoresy) is not unlikely and could be related with the distributional range of *P. winstonae*.

Distribution. Indo-Pacific: China, Islands Solomon and Malaysia (10, 50, 62); Southwestern Atlantic: Brazil (Paraíba, Pernambuco, Alagoas, Bahia, Rio de Janeiro and São Paulo) [22, 63]; present study).

Table 10. Morphometric data of specimens here assigned to *Parasmittina winstonae*. Values represented as minimum–median–maximum (number of zooidal measures). All values in millimeters.

Morphological character	**Taxa / reference**					
	P. winstonae / holotype in Liu *et al*. (2001)	*P. winstonae* / present study	*P. winstonae* / Tilbrook (2006)	*P. winstonae* / Taylor & Tan (2015)	*P. loxoides* / holotype in Winston *et al*. (2014)	*P. loxoides* / Almeida *et al*. (2018)
ZL	0.440–0.660 (10)	0.304–0.530 (15)	0.450 (?)	0.320–0.450 (?)	0.306–0.396 (6)	0.344–0.561 (15)
ZW	0.280–0.420 (10)	0.241–0.424 (15)	0.300 (?)	0.220–0.330 (?)	0.216–0.270 (6)	0.160–0.358 (15)
OL	0.140–0.160 (10)	0.121–0.154 (10)	0.110 (?)	0.100–0.110 (?)	0.081–0.099 (6)	0.113–0.117 (15)
OW	0.100–0.110 (10)	0.073–0.127 (10)	0.110 (?)	0.100 (?)	0.090–0.108 (6)	0.084–0.126 (15)
AvZ1 (subtriangular)	0.102–0.144 (10)	0.069–0.132 (15)	–	0.090–0.120 (?)	0.108–0.126 (4)	0.090–0.116 (15)
AvW1 (subtriangular)	0.058–0.124 (10)	0.032–0.058 (15)	–	0.050–0.060 (?)	0.054–0.054 (4)	0.051–0.061 (15)
AvZ2 (spatulate)	0.270–300 (10)	0.386–0.444 (2)	–	0.350–0.400 (?)	–	0.237–0.360 (15)
AvW2 (spatulate)	0.130–0.150 (10)	0.055–0.074 (2)	–	0.110–0.130 (?)	–	0.069–0.097 (15)
AvZ3 (obovate)	0.062–0.124 (10)	0.041–0.076 (15)	–	0.050–0.060 (?)	–	0.051–0.083 (15)
AvW3 (obovate)	0.042–0.082 (10)	0.032–0.058 (15)	–	0.050–0.080 (?)	–	0.035–0.052 (15)
OvL	0.205–0.225 (10)	0.172–0.208 (15)	–	0.130–0.160 (?)	0.162–0.198 (6)	0.131–0.200 (15)
OvW	0.212–0.292 (10)	0.205–0.273 (15)	–	0.180 (?)	0.234–0.270 (6)	0.154–0.237 (15)

Fig 14. *Parasmittina winstonae* Liu in Liu, Yin & Ma, 2001, UFBA 2159.2 (A, B), UFBA 3028 (C–F). (A) group of young autozooids. (B) detail of autozooid showing small spatulate (green arrow) and large spatulate (pink arrow) adventitious avicularia.

(C) autozooids with small subtriangular (orange arrow), small spatulate (green arrow) and large spatulate (pink arrow) adventitious avicularia. (D) detail of orifice showing small subtriangular (orange arrow) and small spatulate (green arrow) adventitious avicularia. (E) group of ovicelled zooids. (F) detail of ovicelled zooids. Scale bars: A, E = 500 µm; B, F = 200 µm; C = 250 µm; D = 100 µm.

***Parasmittina falciformis* n. sp.**

(Fig 15)

Parasmittina munita: Almeida *et al.* [28]: 4. NOT *Smittina trispinosa* var. *munita*: Marcus, [26]: 108; NOT *Smittina trispinosa* var. *munita*: Marcus, [41]: 44; NOT *Parasmittina munita*: Vieira *et al*. [27]: 26; NOT *Smittia trispinosa* var. *munita* Hincks, [23]: 284.

Material examined. *Holotype*: UFBA 714.1, Camaçari, Bahia, Brazil, 12°49'35.0" S, 38°05'04.2" W, 50 m, coll. 07/2004. *Paratypes*: UFBA 314, Costa do Descobrimento, Banco Charlotte, Bahia, Brazil, 16°07' S, 38°29'W, 35 m coll. 03/1996; UFBA 953, Baía de Todos os Santos, Bahia, Brazil 12°49 'S, 38°37' W, coll. 27/05/1997; UFBA 948, Baía de Todos os Santos, Bahia, Brazil 12°56' S, 38°33' W, coll. 29/05/1997. *Additional specimens*: UFBA 3100 Banco Besnard, Espírito Santo, Brazil, 19°40' S, 38°08' W, coll. 04/1996; UFBA 3073 UFBA 3130.3, Ilhas Rasas, Guarapari, Espírito Santo, Brazil, 20°40' S, 40°21' W, 11–15 m, coll. 27/03/2017; UFBA 3133, UFBA 3135, UFBA 3263, Ilha Escalvada, Guarapari, Espírito Santo, Brazil, 20°41'59.0'S, 40°24'25.2"W, 15m, coll. 29/03/2017.

Etymology. Alluding to the profile of the avicularium, falciform (hooked), as previously stated by Marcus (1937).

Description. Colony encrusting, uni to multilaminar. Autozooids (0.308–0.427–0.545 mm length; n= 15; SD= 0.071 mm; 0.266–0.342–0.470 mm wide; n= 15; SD= 0.067 mm), (Fig 15A and 15B) subrectangular to subquadrangular, limited by slightly raised lateral walls, surrounded by a single row of 14–24 marginal pores (0.011–0.025–0.052 mm in diameter; n = 30; SD = 0.010 mm). Frontal wall with several rounded nodules (Figs 15A and 15B). Primary orifice (0.094–0.118–0.158 mm length; n= 15; SD= 0.018 mm; 0.088–0.101–0.115 mm wide; n=15; SD= 0.007), (Fig 15D) elliptical, longer than wide, distal margin smooth, 1–2 oral spines, lyrula large (0.046–0.054–0.060 mm wide; n = 15; SD = 0.004 mm), comprising three-quarters of the orificial width, a pair of hooked condyles with serrated margins. Secondary orifice forming 2 proximolateral flaps and resulting in a pseudosinus (Fig 15B and 15D), larger in ovicelled zooids (Fig 13E). Adventitious avicularia variable in shapes and sizes (Fig 15B), with two morphologies: (1) small to moderate in size (0.145–0.156–0.173 mm in length; n = 4; SD = 0.015 mm; 0.055–0.064–0.069 mm in wide; n = 4; SD = 0.007 mm), subtriangular avicularia (Fig 15B, orange arrow), with hooked tip and large foramen, placed distolaterally to the orifice, with rostrum oriented proximolaterally; (2) large avicularia (Fig 15B and 15C, red arrow), (0.361–0.403–0.471 mm in length; n = 15; SD = 0.036 mm; 0.077–0.0.090–105 mm in wide; n = 15; SD = 0.008 mm), reaching almost the entire zooidal length, profile subpatulate, broad palate, occupying about half rostrum, foramen elliptical, rostrum subtriangular, with smooth margins, hooked tip and crossbar complete; 3–6 pseudopores adjacent to the avicularia, placed distolaterally to the orifice with rostrum oriented proximally. Ovicells (Figs 15E and 15F) globose, densely surrounded by adjacent frontal wall (Fig 15F, black arrow);

ectooecium perforated by 25–30 medium-sized pseudopores (0.003–0.007–0.012 in diameter; n = 30; SD = 0.002 mm) distributed through the entire ovicell surface.

Remarks. Specimens of *Parasmittina falciformis* n. sp. from northeastern Brazil studied here were previously attributed to *P. munita* [28] that was originally described by Hincks [23] based on colonies from Australia (28). These species can be distinguished, however, by the number of spines (three in *P. munita* and up to two in *Parasmittina falciformis* n. sp.) pseudosinus of secondary orifice (deep in *P. munita* and shallow in *Parasmittina falciformis* n. sp.) and profile of the large adventitious avicularia (oblong in *P. munita* and subtriangular in *Parasmittina falciformis* n. sp.).

However, some specimens of *Parasmittina* from southeastern Brazil were also attributed to *Smittina trispinosa* var. *munita* by Marcus [26, 41]. Although these specimens have adventitious and interzooidal avicularia similar to that of *P. falciformis* n. sp., differences among these taxa include the number of oral spines (3 in specimens from Marcus and 2 in *P. falciformis* n. sp), secondary orifice (shorter in *P. falciformis* n. sp.), pseudosinus (shallower in *P. falciformis*), rostrum of the small adventitious avicularia (straight in specimens from Marcus and curved in *P. falciformis* n. sp.). Moreover, specimens studied by Marcus [26, 41] have also a large interzooidal avicularia, not observed in *P. falciformis* n. sp. Thus, here we consider that *Smittina trispinosa* var. *munita* described by Marcus [26, 41] represent a distinct taxon than *P. munita* and *P. facilformis*.

Other species of *Parasmittina* with same set of adventitious avicularia of *P. falciformis* n sp., are *P. aculeata* Tilbrook, 2006 [10], *P. alanbanneri* Soule & Soule, 1973 [3] *P. aotea* (Brown, 1952) [68] and *P. recidiva* Hayward, 1988 [15]. Differences between species includes the number of oral spines (3 in *P. aotea* and *P. recidiva*, 3–6 in *P. alanbanneri* and 1–2 in *P. aculeata* and *P. falciformis* n. sp); condyles (thin in *P.*

aculeata and P. recidiva and robust in. *P. alanbanneri, P. aotea* and *P. falciformis* n. sp.); lyrula (narrow in *P. aotea*, *P. recidiva* and larger in *P. aculeata*, *P. alanbanneri* and *P. falciformis* n. sp.) and margins of the large avicularia (serrated in *P. aculeata* and *P. recidiva* and smooth in *P. aotea*, *P. alanbanneri* and *P. falciformis* n. sp.). Also, the combination of primary orifice with large lyrula, smooth distally, 1–2 oral spines, serrated condyles with hooked tips and two types of avicularia distinguishes *P. falciformis* n. sp. from all congeners.

Distribution. Southwestern Atlantic: Brazil (Bahia, Espírito Santo and São Paulo) [28, 27]; present study).

Fig 15. *Parasmittina falciformis* n. sp., UFBA 714 (holotype, A–B, D–F) UFBA 953 (paratype, C). (A) group of young autozooids. (B) detail of autozooid showing small subtriangular (orange arrow) and large lanceolate (pink arrow) adventitious avicularia. (C) autozooids with large lanceolate (pink arrow) adventitious avicularia. (D) detail of primary orifice. (E) group of ovicelled zooids. (F) detail of ovicelled zooids. Scale bars: A = 250 µm; B, E, F = 200 µm; C = 500 µm; D = 50 µm.

Discussion

Historically, the morphology and position of the avicularia were considered the main morphologic characteristics to distinguish different *Parasmittina* species, while some other morphological structures (e.g., primary orifice and ovicells) were overlooked [8]. As pointed by Soule & Soule [3, 8], combined morphology of structures such as avicularia, primary orifice (i.e., distal margin, condyles and lyrula) and ovicells, allow distinguishing taxa considered to have an uncommon geographic distribution, such as *P. trispinosa*. However, as showed in this paper, species of *Parasmittina* have been poorly characterized, often based on single colony fragments, and they are not properly compared with congeners or also with type specimens. Thus, among the eleven species of *Parasmittina* reported from the Southwestern Atlantic prior to this study, four were not recognized in this paper – *P. betamorphaea*, *P. munita*, *P. spathulata* and *P. trispinosa*. Previous records of these taxa to the area [26, 27, 28, 41, 65] were not properly characterized and the review of these including analysis of original descriptions of the four species and study of additional specimens from SW Atlantic showed that they truly belong to different taxa. For instance, *P. betamorphaea* is here recognized as part of a species complexes involving the congeners *P. alba* and *P. lavela*; part of the records of *P. munita* [27, 28, 40] is assigned to a *P. falciformis* n. sp. and other records still need review [26, 41]; reports of *P. spathulata* comprise at least two taxa including *P. abrolhosensis* and *P. simpulata*; *P. trispinosa* is assigned to *P. pinctatae.*

Our study also highlighted that there are more than one applicable species name to the same combination of morphological and morphometric characters (i.e., *P. alba*, *P. betamorphea* and *P. lavela*; *P. distincta*, *P. egyptiaca*, *P. floridana* and *P. glomerata*; *P. longirostrata* and *P. serruloides*; *P. simpulata*, *P. barbadensis* and *P. parsevaliformis*). Indeed, variations observed among these taxa include characters that may differ pending on habitat and colonial development and that can represent intraspecific variations rather than different species. Studies including more colonies and other biological data, especially molecular analysis, are needed to help to elucidate the taxonomic identity of these taxa. Thus, in order to prevent to erect new names and new synonymies based on characters that can be considered as intraspecific variations, here we choose to discuss and indicate the occurrence of species complex in

Parasmittina, attributing the most appropriate available name to the studied Brazilian specimens and attempting to maintain some taxonomic stability in the genus.

Interestingly, here we noticed that morphology of the primary orifice provides most reliable taxonomic characters than only the avicularia itself to distinguishes *Parasmittina* species (Fig 16), as previously pointed out by Tilbrook (2006) [10] in specimens from Indo-Pacific. In this sense, analysis including colonies with different astogenetic series, added with characterization of primary orifice, avicularia and ovicell, are strongly required for a reliable taxonomic assignment (i.e., [3, 6, 8, 11, 13, 17, 45].

Fig 16. Primary orifices of the studied *Parasmittina* species. (A) *Parasmittina abrolhosensis*, (B) *Parasmittina alba*, (C) *Parasmittina bimucronata*, (D) *Parasmittina distincta*, (E) *Parasmittina dubitata*, (F) *Parasmittina longirostrata*, (G) *Parasmittina pinctatae*, (H) *Parasmittina egyptiaca*, (I) *Parasmittina serrula*, (J) *Parasmittina simpulata*, (K) *Parasmittina winstonae*, (L) *Parasmittina falciformis* n. sp. Scale bars: A = 50 µm.

Although presence of new species of *Parasmittina* described to Brazil [18, 19, 22], there are no review on historical records on species of that genus in the area. Based on detailed comparison between *Parasmittina* species described from the Southwestern Atlantic and some their congeners (Table 11), we were able to elucidate the identity of specimens studied by Marcus [16, 60] previously attributed *P. nitida* and *P. loxa*, belong to *P. pinctatae* and *P. winstonae* (Fig 17), respectively. Specimens attributed to *P. trispinosa* by Luederwaldt [55] belong to *P. pinctatae* and the record of *P. areolata* [18] is attributed to *P. abrolhosensis*. Additionally, the species recently described as *P. loxoides* is here synonymized under *P. winstonae*, originally described from China.

Fig 17. *Parasmittina* species from Brazil studied by Marcus (1937, 1938, 1939). (A) *Smittina trispinosa*, Marcus, E. det. (1937). (B) *Smittina trispinosa* var. *munita*, Marcus, E. det. (1937) = *Parasmittina bimucronata* (Hincks, 1884b). (C) *Smittina trispinosa* var. *nitida*, Marcus, E. det. (1937) = *Parasmittina pinctatae* Liu in Liu, Yin & Ma, 2001. (D) *Smittina trispinosa* var. *munita* Marcus, E. det. (1937) = *Parasmittina* sp. (E) *Smittina trispinosa* var. *loxa* Marcus, E. det. (1939) = *Parasmittina winstonae* Liu in Liu, Yin & Ma, 2001.

Table 11. Tabular identification key of *Parasmittina* species from the Atlantic Ocean. Present (+) and absent (–), as long as wide (L=W), longer than wide (L>W), wider than long (W/L), number, (N), unknown states (?). The lyrula information correspond to the lyrula width in relation to the orifice width. Species marked with an asterisk correspond to taxa previously attributed to Brazilian specimens.

