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Taxonomia e sistemática de Entomolepididae  
Brady, 1899 (Copepoda, Siphonostomatoida)

Taxonomy and systematic of Entomolepididae Brady, 1899  
(Copepoda, Siphonostomatoida)

Tese apresentada ao Instituto de  
Biociências da Universidade de São  
Paulo, para a obtenção de Título de  
Doutor em Ciências, na Área de  
Zoologia.

Orientador: Carlos Eduardo  
Falavigna da Rocha  
Co-orientador: Rodrigo Johnsson

São Paulo

2018



## Ficha Catalográfica

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Canário Soares, Roberta  
Taxonomia e sistemática de  
Entomolepididae Brady, 1899 (Copepoda,  
Siphonostomatoida)

Número de páginas

Tese (Doutorado) - Instituto de  
Biociências da Universidade de São Paulo.  
Departamento de Zoologia.

1. Crustacea 2. Filogenia 3.  
Copépodes associados I. Universidade de  
São Paulo. Instituto de Biociências.  
Departamento de Zoologia.

### Comissão Julgadora:

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Prof(a). Dr(a).

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Prof(a). Dr(a).

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Prof(a). Dr(a).

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Prof(a). Dr(a).

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Orientador

## Dedicatória

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Dedico esta tese à memória da minha  
mãe, quem sempre me incentivou a  
estudar e buscar uma vida melhor

## Epígrafe

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“Sucesso não é o final, fracasso não é fatal: é a coragem para continuar que conta.”

Winston Churchill

## Agradecimentos

---

Em primeiro lugar eu agradeço a Deus por me manter no caminho e permitir que eu concluísse mais esta etapa.

Agradeço a meus pais Paulo Roberto e Sandra (*in memoria*) pela minha criação e apoio ao longo de toda minha vida acadêmica. Obrigada a meu pai e minha irmã por nos manter unidos no momento mais difícil de nossas vidas. Mãe, sei que você estaria muito feliz por eu ter conseguido chegar até aqui! Embora a perda nunca seja reparada, espero que a nova vida que está a caminho dê mais alegria à nossas vidas. Gostaria de agradecer a Adilton Lopes por ser um companheiro maravilhoso que esteve presente na alegria e na tristeza, na saúde e na doença e espero que esteja por todos os dias da minha vida! Amo muito vocês!

Obrigada ao meu orientador Prof. Dr. Carlos Rocha por ter me aceito como aluna, por todo o auxílio, pelos conselhos sábios e por ser uma pessoa que sempre me socorreu nesses últimos 4 anos! Meu muito obrigada ao meu coorientador Prof. Dr. Rodrigo Johnsson e à Profa. Dra. Elizabeth Neves por esses mais de 10 anos de orientação e amizade! Obrigada pelos conselhos acadêmicos e pelos não acadêmicos! Que nossos caminhos continuem se cruzando! Não poderia deixar de agradecer à Elise Vargas, que não se limitou a ser uma colega de laboratório mas foi um abraço amigo na minha chegada ao IB e em todos os nossos encontros desde então.

Obrigada a CAPES e a Pós-graduação em Zoologia da USP pela bolsa de doutorado e pelo auxílio PROEX que permitiram o desenvolvimento deste trabalho. Agradeço ao Smithsonian Institution National Museum of Natural History, especialmente ao Dr. Rafael Lemaitre, pelo empréstimo de espécimes. Gostaria de agradecer, ao Dr.

Luiz Peixoto (Museu de Zoologia da USP) pela ajuda quando o TNT não quis colaborar... Agradeço ainda aos funcionários do IB, Enio Mattos, Lilian Parpinelli e Erika Takamoto pela disponibilidade e pronta ajuda!

À minha “casa” na Bahia, o LABIMAR, meu muito obrigada à todos os colegas que auxiliaram nas coletas e que tornaram o ambiente de trabalho mais leve e divertido! Em especial, agradeço aos meus amigos Camila Borges, Iaslane Bonfim, Amilcar Farias e Thiego Hubarth: muito obrigada pelo companheirismo, parceria e carinho de sempre! À velha guarda ‘Lapepinê’, Aurinha, Cris, Bereta, Zóiudo, Kina, Nati, Mah, Cata, Pepino e Deli, embora não estivessem no dia a dia do lab, vocês se mantiveram presentes e são amizades pra vida! Licia e Vinicius obrigada também por sempre me receberem tão bem e, se não fosse por vocês, não conseguiria ficar longe de casa... Catarina, muitíssimo obrigada por todas as dicas e avaliações que você fez ao longo desses 4 anos!

Aos meus amigos Renata, Monique e Edgard, muito obrigada por estarem sempre ‘ali’! Monique, obrigada por estar ao meu lado quando eu estive no meu pior momento! Às minhas irmãs metralhas, Pitchê, Naza, Bole e Consul obrigada por terem me adotado! À Renata, Yasmin e Andrea obrigada pela amizade e palavras de conforto! Rê obrigada pela Amanda!!! As Profa. Dra. Moema Bellintani, Profa. Dra. Alessandra Schnadelbach e Profa. Dra. Sheila Resende obrigada por todos os conselhos! Mó, obrigada por todo apoio e amizade!

Por fim, obrigada aos amigos (não dá pra citar todos), professores, ex-alunos e familiares que, direta e indiretamente, contribuíram para o meu crescimento profissional e pessoal. Que o encerramento deste ciclo seja só o início de muitos outros...

# Índice

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<b>Introdução Geral</b>	09
<b>Capítulo 1.</b> Description of a new species of <i>Spongiopsyllus</i> Johnsson, 2000 and redescrptions of <i>Parmulodes verrucosus</i> Wilson, 1944 and <i>Entomopsyllus stocki</i> Kim, 2004 (Copepoda, Siphonostomatoida, Entomolepididae)	16
<i>Abstract</i>	16
1.1. Introduction	17
1.2. Material and Methods	19
1.3. Genus <i>Spongiopsyllus</i> Johnsson, 2000	21
1.4. Genus <i>Entomopsyllus</i> McKinnon, 1988	25
1.5. Genus <i>Parmulodes</i> Wilson, 1944	27
1.6. Acknowledgements	31
1.7. References	31
<b>Capítulo 2.</b> Three new <i>Spongiopsyllus</i> Johnsson, 2000 (Copepoda, Siphonostomatoida, Entomolepididae) associated with <i>Aplysina cauliformis</i> (Carter) (Porifera, Demospongiae) from Todos-os-Santos Bay, Bahia, Brazil	41
<i>Abstract</i>	41
1.1. Introduction	42
1.2. Material and Methods	42
1.3. <i>Spongiopsyllus stocki</i> n. sp. Canário <i>et al.</i>	43
1.4. <i>Spongiopsyllus boxshalli</i> n. sp. Canário <i>et al.</i>	46
1.5. <i>Spongiopsyllus hoi</i> n. sp. Canário <i>et al.</i>	50
1.6. Key to the species of the Entomolepididae	53
1.7. Acknowledgements	55
1.8. References	56



<b>Capítulo 3. Phylogenetic relationships in the family Entomolepididae</b>	
Brady, 1899 (Copepoda, Siphonostomatoida) based on	
morphological characters	66
<i>Abstract</i>	66
1.1. Introduction	67
1.2. Material and Methods	68
1.3. Results	72
1.4. Discussion	75
1.5. Conclusion	86
1.7. Acknowledgements	87
1.8. References	87
<b>Conclusões</b>	<b>107</b>
<b>Resumo</b>	<b>109</b>
<b>Abstract</b>	<b>110</b>
<b>Referências Bibliográficas</b>	<b>111</b>
<b>Anexos</b>	<b>114</b>

## Introdução Geral

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Membros da Classe Copepoda estão entre os organismos mais abundantes e diversos nos ambientes marinhos (Huys & Boxshall, 1991). Copépodes apresentam uma imensa variação morfológica e adaptações à vida nos mais diferentes habitats aquáticos, tendo colonizado com sucesso quase todos os ambientes bentônicos e planctônicos, desde a água doce e hipersalinas continentais até todo o oceano. Sobrevivem também a diversas temperaturas, sendo encontrados desde as águas polares abaixo de 0° até fontes termais, além de exibirem uma grande distribuição vertical, podendo ser encontrados desde os mares profundos até o topo do Himalaia (Huys & Boxshall, 1991). Copépodes são ainda parasitas comuns de peixes e outros vertebrados e realizam uma miríade de associações com os maiores filos de invertebrados, tais como Porifera, Cnidaria, Mollusca e Echinodermata (Huys & Boxshall, 1991; Boxshall & Halsey, 2004; Khodami *et al.*, 2017).

Copepoda é composta, atualmente, por 9 ordens: Calanoida Sars, Cyclopoida Burmeister (incluindo Poecilostomatoida Thorell), Gelyelloida Huys, Harpacticoida Sars, Monstrilloida Sars, Misophrioida Gurney, Mormonilloida Boxshall, Platycopioidea Fosshagen e Siphonostomatoida Thorell. O monofiletismo da Classe foi recentemente confirmado por Eyun (2017) e Khodami *et al.* (2017). Khodami *et al.* (2017) também demonstrou o monofiletismo das ordens de Copepoda, exceto para Harpacticoida a qual mostrou-se um grupo polifilético com duas origens diferentes para Polyarthra e Oligoarthra. Os autores propuseram ainda uma nova ordem, Canuelloida (= Polyarthra) (Khodami *et al.*, 2017).

A ordem Siphonostomatoida é formada, majoritariamente, por organismos parasitas ou associados a outros seres vivos – em sua maioria, animais (Huys & Boxshall, 1991). De acordo com o hospedeiro, os sifonostomatóides podem ser classificados em dois grupos: parasitas de vertebrados ou parasitas de invertebrados, podendo se recto- ou endoparasitas. Comumente usa-se o termo “associado” para os sifonostomatóides que vivem junto a invertebrados devido à ausência/dificuldade de estudos que determinem o tipo de relação envolvida entre hóspede-hospedeiro. Siphonostomatoida apresenta uma enorme variação morfológica, com tipos que possuem a forma do corpo com o típico padrão “ciclopiforme”, comum a muitos copépodes de vida livre, até indivíduos com corpos completamente modificados que tornam difícil até mesmo sua identificação como crustáceos – muito comum entre os parasitas de peixe (Huys & Boxshall, 1991; Boxshall & Halsey, 2004). A principal sinapomorfia da ordem é a modificação do labro e do lábio em um cone oral, por onde passa o estilete da mandíbula (= gnatobase) que, em conjunto, formam o ‘sifão’ (Huys & Boxshall, 1991; Khodami *et al.*, 2017) – a qual confere o nome ao grupo, sendo uma estrutura primariamente associada ao hábito de vida parasitário.

De acordo com Ahyong *et al.* (2011) a ordem contém 43 famílias, 342 gêneros e 2459 espécies. Dentre as famílias que vivem em associação com invertebrados, Entomolepidiade é um grupo que, apesar da sua ampla distribuição mundial, até recentemente, figurava entre as famílias menos diversas de Siphonostomatoida. Estudos realizados na Baía de Todos os Santos (Salvador, Bahia) tem revelado uma diversidade além do esperado, com novos gêneros e novas espécies descritas (Borges *et al.*, in prep.; Farias *et al.*, in prep.).

### **Família Entomolepididae Brady, 1899**

A Família Entomolepididae foi estabelecida por Brady (1899) para acomodar um novo gênero, *Entomolepis*, e uma nova espécie, *E. ovalis*. A nova espécie exibe uma morfologia conspícua: um disco corporal oval e achatado que lembra alguns copépodes parasitas. Quatro anos depois, Thompson & Scott (1903) descreveram o gênero *Lepeopsyllus* composto por duas espécies, *L. ovalis* e *L. typicus*, que possuíam o corpo característico de Entomolepididade; entretanto, os autores posicionaram os novos táxons na família Asterocheridae Giesbrecht. Assim como Thompson & Scott (1903), Wilson (1944) cometeu um engano ao acomodar *Parmulodes*, o qual possui um sifão conspícuo, e que posteriormente foi reconhecido como um Entomolepididae, em Clausidiidae Embleton, uma família da ordem Poecilostomatoida.

A diagnose de Entomolepididade foi estabelecida apenas sessenta anos depois por Eiselt (1959), quem também subdividiu o grupo em duas subfamílias: Entomolepinae e Parmulodinae que diferem, basicamente, pelo número de segmentos pedígeros entre o cefalotórax e o escudo terminal – Entomolepinae tem dois segmentos enquanto Parmulidinae possui apenas um como resultado da fusão entre o terceiro e o quarto segmentos pedígeros. Aparentemente desconhecendo a existência da família, Ummerkuty (1960) descreveu o gênero *Paralepeopsyllus* reconhecendo sua similaridade com *Lepepeopsyllus*, assumiu ambos como um grupo coeso, porém os considerou como intermediários entre Asterocheridae e Dyspontiidae Sars. Quando Mckinnon (1988) realizou uma revisão de Entomolepididae, ele redefiniu a diagnose da família e suas subfamílias para incorporar *Paralepeopsyllus* em Parmulodinae e para incluir a possibilidade do segmento terminal do palpo da mandíbula poder ser muito mais curto que o segmento basal, além de considerar a quarta e quinta pernas como reduzidas ou ausentes nesta subfamília.

Adicionalmente, ele descreveu uma nova espécie de *Entomolepis*, *E. hamondi*, um novo gênero *Entomopsyllus* para acomodar *E. adriae* (Eiselt) e uma nova espécie deste mesmo gênero, *E. nichollsi*. Stock (1992) identificou incongruências em *Parmullela* e *Parmulodes* com relação à diagnose de Parmulodinae e, por este motivo, se absteve em utilizar a classificação de subfamília em seu trabalho.

Até o momento, Entomolepididae é composta por 9 gêneros e 19 species (Borges *et al.*, em prep.; Farias *et al.*, em prep.; Uyeno & Johnsson, em prep.). Parmulodinae, que inclui os gêneros *Parmulodes* Wilson, 1944, *Paralepeopsyllus* Ummerkutty, 1960, *Parmulella* Stock, 1992, *Parmulopsyllus* Borges *et al.*, em prep. e *Neoparmulella* Farias *et al.*, em prep., é caracterizada, entre outras características, pela presença de apenas um segmento entre o cefalotórax e a placa abdominal, e ausência da perna 4, embora a mesma também esteja ausente em *Entomolepis* Brady, 1899. Os gêneros de Entomolepinae, *Entomolepis*, *Entomopsyllus* McKinnon, 1988, *Lepeopsyllus* Thompson & Scott, 1903 e *Spongiopsyllus* Johnsson, 2000 por outro lado, exceto como citado para *Entomolepis*, possuem a perna 4 com exópodo 3-segmentado; o endópodo pode estar reduzido a um lobo com uma cerda, condição observada em *Lepeopsyllus*, ou ausente, como em *Entomopsyllus* e *Spongiopsyllus*.

Entomolepididae apresenta distribuição mundial com maior diversidade, até o momento, no Indo-Pacífico (Stock, 1992; Boxshall & Halsey, 2004). No Oceano Atlântico são registradas espécies de cinco gêneros: *Parmulodes verrucosus* Wilson, 1944, *Parmulella emarginata* Stock, 1992, *Parmulopsyllus breviarticulata* Borges *et al.*, in prep., *Neoparmulella periperiensis* Farias *et al.*, in prep., *Spongiopsyllus adventicius* Johnsson, 2000, *S. redactus* Canário *et al.*, 2012 and *S. intermedius* Borges *et al.*, em prep. Com relação a biologia de Entomolepididae, Boxshall & Halsey (2004) citam a família como

tipicamente associada à esponjas, considerando que a maioria das espécies foram registradas em amostras de Porifera. *Paralepeopsyllus mannarensis* Ummerkutty, 1960 foi encontrada em amostras de diversas esponjas não identificadas; *P. emarginata* e *P. verrucosus* foram ambas descritas em associação com *Chondrilla nucula* Schmidt (Wilson, 1944; Stock, 1992); *E. adriae* (Eiselt, 1959) também vive em esponjas (*Verongia aerophroa* (Schmidt) and *Verongia cavernicola* (Vacelet); por fim, as espécies de *Spongiopsyllus* associam-se ao gênero *Aplysina* Nardo, exceto *S. redactus* que foi encontrada no coral escleractínio *Mussismilia hispida* (Verrill). Entomolepididae também estabelece relação com outros organismos além das esponjas. As espécies do gênero *Entomolepis* foram encontradas em anêmonas (*E. hamondi* McKinnon, 1988) e na ascídia *Botrylloides leachi* (Savigny) (*E. ovalis*) (Brady, 1899; McKinnon, 1988). Kim (2004) descreveu *Entomopsyllus stocki* em associação com o coral *Tubipora musica* (Linnaeus). Apesar das espécies de Entomolepididae que têm seus hospedeiros conhecidos, *Entomopsyllus nichollsi* McKinnon, 1988 (que foi encontrado em rede de plancton) e *Lepeopsyllus typicus* não possuem registro de associação com outros organismos. Entretanto, estas duas espécies não devem ser consideradas como organismos de vida livre, uma vez que compartilham o mesmo formato de corpo e possuem semelhanças em seus apêndices como encontradas em outros Entomolepididae associados (e.g. ambas apresentam longos sifões, que indicam um modo de vida “parasitário”). Os registros esparsos em hospedeiros que não esponjas podem estar relacionados à escassez de estudos que foquem na amostragem mais diversa de potenciais táxons hospedeiros. Por outro lado, é igualmente provável que os membros de Porifera forneçam um habitat propício para o desenvolvimento dos Entomolepididae.

Na literatura não são encontrados trabalhos que objetivaram estudar as relações entre as espécies de Entomolepididae, bem como entre seus gêneros. Em sua tese, ao estudar as famílias de Siphonostomatoida associadas a invertebrados, Johnsson (2003) propôs o monofiletismo de Entomolepididae, embora não tenha publicado seus resultados. A morfologia regular de Entomolepididae dificulta o estabelecimento e a definição dos táxons. É comum encontrar sobreposições nas diagnoses de gêneros assim como nas das subfamílias. Assim, este é o primeiro estudo que busca estudar a família com foco nas relações filogenéticas entre seus membros, incluindo todas as espécies descritas (e as novas), com o objetivo de validar seus gêneros e compreender a evolução do grupo.

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## Capítulos

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**Capítulo 1.** Description of a new species of *Spongiopsyllus* Johnsson, 2000 and redescrptions of *Parmulodes verrucosus* Wilson, 1944 and *Entomopsyllus stocki* Kim, 2004 (Copepoda, Siphonostomatoida, Entomolepididae) – submetido à Zootaxa (ISSN 1175-5326)

**Capítulo 2.** Three new *Spongiopsyllus* Johnsson, 2000 (Copepoda, Siphonostomatoida, Entomolepididae) associated with *Aplysina cauliformis* (Carter) (Porifera, Demospongiae) from Todos-os-Santos Bay, Bahia, Brazil

**Capítulo 3.** Phylogenetic relationships in the family Entomolepididae Brady, 1899 (Copepoda, Siphonostomatoida) based on morphological characters



# Capítulo 1

---

## **Description of a new species of *Spongiopsyllus* Johnsson, 2000 and redescrptions of *Parmulodes verrucosus* Wilson, 1944 and *Entomopsyllus stocki* Kim, 2004 (Copepoda, Siphonostomatoida, Entomolepididae)**

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### **Abstract**

The Family Entomolepididae is composed by 7 genera and 15 species. The family was subdivided in Parmulodinae and Entomolepinae. During a survey on the known species and the search for new species, a new *Spongiopsyllus* is described associated with sponge *Aplysina insularis*. The new species has antennule 14-segmented, four setae on both lobes of maxillule, some unique features on the leg setation and the armature of the maxilliped. These characteristics make the new species different from all other congeners in *Spongiopsyllus*. The diagnosis of *Entomopsyllus* was also revised once it does not consider the differences to *Spongiopsyllus* which was created posteriorly to its erection. An analysis of *Entomopsyllus stocki* also indicated that leg 5 somite and the genital somite are fused, instead of separated as originally stated, the structure is also redescrbed. Finally, *Parmulodes verrucosus* is studied and an up-to-date description is provided, correcting some inconsistencies in the armature formula

of the antennule and the leg setation, and providing re-analysis of the other appendages.

**Key words:** associated copepod, Parmulodinae, Etomolepinae, *Aplysina*, symbiotic fauna

## Introduction

The Family Entomolepididae Brady, 1899 is a worldwide group, composed by 7 genera and 15 species (Canario et al. 2012; Lee & Kim 2017). Eiselt (1959) subdivided the family in Parmulodinae and Etomolepinae.

The diagnosis of Parmulodinae is revised by McKinnon (1988) to accommodate the genus *Paralepeopsyllus* Ummerkutty. New features are considered by McKinnon (1988): “presence of a single thoracic somite between cephalothorax and abdominal pleural plate; mandible not greatly lengthened and retaining a recognizable blade; basal segment of first maxilla small, inner lobe large, outer lobe about a third the length of the inner lobe; leg 4 absent; leg 5 absent or uniramous as in Entomolepidinae, but considerably shorter”. Parmulodinae includes the genera *Parmulodes* Wilson, 1944, *Parmulella* Stock, 1992 and *Paralepeopsyllus* Ummerkutty, 1960. *Paralepeopsyllus* remained monospecific for more than sixty years, until Lee & Kim (2017) described two new species. *Parmulodes* and *Parmulella* have remained monospecific since their original description, although Stock (1992) revised *P. verrucosus* renaming the specific epithet of the species properly, making remarks of certain female characters and describing the male that was unknown.

In Entomolepinae there are 4 genera, *Entomolepis* Brady, 1899; *Entomopsyllus* McKinnon, 1988; *Lepeopsyllus* Thompson & Scott, 1903 and *Spongiopsyllus* Johnsson, 2000. The subfamily is characterized by the following characteristics, according to McKinnon (1988): “2 thoracic somites between cephalotorax and abdominal pleural plate; basal segment of first maxilla large, inner lobe elongate, outer lobe small and bearing 3 setae; mandible stylet-like and greatly lengthened; fourth leg reduced or absent; leg 5 uniramous, long and recurved, short and stick-like, or occasionally absent”. *Entomolepis* is the type genus of the family and possesses two species. A third species, *E. adriae* (Eiselt, 1959), was transferred to *Entomopsyllus* erected by McKinnon (1988) when describing *E. nichollsi* McKinnon, 1988.

Posteriorly two other species were described: *E. stocki* Kim, 2004 found in association to stoloniferan coral *Tubipora musica* (Linnaeus) (Kim 2004) and *E. brevicaudatus* Lee & Kim, 2017 sampled in washings of unidentified sponges (Lee & Kim 2017). Therefore, *Entomopsyllus* is the largest genus of the family, with 4 known species. *Lepeopsyllus* has remained with two species described more than a century ago (Thompson & Scott 1903) and *Spongiopsyllus*, described in the beginning of the XXI century has already two known species (Johnsson 2000; Canario *et al.* 2012). *Spongiopsyllus* has been described to the Brazilian coast and so far, has remained endemic.

The difference between the Entomolepidinae genera relies on leg 4 and urosome segmentation. In *Entomolepis* leg 4 is absent, *Lepeopsyllus* has leg 4 with the endopod reduced to a single segment and in *Entomopsyllus* and *Spongiopsyllus* leg 4 has a 3-segmented exopod but the endopod is totally absent. However, despite this similarity both genera can be distinguished based on the 3 and 4 postgenital

urosomites of the female and male respectively in *Spongiopsyllus* while

*Entomopsyllus* shows 2 and 3 somites on the same region.

*Spongiopsyllus* has been recorded only in the northeastern region of Brazil (Johnsson & Neves 2012) and the main hosts have been sponges for *S. adventicius* Johnsson, 2000 specially the genera *Dysidea* and *Monanchora* but mainly from *Aplysina* (Johnsson 2000; Johnsson & Neves 2012). The other species of the genus, *S. redactus* Canario *et al.* 2012, has recorded in *Mussismilia hispida*, a scleractinian coral (Canario *et al.* 2012).

*Entomopsyllus* has three species recorded from the Indian Ocean region or proximally. *Entomopsyllus stocki* Kim, 2004 was sampled in Madagascar Island in a stoloniferan coral (Kim 2004), *E. nichollsi* McKinnon, 1988 was found in Western Australia, in Shark Bay, in the plankton (McKinnon 1988) and *E. brevicaudatus* Lee & Kim, 2017 was sampled in Anda Island (Philippines). Therefore, these three species are spread along the Western and Central Indo-Pacific regions (Spalding *et al.* 2007). The last species, which is also the type species of the genus, *E. adriae* (Eiselt, 1959) was recorded in Adriatic Sea, near Croatia coast.

Thus, the main aim of this work is to describe a new species of *Spongiopsyllus* found in association with the sponge *Aplysina insularis* (Duchassaing & Michelotti).

Besides that, *Parmulodes verrucosus* and *Entomopsyllus stocki* are redescribed and the diagnosis of *Entomopsyllus* is emended, reinforcing the difference to *Spongiopsyllus*.

## Material and methods

The new species of *Spongiopsyllus* was recovered from samples of *Aplysina insularis* (Duchassaing & Michelotti). The sponges were hand-collected during low tide, at a

maximum depth of 3 m at Porto da Barra Beach, Salvador, Bahia, Brazil (13°00'13.5"S 38°32'02.6"W), in the city of Salvador, Bahia State, Brazil on 31<sup>st</sup>, August 2016.