Species	**Type Locality**	**Primary orifice**				**Adventitious avicularia**				**Ovicell**	
		Distal margin	**Spines (N)**	**Condyles**	**Lyrula**	**Distolateral**	**Proximolateral**	**Marginal**	**Profile**	**Profile**	**Pseudopores (N)**
P. abrolhosensis Ramalho *et al.* 2018	Atlantic (Brazil)	smooth	3–4	serrated	one–quarter	–	elongate	subtriangular	spatulate	W>L	18–25
P. alba Ramalho *et al.* 2011	Atlantic (Brazil)	smooth	1–3	smooth	half	–	subtriangular / oblong	–	spatulate	W>L	20–22
P. areolata (Canu & Bassler, 1927) *	Pacific (Hawaii)	smooth	2	robust / serrated	one–quarter	subtriangular	thin elongate	subtriangular	spatulate	W>L	32
P. bimucronata (Hincks, 1884b)	Indian (India)	smooth	1–2	?	one–quarter	–	subtriangular / oblong	–	sublanceolate	W>L	18 or >
P. distincta Ramalho *et al.* 2018	Atlantic (Brazil)	beaded	2–4	serrated	half	–	oblong / subtriangular		sublanceolate	W<L	20–37
P. dubitata Hayward, 1980	South Atlantic	smooth	2–3	?	half	–	oblong	spatulate	sublanceolate	?	10–13
P. echinata (Canu & Bassler, 1928b)	Caribbean (Gulf of Mexico)	?	?	?	?	subtriangular	–	–	–	?	?
P. floridana Winston, 2005	Atlantic (EUA)	beaded	2–3	smooth	half	–	subtriangular / oblong	–	–	L>W	16
P. glomerata (Thornely, 1912)	Indian (Cargados)	beaded	1–2	serrated	half	–	oblong	oblong	sublanceolate	W>L	?
P. indiginella Winston, 2016	Floridan (EUA)	smooth	5–6	?	three–quarters	thin elongate	–	thin elongate	–	W>L	22–25
P. labellum (Canu & Bassler, 1928b)	Caribbean (Gulf of Mexico)	?	2	?	one–quarter	–	subtriangular / oblong	oblong	spatulate	?	?
P. ligulata (Ridley, 1881)	Atlantic (Brazil)	smooth	?	serrated	one–quarter	–	thin elongate / subtriangular	subtriangular	?	W>L	6–10
P. longirostrata Liu in Liu, Yin & Ma, 2001	Pacific (China)	smooth	3–4	serrated	half	–	thin elongate	–	sublanceolate	W>L	18–24
P. loxa (Marcus, 1937b)	Atlantic (Santa Helena Island)	smooth	2–4	?	?	subtriangular	oblong	–	spatulate	?	?

Species	**Type Locality**	**Primary orifice**				**Adventitious avicularia**				**Ovicell**	
		Distal margin	**Spines (N)**	**Condyles**	**Lyrula**	**Distolateral**	**Proximolateral**	**Marginal**	**Profile**	**Profile**	**Pseudopores (N)**
P. mexicana Pouyet & Herrera–Anduaga, 1986	Caribbean (Gulf Mexico)	?	2	?	?	subtriangular	subtriangular	subtriangular	spatulate	?	> than 20
P. multiaviculata Souto *et al.*, 2016	Atlantic (Portugal)	smooth	1–2	smooth	one–quarter	–	–	oblong	–	W>L	about 30
P. munita (Hincks, 1884) *	Indo–Pacific (Australia)	?	?	?	?	–	oblong	–	sublanceolate	?	?
P. natalensis O'Donoghue, 1957	Atlantic (South Africa)	smooth	2	smooth	half	–	oblong	–	–	?	?
P. nitida (Verrill, 1875)	Atlantic (EUA)	smooth	2	?	one–quarter	–	subtriangular / oblong	subtriangular / oblong	–	W>L	7–24
P. novella Hayward & Cook, 1983	South African	?	2–4	smooth	one–quarter	–	thin elongate	–	spatulate / sublanceolate	?	16–22
P. oculinae Winston, 2016	Floridan (EUA)	smooth	2	smooth	one–quarter	elliptical / subtriangular	–	–	–	W>L	34–44
P. pinctatae Liu in Liu, Yin & Ma, 2001	Pacific (China)	smooth	1–2	serrated	one–quarter	subtriangular	subtriangular	oblong	spatulate	W>L	> than 20
P. simpulata Winston *et al.* 2014	Atlantic (Brazil)	beaded	2–3	robust	one–quarter	subtriangular	oblong	–	spatulate	W>L	8–10
P. serrula Soule & Soule, 1973	Hawaii (EUA)	beaded	3–6	robust	one–quarter	–	thin elongate	subtriangular	spatulate	W>L	12 or >
P. spathulata (Smitt, 1873)	Florida (EUA)	?	2–4	?	half	–	thin elongate	–	spatulate	?	?
P. talismani (Calvet, 1907)	Atlantic (Africa)	smooth	4–5	smooth	three–quarters	oblong	–	oblong	–	W=L	20–35
P. trispinosa (Johnston, 1838) *	(Berwick Bay, United Kingdom)	smooth	2–3	smooth	one–quarter	–	oblong	oblong	subtriangular	W>L	2–4
P. winstonae Liu in Liu, Yin & Ma, 2001	Pacific (China)	smooth	1–2	serrated	one–quarter	subtriangular	–	spatulate	spatulate	W>L	20–32
Parasmittina falciformis n. sp.	Atlantic (Brazil)	smooth	1–2	serrated	three–quarters	–	subtriangular	–	subspatulate	W=L	25–30

Among the 11 species recognized to Brazil (Fig 18), six species were originally described in the area (*P. abrolhosensis*, *P. alba*, *P. distincta*, *P. ligulata*, *P. simpulata* and *P. falciformis* n. sp.), from which at least three, *P. alba*, *P. distincta* and *P. simpulata*, are here recognized as part of species complexes that need further investigations. The remaining five species are mainly known from the Indo–Pacific. Thus, due the unexpected occurrence of *P. bimucronata*, *P. longirostrata*, *P. pinctatae*, *P. serrula* and *P. winstonae* in the Atlantic, we evaluated the exotic status of these species [29–30, 31– 32] (Table 12). Thus, two species were assigned as exotic in SW Atlantic (*P. longirostrata* and *P. serrula*) and the other three were considered cryptogenic (*P. bimucronata*, *P. pinctatae* and *P. winstonae*). The exotic status of *P. longirostrata* and *P. serrula* was based on the same six attributes. At least specimens of *P. serrula* was already reported in artificial substrata from the Caribbean and considered opportunistic in that region [42], but ecological impacts on that species in SW Atlantic are still unknown.

Fig 18. Distribution of *Parasmittina* species studied along the Brazilian coast. Symbols: black circle, *Parasmittina abrolhosensis* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018; white circle, *alba* Ramalho, Muricy & Taylor, 2011; black square, *Parasmittina bimucronata* (Hincks, 1884b); white square, *Parasmittina distincta* Ramalho, Taylor, Moraes, Moura, Amado-Filho & Bastos, 2018; black triangle, *Parasmittina ligulata* (Ridley, 1881); white triangle, *Parasmittina longirostrata* Liu in Liu, Yin & Ma, 2001; grey circle, *Parasmittina pinctatae* Liu in Liu, Yin & Ma, 2001; grey square, *Parasmittina serrula* Soule & Soule, 1973; grey triangle, *Parasmittina simpulata* Winston, Vieira & Woollacott, 2014; black star, *Parasmittina winstonae* Liu in Liu, Yin & Ma, 2001; grey star, *Parasmittina falciformis* n. sp.

Table 12. Correspondence of Chapman and Carlton (1991, 1994) criteria to classify *Parasmittina* species from Brazil as exotic, with the respective number of positive/negative criteria used. 0, criterion not applicable due to lacking data; +, criterion applied positively to exotic status; −, criterion applied negatively to exotic status. N = number of attributes applied positively/negatively. Local criteria: 1 = local appearance where not found previously, 2 = local dispersal after introduction, 3 = association with human mechanisms of dispersal, 4 = prevalence or restriction to new or artificial environment, 5 = restricted distribution when compared to ecologically similar native species. Global criteria: 6 = widespread geographic distribution with isolated populations, 7 = active and passive dispersal mechanisms incapable of achieving the current distribution, 8 = exotic evolutionary origin. Status: E = exotic, C = cryptogenic, Na = native. Criteria applied based on Almeida *et al.* (2015c) and Miranda *et al.* (2018).

Species	**Local criteria**					**Global criteria**			**N**	**Status**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**		
P. bimucronata	−	0	0	−	+	+	+	0	3/2	C
P. longirostrata	+	0	+	+	+	+	+	0	6/0	E
P. pinctatae	−	0	+	−	−	+	+	0	3/3	C
P. serrula	+	0	+	+	+	+	+	0	6/0	E
P. winstonae	−	0	+	−	−	+	+	0	3/3	C

All species here classified as cryptogenic, *P. bimucronata*, *P. floridana*, *P. alba*, *P. pinctatae* and *P. winstonae*, were previously misidentified and thus their occurrences on the Brazilian coast are prior than this study [18–19, 22, 25, 28, 39–40, 55, 63, 65]. Here, these species were collected in artificial surfaces but also on natural rigid substrata such as shells, calcareous nodules and coral reefs. Also, all have a broad distribution along the Brazilian coast with records from northeastern to southeastern Brazil (Fig 18).

Smittinidae fauna from different regions of the world are commonly composed by species recognized as exotic, cryptogenic or species complexes (e.g., [6, 11, 13]). Here we found this same trend. As already noticed in recent studies [29–30, 66], some Brazilian regions, especially close to harbors areas, hosts a higher diversity of non-indigenous species than previously known. Integrative studies, using molecular tools and ecological approaches are recommend to reveal the identity, origin and possible impacts of these species in the environment [30–31, 66].

Acknowledgments

We are grateful to Centro de Pesquisa Gonçalo Moniz (FIOCRUZ/BA), JoAnn Sanner from the Smithsonian Institution’s National Museum of Natural History (USA) and Mary Spencer-Jones from the Natural History Museum, London (NHMUK), Björn Berning, Joachin Scholz and Carsten Lüter from the Museum für Naturkunde, Berlin (MFN), for providing SEM images. We also thank Programa de Pós-Graduação em Biologia Animal of the Universidade Federal de Pernambuco (PPGBA/UFPE) for logistical support. Funding was provided to A.C.S. Almeida by the Fundação de Amparo a Ciência e Tecnologia do Estado de Pernambuco (BFP-FACEPE 0092-2.04/19), Conselho Nacional de Pesquisa (PDJ-CNPq 152608/2018-4 and Chamada MCTIC/CNPq Nº 28/2018 – Universal/Faixa A, Process N. 28/2018 424685/2018-3) and Programa Refauna (MCTIC/SIBBr/CTFB). J. Farias was supported by the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB Nº BOL0431/2019, PEDIDO Nº 659/2019) and L.M. Vieira was by CNPq (Process N. 308768/2018-3).

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001.

References

1. Levinsen G.M.R. Morphological and systematic studies on the cheilostomatous Bryozoa Nationale Forfatterers Forlag, Copenhagen. 1909; 1–431.
2. Vieira LM, Nascimento KB, Almeida ACS. Bryozoa in Catálogo Taxonômico da Fauna do Brasil. PNUD. Accessed through: https://fauna.jbrj.gov.br/fauna/faunadobrasil/ in 2021–01–18.
3. Soule DF, Soule JD. Morphology and speciation of Hawaiian and eastern Pacific Smittinidae (Bryozoa, Ectoprocta). Bull Am Mus Nat Hist. 1973; 152(6): 365–440
4. Osburn RC. Bryozoa of the Pacific coast of America, Part 2. Cheilostomata, Ascophora. R Allan Hancock Pac Exp. 1952; 14: 271–611.
5. Norman A. Notes on the natural history of East Finmark, Polyzoa. Ann Mag Nat Hist. 1903; 7, 11: 567–598.
6. Farias J, Souza FBC, Vieira LM, Almeida ACS. On some Smittinidae (Bryozoa, Cheilostomata) from Bahia, northeastern Brazil, with the description of a new species. Mar Biodivers. 2020; 50(5) 1–17. doi: 0.1007/s12526–020–01088–2
7. Denisenko NV. New species of the genus *Parasmittina* (Bryozoa: Cheilostomata: Smittinidae) from the Chukchi Sea. Zoosyst Ross. 2015; 24(2): 300–306.
8. Soule DF, Soule JD. The Eastern Pacific *Parasmittina trispinosa* Complex (Bryozoa, Cheilostomatida): New and Previously Described Species. Irene McCulloch Foundation Monograph series. 2002; 5: 1–40.

9. Winston JE. Redescription and revision of Smitt's "Floridan Bryozoa' in the Collection of the Museum of Comparative Zoology, Harvard University. Virginia Mus Nat Hist Mem. 2005; 7: 1–150.

10. Tilbrook KJ. Cheilostomatous Bryozoa from the Solomon Islands. Santa Barbara Museum of Natural History Monographs 4 (Studies in Biodiversity Number 3). 2006; 1–386.

11. Harmelin J–G, Bitar G, Zibrowius H. Smittinidae (Bryozoa, Cheilostomata) from coastal habitats of Lebanon (Mediterranean Sea), including new and non–indigenous species. Zoosystema. 2009; 31(1): 163–187.

12. Dick MH, Grichensko AV. Rocky–intertidal cheilostome bryozoans from the vicinity of the Sesoko Biological Station, west– central Okinawa, Japan. J Nat Hist. 2017; 51: 3–4. doi: 10.1080/00222933.2016.1253797.

13. Souto J, Ramalhosa P, Canning–Clode, J. Three non–indigenous species from Madeira harbors, including a new species of *Parasmittina* (Bryozoa). Mar Biodiv. 2016; 1–10. doi: 10.1007/s12526–016–0592–0

14. Baradari H, Nasrolahi A, Taylor, PD. Cheilostome Bryozoa of the northern Persian Gulf, Iran. Zootaxa. 2019; 4619 (3): 459–486. doi: 10.11646/zootaxa.4619.3.3

15. Hayward PJ. Mauritian Cheilostome Bryozoa. J Zoo London. 1988; 215: 269–356.

16. Moyano HI. Magellanic Bryozoa: some ecological and zoogeographical aspects. Marine Biology. 1982; 67: 81–96.

17. Gordon DP. The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. New Zealand Oceanographic Institute Memoir. 1984; 91, 1–198.

18. Ramalho LV, Taylor PD, Moraes FC, Moura R, Amado–Filho GM, Bastos AC. Bryozoan framework composition in the oddly shaped reefs from Abrolhos Bank, Brazil, southwestern Atlantic: taxonomy and ecology. Zootaxa. 2018; 4483(1): 155–186. doi: 10.11646/zootaxa.4483.1.6

19. Ramalho L V, Muricy G, Taylor PD. Taxonomic revision of some lepraliomorph cheilostome bryozoans (Bryozoa: Lepraliomorpha) from Rio de Janeiro State, Brazil. J Nat Hist. 2011; 45(13–14): 767–798

20. Hayward PJ. Cheilostomata (Bryozoa) from the South Atlantic. J Nat Hist. 1980; 14: 701–722.

21. Ridley S O. Polyzoa, in Account of the zoological collections made during the survey of H.M. "Alert" in the Straits of Magellan and on the coast of Patagonia. Proc Zool Soc Lond. 1881; 1881: 44–61.

22. Winston JE, Vieira LM, Woollacott RM. Scientific results of the Hassler expedition. Bryozoa. No. 2. Brazil. Bull Mus Comp Zool. 2014; 161: 139–239. doi: 10.3099/MCZ14.1

23. Hincks T. Contributions towards a General History of the Marine Polyzoa. XIII. Polyzoa from Victoria and Western Australia. Ann and Mag Nat Hist. 1884; 5(13): 363–369.