The hosts were sampled and immediately placed in individual plastic bags with sea water. Ethanol was added to the sea water until a final concentration of 5% was reached. After 30 minutes, the samples were washed and filtered through a 100 µm mesh screen, transferred to a petri dish with ethanol, and sorted for copepods under a dissecting microscope and then fixed in 70% ethanol for subsequent analysis.

The types were cleared in lactic acid, measured, and its body drawn before being stained in Chlorazol Black E, dissected, and permanently mounted in CMC-9® (Masters Chemical Company, Inc.). All drawings were made with the aid of a drawing tube fitted on an Olympus CH30 microscope. All structures were also observed and checked with the aid of a Nikon Eclipse Ci microscope equipped with a digital camera. The length of the antennule segments was measured along the posterior, non-setiferous margin. Antennular segments are denoted by Roman numerals indicating ancestral segments following Huys & Boxshall (1991). For the armature formula of legs 1–4, Roman numerals indicate spines and Arabic numerals indicate setae. Type specimens of the new *Spongiopsyllus* species were deposited in the Museu de Zoologia of the Universidade Federal da Bahia (UFBA) in Brazil. The holotypes of *Entomopsyllus stocki* and *Parmulodes verrucosus* were obtained by loan from United States National Museum of Natural History (USNM) and the specimens were analyzed in a Nikon Eclipse Ci microscope. The illustrations were made with the aid of a drawing tube fitted on an Olympus CH30 microscope.

## **Taxonomy**

## Order SIPHONOSTOMATOIDA Thorell, 1859

### Family ENTOMOLEPIDIDAE Brady, 1899

#### Genus *Spongiopsyllus* Johnsson, 2000

#### *Spongiopsyllus atypicus* n. sp.

(Figs 1–3 A-C)

**Material examined.** Holotype f# (UFBA 3183), alotype m# (UFBA 3295) and paratype f# (UFBA 3296), Porto da Barra Beach, Todos-os-Santos Bay, Salvador city, Bahia State, Brazil, collected by LABIMAR, 31, August 2016. Associated with sponge *Aplysina cauliformis*. Paratype (UFBA 3294) dissected and mounted on slide. Holotype and alotype preserved in ethanol.

**Description of female.** Mean body length (excluding caudal setae) 1,155  $\mu\text{m}$  (1,150–1,160  $\mu\text{m}$  and mean body width 719  $\mu\text{m}$  (717–721  $\mu\text{m}$ ) ( $n=2$ ). Body (Fig. 1A) with prossomal shield flattened showing radiation bands along outer margin. Pedigerous somites 2–4 free. Pedigerous somite 4 expanded, covering urosome except the tip of caudal rami.

Urossome 4-segmented (Fig. 1B). Genital double-somite fused with fifth pedigerous somite, 150  $\mu\text{m}$  long and maximum width 132  $\mu\text{m}$ , length:width ratio = 1.1:1, vestigial leg 6 located anterolaterally with minute seta, close to genital openings. Setulated groove mid posteriorly on genital somite, reaching posterior margin. Three postgenital somites present; first one longer than wide (62  $\times$  60  $\mu\text{m}$ ); second and third somites wider than long (38  $\times$  55, 50  $\times$  60  $\mu\text{m}$ , respectively). Caudal rami enlongate, 120  $\times$  19  $\mu\text{m}$ . Length: width ratio 6.3:1  $\mu\text{m}$ , armed with six setae; seta I absent.

Antennule (Fig. 1C) slender, 257  $\mu\text{m}$  long (not including setae), 14-segmented. Length of segments measured in proximal to distal order: 61, 19, 34, 9, 9,

10, 11, 11, 11, 10, 10, 9, 9, and 18  $\mu\text{m}$ , respectively. Segmental homologies and setation as follows: 1(I)-1; 2(II)-1; 3(III-VIII)-9; 4(IX-XIII)-7; 5(XIV)-1+I; 6(XV)-1; 7(XVI)-1; 8(XVII)-1; 9(XVIII)-2; 10(XIX)-1; 11(XX)-1; 12(XXI)-1+ae; 13(XXII-XXIII)-0; 14(XXIV-XXVIII)-11; all setae smooth. Aesthetasc 82  $\mu\text{m}$  long.

Antenna (Fig. 1D) 218  $\mu\text{m}$  long (including distal claw); coxa and basis unarmed. Exopod 1-segmented, 64  $\mu\text{m}$  long with smooth distal seta and seven lateral setules. Endopod 2-segmented, first segment 54  $\mu\text{m}$  long, unarmed, with setules along outer margin; second segment 27  $\mu\text{m}$  long armed with long proximal lateral seta on outer margin and three subdistal setae on inner, outer and medial margin. The latter seta is the longest one and is located close to distal claw, 46  $\mu\text{m}$  long, slightly curved distally. Two rows of setules on second endopodal segment.

Oral cone 625  $\mu\text{m}$  long, reaching to genital double-somite (Fig. 1A). Mandible comprising stylet and slender 2-segmented palp (Fig. 1E) measuring 43 and 40  $\mu\text{m}$  long, respectively. Second segment with 2 naked distal setae. Both setae broken. Maxillule bilobed (Fig. 1F), both lobes armed with four setae, outer lobe 39  $\mu\text{m}$  long with row of setules on outer margin; inner lobe with 54  $\mu\text{m}$  long. Maxilla (Fig. 1G) with syncoxa 162  $\mu\text{m}$  long and claw with distal portion curved at a 90° angle, 137  $\mu\text{m}$  long.

Maxilliped (Fig. 2A) 5-segmented, 234  $\mu\text{m}$  long; syncoxa 40  $\mu\text{m}$  long with naked seta on inner margin; basis 93  $\mu\text{m}$ , unarmed. Endopod 3-segmented, segments measuring 23, 18 and 22  $\mu\text{m}$  long, respectively; first segment with two long setae; second segment unarmed; third segment with small seta close to distal claw-like element with curved tip and measuring 38  $\mu\text{m}$  long.

Legs 1-3 (Fig. 2B-D) biramous, with 3-segmented rami. Leg 4 (Fig. 2E) with 3-segmented exopod and endopod absent. Armature formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-1	I-1; I-1; II,I,4	0-1; 0-2; 0,5
Leg 2	0-1	1-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
Leg 3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,2
Leg 4	0-0	1-0	I-1; I-1; II,I,3	absent

Leg 1 with very long and naked inner seta on basis, first endopodal segment very enlarged, second and third endopodal segments prolonged distally into sharpened process, therefore distal setae of third segment located sub-distally on inner margin (Fig. 2B). Exopodal segments of legs 1 to 4 with setules on outer margins (Figs 2B-E). Legs 2 and 3 with second endopodal segments with setules on both margins and third endopodal segments with few setules on outer margin (Figs 2C-D). Leg 3 with first endopodal segment unarmed, with setules on outer margin and dilatated subdistally; third endopodal segment very short, half the length of previous segment and armed with 2 setae (Fig. 2D). Leg 4 bearing minute seta on outer margin of basis (Fig. 2E).

Free exopodal segment of P5 (Fig. 1B) elongated, curved, 196  $\mu\text{m}$  long, almost reaching distal margin of first post-genital somite, armed with 2 distal setae and one outer seta medially; all setae plumose.

**Description of male.** Body (Fig. 3A) similar to female, but much smaller. Mean body length (excluding caudal setae) 718  $\mu\text{m}$  and mean body width 535  $\mu\text{m}$ . Prossomal shield flattened with radiation bands along outer margin. Pedigerous somites 2–4 free. Pedigerous somite 4 expanded, covering urosome.

Urosome 5-segmented (Fig. 3B). Genital somite fused with fifth pedigerous somite, 108  $\mu\text{m}$  long and maximum width 151  $\mu\text{m}$ , and length:width ratio 0.7:1. First,



third and fourth postgenital somites wider than long ( $21 \times 53$ ,  $13 \times 48$ ,  $38 \times 48$   $\mu\text{m}$ , respectively); second somite almost as long as wide ( $51 \times 50$   $\mu\text{m}$ ); First and second postgenital somites with tooth-like projections on each distal lateral margins.

Prossome:urossome length ratio 3.4:1. Caudal rami elongated, 55  $\mu\text{m}$  long, armed with six setae; seta I absent, setae II to VII present.

Antennule (Fig. 3C) slender, 219  $\mu\text{m}$  long (not including setae), 14-segmented. Length of segments measured in proximal to distal order: 45, 19, 22, 8, 10, 4, 5, 13, 24, 9, 17, 18, 21 and 15  $\mu\text{m}$ , respectively. Segmental homologies and setation as follows: 1(I)-1; 2(II)-2; 3(III-VI)-8; 4(VII)-1; 5(VIII)-2; 6(IX-XII)-8; 7(XIII)-1; 8(XIV)-1; 9(XV-XVI)-4; 10(XVII)-2; 11(XVIII)-2; 12(XIX-XX)-2; 13(XXI-XXIII)-4+ae; 14(XXIV-XXVIII)-13; all setae smooth. Aesthetasc 85  $\mu\text{m}$  long. Oral cone (Fig. 3A) 400  $\mu\text{m}$  long, reaching first post-genital somite. All other appendages as in the female.

**Type locality.** Porto da Barra Beach ( $13^{\circ}00'13.5''\text{S}$ ,  $38^{\circ}32'02.6''\text{W}$ ), Salvador city, Bahia State, Brazil.

**Etymology.** The specific name '*atypicus*' is a combination of the prefix 'a', that means no, with the Latin word 'typicus', that means 'relative to a type' referring to uncommon and unique characteristics of the new species. Among these characteristics we may point the presence of an outer seta on leg 4 basis, the maxillule with 4 setae on each lobe and the extremely long inner seta on the basis of leg 1.

**Remarks.** *Spongiopsyllus atypicus* **sp. nov.** has antennule 14-segmented differing from all others *Spongiopsyllus* species: *S. adventicius* and *S. redactus* have the antennule 17 and 15-segmented respectively (Johnsson 2000; Canário *et al.* 2012). Indeed, *S. atypicus* sp. nov. possesses four setae on both lobes of maxillule as differing from *S. adventicius* and *S. redactus* that have three setae on each lobe

(Johnsson 2000; Canário *et al.* 2012). The armature formula of the endopod of the maxilliped in the new species is 2,0,1+claw while in *S. adventicius* and *S. redactus* is respectively 0,2,1+claw and 2,1,1+claw (Johnsson 2000; Canário *et al.* 2012). Among the other unique features of the *S. atypicus* sp. nov. are the outer seta on the basis of leg 4, the the extremely long inner seta on the basis of leg 1. These characteristics are not found in any other species of the genus.

### **Genus *Entomopsyllus* McKinnon, 1988**

**Emended diagnosis.** Entomolepididae, sub-family Entomolepinae. Body shield composed by cephalosome and pedigerous somites 2-4; pedigerous somite 4 recovering entirely the prosome. Two postgenital somites in female and one in male. Exopod of antenna hirsute, as long as endopod. Third endopodal segment of leg 1 prolonged distally into sharpened process, therefore distal setae located sub-distally on inner margin. Second endopodal segment of leg 2 with single seta. Third exopodal segment of leg 3 with two lateral spines. Leg 4 with endopod absent and exopod 3-segmented. Leg 5 at least as long as the genital complex.

**Remarks.** The original diagnosis of *Entomopsyllus*, as presented by McKinnon (1988) is very concise and included some characteristics such as (1) exopod of antennule as a single, long, blunt, hirsute segment; (2) endopod of leg 4 absent; and (3) leg 5 as a single segment, at least as long as genital complex. These characteristics were useful to stablish *Entomopsyllus* within the sub-family Entomolepinae. However, Johnsson (2000), when erecting *Spongiopsyllus*, specified the diagnostic characters to differentiate both genera, but the *Entomopsyllus*' diagnosis remained as originally stated. Therefore, *Entomopsyllus* shares these characteristics with *Spongiopsyllus*. Nevertheless, *Entomopsyllus* possesses two and three postgenital

somites in female and male, respectively, instead of three and four as in *Spongiopsyllus*.

***Entomopsyllus stocki* Kim, 2004**

(Fig. 3D)

**Material examined.** Holotype f# (USNM 1027325), associated with *Tubipora musica* collected in Nosy Bé, Madagascar, 05, January 1964.

**Description of female.** Urossome 3-segmented (Fig. 3D). Genital double-somite fused with fifth pedigerous somite forming genital complex, 150  $\mu\text{m}$  long and maximum width anteriorly, 133  $\mu\text{m}$ , length : width ratio = 1.1:1, vestigial leg 6 located anterolaterally with seta, close to genital openings, at 1/3 of the anterior margin. Setulated groove mid-posteriorly on genital somite, reaching posterior margin. Two postgenital somites present. First and second abdominal somites  $52 \times 57$  and  $63 \times 61$   $\mu\text{m}$ , respectively. Posterior margin of anal somite concave at insertion of caudal rami. Caudal rami convergent, and gradually broadening distally,  $110 \times 19$   $\mu\text{m}$ . Length : width ratio 5.8:1, armed with 6; setae I absent. Leg 5 formed by basal segment, enlarged proximally, armed with small, naked seta on outer margin and distal thin segment with 3 naked setae.

All other appendages as in original description by Kim (2004), except for the antennal exopod and the outer lobe of the maxillula which we were unable to study due to the quality of the slide.

**Remarks.** The female of *Entomopsyllus stocki* was described by Kim (2004) based on a single specimen dissected and mounted on permanent slide. In this revision only the genital complex showed differences to the original description (Kim 2004), that was described as unfused to the fifth pedigerous somite. A careful reexamination

indicates that the fifth pedigerous somite is fused, forming a genital complex. The setuled groove in the mid-posterior region was not described originally, as well.

### **Genus *Parmulodes* Wilson, 1944**

#### ***Parmulodes verrucosus* Wilson, 1944**

(Figs 4–6)

**Material examined.** Holotype f# (USNM 79000), collected in tidal pools of coral reefs, Key Matecumbe, Florida, USA, July, 1925.

**Description of female.** Body length (excluding caudal setae) 1,124  $\mu\text{m}$  and body width 841  $\mu\text{m}$ . Body with prosomal shield flattened (Fig. 4A). Pedigerous somite 1 fused to cephalosome with slightly projected margins. Pedigerous somite 2 narrower than others. Pedigerous somite 3 and 4 fused forming posterior shield recovering urosome. Margins of cephalosome and fused pedigerous somites 3 and 4 with digitiform bands (Fig. 4B).

Urosome 4-segmented (Fig. 4C). Genital double-somite 150  $\mu\text{m}$  long and maximum width 106  $\mu\text{m}$ , length:width ratio = 1.4:1, anteriorly enlarged, with set of small setules after genital apertures which are located anterolaterally. Two postgenital somites, both wider than long,  $56 \times 75$ ,  $44 \times 66$   $\mu\text{m}$ , respectively. Anal somite with anal plate on medial-posterior portion. Caudal rami short (Fig. 4D),  $62 \times 47$   $\mu\text{m}$ ; Length: width ratio 1.3:1  $\mu\text{m}$ , armed with six setae; seta I absent.

Antennule (Fig. 4E) slender, 335  $\mu\text{m}$  long (not including setae), and 17-segmented. Length of segments measured in proximal to distal order: 91, 22, 10, 9, 18, 12, 15, 2, 11, 11, 18, 14, 14, 17, 22, 24 and 49  $\mu\text{m}$ , respectively. Segmental homologies and setation as follows: 1(I)-2; 2(II-III)-4; 3(VI)-2; 4(V)-2; 5(VI-VII)-3; 6(VIII)-2; 7(IX-XII)-6; 8(XIII)-1; 9(XIV)-I+1; 10(XV)-2; 11(XVI)-2; 12(XVII)-1;

13(XVIII)-2; 14(XIX)-1; 15(XX)-1; 16(XXI)-1 +ae; 17(XXII–XXVIII)-11. All setae smooth. Aesthetasc 47  $\mu\text{m}$  long.

Antenna (Fig. 5A) 268  $\mu\text{m}$  long (including distal claw); coxa and basis unarmed. Exopod 1-segmented, 52  $\mu\text{m}$  long, with apical seta and 3 small lateral setules. Endopod 3-segmented; first segment 80  $\mu\text{m}$  long, with distal seta and row of setules on outer margin; second segment 15  $\mu\text{m}$  long with subdistal seta; third segment 11  $\mu\text{m}$  long, ornamented with row of setules along outer margin, and armed with 2 naked and thin setae, located proximally and subdistally, and 1 distal robust terminal seta, close to distally straight claw with curved tip, 54  $\mu\text{m}$  long, with row of spinules and 4 teeth distally.

Oral cone 580  $\mu\text{m}$  long, corresponding to half the length of the body, club-shaped, distal part sharp, reaching insertion between of legs 3 and 4 (Fig. 4A). Mandible comprising stylet 319  $\mu\text{m}$  long and slender 2-segmented palp measuring 82 and 27  $\mu\text{m}$  long, respectively (Fig. 5B). Stylet slender and serrated, 480  $\mu\text{m}$  long. Palp with second segment armed with 2 apical, plumose setae, one of them almost twice longer the other. Maxillule bilobed (Fig. 5C), inner lobe 94  $\mu\text{m}$  long, armed with 1 smooth and 3 unilaterally plumose setae. Outer lobe 29  $\mu\text{m}$  long, armed with 4 naked setae, one of them reduced. Maxilla (Fig. 5D) with syncoxa and curved claw measuring 197 and 130  $\mu\text{m}$  long, respectively.

Maxilliped (Fig. 5E) 5-segmented, 275  $\mu\text{m}$  long (excluding claw); syncoxa 63  $\mu\text{m}$  long, unarmed; basis 130  $\mu\text{m}$  long, unarmed with row of setules on medial distal inner margin. Endopod 3-segmented, segments measuring 17, 40 and 25  $\mu\text{m}$  long, respectively; first segment with 2 setae and setules on outer margin; second and third segments both with single seta; curved claw (Fig. 5F) measuring 57  $\mu\text{m}$  long with subdistal inner tooth, both margins with spinules.

Legs 1–3 (Figs. 6A–C) biramous, with 3-segmented rami. Leg 4 (Fig. 6D) reduced to a bud bearing a seta. Armature formula of legs 1–3 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-1; I-1; III,2,2	0-1; 0-2; 1,2,3
Leg 2	0-0	1-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,3
Leg 3	0-1	1-0	I-1; I-1; II,I,4	0-1; 0-2; 1,1,3

Second endopodal segments of leg 1 to leg 3 with two tooth-like processes on distal outer corner (Figs. 6A–C). Setules on outer margin of first exopodal segment of leg 1; and outer margins of most endopodal and exopodal segments of legs 2 and 3.

Leg 5 (Fig. 6E) protopodal fused to fifth pedigerous somite, with single outer seta. Free segment with 3 apical and 1 subdistal setae and setules on outer margin.

**Male.** Material not analyzed.

**Remarks.** The analysis of the holotype shows many differences regarding the original description. Wilson (1944) describes the pedigerous somites 3 to 5 as fused; but, only the pedigerous somites 3 and 4 are fused. The antennule was described as 18-segmented instead of 17-segmented as observed here due to fusions among basal elements II and III. The illustration provided by Wilson (1944, fig. 153) indicates a possible fusion of these segments once there is a seta located in the division of segments I and II. Consequently, if this seta refers to second segment it would imply in the existence of a fused segment as observed in the present redescription.

In the original description, Wilson (1944, pg 544) states: “The basal segment of the second antenna is stout and longer than the other two segments combined, with a short spine at its inner distal corner” that, together with the illustration (Wilson 1944, fig. 154) reinforces the conception that the endopod was formed by only 2 segments, the first unarmed and the second with small spine near to terminal claw,

and the exopod would be the short spine mentioned. In fact, the endopod is 3-segmented, the first and the second segments with a seta both and the third possessing three setae, one of them robust and spine-like. The short spine of the basis refers in fact to the exopod as presently observed.

The endopod of the maxilliped also differs from Wilson's original description (1944) once it is 3-segmented with terminal claw instead large claw as illustrated by the author.

The legs illustrated by Wilson (1944; Figs. 159 and 160) also shows many divergences concerning the holotype analyzed. The main dissemblance consists in the statement made by the author that *Parmulodes verrucosus* has 4 pairs of biramous legs, with 3-segmented rami in each. Leg 4 rises in the adult as a reduced protuberance with a seta on its border as observed in the original slide and also stated by Stock (1992).

*Parmulodes* possess only one species. The material analyzed in this work as the same described by Wilson (1944) and consist of only a female. Posteriorly, Stock (1992) described the male of *P. verrucosus* and discovered that the host of this species is the sponge *Chondrilla nucula* Schmidt. The most of male's appendices resembles those of the female, as described by Stock (1992), only with a reduction of its size. Among the differences observed in both sexes, include (1) Segmental homologies and setation of male's antennule: I-2; II-2; III-2; IV-VII-8; VIII-2; IX-XII-5+ae; XIII-1; XIV-1; XV-XVI-4; XVII-2; XVIII-2; XIX-XX-2; XXI-XXIII-4+ae; XXIV-XXVIII-8+ae reflecting a different fusion pattern in the proximal region of the antennule; and (2) leg 6 represented by two setae.

Despite *Parmulodes verrucosus* was redescribed by Eiselt (1959) and subsequently by Stock (1992), who made some further comments. The original

drawings are too poorly made and a complete redescription was necessary to fulfill gaps concerning details and measures of the appendages.

**Acknowledgements.** The authors thank to Smithsonian Institution National Museum of Natural History for the loan of the holotypes. TH thanks to “FAPESB (Fundação de Amparo à Pesquisa do Estado da Bahia) for financial support. RC thanks ‘Programa de Pós-Graduação em Zoologia’ (USP) and CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for financial support and thanks the ‘Programa de Pós-Graduação em Diversidade Animal’ for the usage of the LaMI (Laboratório de Microscopia e Imagem).

## References

- Canário, R., Neves, E. & Johnsson, R. (2012). *Spongiopsyllus redactus*, a new species of Entomolepididae (Copepoda, Siphonostomatoida) associated with a scleractinian coral in Brazil. *Zoosymposia*, 8, 49–55.  
<http://dx.doi.org/10.11646/zoosymposia.8.1.8>
- Eiselt, J. (1959) *Entomolepis adriae*, ein Beitrag zur Kenntnis der kaum bekannten Gattungen siphonostomer Cyclopiden: *Entomolepis*, *Lepeopsyllus* und *Parmulodes* (Copepoda, Crust.) Sitzber. *Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, 168, 643–660.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468pp.
- Johnsson, R. (2000) *Spongiopsyllus adventicius* new species and genus of Entomolepididae (Copepoda: Siphonostomatoida) associated with sponges in Brazil. *Hydrobiologia*, 417, 115–119.



<https://doi.org/10.1023/A:1003815707337>

- Johnsson, R. & Neves, E. G. (2012) Siphonostomatoid copepods (Crustacea) associated with marine invertebrates and algae in Brazil: a review and future considerations. *Zoosymposia*, 8, 69–80.  
<http://dx.doi.org/10.11646/zoosymposia.8.1.10>
- Kim, I.H. (2004) Two new species of siphonostomatoid copepods (Crustacea) associated with the stoloniferan coral *Tubipora musica* (Linnaeus) from Madagascar. *Korean Journal of Biological Sciences*, 8, 187–196.
- Lee, J. & Kim, I.H. (2017) Siphonostomatoid copepods (Crustacea) associated with sponges from the Philippines and Vietnam. *Animal Systematics, Evolution and Diversity*, 33 (2), 73–99.  
<https://doi.org/10.5635/ASED.2017.33.2.007>
- Mckinnon, A.D. (1988) A revision of Entomolepididae (Copepoda: Siphonostomatoida) with Descriptions of Two New Species from Australia, and Comments on *Entomolepis ovalis* Brady. *Australian Journals of Science Research*, 2, 995–1012.
- Spalding M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, 57, 573–583. <http://dx.doi.org/10.1641/b570707>
- Stock, J.H. (1992) Entomolepididae (Copepoda: Siphonostomatoida) from the Antilles. *Studies on the Natural History of the Caribbean Region*, 71, 53–68.

- Thompson, I.C. & Scott, A. (1903) Report on the Copepoda collected by Prof. Herdman, at Ceylon, in 1902. *Ceylon Pearl Oyster Fish. Gulf of Manaar, Supplementary Reports*, 7, 227–307. pls. 1–20.
- Wilson, C.B. (1944) Parasitic copepods in the United States National Museum. *Proceedings of the United States National Museum*, 94, 529–582.

### Figure captions

**FIGURE 1.** *Songiopsyllus* **sp. nov.**, female paratype (UFBA 3294). A, body dorsal view; B, urosome; C, antennule; D, antenna; E, mandibular palp; F, maxillule; G, maxilliped. Scale bars: A = 200  $\mu\text{m}$ ; B = 50  $\mu\text{m}$ ; E–G = 25  $\mu\text{m}$ .

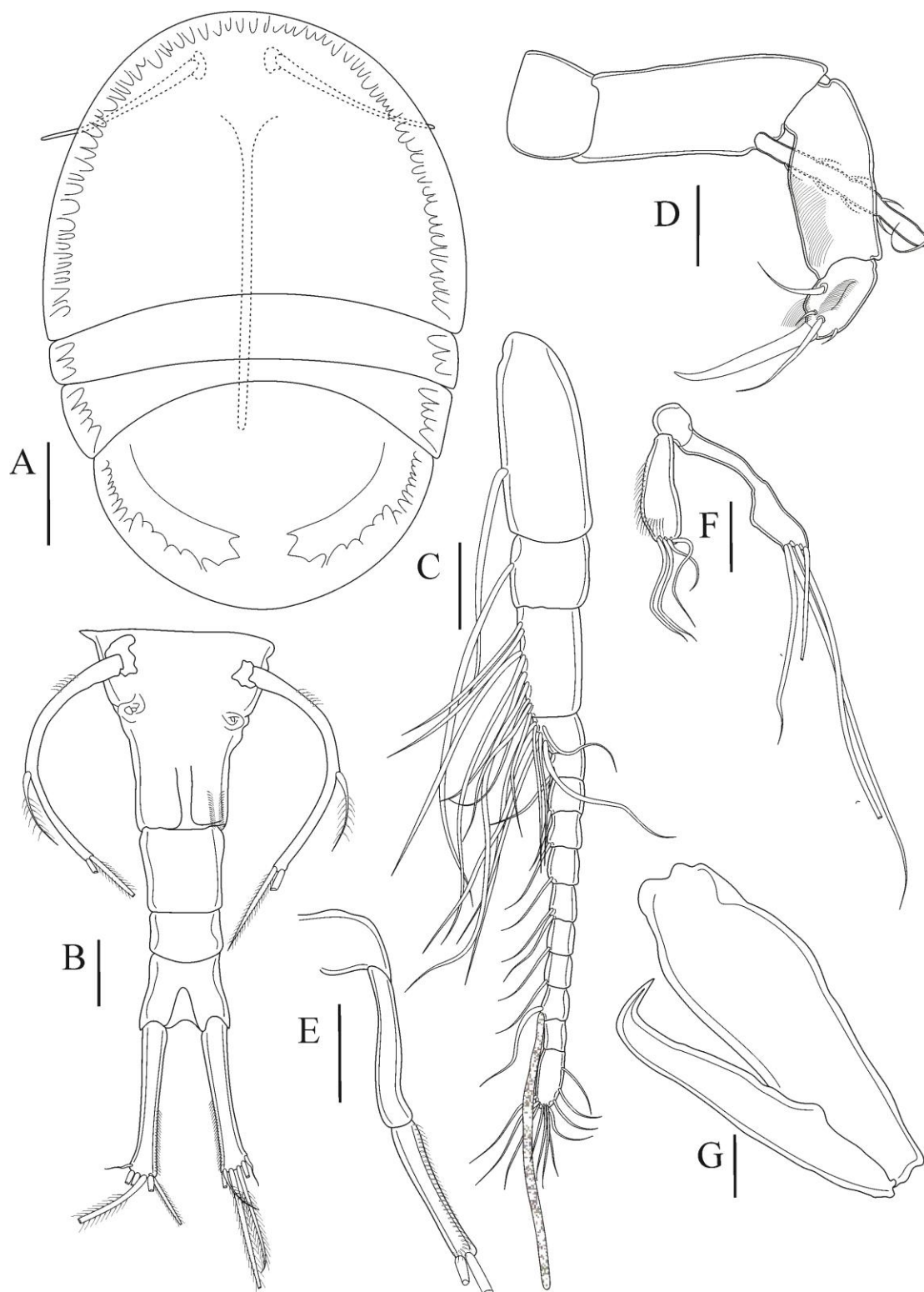
**FIGURE 2.** *Songiopsyllus* **sp. nov.**, female paratype (UFBA 3294). A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4. Scale bars: A–E = 25  $\mu\text{m}$ .

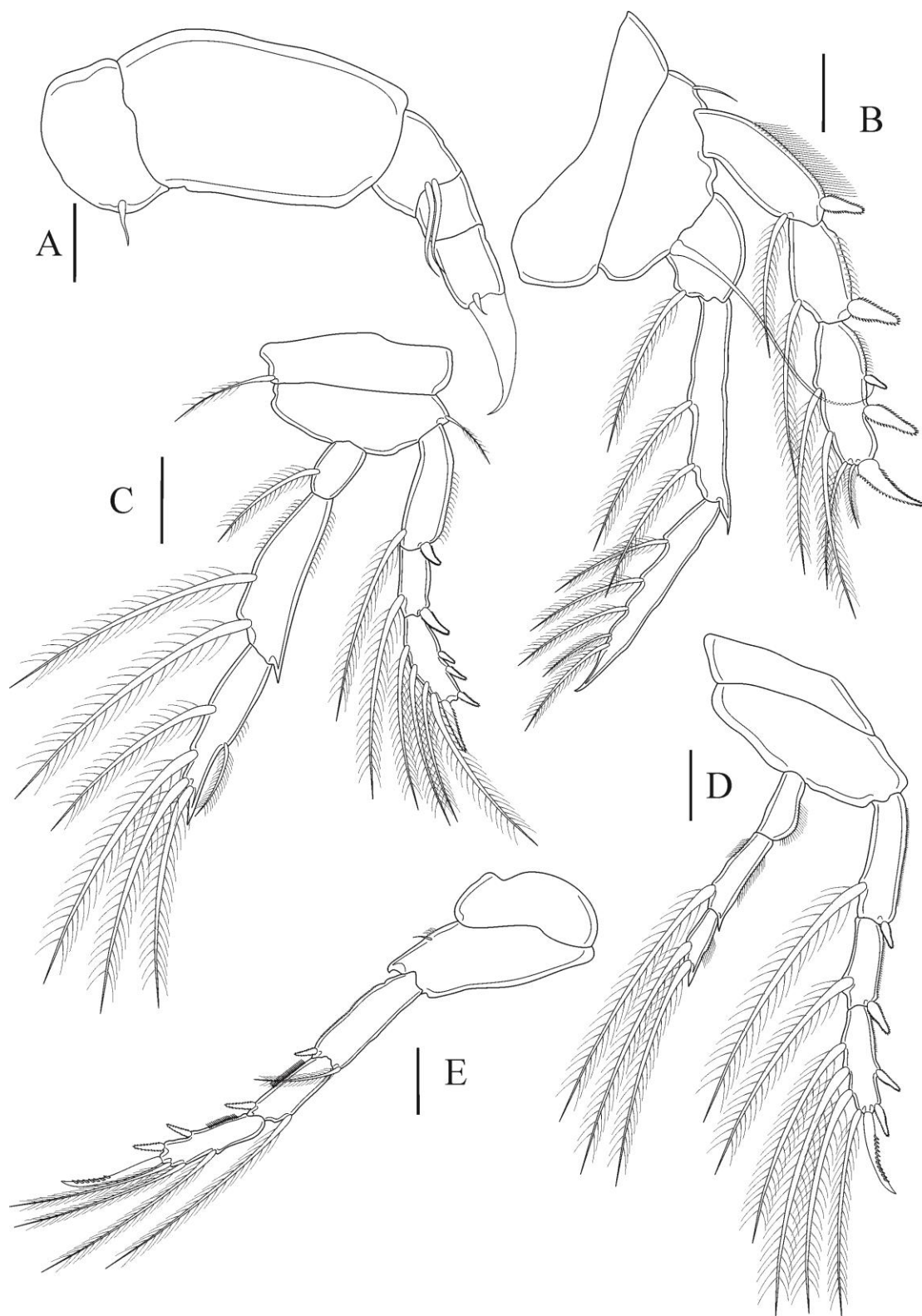
**FIGURE 3.** *Songiopsyllus* **sp. nov.**, male allotype (UFBA 3295). A, body dorsal view; B, urosome; C, antennule; *Entomopsyllus stocki* Kim, 2004 (USNM 1027325). D, urosome. Scale bars: A = 200  $\mu\text{m}$ , B–C = 25  $\mu\text{m}$ ; D = 50  $\mu\text{m}$ .

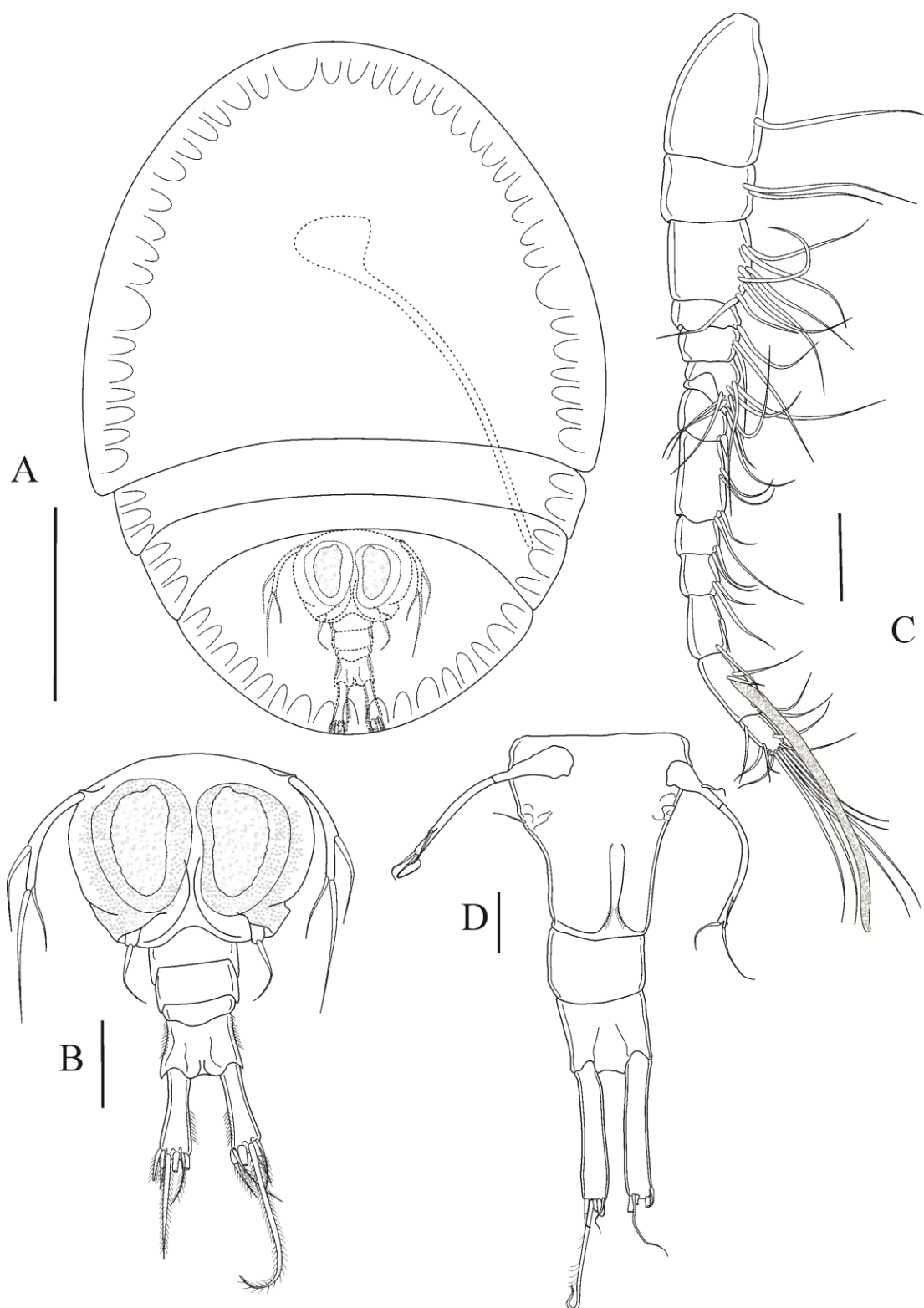
**FIGURE 4.** *Parmulodes verrucosus* Wilson, 1944 (USNM 79000). A, body dorsal view. B, digitiform bands of cephalosome; C, urosome; D, caudal ramus; E, antennule. Scale bars: A = 100  $\mu\text{m}$ ; B–E = 50  $\mu\text{m}$ .

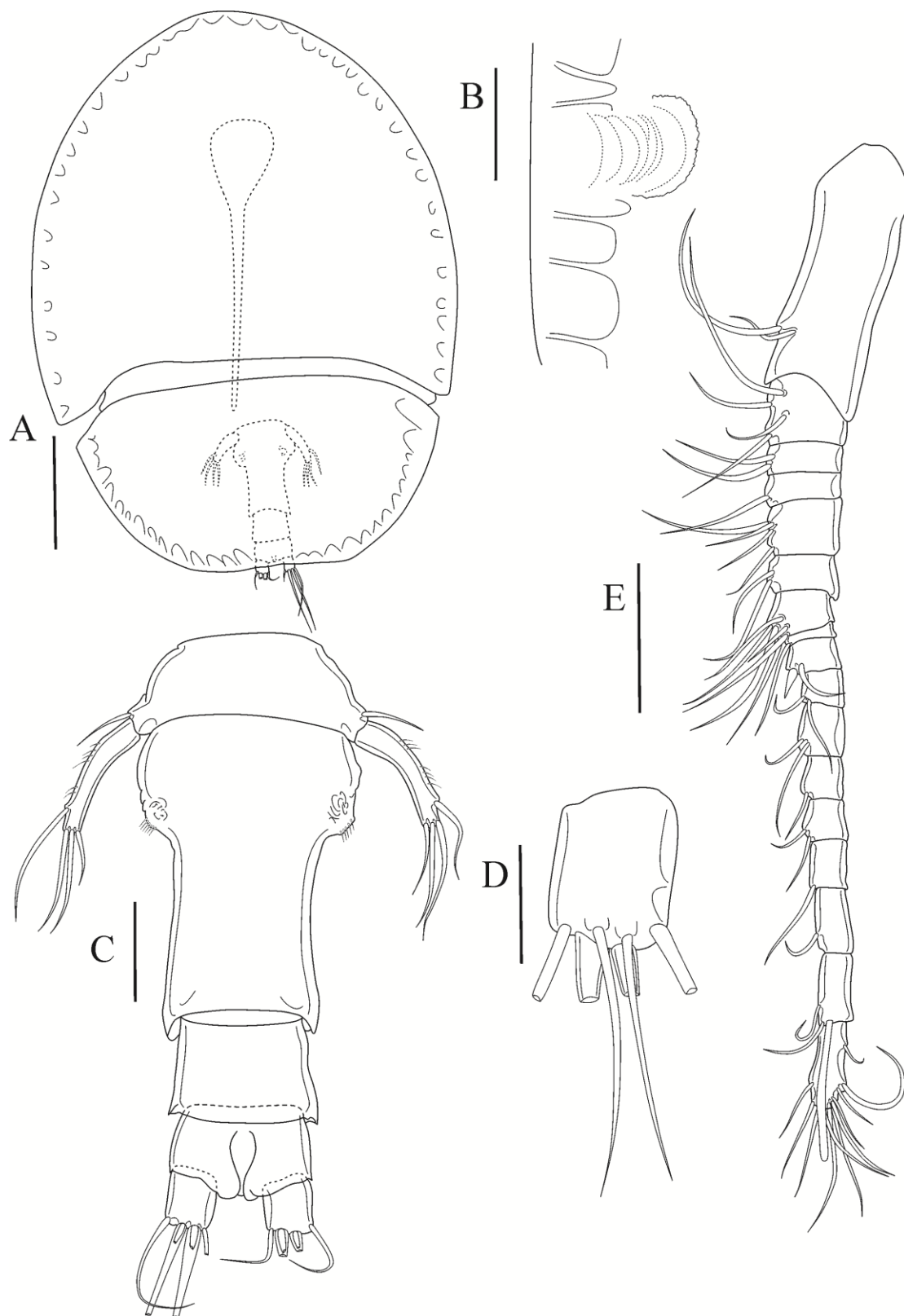
**FIGURE 5.** *Parmulodes verrucosus* Wilson, 1944 (USNM 79000). A, antenna; B, mandible; C, maxillule; D, maxilla; E, maxilliped; F, tip of maxilliped claw. Scale bars: A–F = 50  $\mu\text{m}$ .

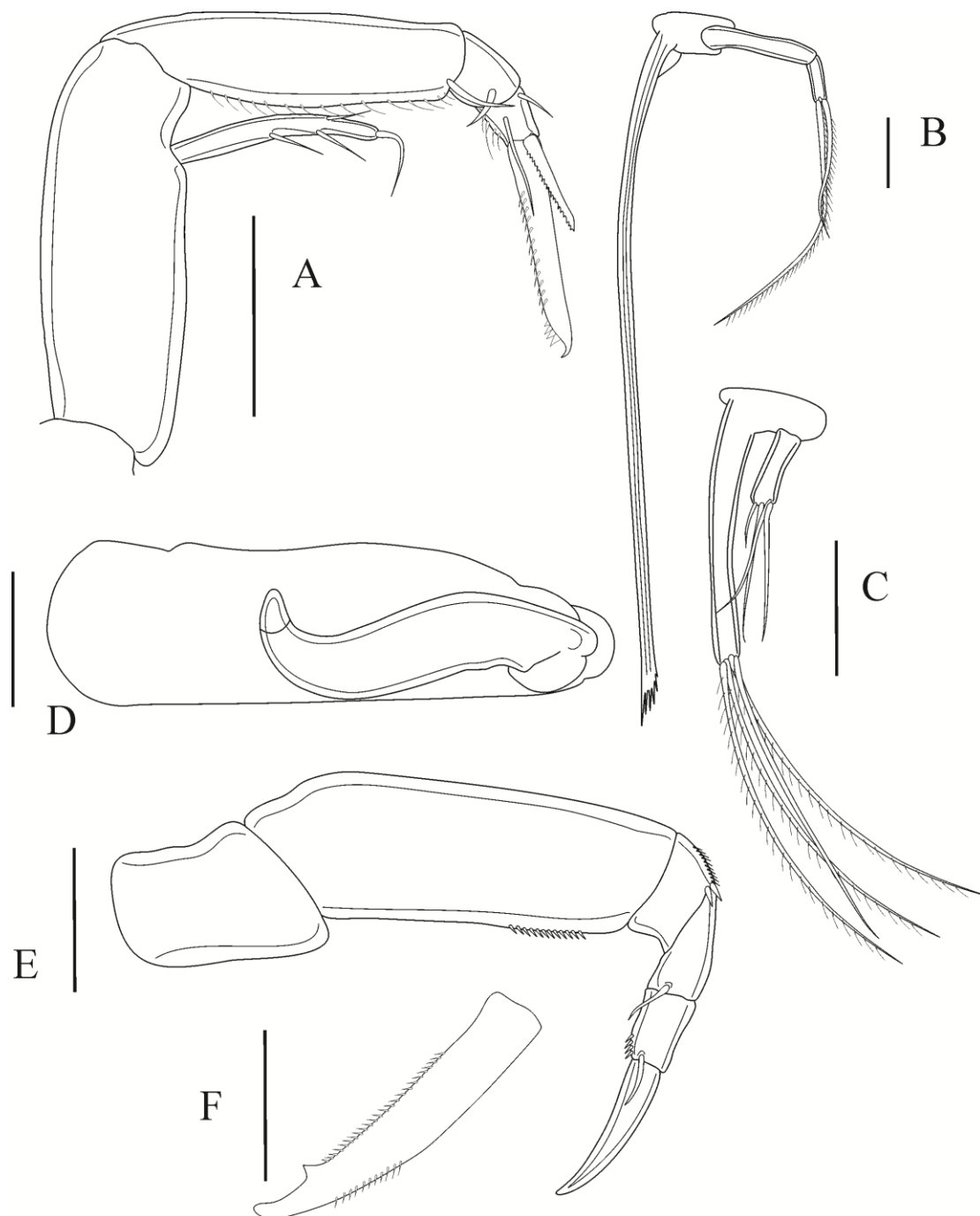
**FIGURE 6.** *Parmulodes verrucosus* Wilson, 1944 (USNM 79000). A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: A–E = 50  $\mu\text{m}$ .



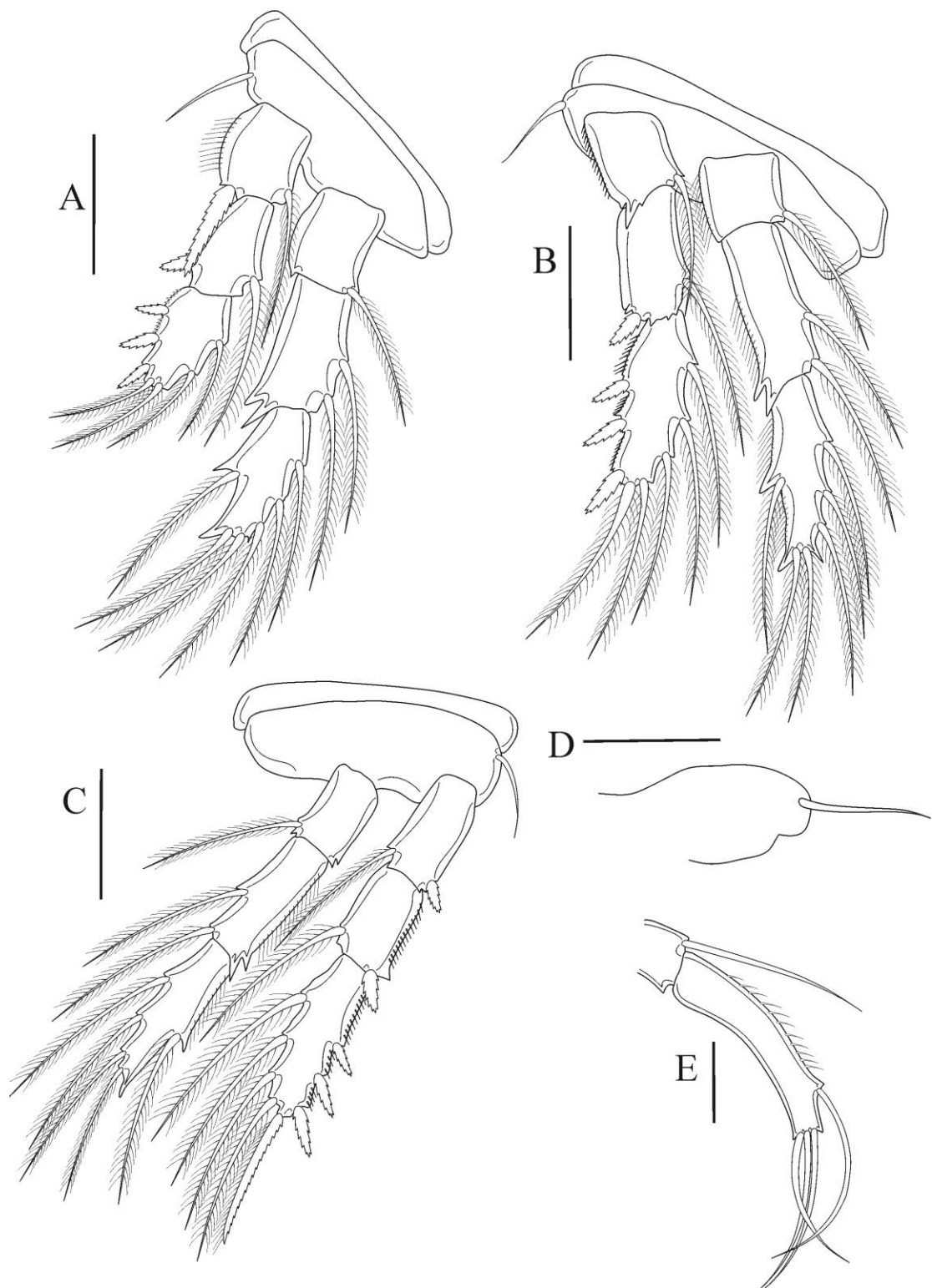












## Capítulo 2

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**Three new *Spongiopsyllus* Johnsson, 2000 (Copepoda, Siphonostomatoida, Entomolepididae) associated with *Aplysina cauliformis* (Carter) (Porifera, Demospongiae) from Todos-os-Santos Bay, Bahia, Brazil**

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### **Abstract**

Entomolepididae is composed by 9 genera and 20 species. In the Atlantic Ocean occurs five genera: *Parmulodes*, *Parmulella*, *Spongiopsyllus*, *Parmulopsyllus* and *Neoparmulella*. *Spongiopsyllus* is the most diverse and restricted to Brazilian coast. Recent studies on Boa Viagem Beach, Todos-os-Santos Bay, Bahia, Brazil, has revealed three new species of this genus, all found associated with the sponge *Aplysina cauliformis*. The new species share a 16-segmented antennule but can be differentiated by a set of characters that include setation of legs, formula of endopod of antenna and maxilliped and number of setae on lobes of maxillule. An updated key to the species of Entomolepididae is also provided.

**Key words:** associated copepod, sponges, *Aplysina*, symbiotic fauna

## Introduction

Entomolepididae Brady, 1899 is a worldwide small family composed by 9 genera and 20 species (Canário *et al.*, in prep.). In the Atlantic Ocean, the family is represented by five genera: *Parmulodes* C. B. Wilson, 1944, *Parmulella* Stock, 1992, *Spongiopsyllus* Johnsson, 2000, *Parmulopsyllus* Borges *et al.* (in prep.) and *Neoparmulella* Farias *et al.* (in prep.). Among then, *Spongiopsyllus* is the most diverse with four described species to Brazilian coast. Johnsson (2000) described the first species of the genus, *S. adventicius* associated with sponge *Aplysina* Nardo. One decade after, the second species, *S. redactus* Canário, Neves & Johnsson, 2012 was found associated with coral *Mussismilia hispida* Verril. Recently, two new species were discovered both associated with species of *Aplysina*: *S. intermedius* Borges *et al.*, in prep. in *A. solangeae* Pinheiro, Hajdu & Custodio and *S. atypicus* Canário *et al.*, in prep. in *A. insularis* (Duchassaing & Michelotti). These new species are in conformity with the expected of a diverse fauna of Entomolepididae in Brazilian coast that is confirmed by recent studies on Todos-os-Santos Bay, which have described new genera and species (Borges *et al.*, in prep.; Farias *et al.*, in prep.). Thus, this work aim to describe three new species of *Spongiopsyllus* associated with the sponge *Aplysina cauliformis* (Carter). An updated key to the species of Entomolepididae is also given.