24. Smitt FA. Floridan Bryozoa collected by Count L.F. de Pourtalès, Part 2. Kongliga Svenska Vetenskaps–Akademiens Handlingar. 1873; 11: 1–83.

25. Johnston G. A history of British Zoophytes. W.H. Lizars, Edinburgh, London & Dublin. 1838; 1–341.

26. Marcus E. Bryozoarios marinhos brasileiros I. Bol Fac Fil Ci Letras Univ São Paulo. 1937 1: 5–224.

27. Vieira LM, Migotto AE, Winston JE. Synopsis and annotated checklist of recent marine Bryozoa from Brazil. Zootaxa. 2008; 1810: 1–39.

28. Almeida ACS, Alves O, Peso–Aguiar M, Dominguez J, Souza FBC. Gymnolaemata bryozoans of Bahia State, Brazil. Mar Biodiv Records. 2015; 8(120): 1–7. doi:10.1017/S1755267215000743.

29. Martha SO, Vieira LM, Souto JD, Grischenko AV, Gordon DP, Ostrovsky AN. Gymnolaemata, Cheilostomata. In: Schwaha T, editor. Phylum Bryozoa. Berlin: de Gruyter. 2020; 317–423.

30. Chapman JW, Carlton JT. A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). J Crustac Biol 1991; 11 (3): 386–400.

31. Chapman JW, Carlton JT. Predicted discoveries of the introduced isopod *Synidotea laevidorsalis* (Miers, 1881). J Crustac Biol. 1994; 14 (4): 700–714.

32. Almeida ACS, Souza FBC, Gordon DP, Vieira LM. The non–indigenous bryozoan *Triphyllozoon* (Cheilostomata: Phidoloporidae) in the Atlantic: morphology and dispersion on the Brazilian coast. Zoologia. 2015; 32(6): 476–484. doi:10.1590/S1984–46702015000600007.

33. Miranda A, Almeida ACS, Vieira LM. Non–native marine bryozoans (Bryozoa: Gymnolaemata) in Brazilian waters: Assessment, dispersal and impacts. Mar Pollut Bull. 2018; 130: 184–191. doi: 10.1016/j.marpolbul.2018.03.023

34. Busk G. An account of the Polyzoa, and sertularian zoophytes, collected in the Voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago. In MacGillivray J, editor. Narrative of the Voyage of the H.M.S. Rattlesnake. London: T. & W. Boone. 1852; 1: 343–402.

35. D'Hondt, JL. Contribution à la systématique des Bryozoaires Eurystomes. Apports récents et nouvelles propositions. Ann Sci Nat Zool Biol Anim. 1985; 7: 1–12.

36. Johnston G. A history of British Zoophytes. Van Voorst, London. 1847; 1: 1–499

37. Hayward PJ, Ryland JS. British Ascophoran Bryozoans. In: Kermack DM, Barnes RSK. Synopses of the British Fauna 14). London: Academic Press for the Linnaean Society. 1979; 1–312.

38. Bock P, Gordon DP. *Parasmittina* Osburn, 1952. World List of Bryozoa. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=110978 in 2021–01–18.

39. Norman AM. On the Polyzoa Hydrozoa, and Spongozoa. Proc Royal Soc of London. 1876; 25: 202–215.

40. Canu F, Bassler RS. Bryozoaires du Brésil. Bulletin de la Société des Sciences de Seine–et–Oise. 1928; 9: 58–110.

41. Marcus E. Bryozoarios marinhos brasileiros II. Bol Fac Fil Ci Letras Univ São Paulo. 1938; 2: 1–137.

42. Harmer SF. The Polyzoa of the Siboga Expedition, Part 4. Cheilostomata Ascophora II. Siboga Expedition Reports. 1957; 28d: 641–1147.

43. Winston JE. Shallow–water Bryozoans of Carrie Bow Cay, Belize. Am Mus Novit. 1984; 2799: 1–38.

44. Winston JE. An annotated check–list of coral–associated bryozoans. Am Mus Novit. 1986; 2859: 1–39.

45. Winston JE, Woollacott RM. Scientific results of the Hassler Expedition. Bryozoa. No. 1. Barbados. Bull Mus Comp Zoo1. 2009; 59: 239–300.

46. Canu F, Bassler RS. Bryozoaires des iles Hawaï. Bulletin de la Société des Sciences de Seine–et–Oise. 1927; 8: 1–67.

47. Pouyet S, Herrera–Anduaga Y. Systematics and palaeogeographical studies of some species of Bryozoa (Cheilostomata) from the Gulf of Mexico. Universidad Nacional Autónoma de México, Inst Geologia. 1986; 6: 204–221.

48. Hincks T. Contributions towards a General History of the Marine Polyzoa. XII. Polyzoa from India (coast of Burmah). Ann and Mag Nat Hist. 1884; 5(13): 356–362.

49. Hayward PJ, Parker SA. Notes on some species of *Parasmittina* Osburn, 1952 (Bryozoa: Cheilostomatida). Zool J Linn Soc. 1994; 110: 53–75.

50. Liu X, Yin X, Ma J. Biology of Marine–Fouling Bryozoans in the Coastal Waters of China. Science Press, Beijing. 2001; 1–860.

51. Thornely LR. Marine Polyzoa of the Indian Ocean. Trans Linn Soc London. 1912*;* 15: 137–157.

52. Audouin JV. Explication sommaire des planches de polypes de l'Egypte et de la Syrie, publiees par Jules–Cesar Savigny. In: Audouin, J. V. (editor) Description de l'Egypte, ou recueil des observations et des recherches qui ont été faites en Egypte pendant l'expédition de l'armée française ... Histoire naturelle Vol. Tome 1, 4 partie: 339. (Imprimerie Impériale, Paris. 1826.

53. Waters AW. Reports on the Marine Biology of the Sudanese Red Sea... 12. The Bryozoa, Part 1, Cheilostomata. Journ Linn Soc Zool London. 1909; 31: 123–181.

54. Winston JE, Woollacott RM. Redescription and revision of some red pigmented species of *Bugula*. Bulletin of the Museum of Comparative Zoology. 2008; 159: 179–212.

55. Luederwaldt H. Resultados de uma excursão científica à Ilha de São Sebastião no litoral do Estado de São Paulo em 1925. Rev Mus Paul. 1929; 16: 1–79.

56. Verrill AE. Brief contributions to zoology from the Museum of Yale College. No.33. Results of dredging expeditions off the New England coast in 1874. Am J Sci Arts. 1875; 10: 36–44.

57. Harmelin JG, Bitar G, Zibrowius H. High xenodiversity versus low native diversity in the south–eastern Mediterranean: bryozoans from the coastal zone of Lebanon. Mediterranean Mar Sci. 2016; 17, 417–439. doi: 10.12681/mms.1429

58. Ryland JS, Hayward PJ. Bryozoa from Heron Island, Great Barrier Reef. Mem Queensl Mus. 1992; 32: 223–30.

59. Gordon DP, d'Hondt JL. Bryozoa: Lepraliomorpha and other Ascophorina from New Caledonian waters. Mém Mus Natl Hist Nat (Résultats des Campagnes MUSORSTOM, Vol. 18). 1997; 176: 9–124.

60. Tilbrook, KJ, Hayward PJ, Gordon DP. Cheilostomatous Bryozoa from Vanuatu. Zoological J Linn Soc. 2001; 131 (1): 35–109. doi: 10.1006/zjls.2000.0249

61. Dick MH, Tilbrook KJ, Mawatari SF. Diversity and taxonomy of rocky–intertidal Bryozoa on the Island of Hawaii, USA. J Nat His. 2006; 40(38): 2197–2257. doi: 10.1080/00222930601062771

62. Taylor PD, Tan, SHA. Cheilostome Bryozoa from Penang and Langkawi, Malaysia. European Journal of Taxonomy. 2015; 149: 1–34. doi: 10.5852/ejt.2015.149

63. Almeida ACS, Souza, FBC, Farias J, Alves OFS, Vieira, LM. Bryozoa on disarticulated bivalve shells from Todos os Santos Bay, northeastern Brazil, with the description of two new species. Zootaxa. 2018; 4434 (3): 401–428. doi: 10.11646/zootaxa.4434.3.1

64. Robertson A. The Incrusting chilostomatous Bryozoa of the west coast of North America. Proc Calif Acad of Sci. 1908; 4: 253–344.

65. Marcus E. Bryozoarios marinhos brasileiros III. Bol Fac Fil Ci Letras Univ São Paulo. 1939; 3: 111–353.

66. Almeida ACS, Souza FBC, Vieira LM. Malacostegine bryozoans (Bryozoa: Cheilostomata) from Bahia State, northeast Brazil: taxonomy and non–indigenous species. Mar Biodiv. 2017; 1–26. doi 10.1007/s12526–017–0639–x.

67. Maturo FJS, Schopf TJM. Ectoproct and entoproct type material: re–examination of species from Bermuda and New England collected by A.E. Verrill, J.W. Dawson and E. Desor. Postilla. 1968; 120: 1–95.

68. Brown DA. The Tertiary cheilostomatous Polyzoa of New Zealand. Trustees Br Mus Nat Hist London. 1952; 1–405.

Fig 1.

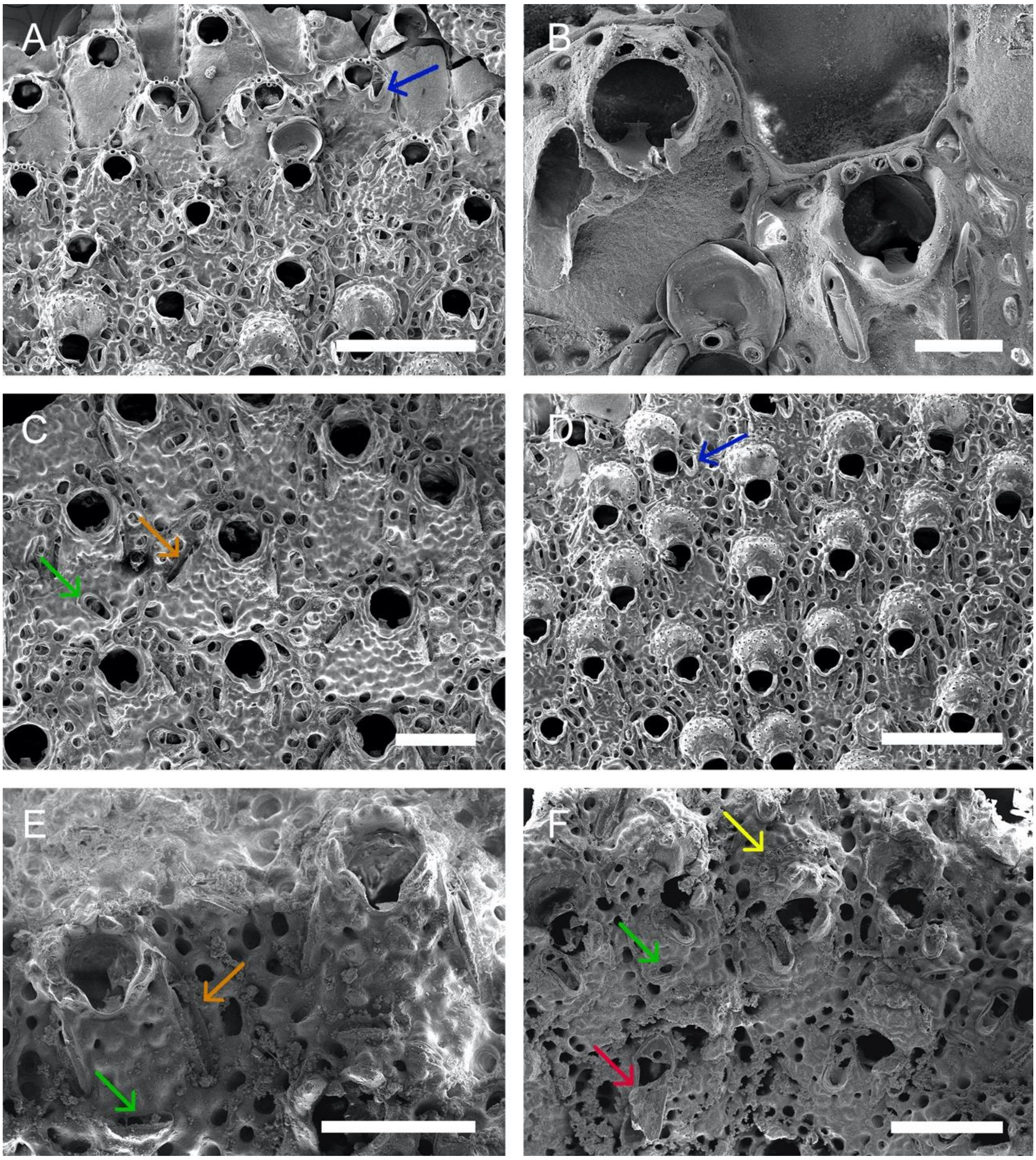


Fig 2.

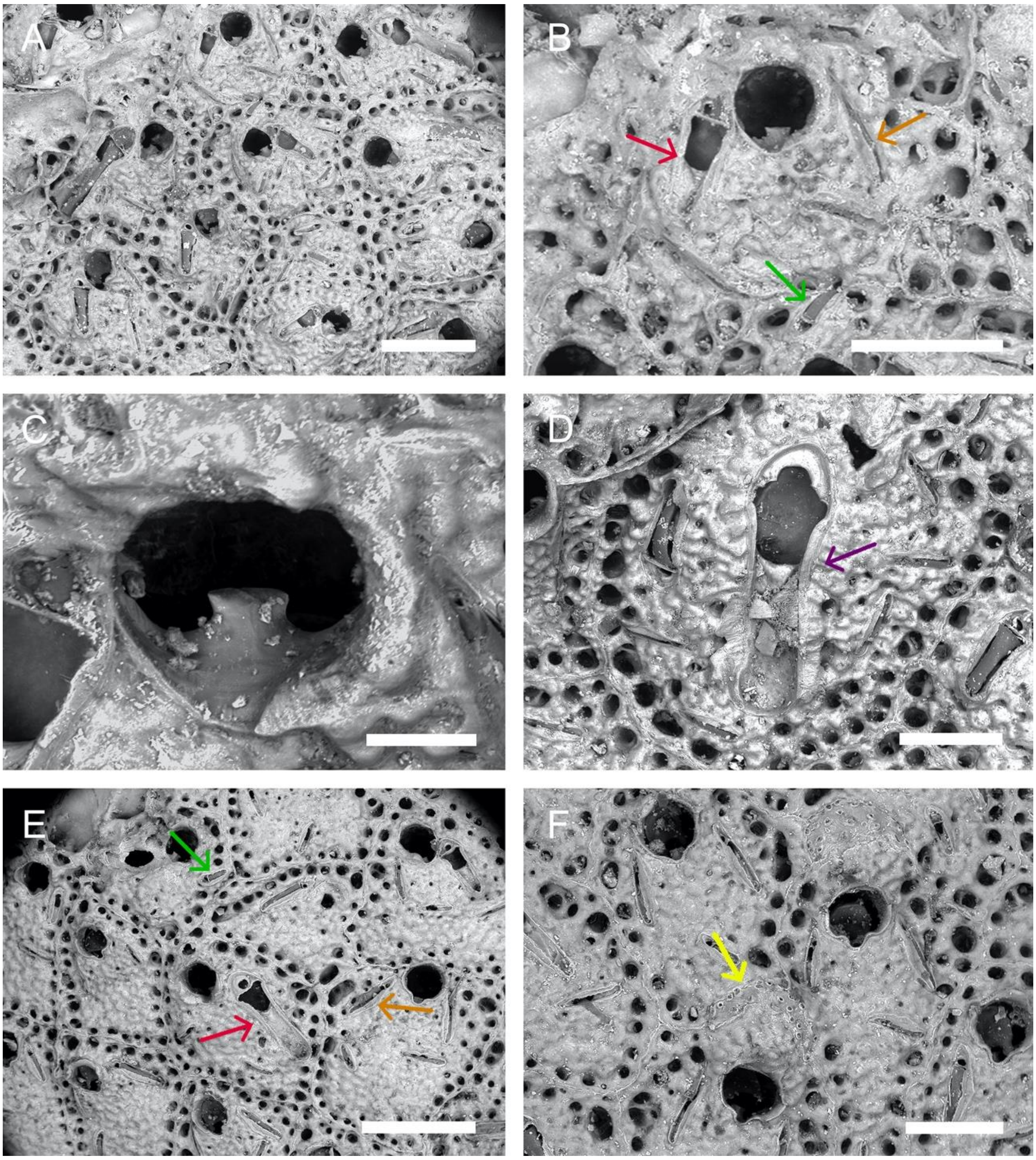


Fig 3.

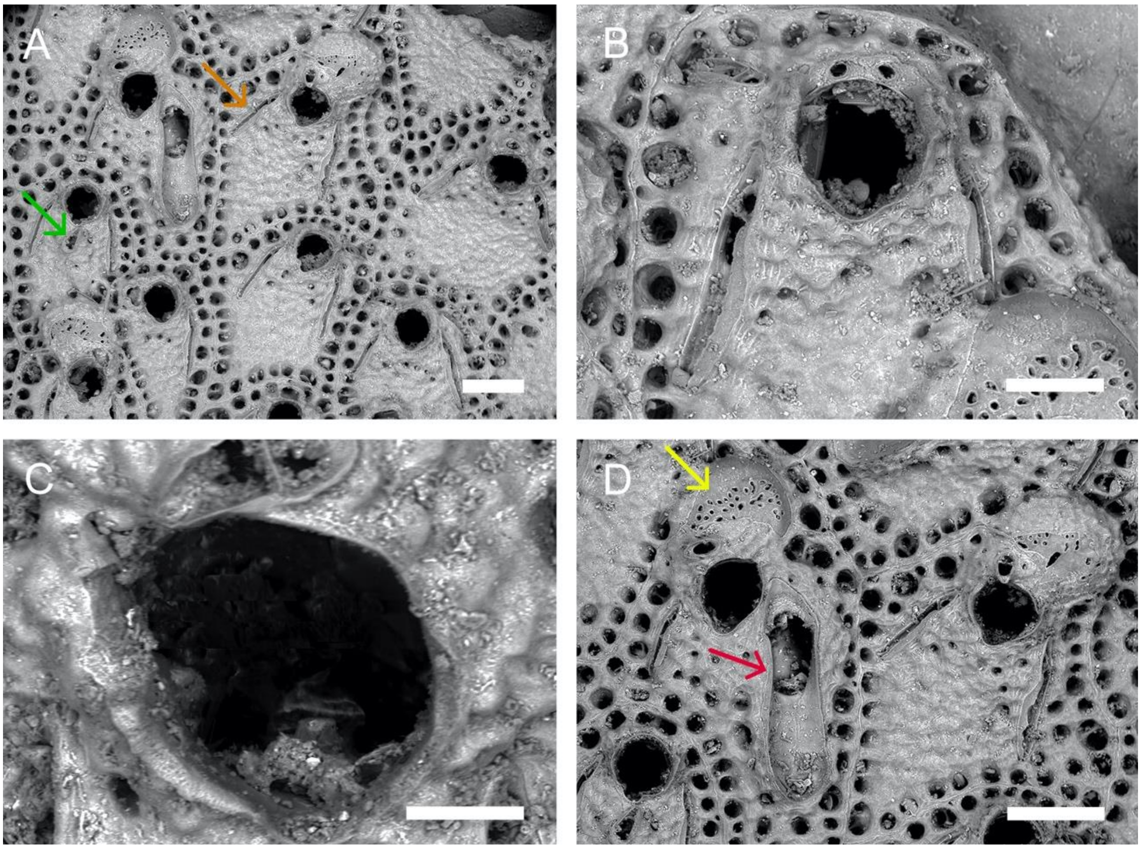


Fig 4.

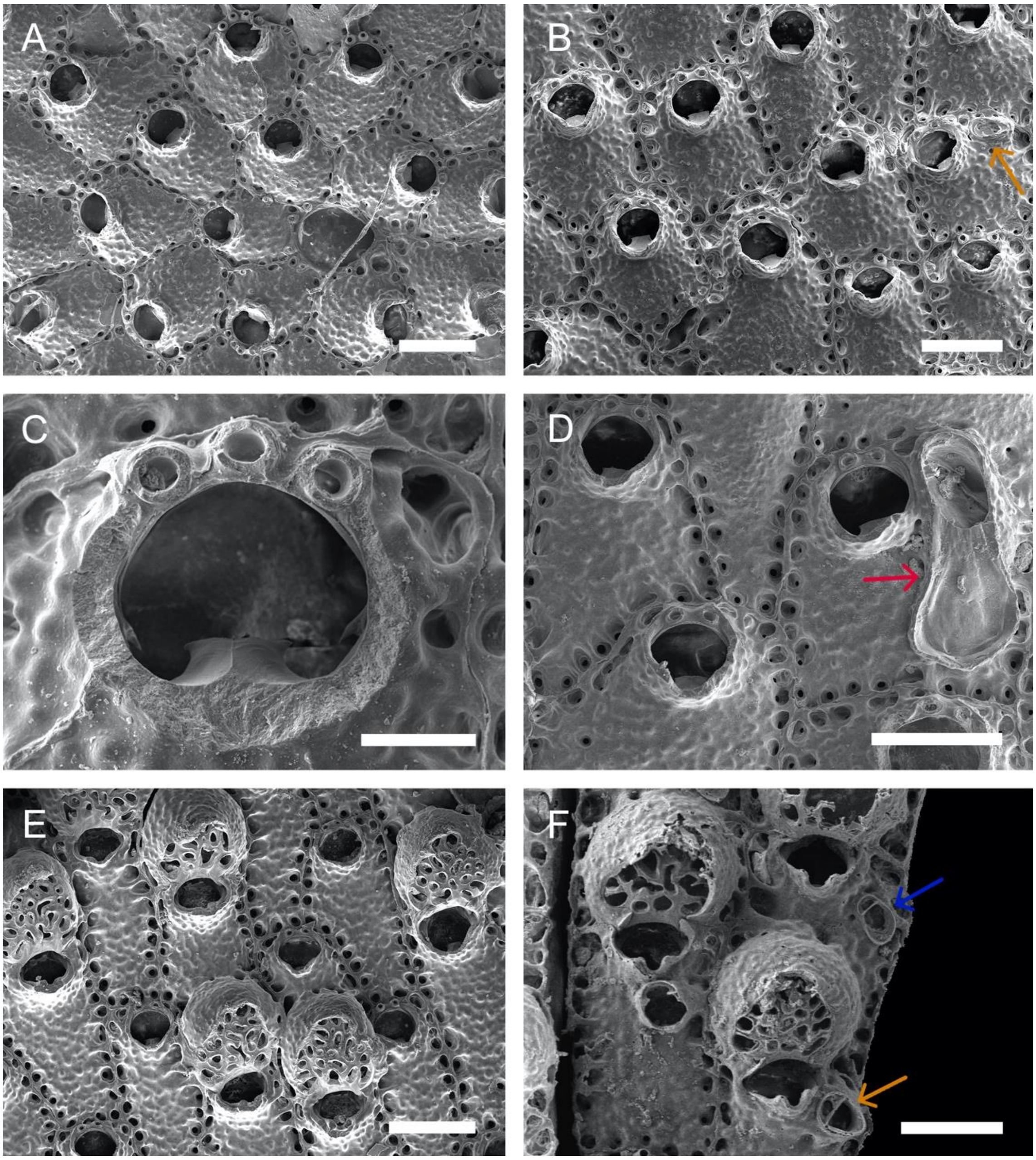


Fig 5.

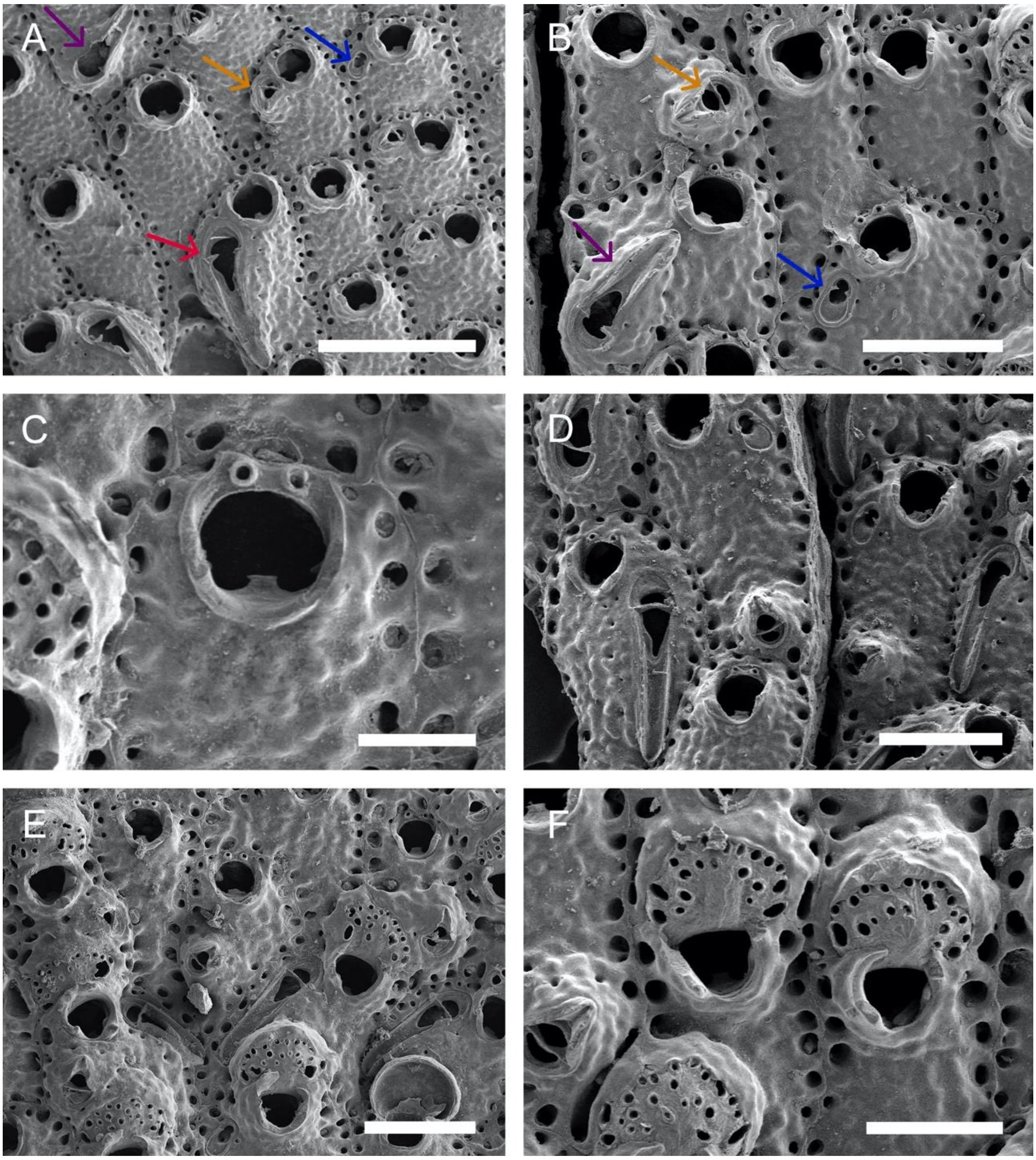


Fig 6.

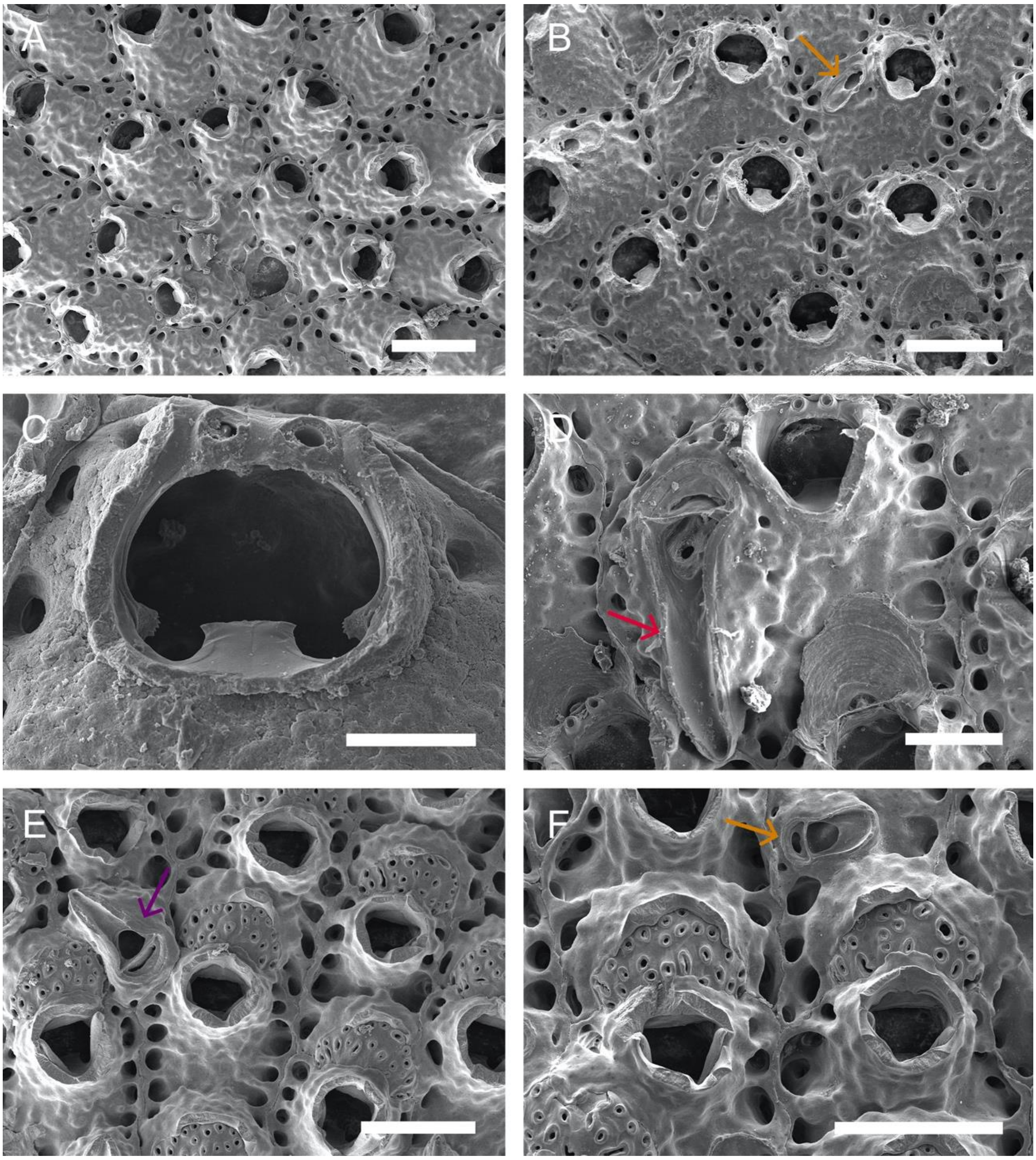


Fig 7.