## Material and methods

The samples of *Aplysina cauliformis* were hand-collected at a depth of 12 m at Cardinal Rock, Todos-os-Santos Bay, Bahia, Brazil (12°50'11.5"S 38°32'48.9"W). The sponges were placed in a plastic bag filled with seawater and then transported to the laboratory. The sample washing was filtered through a 100 µm plankton net,

transferred to a petri dish filled with ethanol, and sorted for copepods under a dissecting microscope.

The types were cleared in lactic acid, measured, and its body drawn before being stained in Chlorazol Black E, dissected, and mounted permanently in CMC-9® (Masters Chemical Company, Inc.) mounting media. All drawings were made with the aid of a drawing tube fitted on an Olympus CH30 microscope. The length of the antennule segments were measured along the posterior, non-setiferous margin. For the antennule formula Roman numerals indicate the ancestral segments followed by the number of setae in Arabic numerals (Huys & Boxshall, 1991). For the armature formula of legs 1–4, Roman numerals represent spines and Arabic numerals indicate setae. The abbreviations P1–P5 refer to legs 1–5.

The specimens studied are deposited in the Museu de Zoologia of the Universidade Federal da Bahia (UFBA).

***Spongiopsyllus stocki* n. sp.**

(Figs 1–2)

**Material examined.** Holotype f# (UFBA 3291), associated with *Aplysina cauliformis* in Cardinal Rock, Todos-os-Santos Bay, Bahia, Brazil, collected by Silvano LCC, 20 May 2017.

**Description of female.** Mean body length (excluding caudal setae) 1170 µm and mean body width 850 µm. Prosomal shield flattened (Fig. 1A), with radiating bands along outer margin. Pedigerous somites 2–4 free.

Urosome (Fig. 1B) 4-segmented. Genital double-somite fused with fifth pedigerous somite, 150 µm long, and with length:width ratio 1.3:1. Three postgenital somites present, all wider than long, 80 × 67, 75 × 47, 65 × 32 µm, respectively.

Prosome:urosoma length ratio 1.5:1. Caudal rami elongate, 107  $\mu\text{m}$  long, with setules along medial-distal inner margin, and armed with 6 setae distally.

Antennule (Fig. 1C) slender, 251  $\mu\text{m}$  long (not including setae), and 16-segmented. Length of segments: 62, 22, 24, 10, 9, 13, 7, 10, 10, 12, 11, 11, 12, 14, 8 and 16  $\mu\text{m}$ , respectively. Segmental homologies and setation as follows: I-1; II-2; III-VI-7; VII-2; VIII-2; IX-XIII-6; XIV-2; XV-2; XVI-2; XVII-1; XVIII-2; XIX-2; XX-2; XXI-1 +ae; XXII-XXIII-2; XXIV-XXVIII-8. All setae naked. Aesthetasc 102  $\mu\text{m}$  long. Antenna (Fig. 1D) 224  $\mu\text{m}$  long (including distal claw); coxa 24  $\mu\text{m}$  long; basis 76  $\mu\text{m}$  long. Exopod 1-segmented, 65  $\mu\text{m}$  long, and with 2 equal distal setae and 4 small spinules along lateral outer margin and 1 spinule on inner margin. Endopod 2-segmented; first segment 53  $\mu\text{m}$  long, unarmed, with 7 spinules on outer margin; second segment 22  $\mu\text{m}$  long, ornamented with row of setules along outer margin, and armed with 2 long and 2 short naked setae; distally curved claw (49  $\mu\text{m}$ ) with a bump-like projection subdistally.

Oral cone 210  $\mu\text{m}$  long, reaching first postgenital somite (Fig. 1A). Mandible comprising stylet and slender 2-segmented palp (Fig. 1E) measuring 40 and 62  $\mu\text{m}$  long, respectively. Stylet slender and pointed, 142  $\mu\text{m}$  long. Palp with second segment armed with 2 apical, plumose setae and ornamented with setules along outer margin.

Maxillule (Fig. 1F) bilobed; inner lobe 68  $\mu\text{m}$  long, armed with 3 long apical setae. Outer lobe 49  $\mu\text{m}$  long, armed with 4 short setae and ornamented with setules along outer margin; all setae naked. Maxilla (Fig. 1G) with syncoxa and curved claw measuring 217 and 134  $\mu\text{m}$  long, respectively; claw with a soft bump-like projection subdistally. Maxilliped (Fig. 2A) 5-segmented, 298  $\mu\text{m}$  long (excluding claw); syncoxa 84  $\mu\text{m}$  long, with inner seta and 3 setules on distal inner margin; basis 138

µm long, unarmed. Endopod 3-segmented, 22, 23 and 31 µm long, respectively; first segment with 2 naked unequal setae; second segment unarmed; third segment with only a curved claw measuring 56 µm long.

P1–P3 (Figs 2B–D) biramous, with 3-segmented rami. P4 (Fig. 2E) with 3-segmented exopod and endopod absent. Armature formula of P1–P4 as follows:

	Coxa	Basis	Exopod	Endopod
P1	0-1	0-1	I-1; I-1; III,3	0-1; 0-2; 1,5
P2	0-1	0-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
P3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,1,1
P4	0-0	0-0	I-1; I-0; II,I,3	Absent

First and second exopodal segments of P1 (Fig. 2B) with setules on outer margins; second segment with setules on inner margin; outer margin of third segment with spinules. Second endopodal segment of P1 (Fig. 2B) with setules on outer margin and moderate sharpened process on distal margin. Third endopodal segment of P1 (Fig. 2B) prolonged distally into sharpened process, therefore distal setae located sub-distally on inner margin. Second exopodal segment of P2 (Fig. 2C) with few setules on medial inner margin; second endopodal segment of P2 (Fig. 2C) with spinules on outer margin and setules on inner margin; third endopodal segment with setules on proximal inner margin; distal margin of second and third endopodal segments as same as observed in second endopodal segment of P1. Basis of P2 and P3 with spinules on inner and outer margins, respectively. P3 exopodal outer margins with spinules (Fig. 2D); first and second endopodal segments with setules on both margins; second endopodal segments with two tiny sharpened process on distal margin; third endopodal segment with one tiny sharpened process on distal margin.

P4 exopodal outer margins with spinules (Fig. 2E,), which are larger on second segment; medial distal margins of first and second segments with two tiny sharpened process on medial distal margin.

Free exopodal segment of P5 (Fig. 1B) elongate, curved, 207  $\mu\text{m}$  long, reaching distal margin of genital double-somite, and armed with 2 distal and one outer plumose setae.

**Male.** Unknown.

**Etymology.** This species is named for D. J. H. Stock who have a monumental contribution to copepod diversity, having published 257 names.

**Remarks.** *Spongiopsyllus stocki* **n. sp.** can be distinguished from *S. adventicius* (17-segmented), *S. redactus* (15-segmented) and *S. atypicus* (14-segmented) by having antennule 16-segmented. *Spongiopsyllus intermedius* as *Spongiopsyllus stocki* **n. sp.** also has a 16-segmented antennule, but they differ in the formula of second endopodal segment of antenna (*S. intermedius* has only 2 setae instead *S. stocki* **n. sp.** has 4 setae). Additionally, *S. stocki* **n. sp.** differs from its four congeners by possess 4 setae on outer of maxillule instead 3 found in *S. adventicius*, *S. redactus* and *S. intermedius*; and by possess 3 setae on inner lobe instead 4 setae found in *S. atypicus*. *Spongiopsyllus stocki* **n. sp.** also have distinct setation of maxiliped endopod differing from its congeners. The absence of a seta on the second endopodal element of P4 is a unique feature of *S.s stocki* **n. sp.** among *Spongiopsyllus* species.

***Spongiopsyllus boxshalli* n. sp.**

(Figs 3–5)

**Material examined.** Holotype f# (UFBA 3292), alotype m# (UFBA 3293) and paratype f# (UFBA 3297) associated with *Aplysina cauliformis* in Cardinal Rock, Todos-os-Santos Bay, Bahia, Brazil, collected by Silvany LCC, 20 May 2017.

**Description of female.** Mean body length (excluding caudal setae) 1220  $\mu\text{m}$  and mean body width 870  $\mu\text{m}$ . Prosomal shield flattened (Fig. 3A), with radiating bands along outer margin. Pedigerous somites 2–4 free.

Urosome (Fig. 3B) 4-segmented. Genital double-somite fused with fifth pedigerous somite, 160  $\mu\text{m}$  long, and with length:width ratio 0,9:1. Three postgenital somites present, first and second wider than long,  $58 \times 84$ ,  $20 \times 78$   $\mu\text{m}$ , respectively; anal somite longer than wide,  $130 \times 70$ . Prosome:urosoma length ratio 2,7:1. Caudal rami elongate, 130  $\mu\text{m}$  long, with setules along medial-distal inner margin, and armed with 6 setae distally.

Antennule (Fig. 3C) slender, 241  $\mu\text{m}$  long (not including setae), and 16-segmented. Length of segments: 58, 25, 27, 7, 9, 13, 10, 10, 12, 9, 11, 12, 12, 14, 7 and 7  $\mu\text{m}$ , respectively. Segmental homologies and setation as follows: I-1; II-2; III–VI-7; VII-2; VIII-2; IX–XIII-7; XIV-1; XV-2; XVI-1; XVII-1; XVIII-1; XIX-2; XX-1; XXI-2 +ae; XXII–XXIII-1; XXIV–XXVIII-7. All setae naked. Aesthetasc 100  $\mu\text{m}$  long. Antenna (Fig. 3D) 222  $\mu\text{m}$  long (including distal claw); coxa 37  $\mu\text{m}$  long; basis 80  $\mu\text{m}$  long. Exopod 1-segmented, 67  $\mu\text{m}$  long, and with 2 subequal distal setae and 2 small spinules along lateral outer margin and 3 spinule on inner margin; setules on distal margin. Endopod 2-segmented; first segment 57  $\mu\text{m}$  long, unarmed, with spinules on outer margin; second segment 27  $\mu\text{m}$  long, ornamented with row of setules along outer margin, and armed with 2 long, one of them with setules on outer margin, and 2 short naked setae; distally slightly curved claw, 58  $\mu\text{m}$  long.



Oral cone 210  $\mu\text{m}$  long, reaching anal somite (Fig. 3A). Mandible comprising stylet and slender 2-segmented palp (Fig. 3E) measuring 52 and 64  $\mu\text{m}$  long, respectively. Palp with second segment armed with 2 apical, smooth setae and ornamented with setules along outer margin.

Maxillule (Fig. 3F) bilobed; inner lobe 86  $\mu\text{m}$  long, armed with 4 setae, 2 longer and plumose. Outer lobe 40  $\mu\text{m}$  long, armed with 4 setae and ornamented with setules along outer margin; all setae naked. Maxilla (Fig. 3G) with syncoxa and curved claw measuring 143 and 147  $\mu\text{m}$  long, respectively; distal claw tip perpendicularly curved. Maxilliped (Fig. 4A) 5-segmented, 298  $\mu\text{m}$  long (excluding claw); syncoxa 84  $\mu\text{m}$  long, unarmed; basis 138  $\mu\text{m}$  long, unarmed. Endopod 3-segmented, 22, 23 and 31  $\mu\text{m}$  long, respectively; first and second segment each with 2 naked setae; third segment with only a curved claw measuring 56  $\mu\text{m}$  long and few setules on outer margin.

P1–P3 (Figs 4B–D) biramous, with 3-segmented rami. P4 (Fig. 4E) with 3-segmented exopod and endopod absent. Armature formula of P1–P4 as follows:

	Coxa	Basis	Exopod	Endopod
P1	0-1	1-1	I-1; I-1; III,4	0-1; 0-2; 1,5
P2	0-1	1-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
P3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,1,1
P4	0-0	0-0	I-1; I-1; II,I,3	Absent

First exopodal segments of P1 and P2 (Fig. 4B–C) with setules on outer margins; second endopodal segments with setules on both margins. Third endopodal segment of P1 and that of P2 with setules on both margins. Second and third exopodal segments of P2 (Fig. 4C) with spinules on outer margins. Exopodal segments of P3

and P4 (Fig. 4D–E) with spinules on outer margins. Spinules on outer margin of P3 basis. P4 with two spinules on basis outer margin. Endopodal segments of P3 with setules on outer margin of first, outer and inner margins of second and third. Third endopodal segment of P4 with setules on inner margin. Distal spines of exopod of P3 and P4 with long setules on inner margin.

Free exopodal segment of P5 (Fig. 3A) elongate, curved, 212  $\mu\text{m}$  long, reaching distal margin of genital double-somite, and armed with 2 distal and one outer setae.

**Male.** Body (Fig. 5A) similar to female, but much smaller. Mean body length (excluding caudal setae) 740  $\mu\text{m}$  and mean body width 510  $\mu\text{m}$ . Prossomal shield flattened with radiation bands along outer margin. Pedigerous somites 2–4 free. Pedigerous somite 4 expanded, covering urosome except caudal rami.

Urossome 5-segmented (Fig. 5B). Genital somite fused with fifth pedigerous somite, 118  $\mu\text{m}$  long, and length:width ratio 0,8:1. Four postgenital somites present; all wider than long (48 x 25, 42 x 25, 38 x 12, 42 x 28  $\mu\text{m}$ , respectively. First and second postgenital somites with one spine on each distal lateral margins. Prossome:urossome length ratio 2.9:1. Caudal rami enlongate, 48  $\mu\text{m}$  long, armed with six setae.

Antennule (Fig. 5C) slender, 223  $\mu\text{m}$  long (not including setae), 13-segmented. Length of segments measured along anterior to posterior margins: 42, 17, 22, 6, 8, 12, 11, 25, 11, 9, 18, 23 and 19, respectively. Segmental homologies and setation as follows: I-2; II-2; III-VI-7; VII-2; VIII-2; IX–XIII-9; XIV-1; XV-XVI-4; XVII-2; XVIII-2; XIX-XX-3; XXI-XXIII-4+ae; XXIV-XXVIII-11; all setae smooth. Aesthetasc 86  $\mu\text{m}$  long. Oral cone (Fig. 5A) 350  $\mu\text{m}$  long, reaching genital somite. All other appendages as in the female.

**Etymology.** This species is named for G. Boxshall an important present-day copepodologist with contributions from Copepoda taxonomy, systematics and biology.

**Remarks.** As *Spongiopsyllus stocki* **n. sp.**, *S. boxshalli* **n. sp.** has 16-segmented antennule. However, can be distinguished from *S. stocki* **n. sp.** by possess 4 setae on both lobes of maxillule instead 3 on inner lobe of *S. stocki* **n. sp.** The maxilliped of *Spongiopsyllus stocki* **n. sp.** show 1 seta and setules on coxa and setation of endopod as 2, 1, 1+claw differing from *S. boxshalli* **n. sp.** that has unarmed coxa and setation of endopod as 2, 2, 0+claw. Other differences includes (1) setation of antennule, (2) the format of antenna claw and (3) presence of the seta on second endopodal element of P4 (absent in *Spongiopsyllus stocki* **n. sp.**).

***Spongiopsyllus hoi* **n. sp.****

(Figs 5–7)

**Material examined.** Holotype f# (UFBA 3298) and paratypes f# (UFBA 3299, 3300, 3301) associated with *Aplysina cauliformis* in Cardinal Rock, Todos-os-Santos Bay, Bahia, Brazil, collected by Silvany LCC, 20 May 2017.

**Description of female.** Mean body length (excluding caudal setae) 1190  $\mu\text{m}$  and mean body width 840  $\mu\text{m}$ . Prosomal shield flattened (Fig. 5D), with radiating bands along outer margin. Pedigerous somites 2–4 free.

Urosome (Fig. 5E) 4-segmented. Genital double-somite fused with fifth pedigerous somite, 175  $\mu\text{m}$  long, and with length:width ratio 1.2:1. Three postgenital somites present, all wider than long,  $72 \times 55$ ,  $70 \times 30$ ,  $55 \times 32$   $\mu\text{m}$ , respectively. Prosome:urosoma length ratio 3:1. Caudal rami elongate, 108  $\mu\text{m}$  long, with setules along medial-distal inner margin, and armed with 6 setae distally.

Antennule (Fig. 6A) slender, 220  $\mu\text{m}$  long (not including setae), and 16-segmented. Length of segments: 54, 20, 25, 7, 9, 13, 9, 10, 9, 9, 11, 10, 11, 12, 9 and 13  $\mu\text{m}$ , respectively. Segmental homologies and setation as follows: I-1; II-2; III–VI-7; VII-2; VIII-2; IX–XIII-7; XIV-1; XV-2; XVI-1; XVII-1; XVIII-1; XIX-2; XX-1; XXI-2 +ae; XXII–XXIII-1; XXIV–XXVIII-7. All setae naked.

Antenna (Fig. 6B) 226  $\mu\text{m}$  long (including distal claw); coxa 36  $\mu\text{m}$  long; basis 62  $\mu\text{m}$  long. Exopod 1-segmented, 45  $\mu\text{m}$  long, and with 2 subequal distal setae and 2 small spinules along lateral outer margin and 3 spinule on inner margin; setules on distal margin. Endopod 2-segmented; first segment 54  $\mu\text{m}$  long, unarmed; second segment 23  $\mu\text{m}$  long, ornamented with row of setules along outer margin, and armed with 2 setae; distally slightly curved claw, 51  $\mu\text{m}$  long.

Oral cone 800  $\mu\text{m}$  long, reaching prosomal distal margin (Fig. 5D). Mandible comprising stylet (Fig. 6C) and slender 2-segmented palp (Fig. 6D) measuring 36 and 67  $\mu\text{m}$  long, respectively. Palp with second segment armed with 2 apical, smooth setae and ornamented with setules along outer margin.

Maxillule (Fig. 6E) bilobed; inner lobe 80  $\mu\text{m}$  long, armed with 4 setae, 2 longer and plumose. Outer lobe 42  $\mu\text{m}$  long, armed with 4 setae and ornamented with setules along outer margin; all setae naked. Maxilla (Fig. 6F) with syncoxa and curved claw measuring both 152  $\mu\text{m}$  long, respectively; distal claw tip perpendicularly curved. Maxilliped (Fig. 6G) 5-segmented, 326  $\mu\text{m}$  long (excluding claw); syncoxa 80  $\mu\text{m}$  long, unarmed; basis 122  $\mu\text{m}$  long, unarmed. Endopod 3-segmented, 18, 20 and 32  $\mu\text{m}$  long, respectively; first and second segment each with 2 naked setae; third segment with only a curved claw measuring 53  $\mu\text{m}$  long and few setules on outer margin.

P1–P3 (Figs 7A–C) biramous, with 3-segmented rami. P4 (Fig. 7D) with 3-segmented exopod and endopod absent. Armature formula of P1–P4 as follows:

	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	I-1; I-1; III,4	0-1; 0-2; 1,5
P2	0-1	1-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,2
P3	0-0	0-0	I-1; I-1; II,I,4	0-0; 0-1; 0,1,1
P4	0-0	0-0	I-1; I-1; II,I,3	Absent

First exopodal segments of P1 and P3 (Fig. 7A, C) with setules on outer margins; second and third exopodal segments with spinules on other margins. Endopodal segments of P1 to P3 (Fig. 7A–C) with setules on outer margins. Exopodal segments of P2 and P4 (Figs. 7B, D) with spinules on outer margins; second segment with setules on inner margin in both legs. Spinules on outer margin of P4 basis. Distal spines of exopod of P2 to P4 with long setules on inner margin.

Free exopodal segment of P5 (Fig. 5E) elongate, curved, 207  $\mu\text{m}$  long, reaching first postgenital somite, and armed with 2 distal and one outer setae.

**Male.** Unknown.

**Etymology.** This species is named for Ju-shey Ho, who has significant contributions from symbiotic Copepoda, having described an extensive list of parasitic species of fish and marine invertebrates.

**Remarks.** As *Songiopsyllus stocki* **n. sp.** and *S. boxshalli* **n. sp.**, *S. hoi* **n. sp.** has 16-segmented antennule. *Songiopsyllus hoi* **n. sp.** differs from its 16-segmented antennule congeners by possess only two setae on second endopodal segment of antenna (instead 4 in *S. stocki* **n. sp.** and *S. boxshalli* **n. sp.**). Additionally, the format of maxillar claw is distinct between *S. hoi* **n. sp.** and *S. stocki* **n. sp.**; besides that *S.*

*hoi* **n. sp.** has the seta on the second endopodal element of P4 absent in *S. stocki* **n. sp.** *Spongiopsyllus hoi* **n. sp.** can be differentiated from *S. boxshalli* **n. sp.** by the formula of endopod of maxilliped: 2,1,1+claw instead 2,2,0+claw observed in *S. boxshalli* **n. sp.**.

**Key to the species of the Entomolepididae (adapted from Borges *et al.*, in prep. and Uyeno & Johnsson, in prep.)**

- 1 Pedigerous somite 2 free in dorsal view (Parmulodinae Eiselt, 1959) ... 2
  - Pedigerous somites 2 and 3 free in dorsal view (Entomolepidinae Eiselt, 1959) ... 8
- 2 Most of urosome hidden under body shield ... 3
  - Most of urosome exposed ... 7
- 3 P3 biramous ... 4
  - P3 uniramous (*Paralepeopsyllus* Ummerkutty, 1960) ... 5
- 4 Antennule 17-segmented ... *Parmulodes verrucosus* C. B. Wilson, 1944
  - Antennule 16- segmented ... *Parmulopsyllus breviarticulata* Borges *et al.* (in press)
- 5 Antennule 15-segmented ... *Paralepeopsyllus leei* Lee & Kim, 2017
  - Antennule 14-segmented ... 6
- 6 Third exopodal segment of P3 with only three setae ... *Paralepeopsyllus mannarensis* Ummerkutty, 1960
  - Third exopodal segment of P3 with four spines and three setae ... *Paralepeopsyllus dambayensis* Lee & Kim, 2017
- 7 P4 reduced to a knob, antennule 18-segmented ... *Parmulella emarginata* Stock, 1992
  - P4 bireme with three segmented rami, antennule 17-segmented ... *Neoparmulella periperiensis* Farias & Johnsson (in prep.)

- 8 P4 absent (*Entomolepis* Brady, 1899) ... 9
- P4 present ... 10
- 9 Caudal ramus 5–6 times longer than wide ... *E. ovalis* Brady, 1899
- Caudal ramus at least 10 times longer than wide ... *E. hamondi* McKinnon, 1988
- 10 P4 endopod absent ... 11
- P4 endopod reduced to a single small segment (*Lepeopsyllus* Thompson & Scott, 1903) ... 18
- 11 Three postgenital somites in female and four in male (*Spongiopsyllus* Johnsson, 2000) ... 12
- Two postgenital somites in female and three in male (*Entomopsyllus* McKinnon, 1988) ... 19
- 12 Female antennule 16 or 17-segmented ... 13
- Female antennule 14 or 15-segmented ... 17
- 13 Female antennule 17-segmented ... *Spongiopsyllus adventicius* Johnsson, 2000
- Female antennule 16-segmented ... 14
- 14 Second exopodal segment of P4 with formula I-0 ... ***S. stocki* n. sp.**
- Second exopodal segment of P4 with formula I-1 ... 15
- 15 Maxillule with three setae on outer lobe and two setae on inner lobe ... *S. intermedius* Borges *et al.* (in press)
- Maxillule with other setation ... 16
- 16 Endopod of maxilliped with formula 2,2,0+claw ... ***S. boxshalli* n. sp.**
- Endopod of maxilliped with formula 2,1,1+claw ... ***S. hoi* n. sp.**
- 17 Antennule 15-segmented, outer seta of P4 basis absent ... *S. redactus* Canário *et al.*, 2012

- Antennule 14-segmented, outer seta of P4 basis present ... *Spongiopsyllus atypicus* Canário *et al.* (in prep.)
- 18 Female antennule 15-segmented ... *L. typicus* Thompson & Scott, 1903
- Female antennule 13-segmented ... *L. ovalis* Thompson & Scott, 1903
- 19 Second endopodal segment of the leg 2 bearing one seta ... 20
- Second endopodal segment of the leg 2 bearing two setae ... 21
- 20 Antennule of female 11-segmented; the distal exopodal segment of the leg 4 bearing four inner setae ... *E. nichollsi* McKinnon, 1988
- Antennule of female 15-segmented; the distal exopodal segment of the leg 4 bearing two inner setae ... *E. stocki* Kim, 2004
- 21 Third exopodal segment of the leg 4 bearing three inner setae ... *E. adriae* (Eiselt, 1959)
- Third exopodal segment of the leg 4 bearing four inner setae ... 22
- 22 Third endopodal segment of the leg 2 bearing four setae ... *E. brevicaudatus* Lee & Kim, 2017
- Third endopodal segment of the leg 2 bearing five setae ... *E. takara* Uyeno & Johnsson, in prep.