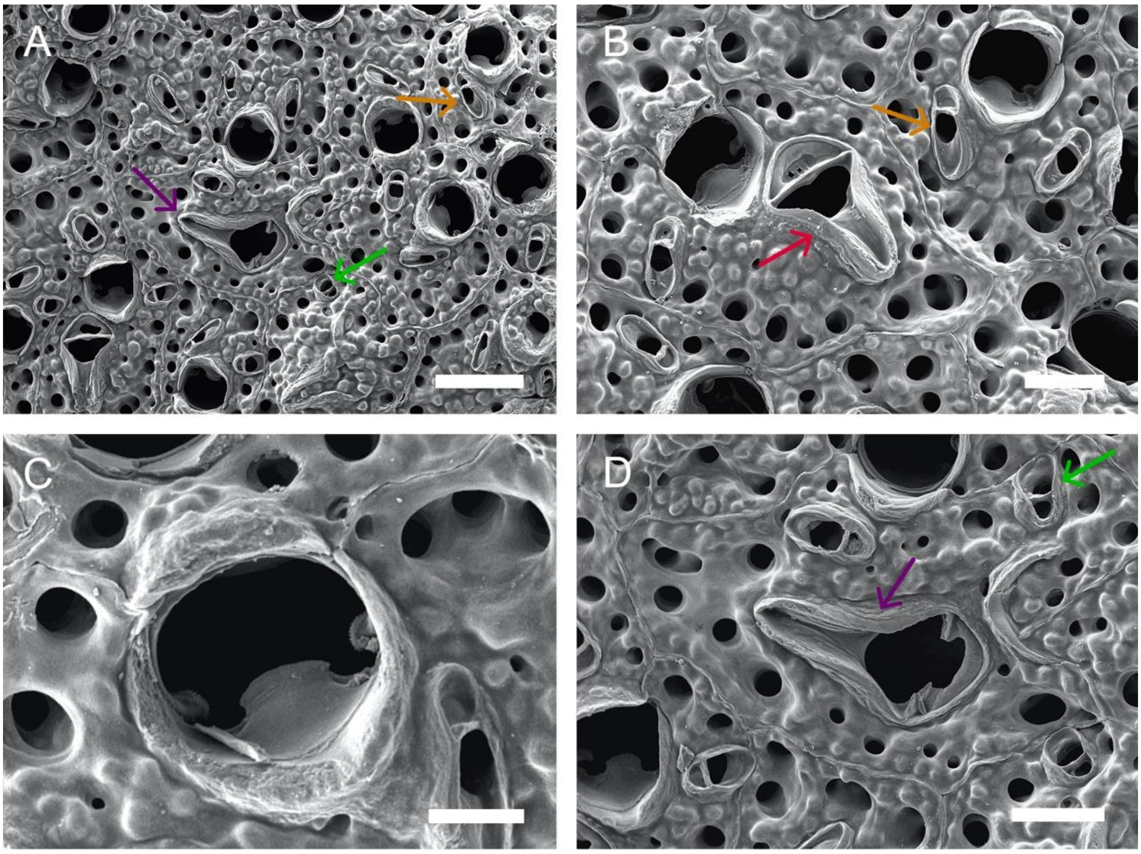


Fig 8.

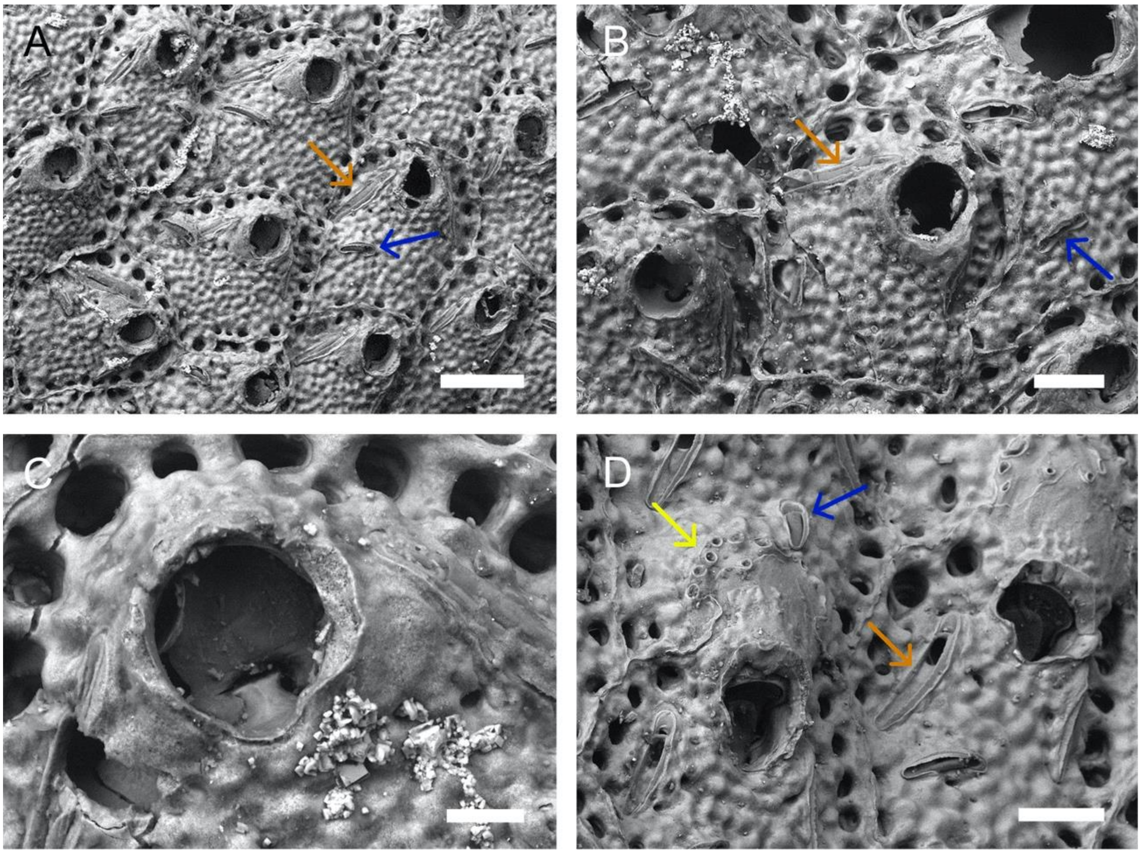


Fig 9.

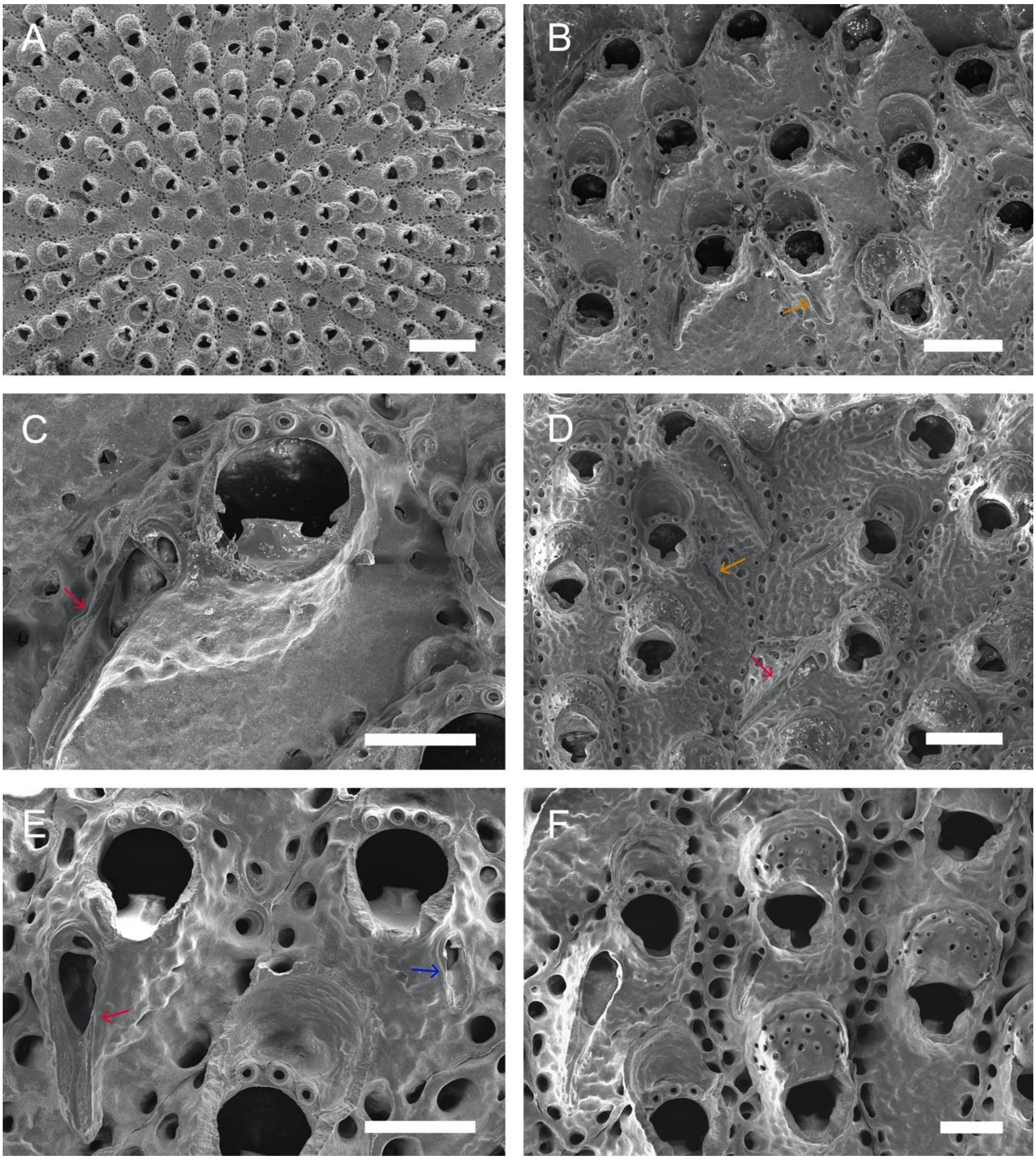


Fig 10.

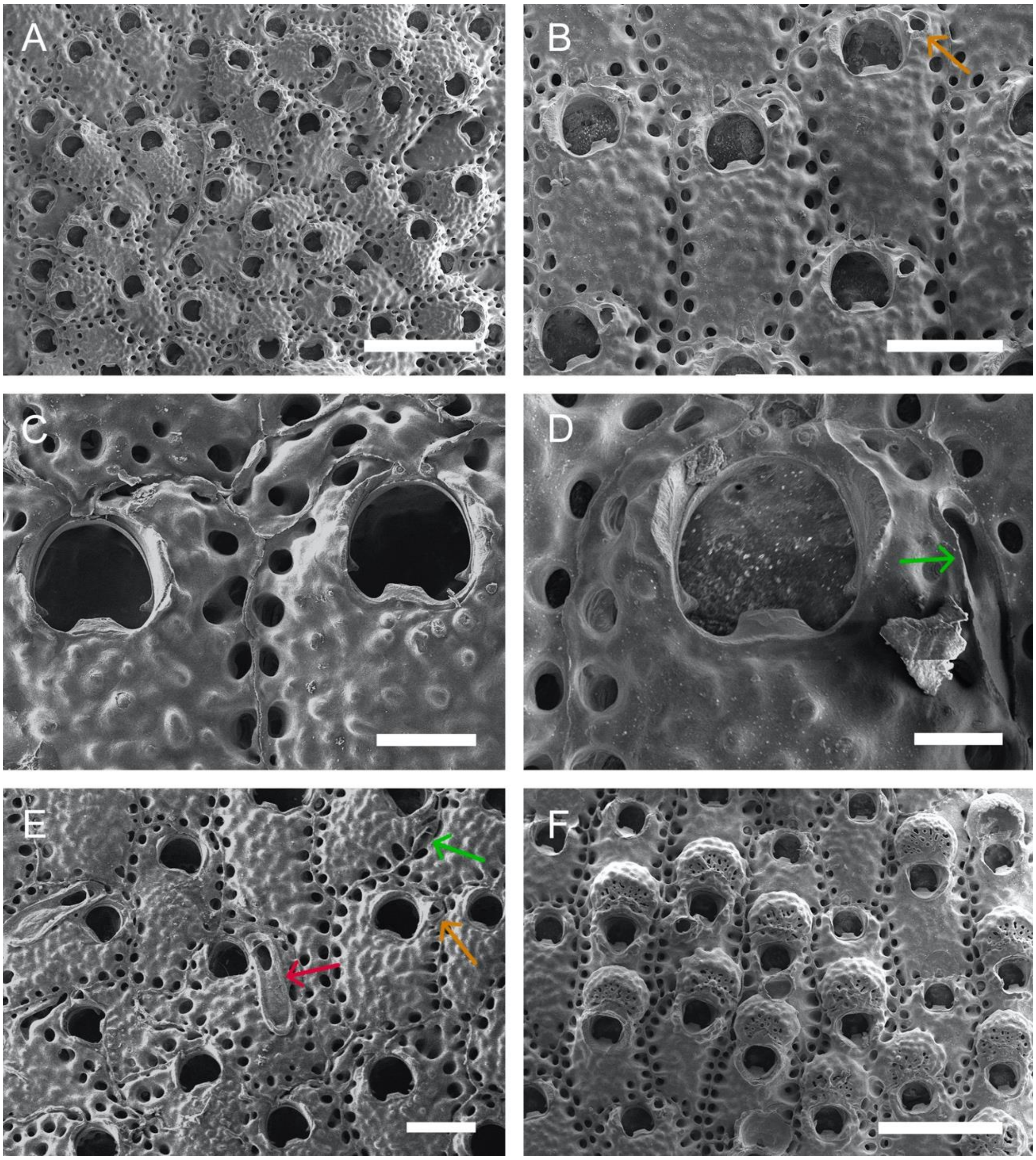


Fig 11.

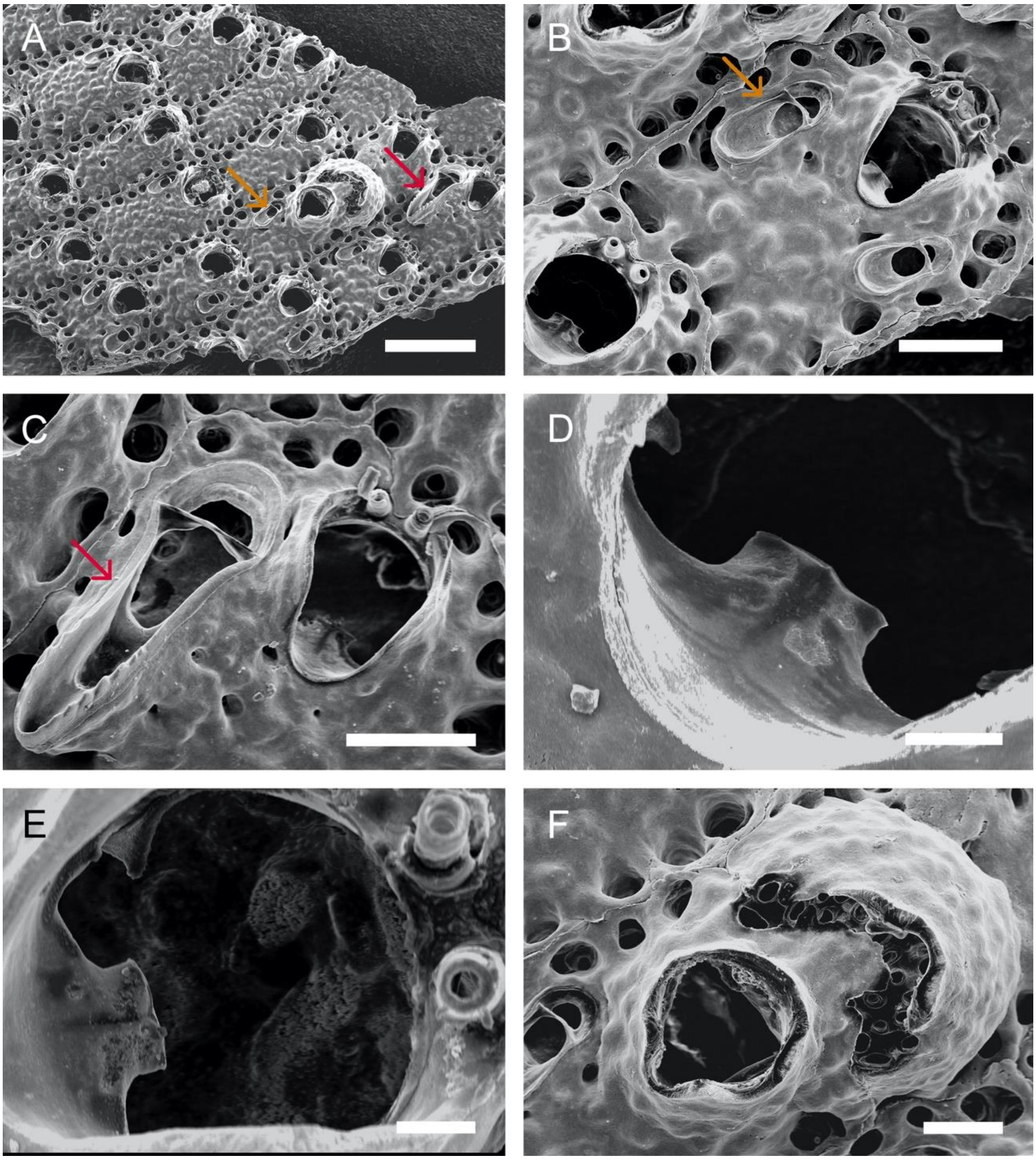


Fig 12.