**Acknowledgements.** The authors thank to Silvany LCC and ‘CNPq Edital Universal 14/2014, Processo 459241/2014-1’ for the collection of the specimens analyzed here and the ‘Programa de Pós-Graduação em Diversidade Animal’ (UFBA) for logistical support. CB thanks ‘Fundação de Amparo à Pesquisa do Estado da Bahia’ for financial support. RC thanks ‘Programa de Pós-Graduação em Zoologia’ (USP) and ‘CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior)’ for financial support.



## References

- Brady, G.S. (1899) On the marine Copepoda of New Zealand. *Transactions of the Zoological Society of London*, 15, 31–54.
- Borges, C., Neves, E.G. & Johnsson, R. (in press) A new Entomolepididae genus and a new species of *Spongiopsyllus* associated with sponges in Todos-os-Santos Bay, Bahia, Brazil.
- Canário, R., Neves, E. & Johnsson, R. (2012). *Spongiopsyllus redactus*, a new species of Entomolepididae (Copepoda, Siphonostomatoida) associated with a scleractinian coral in Brazil. *Zoosymposia*, 8, 49–55.
- Canário, R., Hurbath, T., Rocha, C.E.F., Neves, E. & Johnsson, R. (in preparation) Redescription of *Parmulodes verrucosus* Wilson, 1944 with notes of *Entomopsyllus stocki* Kim, 2004 and description of a new species of *Spongiopsyllus* Johnsson, 2000 (Copepoda, Siphonostomatoida, Entomolepididae).
- Eiselt, J. (1959) *Entomolepis adriae*, ein Beitrag zur Kenntnis der kaum bekannten Gattungen siphonostomer Cyclopoiden: *Entomolepis*, *Lepeopsyllus* und *Parmulodes* (Copepoda, Crust.) Sitzber. Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, 168, 643–660.
- Farias, A., Neves, E.G. & Johnsson, R. (in preparation) A new species and genus of Entomolepididae Brady, 1899 (Copepoda Siphonostomatoida) associated with the endemic octocoral *Phyllogorgia dilatata* (Esper, 1900) (Cnidaria, Octocorallia) from Northeastern Brazil.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468pp.

- Johnsson, R. (2000) *Spongiopsyllus adventicius* new species and genus of Entomolepididae (Copepoda: Siphonostomatoida) associated with sponges in Brazil. *Hydrobiologia*, 417, 115–119.
- Kim, I.H. (2004) Two new species of siphonostomatoid copepods (Crustacea) associated with the stoloniferan coral *Tubipora musica* (Linnaeus) from Madagascar. *Korean Journal of Biological Sciences*, 8, 187–196.
- Lee, J. & Kim, I.H. (2017) Siphonostomatoid Copepods (Crustacea) Associated with Sponges from the Philippines and Vietnam. *Animal Systematics, Evolution and Diversity*, 33(2), 73–99.
- Mckinnon, A.D. (1988) A revision of Entomolepididae (Copepoda: Siphonostomatoida) with Descriptions of Two New Species from Australia, and Comments on *Entomolepis ovalis* Brady. *Australian Journals of Science Research*, 2, 995–1012.
- Stock, J.H. (1992) Entomolepididae (Copepoda: Siphonostomatoida) from the Antilles. *Studies on the Natural History of the Caribbean Region*, 71, 53–68.
- Thompson, I.C. & Scott, A. (1903) Report on the Copepoda collected by Prof. Herdman, at Ceylon, in 1902. *Ceylon Pearl Oyster Fish. Gulf of Manaar, Supplementary Reports*, 7, 227–307. pls. 1–20.
- Ummerkutty, A.N.P. (1960) Studies on indian copepods I. *Paralepeopsyllus mannarensis*, a new genus and species of Cyclopoid Copepod from the Gulf of Mannar. *Journal of Marine Biology*, 2, 105–114.
- Uyeno, D. & Johnsson, R. (in preparation) Two new species of Siphonostomatoida (Copepoda) found on cnidarians in Tokara Islands, Southern Japan.
- Wilson, C.B. (1944) Parasitic copepods in the United States National Museum. *Proceedings of the United States National Museum*, 94, 529–582.

## Figure Captions

**FIGURE 1.** *Spongiopsyllus stocki* **n. sp.**, female holotype (UFBA 3291). A, habitus, dorsal view; B, urosome; C, antennule; D, antenna; E, mandibular palp; F, maxillule; G, maxilla. Scale bars: A = 200  $\mu\text{m}$ ; B–G = 50  $\mu\text{m}$ .

**FIGURE 2.** *Spongiopsyllus stocki* **n. sp.**, female holotype (UFBA 3291). A, maxilliped; B, P1; C, P2; D, P3; E, P4. Scale bars: A–E = 50  $\mu\text{m}$ .

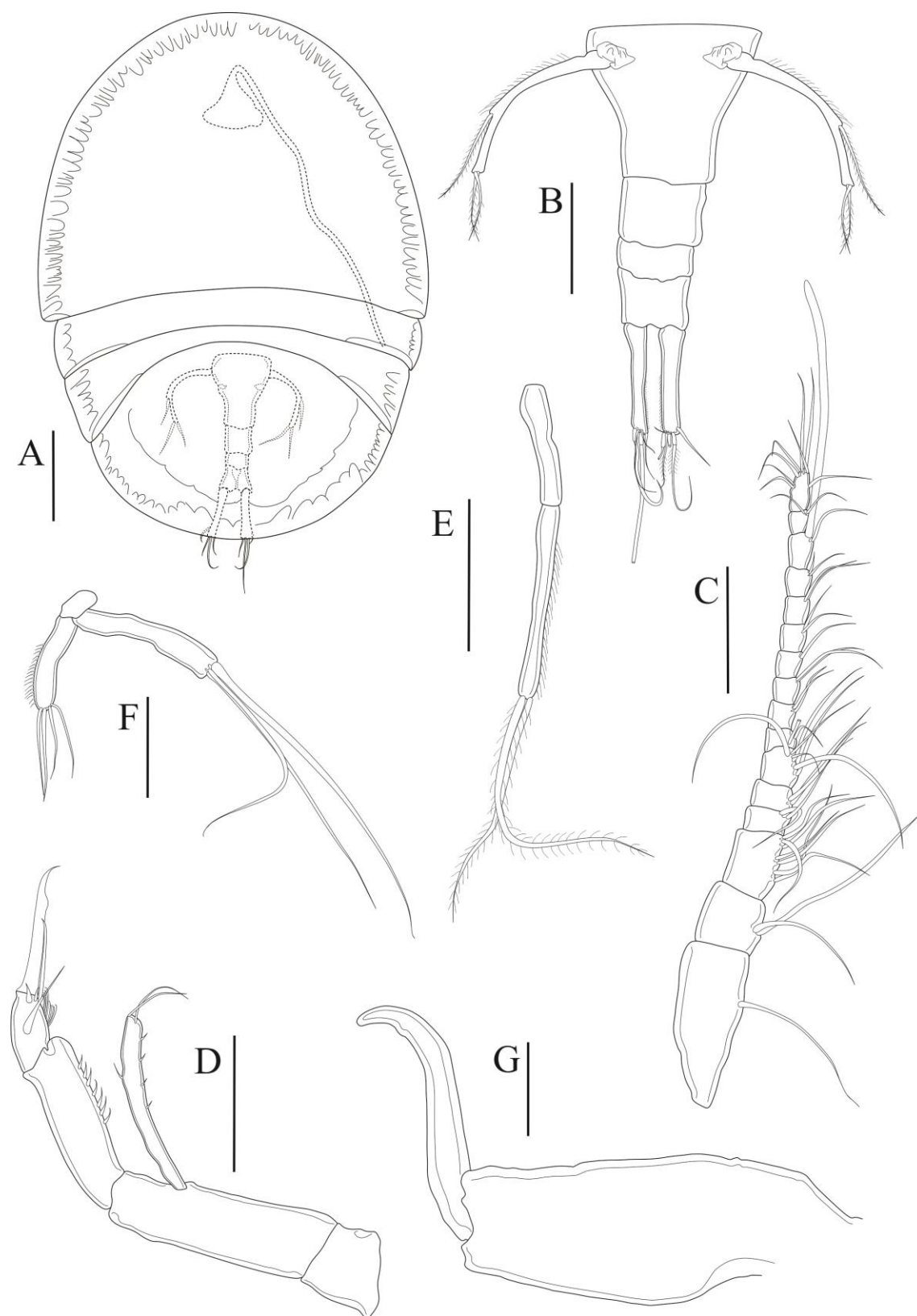
**FIGURE 3.** *Spongiopsyllus boxshalli* **n. sp.**, female holotype (UFBA 3292). A, habitus, dorsal view; B, urosome; C, antennule; D, antenna; E, mandibular palp; F, maxillule. Scale bars: A = 200  $\mu\text{m}$ ; B = 50  $\mu\text{m}$ ; C–E = 25  $\mu\text{m}$ .

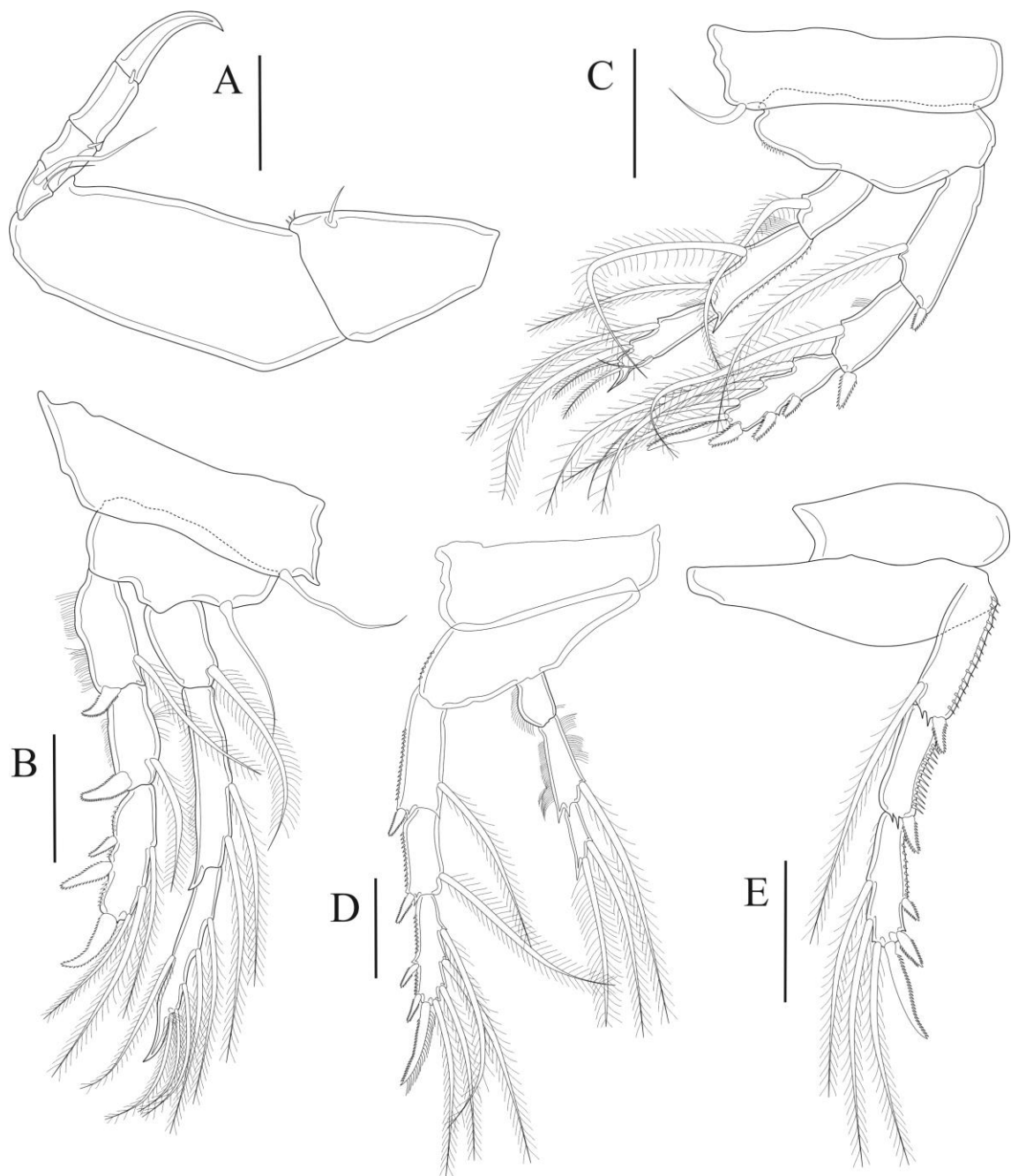
**FIGURE 4.** *Spongiopsyllus boxshalli* **n. sp.**, female holotype (UFBA 3292). A, maxilliped; B, P1; C, P2; D, P3; E, P4. Scale bars: A–E = 50  $\mu\text{m}$ .

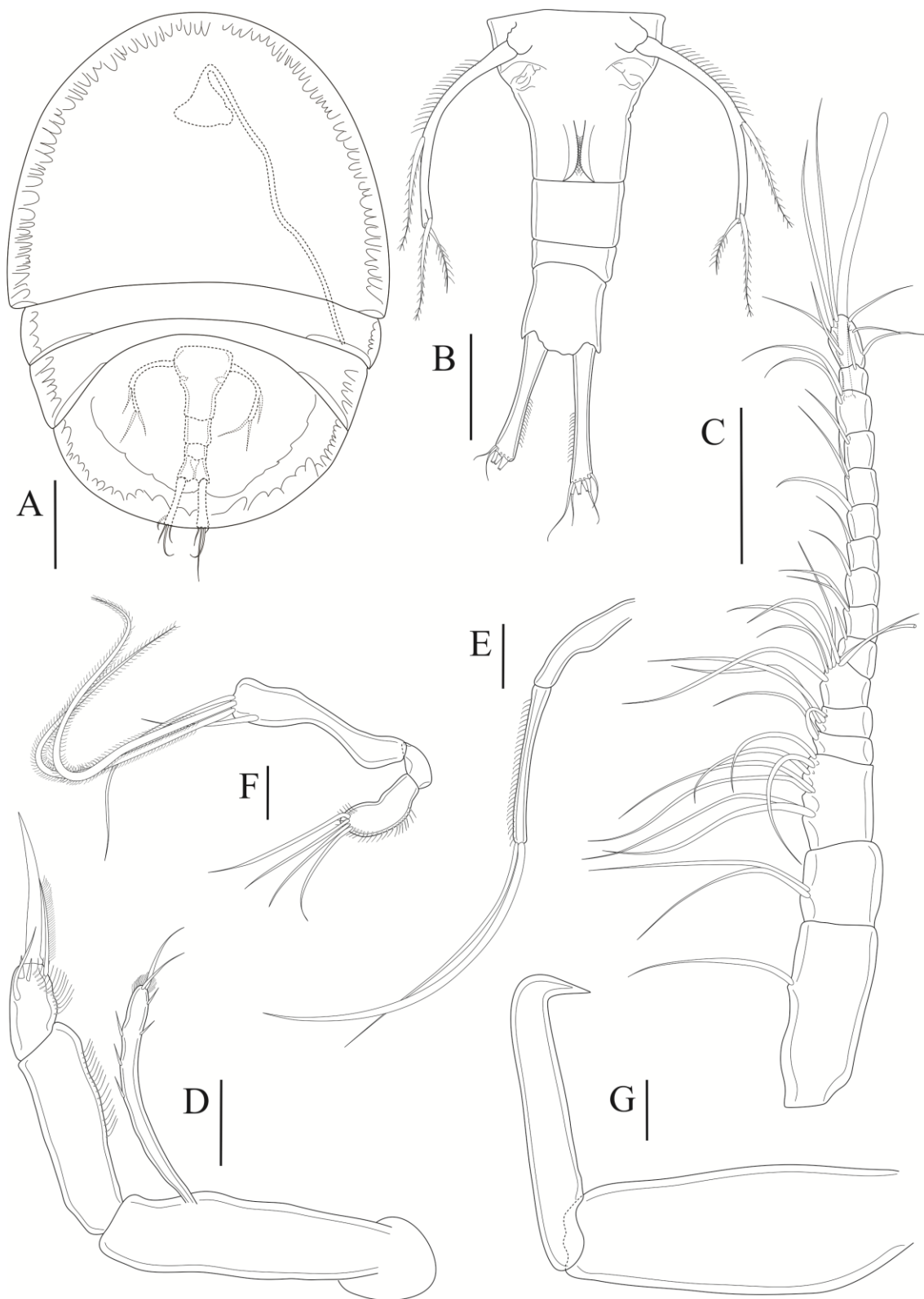
**FIGURE 5.** *Spongiopsyllus boxshalli* **n. sp.**, male allotype (UFBA 3293). A, habitus, dorsal view; B, urosome; C, antennule. *Spongiopsyllus hoi* **n. sp.**, female paratype (UFBA 3299). D, habitus, dorsal view; E, urosome. Scale bars: A, E = 100  $\mu\text{m}$ ; B, C = 25  $\mu\text{m}$ ; D = 200  $\mu\text{m}$ .

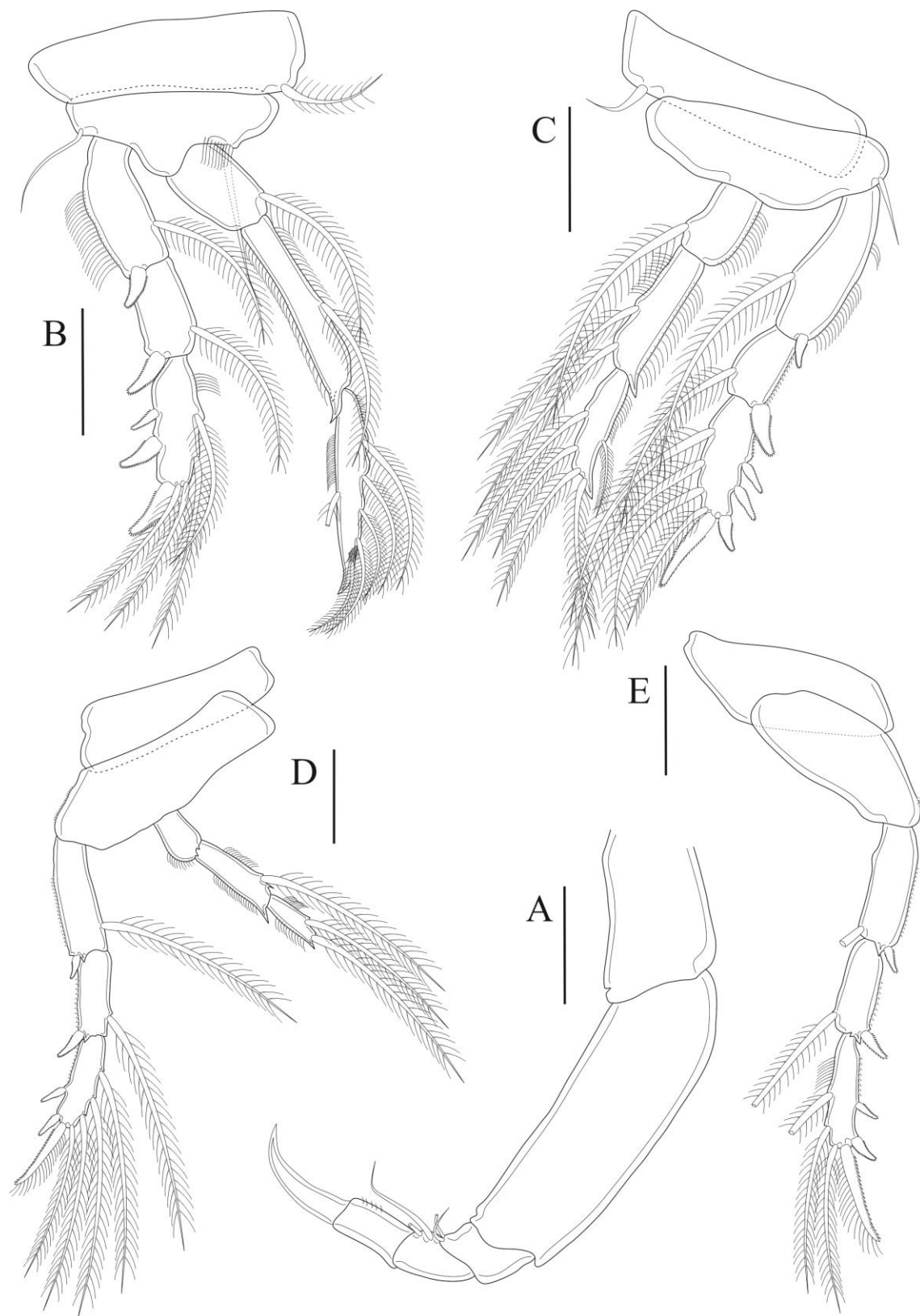
**FIGURE 6.** *Spongiopsyllus hoi* **n. sp.**, female paratype (UFBA 3299). A, antennule; B, antenna; C, mandibular palp; D, stilette; E, maxillule; F, maxilla; G, maxilliped. Scale bars: A–E = 25  $\mu\text{m}$ ; F, G = 50  $\mu\text{m}$ .

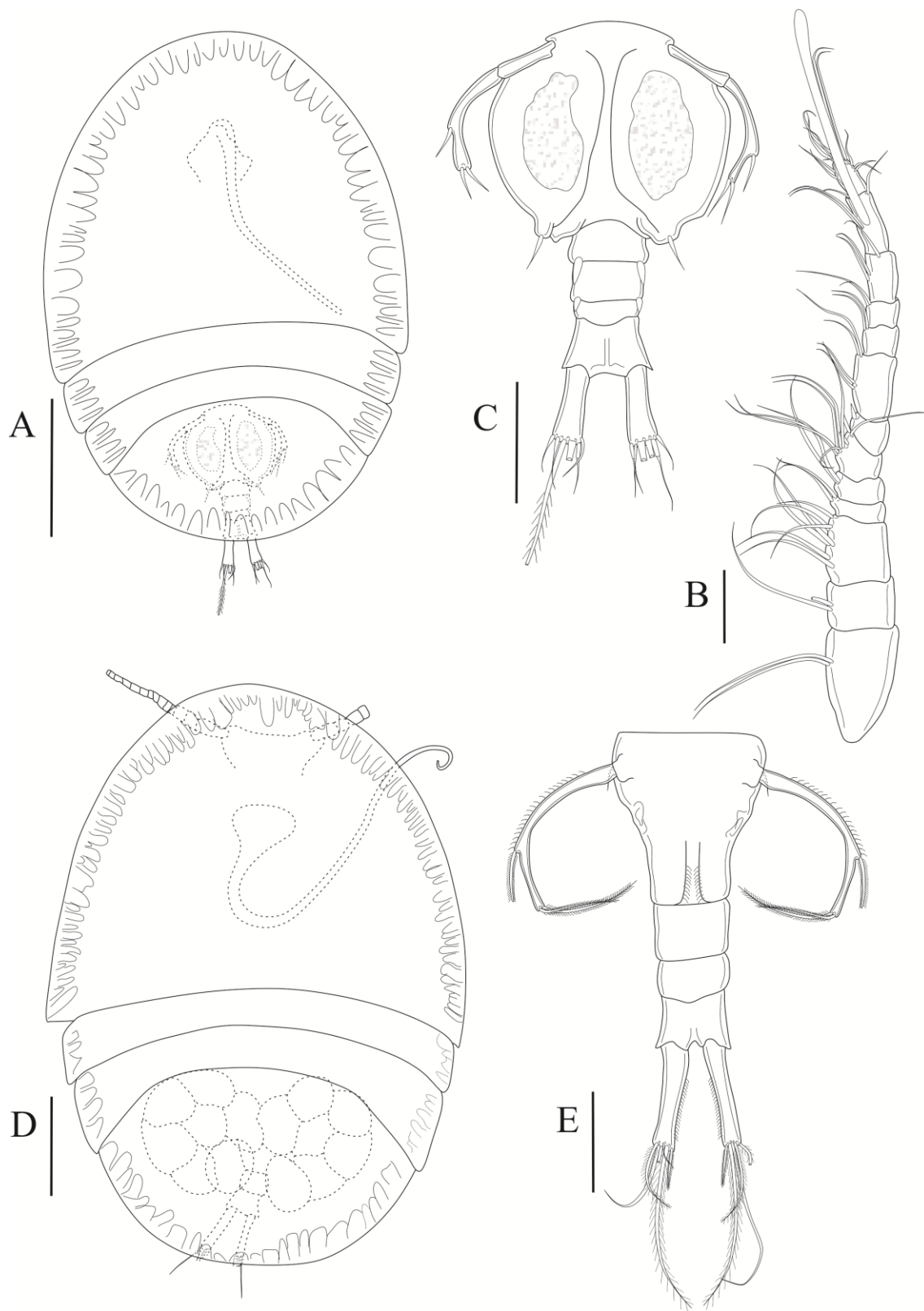
**FIGURE 7.** *Spongiopsyllus hoi* **n. sp.**, female paratype (UFBA 3300). A, P1; B, P2; C, P3; D, P4. Scale bars: A–D = 50  $\mu\text{m}$ .



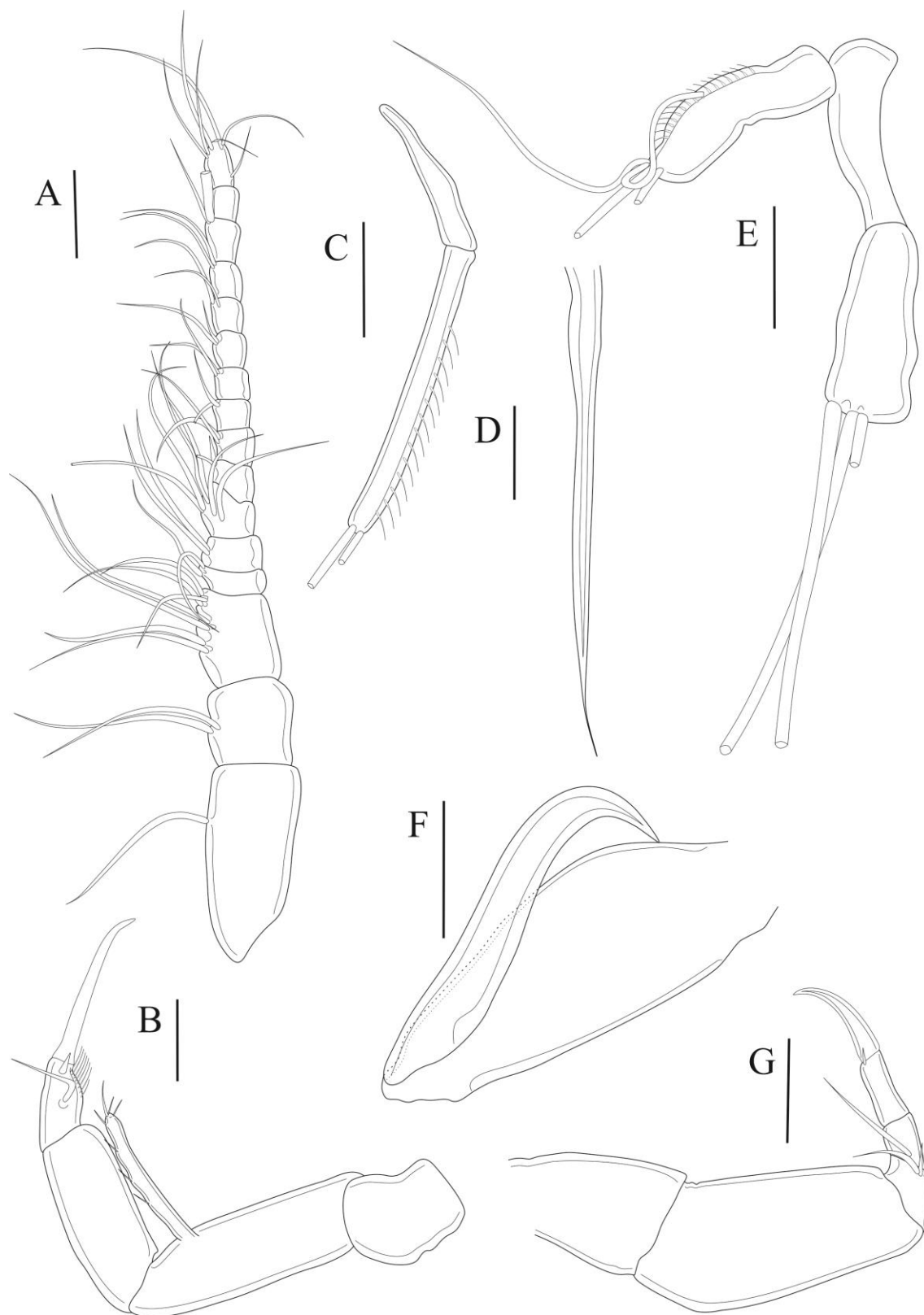


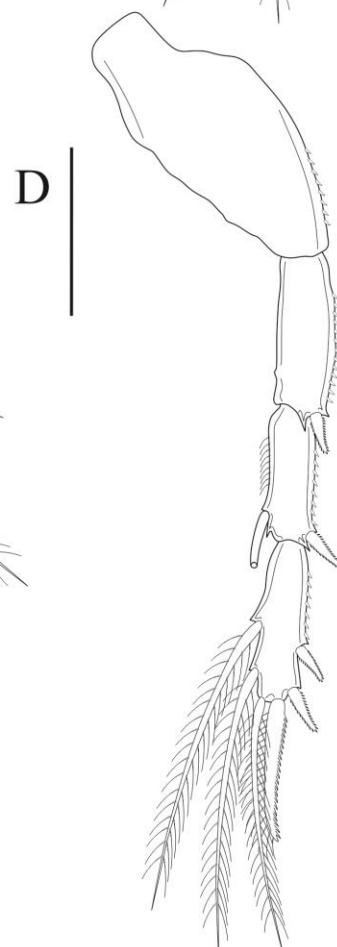
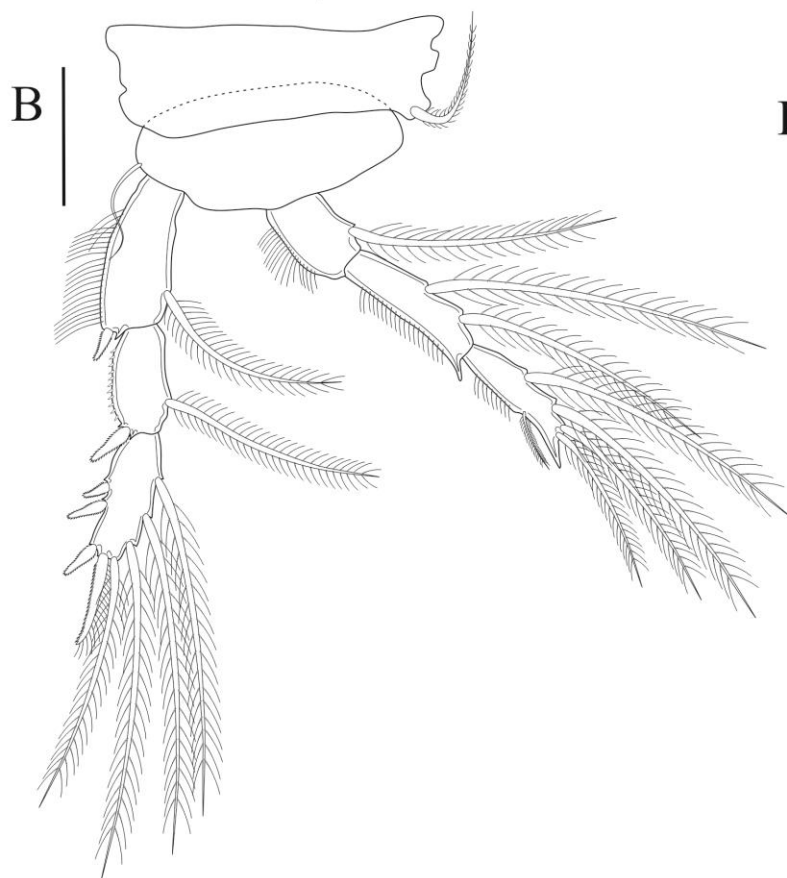
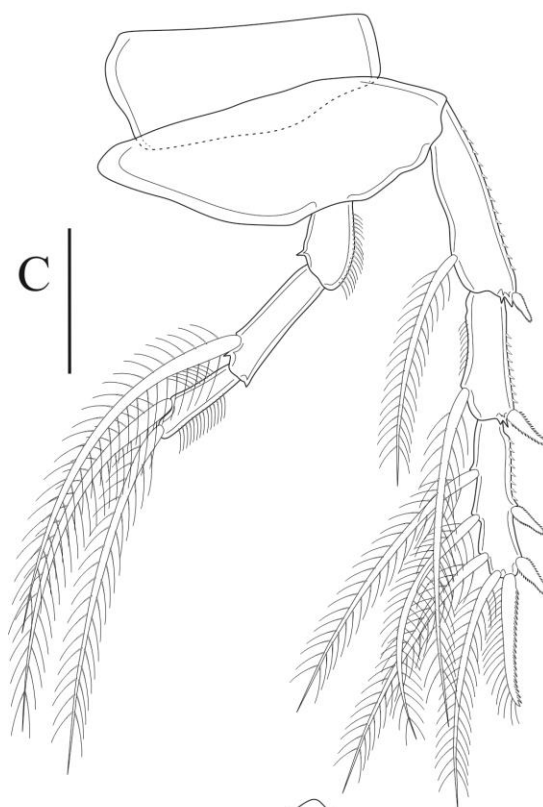
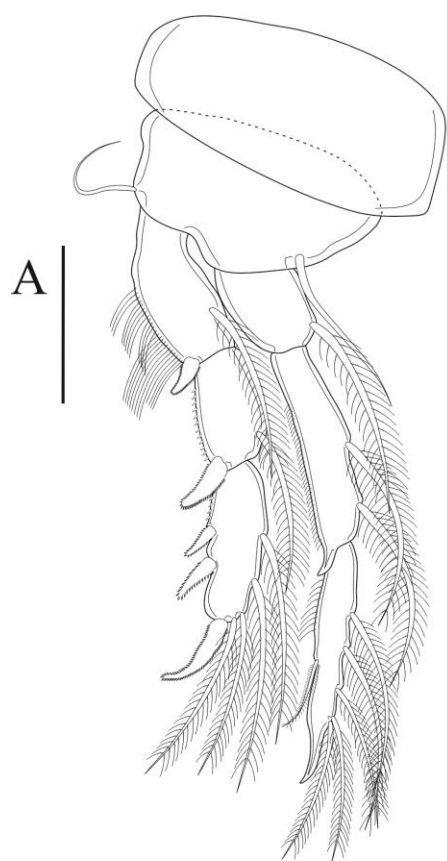












## Capítulo 3

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### **Phylogenetic relationships in Family Entomolepididae Brady, 1899 (Copepoda, Siphonostomatoida) based on morphological characters**

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#### **Abstract**

Entomolepididae is a Siphonostomatoida family that possesses a conspicuous morphology: a flattened body shield. Morphological data are used to examine the interrelationships within Entomolepididae at first time. All entomolepidids species known, until now, are included in the analysis. The classification of Entomolepididae into two subfamilies was rejected – Parmulodinae do not constitute a monophyletic group; only Entomolepinae was recovered as monophyletic group. Most Entomolepididae genera are monophyletic; the exception is *Entomopsyllus* that appears as paraphyletic in IW topology, related with *Spongiopsyllus*. However, due to many homoplasies and low supports values, it is not possible with certainty to include *Spongiopsyllus* into *Entomopsyllus*. An emended diagnosis is proposed to the genera.

**Key words:** Phylogeny, associated copepods, morphology.

## Introduction

The Family Entomolepididae Brady 1899 was created to a new species of siphonostome that exhibit a conspicuous morphology, a flattened body shield. In 1959, this family had four species already described when Eiselt (1959) established its diagnoses and subdivided into two subfamilies, Parmulodinae and Entomolepinae. Almost three decades later, Mckinnon (1988) revised the diagnoses of Entomolepididae and its subfamilies, expanding them to accommodate his new species. Stock (1992) found incongruities on Mckinnon's diagnosis, and declined to use the subfamily classification in his work. Indeed, the only feature that really differentiates Parmulodinae from Entomolepinae is the number of pedigerous somites between the cephalothorax and the terminal shield: Entomolepinae shows two somites while Parmulodinae has only one somite resulted from the fusion of third and fourth pedigerous somites. The following authors, disregarding the observations made by Sotck (1992), maintained the use of subfamilies classification. So far, no one tested the validity of subfamilies from the perspective of phylogenetics analysis.

The conservative morphology of Entomolepididae makes the limits among genera a thin line and it is not difficult to find overlaps in theirs diagnosis. As mentioned above, the same scenario is true to both subfamilies. Notwithstanding, morphological characters are central in Copepoda taxonomy, and are the primary source for establishment of species and supra specific taxa. According to Giribet (2015), morphological data play an important role in animal phylogentic studies. This is especially true in cases where no specimens are available for molecular analysis, either by lack of copies donated by museums, difficulty in collecting accurate new material, or when data are accessible only in literature. That is the case of many siphonostomes, mainly when referring to Entomolepididade that had several species

collected once but this material is not made available by museums. A phylogenetic study can elucidate the question of limits between taxa and allows the identification of synapomorphies, which can be useful in redefining diagnosis.

Currently, Entomolepididae is composed by 9 genera and 23 species (Canário *et al.*, in prep.). In the last two decades, the diversity had increased to the description of eight new species at South Atlantic Ocean (*Spongiopsyllus adventicius* Johnsson, 2000, *S. redactus* Canário *et al.*, 2012, *S. atypicus* Canário *et al.*, in prep., *S. stocki* Canário *et al.*, in prep., *S. boxshalli* Canário *et al.*, in prep., *S. hoi* Canário *et al.*, in prep., *Parmullopsyllus breviarticulata* Borges *et al.*, in prep. and *Neoparmullela periperiensis* Farias *et al.*, in prep.) and one species at Southern Japan (*Entomopsyllus takara* Uyeno & Johnsson, in prep.). However, none of these works, as previous studies, were made in light of a phylogenetic study that aimed to evaluate the relationships, as well as validate genus and species proposed. Thus, this work aims to examine the interrelationships within Entomolepididae based on morphological characters, testing subfamilies and genus monophylies, and relations among species.

## **Material and Methods**

### *Morphological characters*

From 157 characters selected (Table 1), 143 were binary and 14 were multistate. Among the multistate, the characters 48, 50, 60, 61, 63, 64, 70, 71, 155 and 156 were coded as ordered, considering ontogenetic sequences known for Siphonostomatoida (Ivanenko & Ferrari, 2003). Missing data was coded as “?” and inapplicable information as “-“, although both were analyzed as the same by TNT 1.5 (Goloboff & Catalano, 2016). Morphological matrix are shown in the appendix. For better understanding of the nomenclature used for morphological features listed in Table 1,

it is necessary to describe briefly some of the characters. First, the structures are viewed from anterior to posterior and from general to particular, considering the ancestral pattern attributed to siphonostomatoids.

Antenna – characters 48 to 55. In the plesiomorphic state, the antennal endopod possess three segments, named as I, II and III (Figure 1A). These segments could be fused in different degrees. The endopod I is unarmed; the endopod II may have a distal seta on its inner margin (Seta I). The endopod III possess four setae (Seta II, III, IV, and V) (Figure 1A). The antennal exopod in Siphonostomatoida has only one segment, reduced or absent, with up to three setae, one lateral and two distal.

Maxilla – characters 62 to 67. The maxilla in siphonostomatoida is formed by a syncoxa plus a claw. The distal claw is a result of specialization of the basis, which may possess up to three setae (Figure 1B). In Entomolepididae these setae generally are fused with basis or are absent.

Maxilliped – characters 68 to 74. The maxilliped is formed by syncoxa, basis and endopod (with four segments in the plesiomorphic forms: I, II, III and IV). Ancestrally, the syncoxa has one seta and the basis has two setae. The endopod I may possess up to two setae; endopod II and III have one seta each; the last endopodal segment shows a distal seta located near the claw.

Swimming legs (P1 to P4) – characters 75 to 150. The pattern of legs in Copepoda includes coxa, basis and a 3-segmented exopod and endopod. The description of spines (represented by Roman numerals) and setae (represented by Arabic numerals) starts with outer to inner margins. To identify each element of the rami, each segment received a denomination by means of a letter. Thus, the exopod has the segments “a”, “b” and “c” and the endopod has the segments “d”, “e” and “f” (Figure 1C). The

spines and setae were numbered always from the outer proximal to the inner proximal margin (Figure 1C).

#### *Ingroup selection*

The ingroup include all Entomolepididae species, already described, and new species ready for publication, which are known at the time of preparation of this manuscript.

Character states were scored from direct observations of specimens and/or from published accounts (Table 2) – where no samples were available but for which reliable drawings were at hand in literature. The species *Lepeopsyllus typicus* (Thompson & Scott, 1903) and *L. ovalis* (Thompson & Scott, 1903) were incompletely described, but literature has enough information that allowed the inclusion of them in the analysis. The species *Entomolepis ovalis* Brady, 1899, *Entomopsyllus brevicaudatus* Lee & Kim, 2017, *E. stocki* Kim, 2004, *L. typicus*, *L. ovalis*, *Paralepeopsyllus dambayensis* Lee & Kim, 2017, *P. leei* Lee & Kim, 2017, *Parmulopsyllus breviarticulata* Borges *et al.*, in prep., *Spongiopsyllus redactus* Canário *et al.*, 2012, *S. stocki* Canário *et al.*, in prep., *S. hoi* Canário *et al.*, in prep. and *S. intermedius* Borges *et al.*, in prep., does not have a known male.

#### *Outgroup selection*

The affinities of Entomolepididae and Asterocheridae Giesbrecht were suggested early in history of entomelepidids. Thompson & Scott (1903) described the genus *Lepeopsyllus*, which possesses the body shape of a typical Entomolepididae, as member of Asterocheridae. Posteriorly, seemingly unaware of the existence of Entomolepididae, Ummerkuty (1960) described *Paralepeopsyllus* recognizing its similarity with *Lepeopsyllus*, but considering both genera as a cohesive group near

to Asterocheridae. When described *Parmulella*, Stock (1992) emphasized that the only difference between these two families is the modified body of entomolepidids. In his thesis, Johnsson (2003) made the unique phylogenetic study of siphonostome families associated with invertebrates, including Entomolepididae. The author validated the family Entomolepididae and found it as a group near to Asterocheridae (unpublished data). Thus, we chose to include the type species of the most basal genera of Asterocheridae, *Asterocheres lilljeborgi* Boeck, 1859, *Cheramomyzon abyssale* Humes, 1989 and *Dermatomyzon nigripes* (Brady & Robertson, 1876), as outgroups of our analysis. The character states were scored from the original descriptions and redescrptions of cited species (Boeck, 1859; Brady & Robertson, 1876; Humes, 1989; Ivanenko & Ferrari, 2003).

#### *Analytical methods*

The database was created initially by using Nexus Data Editor 0.5.0 (Page, 2001) software and was composed by 26 taxa and 157 morphological characters. Next, the Nexus matrix was exported in a .txt file for input into TNT 1.5 (Goloboff & Catalano, 2016). Parsimony-based phylogeny was conducted with a heuristic search in two steps: first with equal weight (EW) and second with implied weighting (IW) against homoplasy.

The first stage of the analysis involved a Traditional search of Wagner trees option of TNT 1.5; 1500 replications with random input order; branch swapping: tree-bisection-reconnection. Symmetric resampling support on unweighted data was determined ( $p = 33$ ; frequencies differences – GC; 5000 replicates; collapse groups below 1). The second search was made with Implied weighting with  $k=1$ . The Traditional search was performed with 200 and random input order; branch



swapping: tree-bisection-reconnection. Symmetric resampling support was determined with the same specifications of EW. The resulting trees were edited using CorelDraw X7.

## Results

### *General results*

The EW search in TNT 1.5 retrieved one most parsimonious trees (MPT) (length 372, consistency index 0.42, and retention index 0.55) shown in Figure 2A. Monophyly of Entomolepididae received moderated symmetric resampling support (GC = 83) as same as found at the genus *Entomolepis* (Figure 2B). The subfamilies division was not validated; Parmulodinae do not constitute a monophyletic group instead Entomolepinae was recovered but with low support (GC = 64) (Figure 2B). The genera *Lepeopsyllus*, *Paralepeopsyllus* and *Spongiopsyllus* appeared as monophyletic groups in symmetric resampling analysis, although it showed low GC values (24, 35 and 30, respectively) (Figure 1B).

Implied weighting yielded one MPT (best score = 56.77659) (Figure 2), differing substantially from the EW result (compare Fig. 2A with Fig. 3). In the IW topology, *Parmulodes* is the sister genus of *Parmullela*, and *Parmulopsyllus* the sister of *Paralepeopsyllus*. The monophyletic genera *Entomolepis* and *Lepeopsyllus* formed a clade sister to the clade formed by polyphyletic *Entomopsyllus* plus *Spongiopsyllus* (Figure 3). In both analysis, EW and IW, the recent discovered of genus *Neoparmullela* appeared as most basal taxa of Entomolepididae; both agreed about the monophyletic condition to Entomolepinae, *Entomolepis*, *Lepeopsyllus* and *Spongiopsyllus*.

Symmetric resampling of IW (Figure 4) did not recover the relationship between *Entomolepis* and *Lepeopsyllus*, but both genus still formed monophyletic groups with low supports (52 and 53, respectively). The same was found at *Entomopsyllus-Spongiopsyllus* clade: in symmetric resampling, *Lepeopsyllus* was included as sister of clade formed by *E. stocki* and *E. nichollsi*. Although with low supports (GC = 36), *Spongiopsyllus* are still monophyletic. As indicated by the retention index (RI) for each character (Table 1), 49 of 157 characters made a small contribution (RI < 0.50) to the topology (Figure 3). Only 21 characters (1, 5, 14; 31, 39, 58, 76, 80, 90, 96, 97, 99, 102, 106, 108, 110, 118, 121, 139, 144 and 153) showed unambiguous states change (Table 3) which is shown by the retention index = 1.0 (Table 1).

#### *Clades, synapomorphies and supports*

The clades presented in this section were a result of IW analyzsis and are shown in Figure 2. Clade 1 represents the family Entomolepididae; the only unambiguous sinapomorphy of this clade is the absence of seta P4f1 (character 144: 0 → 1). The transition states of 0 to 1 of the characters 4, 17, 60 and 123 are synapomorphies of Entomolepididae; other homoplastic synapomorphies includes characters 2, 18, 71 and 83. The absence of articulation between third and fourth pedigerous somites (character 4) appears as a primitive condition for entomolepidids. The Symmetric resampling showed a moderated support for the family (Figure 4) whereas the Bremer support was low (Figure 3).

Clade 2 includes all entomolepidids with exception of *Neoparmulella periperiensis* (Bremer = 27; CG = 25). As synapomorphies, includes characters 8 (0 → 1), 12 (0 → 3), 19 (0 → 1) and 39 (0 → 1; unambiguous). This clade includes

Clade 3 formed by *Parmulodes verrucosus* and *Parmulella emarginata*, united by the possession of posterior region of siphon reaching leg 3 and reduction of leg 4 to a lobe (characters 56 and 121, respectively), with low supports in Bremer (= 57) and Symmetric resampling (= 22) approaches. Additionally, Clade 4 is included in Clade 2 composed by others species of Entomolepididae.

*Parmulopsyllus breviarticulata* appears as sister of genus *Paralepeopsyllus* in Clade 5; this genus share ambiguous states which are the absence of articulation between genital and second abdominal somite in females (character 6), absence of leg 4 (character 120) and absence of an inner seta on leg 5 protopod (character 152). The genus *Paralepeopsyllus* (Clade 7) are defined mainly by three unambiguous synapomorphies: absence of setae P3a3, absence of endopod on leg 3 and absence of exopod on leg 5, characters 99, 108 and 153, respectively. The monophyly of this genus is supported by the highest values of supports observed in this analyze (Bremer = 97; CG = 93). Among the *Paralepeopsyllus* species, *P. mannarensis* and *P. leei* are sister group (Clade 8) based in four synapomorphies, two of them unique: absences of spine P3c2 and the seta P3c7.

The subfamily Entomolepinae (Clade 6) was recovered as a monophyletic group (Figure 2) although with low support value (CG = 30; Figure 4). Its synapomorphies include characters 1, 4, 13, 50, 56, 78 and 119, most of them ambiguous. The subfamily includes monophyletic genera *Entomolepis*, *Lepeopsyllus* and *Spongiopsyllus*, and paraphyletic genus *Entomopsyllus*. *Entomolepis* and *Lepeopsyllus* are sister groups (Clade 9) sharing the absence of seta P1e2 (character 80). The two species of *Lepeopsyllus* (Clade 11), *L. typicus* and *L. ovalis* shared reduction of mandible stilete as sinapomorphy; additionally the shift of state 1 to 2 in the character 71 appears as homoplastic sinapomorphy of this genus. On the other

hand, *Entomolepis* (Clade 12) possesses more synapomorphies that support its monophyletic status (characters 14, 16, 71, 73, 120, 152, 155) although most of it represented homoplasies and their support were low (CG = 52). The relationship between *Lepeopsyllus* and *Entomolepis* was not recovered in the resampling (Figure 4).

*Entomopsyllus* and *Songiopsyllus* are genera closely related and comprises a monophyletic group (Clade 10) based on mainly two synapomorphies: the absences of seta P3f6 (character 118) and endopod of leg 4 (character 139). Among species formally known of *Entomopsyllus* (Clade 17), *E. stocki* and *E. nichollsi* it appears as sister (synapomorphies include characters 19, 20, 77 and 90; the last one is the only one that is unambiguous) with similar low supports values (Bremer = 25; CG = 26). The monophyly of *Songiopsyllus* (Clade 16) was weakly supported (Bremer = 30; CG = 36) even when the group showed a sinapomorphy which is the absence of seta P3e1 (character 110), in addition to the homoplastic synapomorphies that included characters 78, 81, 83, 91 and 93. *Songiopsyllus redactus* and *S. adventicius* (Clade 19) were recovered as sister species with substantial support in Symmetric resampling (CG = 89) (Figure 4). The species *S. hoi* and *S. stocki* formed a clade with 100% of Bremer support, sharing the absence of outer seta of the basis of leg 1 (character 76). The CG value of this clade was moderate (Figure 4). At last, *S. boxshalli* and *S. atypicus* are sister taxa with significant Bremer support (= 80) and low CG value (= 23). These two species shared only one ambiguous synapomorphie: the presence of 4 setae on inner lobe of maxílule (character 30, 3 → 2).