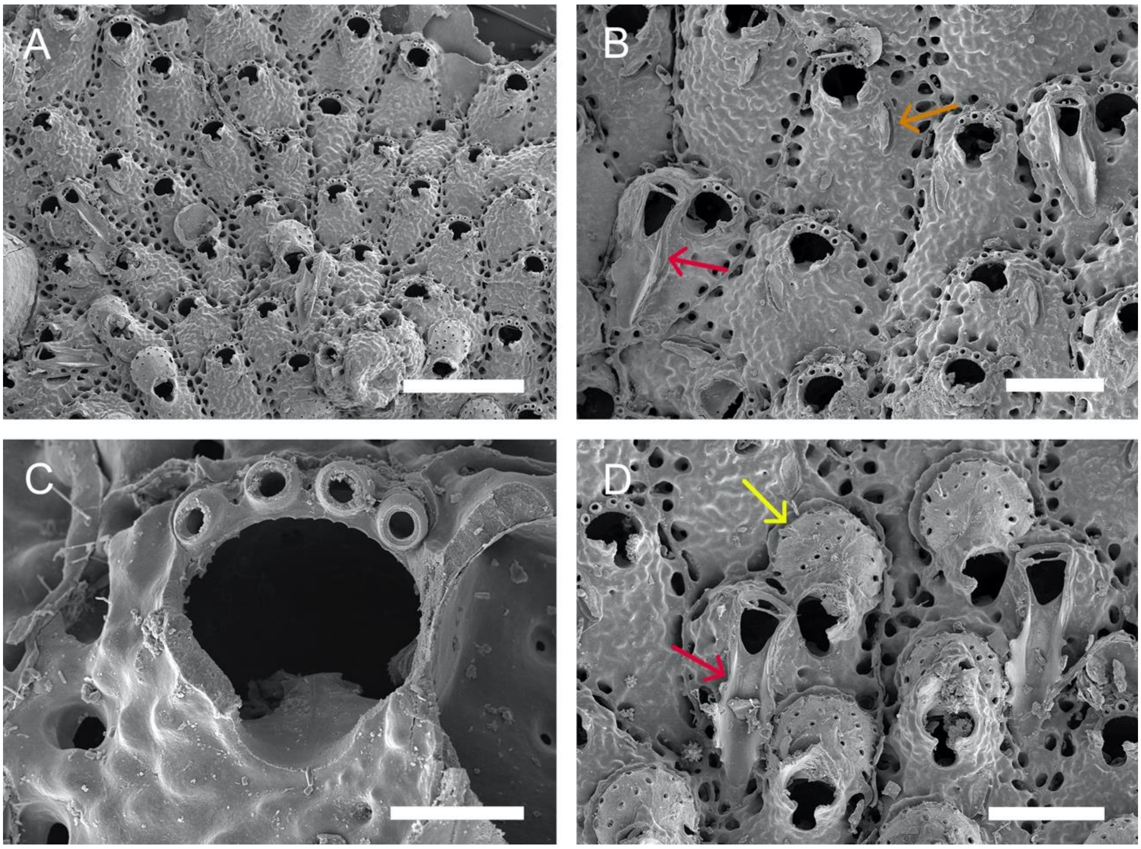


Fig 13.

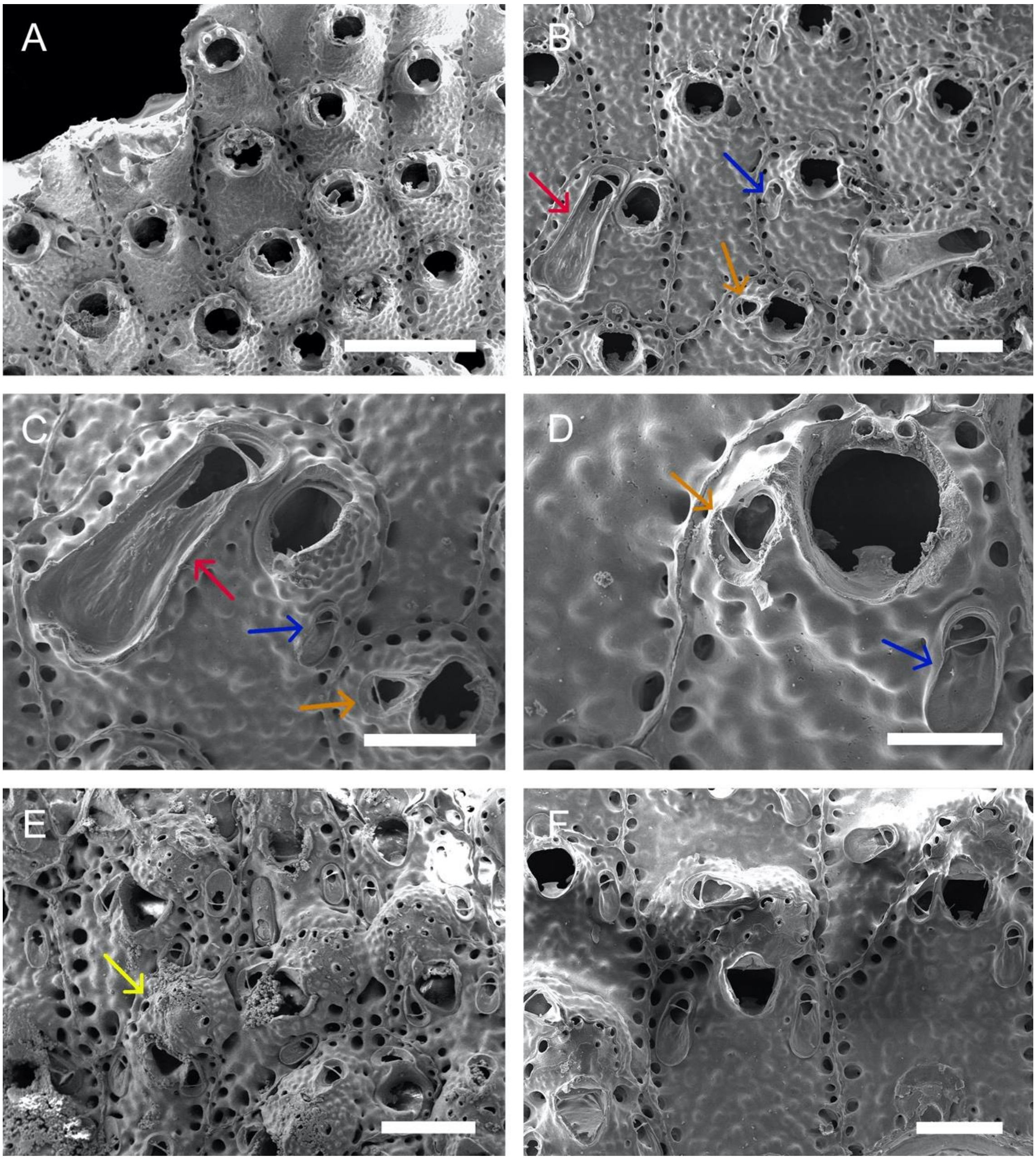


Fig 14.

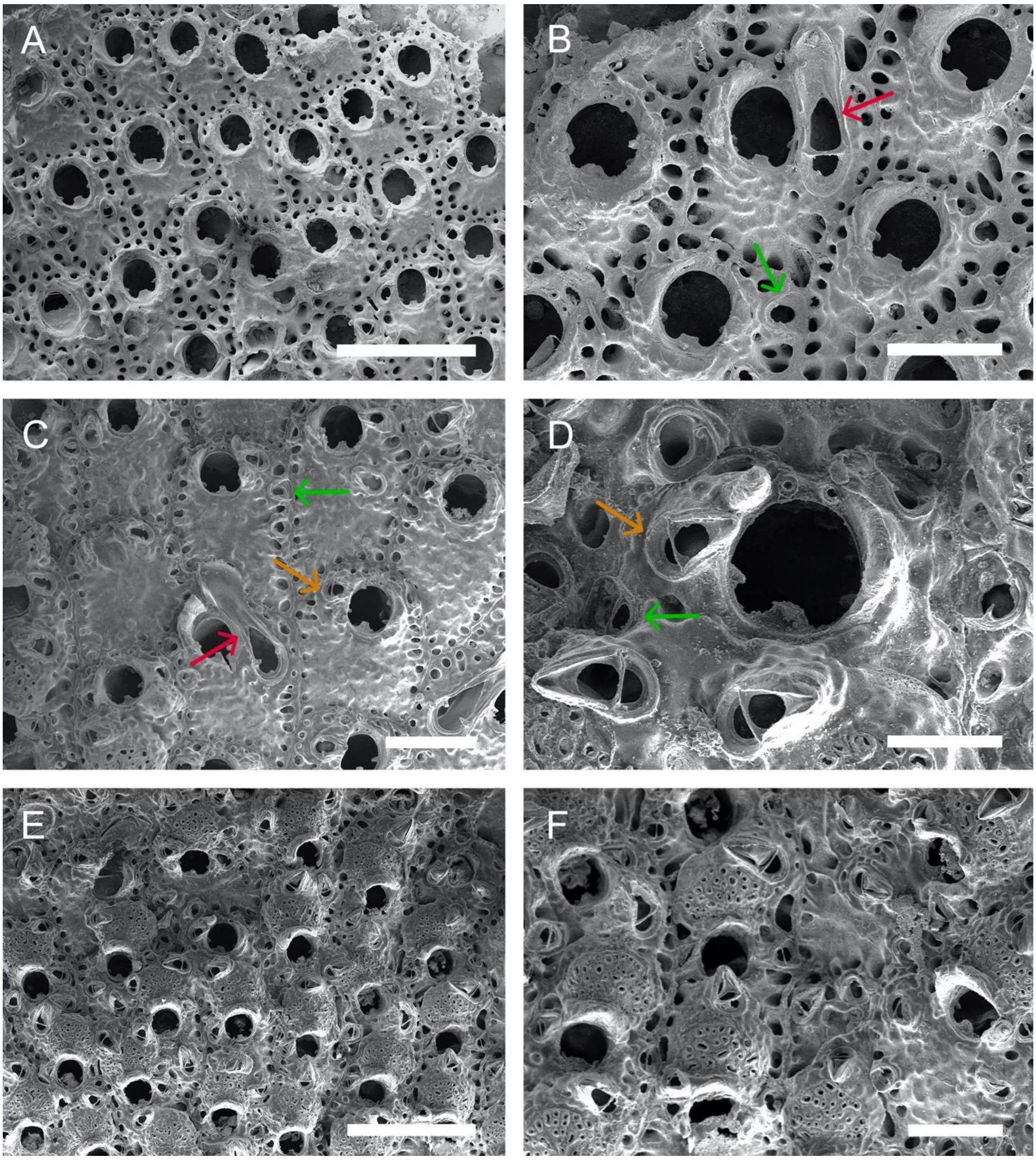


Fig 15.

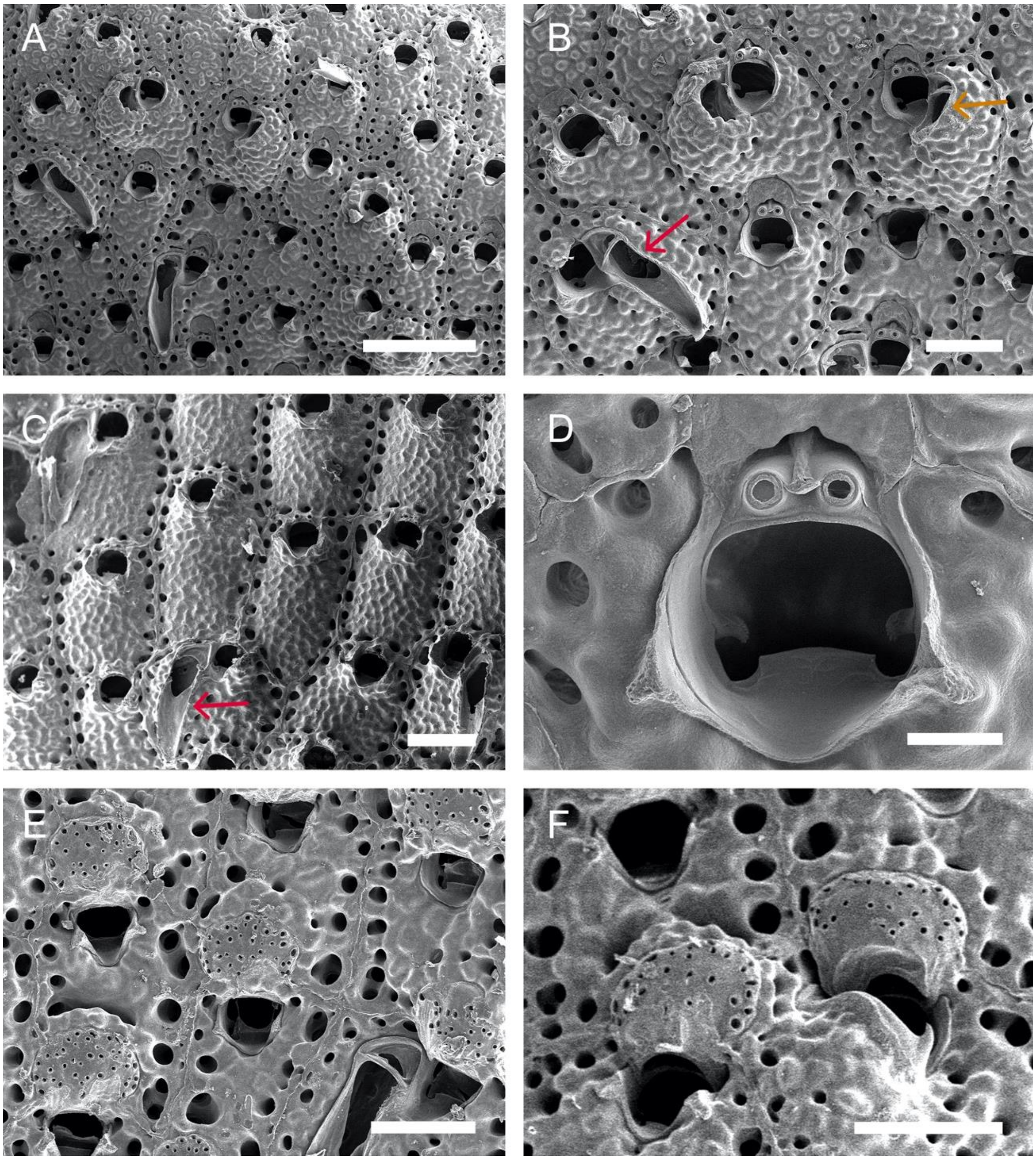


Fig 16.

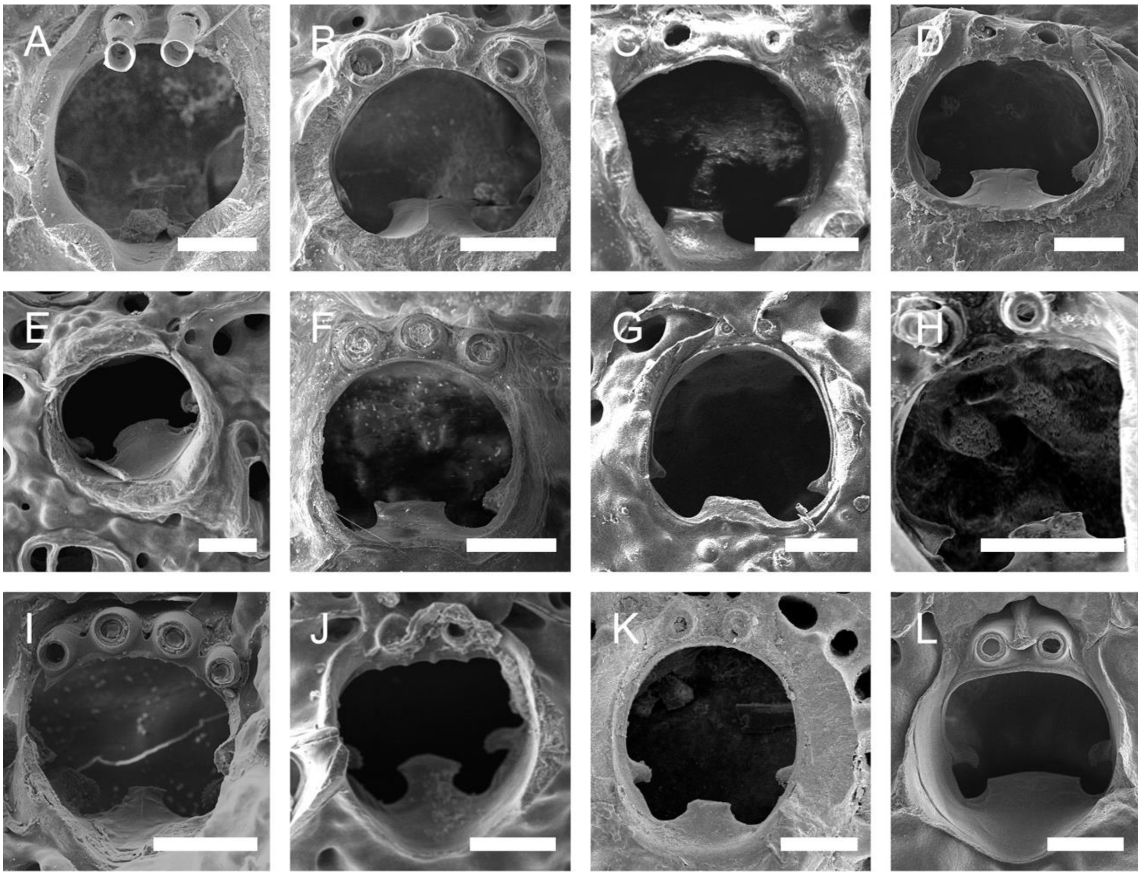


Fig 17.

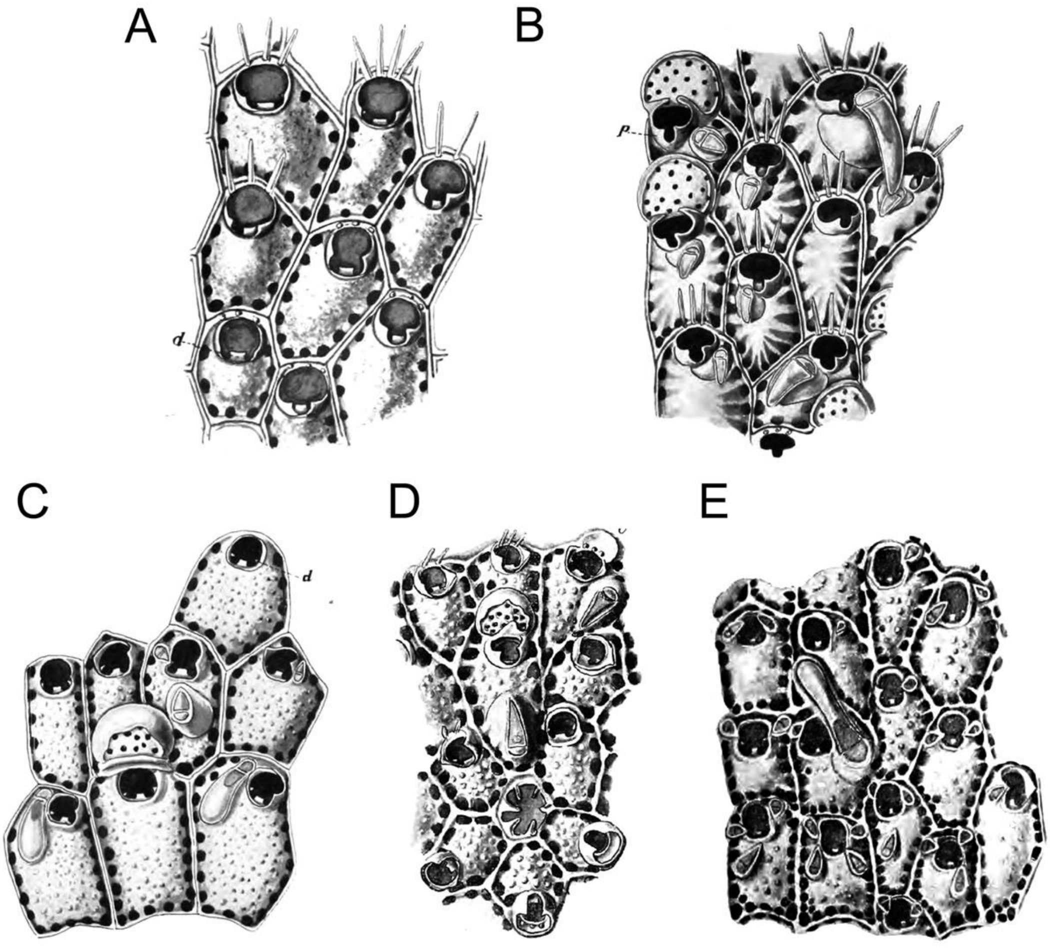
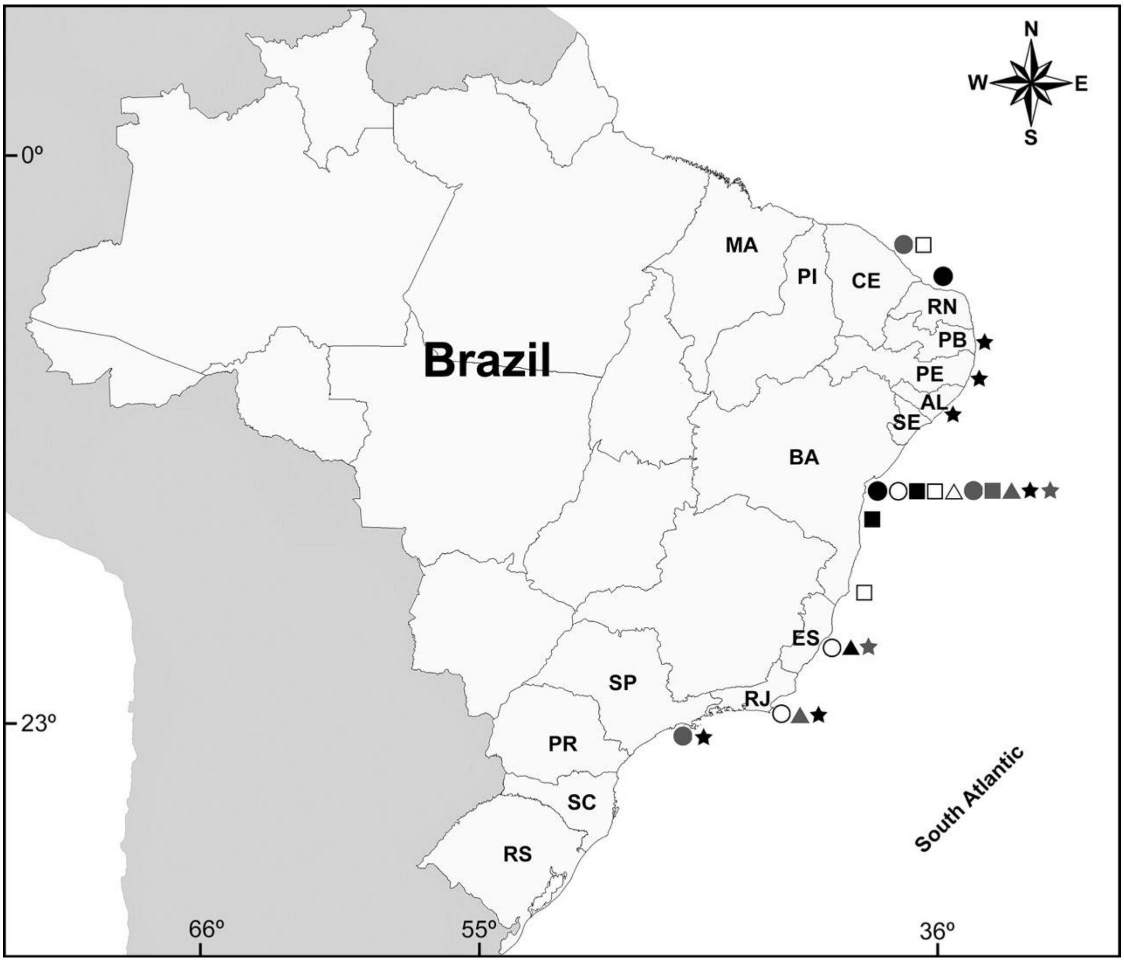


Fig 18.


N
W
E
S
0º
23º
66º
55º
36º
Brazil
MA
PI
CE
RN
PB
PE
AL
SE
BA
ES
RJ
SP
PR
SC
RS
South Atlantic

Considerações finais

- O gênero *Parasmittina* está entre os mais diversos do filo Bryozoa com espécies distribuídas em todos os mares e Oceanos e capazes de se estabelecer em qualquer tipo de superfície disponível.
- A revisão das espécies de *Parasmittina* do Oceano Atlântico Ocidental possibilitou a delimitação de caracteres diagnósticos para esses táxons, evidenciando a necessidade de utilização de um conjunto de características para determinação específica confiável. A necessidade de análise de colônias em diferentes estágios de desenvolvimento também foi evidenciada.
- Ao menos três espécies (*P. alba*, *P. distincta* and *P. simpulata*) foram reconhecidas como parte de complexos de espécies que necessitam de mais estudos utilizando outras bases de dados, como análises moleculares e investigações das influências ambientais na morfologia e morfometria.
- Duas espécies foram classificadas como exóticas (*P. longirostrata* and *P. serrula*) e três foram classificadas como criptogênicas (*P. bimucronata*, *P. pinctatae* and *P. winstonae*) no Oceano Atlântico Ocidental. Esses táxons foram encontrados principalmente em substratos artificiais e em áreas portuárias e adjacências.
- A identificação taxonômica confiável é imprescindível para deteção e controle de eventos de invasão biológica.
- O entendimento de padrões de distribuição das espécies de *Parasmittina* deve auxiliar a identificar possíveis rotas de introdução de espécies exóticas para prevenção e controle dos impactos causados pela bioinvasão, considerada um dos maiores impactos resultantes de atividade humana em ambientes aquáticos.
- Registros históricos do Brasil das espécies *P. areolata*, *P. spathulata* e *P. trispinosa* foram invalidados e atribuídos às espécies *P. abrolhosensis*, *P. simpulata* e *P. falciformis* n. sp., respectivamente.
- A análise do espécime–tipo de todas as espécies descritas é fundamental para descrição de novas especies, assim como representa o primeiro passo para resolver problemas taxonômicos no grupo.

Referências bibliográficas

AFFANDY, M.M.A.; MADIN, J.; JAKOBSEN, K. P.; AULUCK., M. Macrofouling Development on Artificial Structure at Karambunai Bay, Sabah Malaysia. **Journal of Physics: Conference Series**, v. 1358, n. 012011, p. 1–7, 2019.

ALLMANN, G. J. **A monograph of the Freshwater Polyzoa, including all the known species, both British and Foreign.** London: The Ray Society, 1856. 119 p.

ALMEIDA, A. C. S.; ALVES, O.; PESO–AGUIAR, M.; DOMINGUEZ, J.; SOUZA, F. Gymnolaemata bryozoans of Bahia State, Brazil. **Marine Biodiversity Records**, v. 8, p. e120, 2015a.

ALMEIDA, A. C. S.; SOUZA, F. B. C.; GORDON, D.; VIEIRA, L. M. The non–indigenous bryozoan *Triphyllozoon* Canu & Bassler, 1917 in the Atlantic: morphology and dispersion on the Brazilian coast. **Zoologia**, v. 32, n. 6, p. 476–484, 2015b.

ALMEIDA, A. C. S.; SOUZA, F. B. C.; FARIAS, J.; ALVES, O.; VIEIRA, L. M. Bryozoa on disarticulated bivalve shells from Todos os Santos Bay, Northeast Brazil, with the description of a new species. **Zootaxa**, v. 4434, n. 3, p. 401–428, 2018.

AMINI, Z. Z.; ADABI, M. H.; BURRETT, C. F.; QUILTY, P. G. Bryozoan distribution and growth form associations as a tool in environmental interpretation, Tasmania, Australia. **Sedimentary Geology**, v. 167, p. 1–15, 2004.

BARADARI, H.; NASROLAHI, A.; TAYLOR, P.D. Cheilostome Bryozoa of the northern Persian Gulf, Iran. **Zootaxa**, n. 4619, n. 3, p. 459–486, 2019.

BERNING, B.; TILBROOK, K. J.; OSTROVSKY, A. N. What, if anything, is a lyrula? In: Bryozoan Studies 2013, (Eds, Rosso, Antonietta, Wyse Jackson, Patrick N. & Porter, Joanne S.) (**Museo delle Scienze, Trento),** 21–28, 2014.

BOARDMAN, R.S.; CHEETHAM, A.H.; COOK, P.L. Introduction to the Bryozoa. In: Boardman, R.S.; Cheetham, A.H.; Blake, D.B.; Utgaard, J.; Karklins, O.L.; Cook, P.L.; Sandberg, P.A.; Lutaud, G.; Wood, T.S. (Eds), Bryozoa. **Treatise on Invertebrate Paleontology Part G, Revised.** Kansas: Geological Society of America and University of Kansas, Boulder and Lawrence, p. 3–48, 1983.

BOCK, P.; GORDON, D. (2021). *Parasmittina* Osburn, 1952. World List of Bryozoa. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=110978 em 2021–01–18.

BORG, F. Studies on Recent Cyclostomatous Bryozoa. **Zoologiska Bidrag från Uppsala**, v. 10, p. 181–507, 1926.

BREVES–RAMOS, A.; LAVRADO, H.P.; JUNQUEIRA, A.O.R.; SILVA, S.H.G. Succession in rocky intertidal benthic communities in areas with different pollution levels at Guanabara Bay (RJ–Brazil). **Brazilian Archives of Biology and Technology**. 48, 951– 965, 2005.

BUSK, G. An Account of the Polyzoa, and Sertularian Zoophytes, collected in the Voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago, & C. In: MACGILLIVRAY, J. (Ed). Narrative of Voyage of H.M.S. Rattlesnake, commanded by the late Captain Owen Stanley, R.S., F.R.S. &C. during the years 1846–1850; including discoveries and surveys in New Guinea, the Lousiade Archipelago, etc., to which is added the Account of Mr. E. B. Kennedy's expedition for the exploration of the Cape York Peninsula, 1. London: T.W. Boone, 1852.