## Discussion

The topologies generated by EW and IW differ in several points (Figures 2 and 3). The sisters groups *P. leei*–*P. manarensis*, *L. typicus*–*L. ovalis*, *E. ovalis*–*E. hamondi*, *E. nichollsi*–*E. adriae* and *S. redactus*–*S. adventicius* were recovered in both analysis, although high support (Bremer = 91) was found only on *L. typicus*–*L. ovalis* in IW. The clade formed between *E. ovalis* and *E. hamondi* had a moderated support in Symmetric resampling of EW (CG = 83). All other clades had supports below 70, most of them with even lower values (> 50). In general, the IW analysis showed higher support values for both Bremer and Symmetric resampling. Considering that, in addition to the penalization of homoplasies, we chose to discuss the results concerning the IW topology.

The low number of unambiguous synapomorphies joining lineages within the Entomolepididae contrasted with the greater number of homoplasious transformations in character states occurring within clades. Bradford-Grieve & Ahyong (2010) found similar results to phylogeny of Calanidae genera, where many of the synapomorphies that defined clades also were homoplastic. In our analysis, only 21 characters, 13,4% of total, showed CI and RI = 1.0 (Table 1). Others characters (e.g. 21, 63, 125 and 133) were not ambiguous, but did not have the indexes calculated by being states transitions restricted to one node or to all nodes; both cases represented non-informative characters (see the representation “-“ on Table 1) (de Pinna et al., 2007). Homoplastic transformations are present in articulation of thoracic and abdominal somites, articles of female and male antennule and setation of cephalosome appendages and rami of legs. The high number of homoplasies made it very difficult to recognize trends in Entomolepididae evolution.

Entomolepididae formed a clade defined by the following shared derived characters states: posterior corners of second and third pedigerous somites not

projected (2); absence of articulation between third and fourth pedigerous somites (4); articles IV and V of female antennule fused (17); articles V and VI of female antennule fused (18); four setae on inner lobe of maxillule (60); one seta on first maxilliped endopodal segment (71); absence of P2 inner coxal seta (83); absence of P4 inner coxal seta (123); absence of seta P4f1 (144). The number in parenthesis represents the characters. The character 144 is the only synapomorphy that has CI = 1.0. The characters 4, 17, 60 and 123 have CI = 0.5 because there is more than one possible step for transformations in states. Entomolepinae showed the apomorphic condition to character 4 (third and fourth pedigerous somite free). *Parmulodes verrucosus* is the only entomolepidid species that has articles IV and V of female antennule not fused, representing a reversion in character 17. The shared condition of four setae on inner lobe of maxilla is presented on most basal species (*N. periperiensis*, *P. verrucosus*, *P. emarginata* and *P. breviarticulata*) and reversibly in *P. mannarensis*, *S. boxshalli* and *S. atypicus*. *Entomopsyllus nichollsi* is the only species that possesses inner seta on P4 coxa, differing from all other entomolepidids.

*Neoparmulella periperiensis* is the most basal species of the family and is sister to all other entomolepidids. The autapomorphic fusion between articles XV and XVI of male antennule, absent in *Neoparmulella*, agroups the entomolepidids in Clade 2. *Parmulodes* and *Parmulella* are monospecific sister genera that share the reduction of P4, which is the only unambiguous synapomorphie of Clade 3. The higher and congruent support value was found to the genus *Paralepeopsyllus*: Bremer = 97 and CG = 93. Five synapomorphies defines this clade, from which, three are autapomorphic: the absence of setae P3a3 and P3c8 (characters 99 and 107, respectively), the absence of P3 endopod (character 108) and the absence of P5 exopod (character 153). This genus is composed by *P. dambayensis*, *P. leei*, both

recently described by Lee & Kim (2017), and *P. mannarensis*, the type species. The last two, appeared as sister although with low supports values. In fact, the monophyly of *Paralepeopsyllus* is unquestionable and the clade formed by this genus plus *Paralepeopsyllus* is the sister group of Neoentomolepinae, although the relationship get low support values (Bremer = 56; CG = 75). Only the absence between the fifth pedigerous somite and the genital somite support unambiguously this clade.

Eiselt (1959) divided Entomelipidae in two subfamilies, Parmulodinae and Entomolepinae, which can be distinguished almost exclusively by the numbers of pedigerous somite between the cephalosome and the posterior shield. The Parmulodinae species showed only one free segment, which is the second pedigerous somite, as a result of the fusion between the third and the fourth pedigerous somite. On the other hand, Entomolepinae possesses two free segments; the second, third and fourth pedigerous somites are present. In our phylogenetic analysis, the articulation between third and fourth pedigerous somites (character 4) were plesiomorphic fused in genera *Neoparmulella*, *Parmulodes*, *Parmulella*, *Parmulopsyllus* and *Paralepeopsyllus*. The presence of third and fourth pedigerous somites as free, is present in Entomolepinae genera (*Lepeopsyllus*, *Entomolepis*, *Entomopsyllus* and *Spongiopsyllus*) and, with other synapomorphic states, designates them as a clade. Thus, the Eiselt (1959) subfamilies classification was invalid since Parmulodinae did not recover as a monophyletic unit. Consequently, to avoid misunderstandings, we proposed a new name to designate the clade formed by previous “Entomolepinae” genera: Neoentomolepididae, which does not possess a hierarchical category. The prefix ‘neo’ means ‘new’ in Greek and refers to the derived status of the Clade 6 (Figure 3). The posterior corners of cephalosome non-projected (character 1), the endopod segments of antenna free (character 50, with reversion in *L. typicus* and

convergence in *P. emarginata*), the absence of spine P1c1 (character 78, presented in *Spongiopsyllus*) and the absence of seta P3f7 (character 119) are synapomorphic features of Neoentomolepididae.

*Lepeopsyllus* and *Entomolepis* are both monophyletic and a sister group with low Bremer support (= 6), probably resulted of a unique unambiguous synapomorphie that united them (character 80). The relationship between these genera did not recovered in resampling; instead, both formed a low supported clade with *Entomopsyllus adriae*. As mentioned on the results, *Entomopsyllus* was the only non-monophyletic among Entomolepididae genus. This can be attributed to several resemblances that *Entomopsyllus* shared with *Spongiopsyllus*, shown by sister relationship between Clade 15 (formed by *E. adriae*, *E. stocki* and *E. nicholli*) and the later. Differently, *Spongiopsyllus* species are grouped into a monophyletic clade based manly on an autapomorphic character: the absence of setae P3e1. In fact, it is possible that both *Entomopsyllus* and *Spongiopsyllus* represent only a genus. Data presented here are not sufficient to suggest the inclusion of *Spongiopsyllus* into *Entomopsyllus*, therefore, we awaiting for more specific morphological or/and genetic data that may solve this problem. Similarly, development studies with Enomolepididade species could improve the propositions of primary homology and sorting of characters for better estimates of support values, which are, in general, low in our analysis. It is worth nothing that, we have been restricted to delimit the characters based on knowledge of developmental series of other close siphonostomatoids species (Ivanenko & Ferrari, 2003) included here as outgroups.

Based in the unambiguous synapomorphies identified in our IW analysis, we proposed an emendation on diagnosis of monophyletic Entomolepididae genera. Only characters that showed CI = 1.0 were added to current diagnosis of genera.



Additionally, some of the diagnosis were revised and summarized to be more objective and/or to be according to nomenclature currently used in Siphonostomatoida.

*Revised diagnosis of the Entomolepididae genera*

***Entomolepis* Brady, 1899 (modified from MacKinnon, 1988)**

Body shield flattened; prosome composed by 4-segments, the fourth recovering entirely the urosome. Urosome 3-segmented in both sexes. Ancestral articles I and II of female antennule fused. Exopod of antenna with an annulated process produced anteriorly from about mid-length, bearing a number of hairs. Terminal segments of mandibular palp about half as long as basal segment. Fourth leg absent. Leg 5 greatly reduced in female, consisting of a single small segment and a short terminal seta. Leg 5 absent in male.

*Remarks*

The first diagnosis of *Entomolepis* made by Brady (1899) was very general and included common features to all Entomolepididae. MacKinnon (1998) noted this and redefined it. Here, the fusion between the ancestral segments I and II of female antennule was included in the *Entomolepis* diagnosis because it represented the only unambiguous synapomorphie of the group, identified in our phylogeny. Afterwards, we included a description of the body shape and prosomal and urosomal segmentation that were lacking in the original diagnosis.

***Entomopsyllus* MacKinnon, 1988**

*Entomopsyllus* was the only genus that was not recovered as monophyletic. Thus, there is no sinapomorphy to define it as clade. Therefore, the diagnosis of this genus remained as established by McKinnon (1988).

***Lepeopsyllus* Thompson & Scott, 1903**

Body shield oval, flattened, composed by 4 segments. Female abdomen 3-segmented and completely covered by the fourth pedigerous somite. Caudal rami partially or completely covered by the same segment. Siphon long, reaching to about the end of the anal somite. Antennule 13-15-segmented. Mandible stylet reduced, consisting of a long hair attached to a short slender basal segment; palp 2-segmented, with equal length, second segment hisurte. Maxilla with 2 lobes. P1 to P3 biramous with 3-segmented rami; P4 exopod 3-segmented, endopod reduced, consisting of a minute knob with one hair; P5 consist of a long curved hairy appendage. Caudal rami long and narrow.

*Remarks*

The wording of original diagnosis was revised for adequation of modern nomenclature used in Siphonostomatoida taxonomy and to include the reduction of mandible stylet, sinapomorphic to the genus.

***Paralepeopsyllus* Ummerkutty, 1960**

Body thin, sacale-like, oval or circular; prosome 3-segmented and urosome 4-segmented in both sexes; urosome completely overlapped by the last prosomal segment; the margin of all prossomal segments thickly lined with papila-like prolongations of irregular lengths, forming an ornamentation. Antennule 14-segmented or 15-segmented in female. Antenna 5-segmented, the last segment carrying

terminal claw; exopod very short. Siphon rather short and shield-shaped. Mandible comprising stylet and palp carrying two terminal unequal setae. Maxillule bilobed, lobes with unequal length, both lobes carrying four setae. Maxilla 1-segmented, strongly built and carrying a stout terminal claw. Maxilliped 5 or 6-segmented, with terminal claw. P1 and P2 biramous with 3-segmented rami; P3 uniramous with 3-segmented exopod; inner setae of first exopodal segment of P3 absent. P5 absent; Caudal rami moderately divergent and cylindrical.

#### *Remarks*

Lee and Kim (2017) described two new species of *Paralepeosyllus* with some divergences with the diagnosis of this genus made by Ummerkutty (1960). Thus, we proposed an emendation in diagnosis to expand it to accommodate *P. leei* and *P. dambayensis*, with inclusion of the two non-homoplastic synapomorphies of *Paralepeosyllus*. Additionally, we modified the sentence “the second segment carries a rudimentary endopod provided with terminal setae” because it is a misinterpretation of the antenna exopod. The general text of diagnosis was revised aiming to reduce it and make it more objective.

#### ***Parmulella* Stock, 1992**

Body shield composed of cephalosome and pedigerous segments 2 and 4 (segment 3 not free); body shield not covering the urosome. Genital segment of female wider than long. Two post-genital segments in both sexes. Mandible blade greatly lengthened, almost setiform. Syncoxa of maxilla with one seta. P1 to P3 biramous, P4 present as knob in female or monomeric rudiment in male. Third endopodal segment of P3 with one distal seta. Leg 5 leaf-shaped (female) or clavate (male). Caudal rami shorter than anal segment.

*Remarks*

The new *Parmulella* diagnosis included an autapomorphic character of *P. emarginata*, ‘the presence of one seta on syncoxa of maxilla’ (= character 63).

***Parmulodes* Wilson, 1944 (modified from Eiselt, 1959 and Stock, 1992)**

Body suborbicular and flattened; prosome composed by cephalosome and two pedigerous somites; second segment free; third and fourth pedigerous somite fused. Urosome completely recovered by prosome, except half of caudal rami. Two post-genital somites present. Antennule usually 17 or 18-segmented. Antenna 4-segmented, third segment indistinctly divided into two segments; exopod absent. Siphon long and narrow. Mandible comprising stylet and two segmented palp with two unequal setae. Maxillule bilobed, lobes unequal; both lobes with four setae. Maxila and maxilliped with a hooked shape. P1 to P3 biramous with 3-segmented rami; outer distal seta of third endopodal segment of P3 absent. P4 reduced a small unsegmented bud with a minute distal seta. P5 1-segmented bearing three seta.

*Remarks*

The *Parmulodes* diagnose was revised, rewritten and the feature “outer distal seta of third endopodal segment of P3 absent” (= absence of seta P3f3, character 114) was included.

***Parmulopsyllus* Borges et al. (in prep.) and *Neoparmulella* Farias et al., in prep.**

Both genera were recently discovered and their description are in process of finalization. In this phylogenetic analysis, all the autapomorphic characters of *Parmulopsyllus*, as well as of *Neoparmulella*, are homoplastic. Thus, we did not add any feature for both diagnoses.

***Spongiopsyllus* Johnsson, 2000**

Body shield composed of cephalothorax and pedigerous somites 2–4. Body shield covering urosome, except for the tip of the caudal rami. Three postgenital urosomites in females and four in males. P1 to P3 biramous with 3-segmented rami; inner seta of first endopodal segment of P3 absent. P4 uniramous with 3-segmented exopod.

*Remarks*

*Spongiopsyllus* is a monophyletic group and the absence of inner seta for the first endopodal segment of P3 is its only non-homoplastic sinapomorphy which was included in its diagnosis. Additionally, we included the description of legs and its rami to complete the diagnosis.

*On the distribution and guest-host relationships*

Entomolepididae has a worldwide distribution with major diversity on Indo-Pacific Ocean. However, the early genera *Neoparmulella*, *Parmolodes* and *Parmulella* occurred on Atlantic Ocean, the first on South then both later on North (Wilson, 1944; Stock, 1992; Farias *et al.*, in prep.). *Neoparmulella periperiensis* and *P. emarginata* were found only in the type locality, Periperi Beach (Salvador, Bahia, Brazil) and Piscadera Bay (Curaçao), respectively. Their congenerer, *P. verrucosus* has a wider distribution, occurring on several sites at Caribbean Sea (Cayo Caracoles, San Christóbal Reef, Piscadera Bay, Fuik Bay and Aruba) and Florida (EUA). On the other hand, the *Paralepeopsyllus* species, are known only on Indo-Pacific Ocean, in the Gulf of Mannar (*P. mannarensis*), Bohol Island (*P. leei*) and Dam Bay (*P. dambayensis*) (Ummerkutty, 1960; Lee & Kim, 2017).

Most of the Neoentomolepididae genera occur on Indo-Pacific Ocean.

*Lepeopsyllus* and *Entomolepis* are only found on Indo-Pacific waters, the first on Indic Ocean (Brady, 1899; Thompson & Scott, 1903; McKinnon, 1988). The species *E. ovalis* is restricted to New Zealand coast and *E. hamondi* has a broad distribution along the Bass Strait (Tasmania), also occurring in Britomart Reef (North Queensland) (Brady, 1899; McKinnon, 1988). *Entomopsyllus* was also registered on Indo-Pacific with exception of *E. adriae*, which was found on Adriatic Sea (Eiselt, 1959). The other species, *E. nicholli*, *E. stock*, *E. brevicaudatus* and *E. takara* were found on Shark Bay (Western Australia), Nosy Bé (Madagascar), Bohol Island (Philippines) and on North Pacific Ocean coast (Tokara Islands, Japan), respectively (McKinnon, 1988; Kim, 2004; Lee & Kim, 2017; Uyeno & Johnsson, in prep.). *Spongiopsyllus* is the only genus that is registered on Atlantic Ocean, with distribution along Northeast Brazilian coast, at Pernambuco and Bahia States (Johnsson, 2000; Canário *et al.*, 2012; Borges *et al.*, in prep.; Farias *et al.*, in prep.; Canário *et al.*, in prep.).

Sponges are typical hosts for entomolepidids: among 23 species known until now, 14 are associated with sponges. It is difficult to find a pattern of evolutionary radiation of guest-host relationship. Although it is evident on Neoentomolepididae a trend of colonization of Porifera among *Spongiopsyllus* species – only *S. redactus* were not found in a sponge. However, Canário *et al.* (2012) described *S. redactus* based on a single female discovered in a sample of the coral *Mussismilia hispida* (Verrill), which can be, in fact, an accidental host. The sponges of genus *Aplysina* is the preferential host of *Spongiopsyllus*: *S. hoi*, *S. stocki* and *S. boxshalli* were all found associated with *A. cauliformis* (Carter); *S. intermedius* is associated to *A. solangeae* Pinheiro, Hajdu & Custodio; and *S. atypicus* was found in *A. insularis* (Duchassaing & Michelotti) (Borges *et al.*, in prep.; Canário *et al.*, in prep.). The type

species *S. adventicius* also occurs on *Aplysina* (*Aplysina lacunosa* (Lamarck)) and additionally was found with *Dysidea janiae* (Duchassaing & Michelotti) and *Monanchora* Carter (Johnsson, 2000; Canário *et al.*, 2012). Other Entomolepididae species associated with sponges include: *P. verrucosus* and *P. emarginata*, both associated with *Chondrilla nucula* Schmidt (Stock, 1992); *P. breviarticulata* was found with *Aplysina cauliformis* (Carter); and *P. dambayensis*, *P. mannarensis*, *P. leei* and *E. brevicaudatus* all registered on samples of unidentified sponges (Ummerkutty, 1960; Lee & Kim, 2017; Borges *et al.*, in prep.).

*Entomopsyllus* include species with more diverse host taxa, including besides sponge as mentioned above, the cnidarians *Tubipora musica* (Linnaeus) for *E. stocki* and *Heliopora coerulea* (Pallas) for *E. takara* (Kim, 2004; Uyeno & Johnsson, in prep.); the algae *Sargassum* C.Agardh for *E. adriae* (Eiselt, 1959); and a sample of plankton for *E. nichollsi*, but McKinnon (1988) assumes that this species is in fact associated with benthic invertebrates. Among the last two Entomolepididae genera, *Entomolepis* and *Lepeopsyllus*, only *E. ovalis* has its host determined: the ascidian *Botrylloides leachii* (Savigny) (McKinnon, 1988). *Entomolepis hamondi* has unknown host and *L. ovalis* and *L. typicus* were found in washings of invertebrates and oyster, respectively.

## Conclusion

Based on morphological data here analyzed, the evolution of Entomolepididae involved many homoplastic characters, which include fusion between antennule segments and rami setation of legs. The previous division of Family into two subfamilies was rejected: Parmulodinae do not constitute a monophyletic unity. Instead, Entomolepinae, now named as Neoentomolepididae, was monophyletic

based on a seven sinapomorphy, among then the presence of articulation between third and fourth pedigerous somites.

The genus *Entomopsyllus* was the only taxa that was not recovered as monophyletic. The *Entomopsyllus* species formed a monophyletic group with *Songiopsyllus* genera, although with low Bremer support, the same was not recovered in Symmetric resampling. Thus, we are not able to include *Songiopsyllus* into *Entomopsyllus*. As mentioned above, *Songiopsyllus* is monophyletic but the relationship among its species was not congruent among the various analysis, except for the relationship between *S. adventicius* and *S. redactus*. In IW, the genus *Entomolepis* and *Lepeopsyllus* are sister with no consensus in Symmetric resampling. The same scenario was not found for the relationship between *Parmulopyllus* and *Paralepeopsyllus*, which was sister, recovered also in resampling round.

Data showed here was the first attempt to test the relationship among Entomolepididae taxa. The amount of homoplasies involved in evolution of Entomolepididae highlights the necessity to improve data survey, but serve as a working hypothesis that can be tested using newly morphological and molecular data.

## Acknowledgment

The authors thank to Smithsonian Institution National Museum of Natural History for the loan of the holotypes and to the Luiz Peixoto (Museu de Zoologia da USP) for the technical supports with TNT 1.5. RC thanks ‘Programa de Pós-Graduação em Zoologia’ (USP) and CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for financial support.

## References



- Boeck, A. (1859) Tvende nye parasitiske Krebsdyr, *Artotrogus orbicularis* og *Asterocheres Liljeborgii*. *Forhandlinger i Videnskabs-Selskabet i Christiana*, 2, 171–182.
- Borges, C., Neves, E.G. & Johnsson, R. (in preparation) A new Entomolepididae genus and a new species of *Spongiopsyllus* associated with sponges in Todos-os-Santos Bay, Bahia, Brazil.
- Bradford-Grieve, J.M. & Ah Yong, S.T. (2010) Phylogenetic relationships among genera in the Calanidae (Crustacea: Copepoda) based on morphology. *Journal of Natural History*, 44(5-6), 279–299.
- Brady, G.S. (1899) On the marine Copepoda of New Zealand. *Transactions of the Zoological Society of London*, 15, 31–54.
- Brady, G.S. & Robertson, D. (1876) Report on dredgings off the coast of Durham and North-Yorkshire in 1874. *Report to the British Association for the Advancement of Science*, 45, 185–199.
- Canário, R., Neves, E. & Johnsson, R. (2012). *Spongiopsyllus redactus*, a new species of Entomolepididae (Copepoda, Siphonostomatoida) associated with a scleractinian coral in Brazil. *Zoosymposia*, 8, 49–55.
- Canário, R., Hurbath, T., Rocha, C.E.F., Neves, E. & Johnsson, R. (in preparation) Redescription of *Parmulodes verrucosus* Wilson, 1944 with notes of *Entomopsyllus stocki* Kim, 2004 and description of a new species of *Spongiopsyllus* Johnsson, 2000 (Copepoda, Siphonostomatoida, Entomolepididae).
- Canário, R., Borges, C., Rocha, C.E.F., Neves, E. & Johnsson, R. (in preparation) Three new *Spongiopsyllus* Johnsson, 2000 (Copepoda, Siphonostomatoida,

- Entomolepididae) associated with *Aplysina cauliformis* (Carter) (Porifera, Demospongiae) from Todos-os-Santos Bay, Bahia, Brazil.
- De Pinna, M.C.C., Ferraris Jr, C.J. & Vari Fls, R.P. (2007) A phylogenetic study of the neotropical catfish family Cetopsidae (Osteichthyes, Ostariophysi, Siluriformes), with a new classification. *Zoological Journal of the Linnean Society*, 150, 755–813.
- Eiselt, J. (1959) *Entomolepis adriae*, ein Beitrag zur Kenntnis der kaum bekannten Gattungen siphonostomer Cyclopoiden: *Entomolepis*, *Lepeopsyllus* und *Parmulodes* (Copepoda, Crust.) Sitzber. *Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, 168, 643–660.
- Farias, A., Neves, E.G. & Johnsson, R. (in preparation) A new species and genus of Entomolepididae Brady, 1899 (Copepoda Siphonostomatoida) associated with the endemic octocoral *Phyllogorgia dilatata* (Esper, 1900) (Cnidaria, Octocorallia) from Northeastern Brazil.
- Giribet, G. (2015) Morphology should not be forgotten in the era of genomics – a phylogenetic perspective. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 256, 96–103.
- Goloboff, P.A. & Catalano, S.A. (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32, 1–18.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468pp.
- Humes, A.G. (1989) Copepoda from deep-sea hydrothermal vents at the East Pacific Rise. *Bulletin du Museum National d'Histoire Naturelle*, 11(A, 4), 829–849.
- Ivanenko, V.N. & Ferrari, F.D. (2003) Redescription of adults and description of copepodid development of *Dermatomyzon nigripes* (Brady & Robertson, 1876)

- and of *Asterocheres lilljeborgi* Boeck, 1859 (Copepoda: Siphonostomatoida: Asterocheridae). *Proceedings of the Biological Society of Washington*, 116(3), 661–691.
- Johnsson, R. (2000) *Spongiopsyllus adventicius* new species and genus of Entomolepididae (Copepoda: Siphonostomatoida) associated with sponges in Brazil. *Hydrobiologia*, 417, 115–119.
- Kim, I.H. (2004) Two new species of siphonostomatoid copepods (Crustacea) associated with the stoloniferan coral *Tubipora musica* (Linnaeus) from Madagascar. *Korean Journal of Biological Sciences*, 8, 187–196.
- Lee, J. & Kim, I.H. (2017) Siphonostomatoid Copepods (Crustacea) Associated with Sponges from the Philippines and Vietnam. *Animal Systematics, Evolution and Diversity*, 33(2), 73–99.
- Mckinnon, A.D. (1988) A revision of Entomolepididae (Copepoda: Siphonostomatoida) with Descriptions of Two New Species from Australia, and Comments on *Entomolepis ovalis* Brady. *Australian Journals of Science Research*, 2, 995–1012.
- Stock, J.H. (1992) Entomolepididae (Copepoda: Siphonostomatoida) from the Antilles. *Studies on the Natural History of the Caribbean Region*, 71, 53–68.
- Thompson, I.C. & Scott, A. (1903) Report on the Copepoda collected by Prof. Herdman, at Ceylon, in 1902. *Ceylon Pearl Oyster Fish. Gulf of Manaar, Supplementary Reports*, 7, 227–307. pls. 1–20.
- Ummerkutty, A.N.P. (1960) Studies on indian copepods I. *Paralepeopsyllus mannarensis*, a new genus and species of Cyclopoid Copepod from the Gulf of Mannar. *Journal of Marine Biology*, 2, 105–114.