CANU, F.; BASSLER, R. S. Bryozoaires des iles Hawaï. **Bulletin de la Société des Sciences de Seine–et–Oise**, v. 8, p. 1–67, 1927.

CANU, F.; BASSLER, R. S. **Bryozoaires du Brésil. Bulletin de la Société des Sciences de Seine–et–Oise**, v. 9, p. 58–110, 1928.

CARTER, M. C. **The functional morphology of avicularia in Cheilostome Bryozoans**. Tese (Doutorado em Biologia Marinha) – Victoria University of Wellington, Nova Zelândia, p. 233, 2008.

CIAVATTA, M. L.; LEFRANC, F.; VIEIRA, L. M.; KISS, R.; CARBONE, M.', VAN OTTERLOO, W.A.L.; LOPANIK, N. B.; WAESCHENBACH, A. The Phylum Bryozoa: From Biology to Biomedical Potential. **marine drugs**, 18: 200, 2020.

COOK, P. L.; BOCK, P. E.; GORDON, D. P.; WEAVER, H. J. **Australian Bryozoa volume 2: taxonomy of Australian Families**. CSIRO Publishing, Melbourne, 320 p., 2018.

FARIAS, J.; SOUZA, F. B. C.; VIEIRA, L. M.; ALMEIDA, A. C. S. On some Smittinidae (Bryozoa, Cheilostomata) from Bahia, northeastern Brazil, with the description of a new species. **Marine Biodiversity**, v. 50, n. 5, p. 1–17, 2020.

GORDON, D. P. The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. **New Zealand Oceanographic Institute Memoir**, v. 91, p. 1–198, 1984.

GORDON, D. P. Bryozoan frontal shields: studies on umbonulomorphs and impacts on classification. **Zoologica Scripta**, v. 22, n. 2, p. 203–221, 1993.

GORDON, D. P. Living Lace. **New Zealand Geographic**, n. 61, p. 80–95, 2003.

GORDON, D. P. D.; MAWATARI, S. F. Atlas of marine fouling Bryozoa of New Zealand ports and harbours. **Miscellaneous publications of the New Zealand Oceanographic Institute**, n. 107, p. 1–52, 1992.

HARMELIN, J. –G.; BITAR, G.; ZIBROWIUS, H. Smittinidae (Bryozoa, Cheilostomata) from coastal habitats of Lebanon (Mediterranean Sea), including new and non–indigenous species. **Zoosystema**, v. 31, n. 1, p. 163–187, 2009.

HAYWARD, P. J. Cheilostomata (Bryozoa) from the South Atlantic. **Journal of Natural History**, v. 14, p. 701–722, 1980.

HAYWARD, P. J.; PARKER, S. A. Notes on some species of *Parasmittina* Osburn, 1952 (Bryozoa: Cheilostomatida). **Zoological Journal of the Linnean Society**, v. 110, p. 53–75, 1994.

HEYSE, H.L. **Briozoários como bioindicadores de qualidade ambiental na Baía da Babitonga, Santa Catarina.** 2012. Dissertação (Mestrado em Ecologia e Conservação) – Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba.

HINCKS, T. Contributions towards a general history of the marine Polyzoa. Part XIII (cont.). Polyzoa from Victoria (continued). **Annals and Magazine of Natural History**. p. 276–285, 1884.

HIROSE, M. Diversity of Freshwater and Marine Bryozoans in Japan. In: MOTOKAWA, M., KAJIHARA, H. (Eds). **Species Diversity of Animals in Japan, Diversity and Commonality in Animals.** Japan: Springer, p. 629–649, 2017.

IGNACIO, B.L.; JULIO, L.M.; JUNQUEIRA, A.O.R.; FERREIRA–SILVA, M.A.G. Bioinvasion in a Brazilian bay: filling gaps in the knowledge of southwestern Atlantic biota. **PLoS One**, v. 5, n. 9, p. e13065, 2010.

JOHNSTON, G. A History of British Zoophytes. **W.H. Lizars, Edinburgh**. 1838.

LEVINSEN, G. M. R. **Morphological and systematic studies on the cheilostomatous Bryozoa.** Nationale Forfatterers Forlag, Copenhagen, p. 1–431, 1909.

LOPES, R. M. Métodos. Informe sobre as espécies exóticas invasoras marinhas no Brasil. **Ministério do Meio Ambiente** – Secretaria de Biodiversidade e Florestas, Brasília, p.11–139, 2009.

LÓPEZ GAPPA, JUAN. *Smiltina oblita* sp. nov., a new cheilostomatous bryozoan from the southwest Atlantic. **Revista del Museo Argentino de Ciencias Naturales nueva serie**, v. 4, n. 2, p. 187–190, 2002.

MARCUS, E. Bryozoarios marinhos brasileiros I. **Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia**, v. 1, p. 5–224, 1937.

MARCUS, E. Bryozoarios Marinhos Brasileiros, 2. **Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia**, v. 2, p. 1–196, 1938.

MARQUES, A. C. et al. Rapid assessment survey for exotic benthic species in the São Sebastião Channel, Brazil. **Latin American Journal of Aquatic Research**, v. 41, p. 265–285, 2013.

MARTHA, S. O.; VIEIRA, L.M., SOUTO–DERUNGS, J.; GRISCHENKO, A.V., GORDON, D. P.; OSTROVSKY, A. N. 11. Gymnolaemata, Cheilostomata. In: *Phylum Bryozoa*, **(Ed, Schwaha, Thomas):** 317–423, 2020. (de Gruyter, Berlin).

MCKINNEY, F. K.; JACKSON, J. B. C. **Bryozoan Evolution**. Studies in Paleobiology. Boston: Unwin Hyman. p. 238, 1989.

MIRANDA, A. A., ALMEIDA, A. C. S.; VIEIRA, L. M. Non–native marine bryozoans (Bryozoa: Gymnolaemata) in Brazilian waters: Assessment, dispersal and impacts. **Marine Pollution Bulletin**, v. 130, p. 184–191, 2018.

MUKAI, H.; TERAKADO, K.; REED, C. G. Bryozoa. In: HARRISON, F.W.; WOOLLACOTT, R. M. (Eds). **Microscopic anatomy of invertebrates.** New York, Chichester, etc: Wiley–Liss, p. 45–206, 1997.

MAYER–PINTO, M., JUNQUEIRA, A.O.R., 2003. Effects of organic pollution on the initial development of fouling communities in a tropical bay, Brazil. **Marine Pollution Bulletin**, 46, 1495–1503, 2003.

O'DONOGHUE, C. H. Some South African Bryozoa. **Transactions of the Royal Society of South Africa** 35: 71–95, 1957.

OKEN, L. **Lehrbuch der Naturgeschichte, III, Zoologie. Abtei–lung 1, Fleischlose Thiere.** Leipzig: Jena, 1815.

OSBURN, R.C. Bryozoa of the Pacific coast of America, Part 2. Cheilostomata, Ascophora. **Report of the Allan Hancock Pacific Expeditions**, v. 14, p. 271–611, 1952.

OSTROVSKY, A. **Evolution of Sexual Reproduction in Marine Invertebrates: Example of Gymnolaemate bryozoans**. Springer: Dordrecht. 356 p. 2013.

PORTER, J. S.; SPENCER JONES M. E.; KUKLINSKI P.; ROUSE S. First records of marine invasive non–native Bryozoa in Norwegian coastal waters from Bergen to Trondheim. **BioInvasions Records**, v. 4, n. 3, p. 157–169, 2015.

POUYET, S.; HERRERA–ANDUAGA, Y. Systematics and palaeogeographical studies of some species of Bryozoa (Cheilostomata) from the Gulf of Mexico. **Universidad Nacional Autónoma de México, Instituto de Geologia, Revista** 6, p. 204–221, 1986.

RAMALHO, L. V.; MURICY, G.; TAYLOR P. D. Taxonomic revision of some lepraliomorph cheilostome bryozoans (Bryozoa: Lepraliomorpha) from Rio de Janeiro State, Brazil. **Journal of Natural History**, v. 45, p. 767–798, 2011.

RAMALHO, L. V.; TAYLOR, P.D.; MORAES, F.C.; MOURA, R.; AMADO–FILHO, G.M.; BASTOS, A.C. Bryozoan framework composition in the oddly shaped reefs from Abrolhos Bank, Brazil, southwestern Atlantic: taxonomy and ecology. **Zootaxa**, v. 4483, n. 1, p. 155–186, 2018.

RIDLEY, S. O. Account of the zoological collections made during the survey of H.M.S. Alert in the straits of Magellan and on the coast of Patagonia. **Proceedings of the Zoological Society of London**, p. 44–61, 1881.

RYLAND, J. S. Bryozoans**.** London: **Hutchinson University Library**, p. 11–175, 1970.

RYLAND, J. S. Bryozoa: an introductory overview. **Denisia**, v. 16, p. 9–20, 2005.

SEO, J. E. A new Parasmittinid bryozoan (Cheilostomata) from Korea. **Korean Journal of Biological Sciences**, v. 6, n. 1, p. 41–43, 2002.

SIMA, P.; VETVICKA, V. Bioactive substances with anti–neoplastic efficacy from marine invertebrates: Bryozoa, Mollusca, Echinodermata and Urochordata. **World Journal of Clinical Oncology**, v. 2, n. 11, 362–366, 2011.

SMITH, A. M. Palaeoenvironmental interpretation using bryozoans: a review. **Geological Society of London Special Publication**, n. 83, p. 231–243, 1995.

SMITT, F. A. Floridan Bryozoa collected by Count L.F. de Pourtales, Part 2. **Kongliga Svenska Vetenskaps–Akademiens Handlingar**, v. 11, n. 4, p. 1–83, 1873.

SOULE, D. F.; SOULE, J. D. Morphology and speciation of Hawaiian and eastern Pacific Smittinidae (Bryozoa, Ectoprocta). **Bulletin of the American Museum of Natural History**, v.152, n. 6, p. 365–440, 1973.

SOULE, D. F.; SOULE, J. D. The Eastern Pacific Parasmittina trispinosa Complex (Bryozoa, Cheilostomatida): New and Previously Described Species. **Irene McCulloch Foundation Monograph**, v. 5, p. 1–40, 2002.

SOUTO, J.; RAMALHOSA, P.; CANNING–CLODE, J. Three non–indigenous species from Madeira harbors, including a new species of *Parasmittina* (Bryozoa). **Marine Biodiversity**, v. 48, n. 2, p. 977–986, 2016.

TAYLOR, P. D.; TAN, S. Cheilostome bryozoa from Penang and Langkawi, Malaysia. **European Journal of Taxonomy**, v. 149, p. 1–34, 2015.

UTTLEY, G. H. The Recent and Tertiary Polyzoa (Bryozoa) in the collection of the Canterbury Museum. Part 2. **Records of the Canterbury Museum**, v. 6, p. 15–39, 1951.

VIEIRA, L. M.; MIGOTTO, A. E.; WINSTON, J. E. Synopsis and annotated checklist of Recent marine Bryozoa from Brazil. **Zootaxa**, v. 1810, p. 1–39, 2008.

VIEIRA, L.; ALMEIDA, A. C. S.; Fehlauer–Ale, K. H.; MIGOTTO, A. E. Filo Bryozoa: novas perspectivas no estudo da biodiversidade marinha no Brasil. **Boletim informativo Sociedade Brasileira de Zoologia**, São Paulo, v. 27, n. 113, 2015.

WINSTON, J. E. Why bryozoans have avicularia? A review of the evidence. **American Museum Novitates**, n. 2789, p. 1–26, 1984.

WINSTON, J. E. An annotated check–list of coral–associated bryozoans. **American Museum Novitates**, n. 2859, p. 1–39, 1986.

WINSTON, J. E. Re–description and revision of Smitt's "Floridan Bryozoa" in the collection of the Museum of Comparative Zoology, Harvard University. **Virginia Museum of Natural History Memoir**, n. 7, p. 1–147, 2005.

WINSTON, J. E.; VIEIRA, L. M.; WOOLLACOTT, R. M. Scientific results of the Hassler expedition. Bryozoa. No. 2. Brazil. **Bulletin of the Museum of Comparative Zoology**, v. 161, n. 5, 139–239, 2014.

Anexo

Normas do periódico científico PLoS One

Style and Format

File format	Manuscript files can be in the following formats: DOC, DOCX, or RTF. Microsoft Word documents should not be locked or protected. LaTeX manuscripts must be submitted as PDFs. Read the LaTeX guidelines.
Length	Manuscripts can be any length. There are no restrictions on word count, number of figures, or amount of supporting information. We encourage you to present and discuss your findings concisely.
Font	Use a standard font size and any standard font, except for the font named “Symbol”. To add symbols to the manuscript, use the Insert → Symbol function in your word processor or paste in the appropriate Unicode character.
Headings	Limit manuscript sections and sub–sections to 3 heading levels. Make sure heading levels are clearly indicated in the manuscript text.
Layout and spacing	Manuscript text should be double–spaced. Do not format text in multiple columns.
Page and line numbers	Include page numbers and line numbers in the manuscript file. Use continuous line numbers (do not restart the numbering on each page).
Footnotes	Footnotes are not permitted. If your manuscript contains footnotes, move the information into the main text or the reference list, depending on the content.
Language	Manuscripts must be submitted in English. You may submit translations of the manuscript or abstract as supporting information. Read the supporting information guidelines.
Abbreviations	Define abbreviations upon first appearance in the text. Do not use non–standard abbreviations unless they appear at least three times in the text. Keep abbreviations to a minimum.
Reference style	PLOS uses “Vancouver” style, as outlined in the ICMJE sample references. See reference formatting examples and additional instructions below.
Equations	We recommend using MathType for display and inline equations, as it will provide the most reliable outcome. If this is not possible, Equation Editor or Microsoft's Insert→Equation function is acceptable. Avoid using MathType, Equation Editor, or the Insert→Equation

function to insert single variables (e.g., “$a^2 + b^2 = c^2$”), Greek or other symbols (e.g., β, Δ, or ′ [prime]), or mathematical operators (e.g., x, ≥, or ±) in running text. Wherever possible, insert single symbols as normal text with the correct Unicode (hex) values.

Do not use MathType, Equation Editor, or the Insert→Equation function for only a portion of an equation. Rather, ensure that the entire equation is included. Equations should not contain a mix of different equation tools. Avoid “hybrid” inline or display equations, in which part is text and part is MathType, or part is MathType and part is Equation Editor.

Nomenclature

Use correct and established nomenclature wherever possible.

Units of measurement	Use SI units. If you do not use these exclusively, provide the SI value in parentheses after each value. Read more about SI units.
Drugs	Provide the Recommended International Non–Proprietary Name (rINN).
Species names	Write in italics (e.g., *Homo sapiens*). Write out in full the genus and species, both in the title of the manuscript and at the first mention of an organism in a paper. After first mention, the first letter of the genus name followed by the full species name may be used (e.g., *H. sapiens*).
Genes, mutations, genotypes, and alleles	Write in italics. Use the recommended name by consulting the appropriate genetic nomenclature database (e.g., HGNC for human genes; we strongly recommend using this tool to check against previously approved names). It is sometimes advisable to indicate the synonyms for the gene the first time it appears in the text. Gene prefixes such as those used for oncogenes or cellular localization should be shown in roman typeface (e.g., v–fes, c–MYC).
Allergens	The systematic allergen nomenclature of the World Health Organization/International Union of Immunological Societies (WHO/IUIS) Allergen Nomenclature Sub–committee should be used for manuscripts that include the description or use of allergenic proteins. For manuscripts describing new allergens, the systematic name of the allergen should be approved by the WHO/IUIS Allergen Nomenclature Sub–Committee prior to manuscript publication. Examples of the systematic allergen nomenclature can be found at the WHO/IUIS Allergen Nomenclature site.