Uyeno, D. & Johnsson, R. (in preparation) Two new species of Siphonostomatoida (Copepoda) found on cnidarians in Tokara Islands, Southern Japan.

Wilson, C.B. (1944) Parasitic copepods in the United States National Museum.

*Proceedings of the United States National Museum*, 94, 529–582.

## Tables

Table 1: Morphological characters/states used for phylogenetic analysis followed by the consistency index and retention index (bold) in IW analysis. Index for characters that have one state in a single terminal and another state in all other terminals are mathematically indeterminate (de Pinna et al., 2007), and thus are indicated as “-“. The number of characters starts at ‘0’ following the pattern adopted by TNT 1.5.

0. Radial Bands on the external margin of female prosome and pedigerous somites (absent, present)	0.25	<b>0.25</b>
1. Posterior corners of cephalosome (not projected, projected)	1.00	<b>1.00</b>
2. Posterior corners of second and third pedigerous somites (not projected, projected)	0.33	<b>0.60</b>
3. Posterior corners of fourth pedigerous somite (not projected, projected)	0.50	<b>0.00</b>
4. Articulation between third and fourth pedigerous somites (present, absent)	0.50	<b>0.83</b>
5. Articulation between fifth pedigerous somite and genital somite (present, absent)	1.00	<b>1.00</b>
6. Articulation between genital somite and second abdominal somite in females (present, absent)	0.25	<b>0.25</b>
7. Articulation between second and third abdominal somites in females (present, absent)	0.17	<b>0.50</b>
8. Articulation between genital somite and first abdominal somite in males (present, absent)	0.50	<b>0.80</b>
9. Articulation between first and second abdominal somite in males (present, absent)	-	-
10. Articulation between second genital somite and third abdominal somite in males (present, absent)	0.25	<b>0.00</b>
11. Relative size of third pedigerous somite (not over fourth pedigerous somite, over fourth pedigerous somite, partially over genital somite, over anterior margin of anal somite, over beyond anal somite)	0.67	<b>0.00</b>
12. Relative size of fourth pedigerous somite (not over fifth pedigerous somite, over fifth pedigerous somite, partially over genital somite, partially over caudal rami, over caudal ramio, over anal somite)	0.50	<b>0.43</b>
13. Shape of anal somite (longer than wider, wider than longer)	0.17	<b>0.54</b>
14. Articles I and II of female antennule (separate, fused)	1.00	<b>1.00</b>
15. Articles II and III of female antennule (separate, fused)	0.14	<b>0.25</b>
16. Articles III and IV of female antennule (separate, fused)	0.17	<b>0.44</b>
17. Articles IV and V of female antennule (separate, fused)	0.50	<b>0.67</b>

18. Articles V and VI of female antennule (separate, fused)	0.33	<b>0.50</b>
19. Articles VI and VII of female antennule (separate, fused)	0.20	<b>0.60</b>
20. Articles VII and VIII of female antennule (separate, fused)	0.20	<b>0.43</b>
21. Articles XIV and XV of female antennule (separate, fused)	-	-
22. Articles XV and XVI of female antennule (separate, fused)	0.50	<b>0.00</b>
23. Articles XVI and XVII of female antennule (separate, fused)	-	-
24. Articles XVII and XVIII of female antennule (separate, fused)	0.50	<b>0.00</b>
25. Articles XVIII and XIX of female antennule (separate, fused)	-	-
26. Articles XIX and XX of female antennule (separate, fused)	-	-
27. Articles XXI and XXII-XXIII of female antennule (separate, fused)	0.50	<b>0.00</b>
28. Articles XXII-XXIII and XXIV-XXV of female antennule (separate, fused)	0.14	<b>0.33</b>
29. Articles XXIV-XXV and XXVI-XXVIII of female antennule (separate, fused)	0.33	<b>0.00</b>
30. Articles I and II of male antennule (separate, fused)	-	-
31. Articles II and III of male antennule (separate, fused)	1.00	<b>1.00</b>
32. Articles III and IV of male antennule (separate, fused)	0.33	<b>0.60</b>
33. Articles IV and V of male antennule (separate, fused)	0.33	<b>0.00</b>
34. Articles V and VI of male antennule (separate, fused)	0.50	<b>0.00</b>
35. Articles VI and VII of male antennule (separate, fused)	0.25	<b>0.25</b>
36. Articles VII and VIII of male antennule (separate, fused)	0.50	<b>0.00</b>
37. Articles VIII and IX-XII of male antennule (separate, fused)	-	-
38. Articles XIV and XV of male antennule (separate, fused)	-	-
39. Articles XV and XVI of male antennule (separate, fused)	1.00	<b>1.00</b>
40. Articles XVI and XVII of male antennule (separate, fused)	0.50	<b>0.00</b>
41. Articles XVII and XVIII of male antennule (separate, fused)	0.50	<b>0.00</b>
42. Articles XVIII and XIX of male antennule (separate, fused)	-	-
43. Articles XIX and XX of male antennule (separate, fused)	-	-
44. Articles XX and XXI of male antennule (separate, fused)	-	-
45. Articles XXI and XXII-XXIII of male antennule (separate, fused)	0.25	<b>0.40</b>
46. Articles XXII-XXIII and XXIV-XXV of male antennule (separate, fused)	0.25	<b>0.40</b>
47. Articles XXIV-XXV and XXVI-XXVIII of male antennule (separate, fused)	-	-
48. Number of distal setae on antenna exopod (2, 1, none)	0.25	<b>0.33</b>
49. Lateral setae on antenna exopod (present, absent)	0.14	<b>0.40</b>
50. Fusion among endopod segments of antenna (separate, II and III fused, I to III fused)	0.25	<b>0.57</b>
51. Seta I of antenna endopod (present, absent)	0.25	<b>0.00</b>
52. Seta II of antenna endopod (present, absent)	0.20	<b>0.00</b>
53. Seta III of antenna endopod (present, absent)	0.14	<b>0.00</b>
54. Fusion between seta IV and endopodal segment of antenna (absent, present)	0.50	<b>0.00</b>
55. Seta V of antenna endopod (present, absent)	0.14	<b>0.25</b>
56. Posterior region of oral cone (not over cephalosome, longer than prosome, reaching P3, reaching anal somite, over genital somite, over urosome)	0.50	<b>0.58</b>
57. Number of articles of mandibular palp (more than 2, 2, 1, none)	0.50	<b>0.00</b>

58. Reduction of mandibular stilet (absent, present)	1.00	<b>1.00</b>
59. Number of maxillula lobes (2, 1)	-	-
60. Number of setae on inner lobe of maxillule (more than 5, 5, 4, 3, 2, 1)	0.50	<b>0.75</b>
61. Number of setae on outer lobe of maxillule (more than 4, 4, 3, 2, 1)	0.50	<b>0.50</b>
62. Aestetasc of maxilla syncoxa (absent, present)	0.33	<b>0.00</b>
63. Setae of maxilla syncoxa (more than 2, 2, 1, none)	-	-
64. Seta I of maxilla (separate, partially fused, fused)	0.50	<b>0.00</b>
65. Seta II of maxilla (present, absent)	0.33	<b>0.00</b>
66. Fusion between seta II and maxilla basis (separate, fused)	-	-
67. Seta III of maxilla (present, absent)	1.00	<b>1.00</b>
68. Seta of maxilliped syncoxa (present, absent)	0.14	<b>0.00</b>
69. Setae of maxilliped basis (2, 1, none)	0.25	<b>0.00</b>
70. Segments of maxilliped endopod (separate, I and II fused, II and III fused, III and IV fused, all fused)	0.30	<b>0.12</b>
71. Number of setae on first maxilliped endopodal segment (2, 1, none)	0.14	<b>0.29</b>
72. Seta of second maxilliped endopodal segment (present, absent)	0.17	<b>0.29</b>
73. Seta of third maxilliped endopodal segment (present, absent)	0.11	<b>0.11</b>
74. Distal seta of maxilliped endopodal (present, absent)	0.33	<b>0.00</b>
75. Inner seta of P1 coxa (present, absent)	0.14	<b>0.40</b>
76. Outer seta of P1 basis (present, absent)	1.00	<b>1.00</b>
77. Inner seta of P1 basis (present, absent)	0.33	<b>0.33</b>
78. Spine P1c1 (present, absent)	0.50	<b>0.86</b>
79. Transformation of seta P1c4 in spine (absent, present)	-	-
80. Seta P1e2 (present, absent)	1.00	<b>1.00</b>
81. Seta P1f1 (present, absent)	0.25	<b>0.50</b>
82. Seta P1f7 (present, absent)	-	-
83. Inner seta of P2 coxa (present, absent)	0.20	<b>0.50</b>
84. Outer seta of P2 basis (present, absent)	0.50	<b>0.00</b>
85. Spine P2a2 (present, absent)	-	-
86. Spine P2c1 (present, absent)	0.50	<b>0.67</b>
87. Spine P2c2 (present, absent)	-	-
88. Transformation of seta P2c4 in spine (absent, present)	0.25	<b>0.00</b>
89. Seta P2c8 (present, absent)	0.50	<b>0.00</b>
90. Seta P2e2 (present, absent)	1.00	<b>1.00</b>
91. Seta P2f1 (present, absent)	0.25	<b>0.25</b>
92. Transformation of seta P2f4 in spine (absent, present)	-	-
93. Seta P2f7 (present, absent)	0.33	<b>0.75</b>
94. Fusion between coxa and basis of P3 (absent, present)	0.33	<b>0.00</b>
95. Inner seta of P3 coxa (present, absent)	0.50	<b>0.83</b>
96. Outer seta of P3 basis (present, absent)	1.00	<b>1.00</b>
97. Inner seta of P3 basis (present, absent)	1.00	<b>1.00</b>
98. Spine P3a2 (present, absent)	-	-
99. Seta P3a3 (present, absent)	1.00	<b>1.00</b>
100. Seta P3b2 (present, absent)	-	-
101. Spine P3c1 (present, absent)	0.50	<b>0.91</b>
102. Spine P3c2 (present, absent)	1.00	<b>1.00</b>

103. Seta P3c5 (present, absent)	-	-
104. Reduction of Seta P3c5 (absent, present)	-	-
105. Seta P3c6 (present, absent)	-	-
106. Seta P3c7 (present, absent)	1.00	<b>1.00</b>
107. Seta P3c8 (present, absent)	0.50	<b>0.67</b>
108. P3 endopod (present, absent)	1.00	<b>1.00</b>
109. Reduction of P3 endopod (absent, present)	-	-
110. Seta P3d1 (present, absent)	1.00	<b>1.00</b>
111. Seta P3e1 (present, absent)	0.33	<b>0.67</b>
112. Seta P3e2 (present, absent)	0.33	<b>0.67</b>
113. Seta P3f1 (present, absent)	0.50	<b>0.86</b>
114. Seta P3f3 (present, absent)	-	-
115. Seta P3f4 (present, absent)	0.33	<b>0.00</b>
116. Transformation of seta P3f4 in spine (absent, present)	-	-
117. Seta P3f5 (present, absent)	0.50	<b>0.83</b>
118. Seta P3f6 (present, absent)	1.00	<b>1.00</b>
119. Seta P3f7 (present, absent)	0.50	<b>0.80</b>
120. P4 (present, absent)	0.50	<b>0.80</b>
121. Reduction of P4 to a lobe (absent, present)	1.00	<b>1.00</b>
122. Fusion between coxa and basis of P4 (absent, present)	0.50	<b>0.00</b>
123. Inner seta of P4 coxa (present, absent)	0.50	<b>0.67</b>
124. Outer seta of P4 basis (present, absent)	0.25	<b>0.50</b>
125. Inner seta of P4 basis (present, absent)	-	-
126. Spine P4a2 (present, absent)	-	-
127. Seta P4a3 (present, absent)	-	-
128. Spine P4b1 (present, absent)	-	-
129. Seta P4b2 (present, absent)	-	-
130. Spine P4c1 (present, absent)	0.50	<b>0.75</b>
131. Spine P4c2 (present, absent)	-	-
132. Spine P4c3 (present, absent)	-	-
133. Seta P4c5 (present, absent)	-	-
134. Reduction on seta P4c5 (absent, present)	-	-
135. Seta P4c6 (present, absent)	-	-
136. Seta P4c7 (present, absent)	-	-
137. Seta P4c8 (present, absent)	0.50	<b>0.86</b>
138. Seta P4c9 (present, absent)	-	-
139. P4 endopod (present, absent)	1.00	<b>1.00</b>
140. Reduction on P4 endopod absent, present)	-	-
141. Seta P4d1 (present, absent)	-	-
142. Seta P4e1 (present, absent)	-	-
143. Seta P4e2 (present, absent)	-	-
144. Seta P4f1 (present, absent)	1.00	<b>1.00</b>
145. Seta P4f3 (present, absent)	-	-
146. Transformation of seta P4f3 in spine (absent, present)	1.00	<b>1.00</b>
147. Seta P4f4 (present, absent)	1.00	<b>1.00</b>
148. Transformation of seta P4f4 in spine (absent, present)	-	-

149. Seta P4f5 (present, absent)	-	-
150. Seta P4f6 (present, absent)	-	-
151. P5 protopod (present, absent)	0.25	<b>0.25</b>
152. Inner seta of P5 protopod (present, absent)	0.20	<b>0.60</b>
153. P5 exopod (present, absent)	1.00	<b>1.00</b>
154. Localization of P5 (ventral, lateral)	-	-
155. Number of setae on female P5 exopod (5, 4, 3, 2, ,1)	0.80	<b>0.75</b>
156. Number of setae on male P5 exopod (5, 4, 3, 2, ,1)	-	-

Table 2: Entomolepididae species used as ingroup in the phylogenetic analysis.

Species	Material analyzed
<i>Entomolepis hamondi</i> McKinnon, 1988	literature
<i>Entomolepis ovalis</i> Brady, 1899	literature
<i>Entomopsyllus adriae</i> (Eiselt, 1959)	literature
<i>Entomopsyllus brevicaudatus</i> Lee & Kim, 2017	literature
<i>Entomopsyllus nicholli</i> McKinnon, 1988	literature
<i>Entomopsyllus stocki</i> Kim, 2004	USNM 1027325 holotype
<i>Entomopsyllus takara</i> Uyeno & Johnsson, in prep.	literature
<i>Lepeopsyllus ovalis</i> Thompson I.C. & Scott A., 1903	literature
<i>Lepeopsyllus typicus</i> Thompson I.C. & Scott A., 1903	literature
<i>Paralepeopsyllus leei</i> Lee & Kim, 2017	literature
<i>Paralepeopsyllus dambayensis</i> Lee & Kim, 2017	literature
<i>Paralepeopsyllus mannarensis</i> Ummerkutty, 1960	literature
<i>Parmulella emarginata</i> Stock, 1992	literature
<i>Parmulodes verrucosus</i> Wilson C.B., 1944	USNM 79000 holotype
<i>Parmulopsyllus breviarticulata</i> Borges <i>et al.</i> , in prep.	UFBA 3290 holotype
<i>Neoparmulella periperiensis</i> Farias <i>et al.</i> , in prep.	UFBA 3302 holotype
	UFBA 3303 alotype
<i>Spongiopsyllus adventicius</i> Johnsson, 2000	UFBA 861
<i>Spongiopsyllus atypicus</i> Canário <i>et al.</i> , in prep.	UFBA 3294 holotype
	UFBA 3295 alotype
<i>Spongiopsyllus boxshalli</i> Canário <i>et al.</i> , in prep.	UFBA 3292 holotype
	UFBA 3293 holotype
<i>Spongiopsyllus hoi</i> Canário <i>et al.</i> , in prep.	UFBA 3298 alotype
<i>Spongiopsyllus intermedius</i> Borges <i>et al.</i> , in prep.	UFBA 3185 holotype



*Spongiopsyllus redactus* Canário *et al.*, 2012

UFBA 400 holotype

*Spongiopsyllus stocki* Canário *et al.*, in prep.

UFBA 3291 holotype

Table 3. Unambiguous character state changes for the single MPT of Entomolepididae phylogeny following implied weighting. Clades with no unambiguous changes are represented by “-”.

Clade 1	144: 0 → 1
Clade 2	39: 0 → 1
Clade 3	121: 0 → 1
Clade 4	5: 0 → 1
Clade 5	-
Clade 6	1: 1 → 0
Clade 7	99: 0 → 1, 108: 0 → 1, 153: 0 → 1
Clade 8	102: 0 → 1, 106: 0 → 1
Clade 9	80: 0 → 1
Clade 10	118: 0 → 1, 139: 0 → 1
Clade 11	58: 0 → 1
Clado 12	14: 0 → 1
Clado 13	-
Clado 14	-
Clado 15	31: 0 → 1
Clado 16	110: 0 → 1
Clado 17	90: 0 → 1
Clado 18	-
Clado 19	97: 1 → 0
Clado 20	96: 0 → 1
Clado 21	76: 0 → 1
Clado 22	-

#### Figure captions:

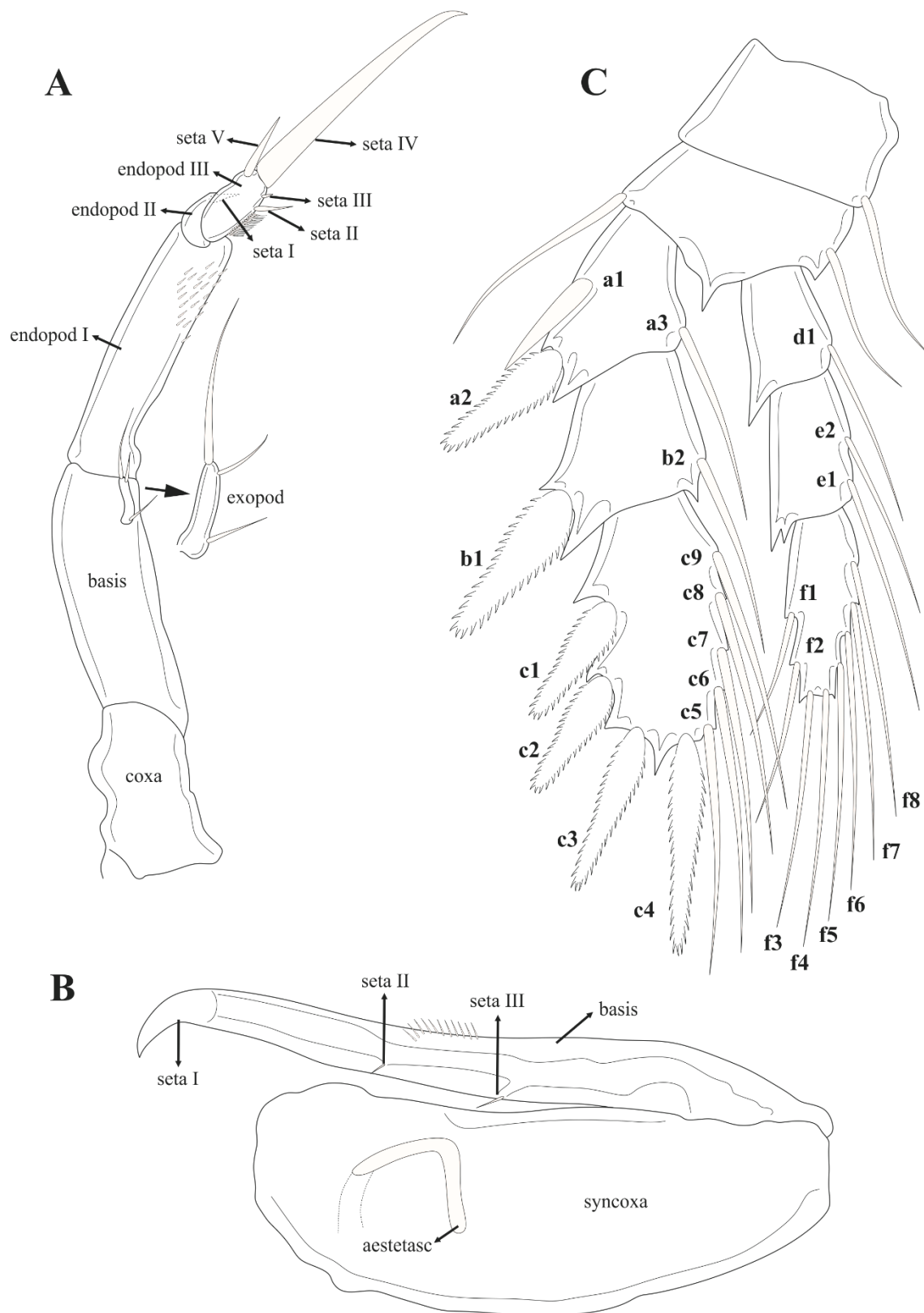
**FIGURE 1.** Ancestral structure of Siphonostomatoida appendages. A, *Asterocheres lilljeborgi*, showing the plesiomorphic condition with the 3-segmented endopod and seta I to V present (modified from Ivanenko & Ferrari, 2003). B, *Dermatomyzon*

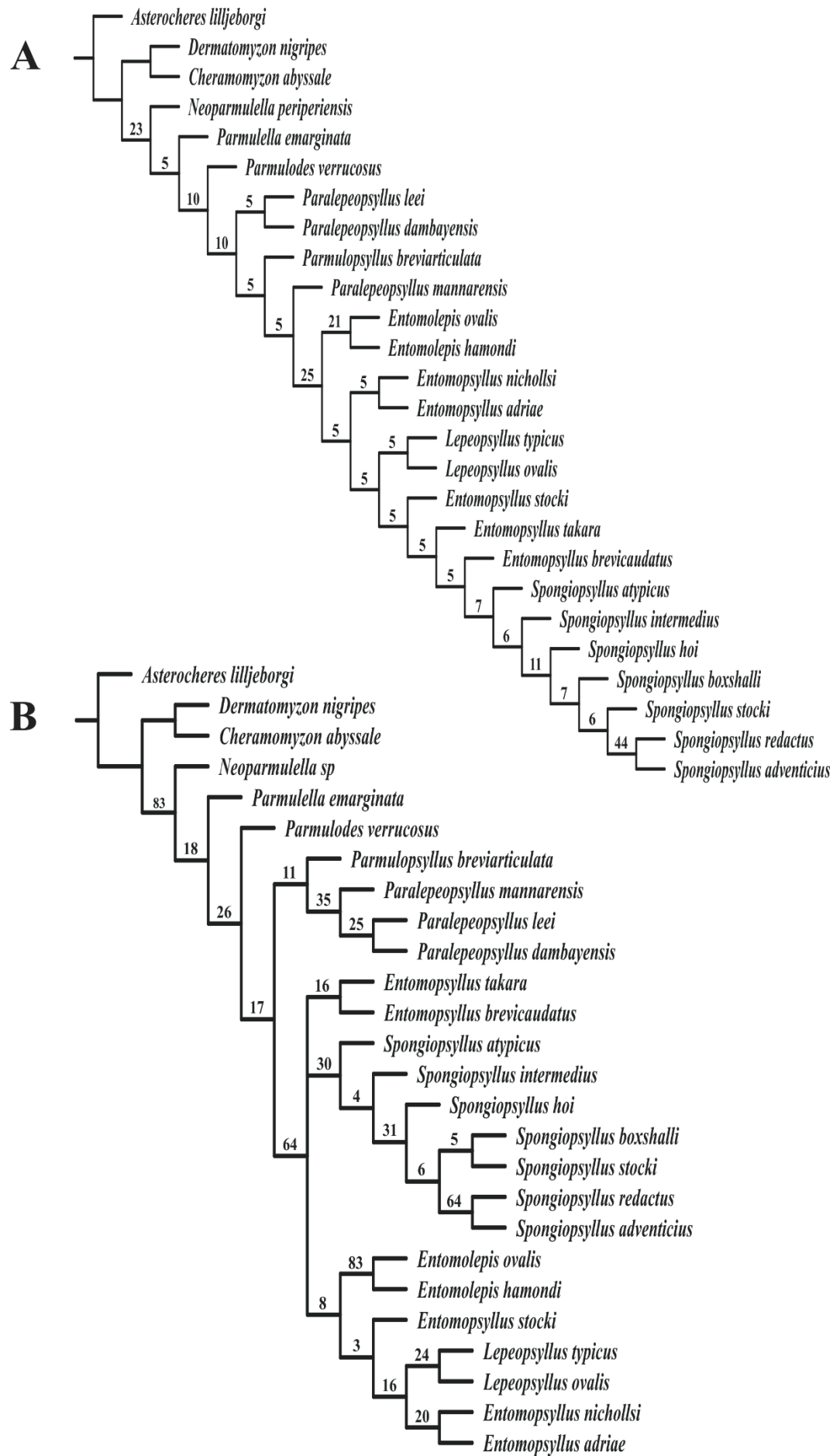
*nigripes*, maxilla with setae I to III identifiable on basis (modified from Ivanenko & Ferrari, 2003). C, Basic pattern of a copepod swimming leg, showing the maximum setation of P2 and the nomenclature of each element (modified from Huys & Boxshall, 1991).

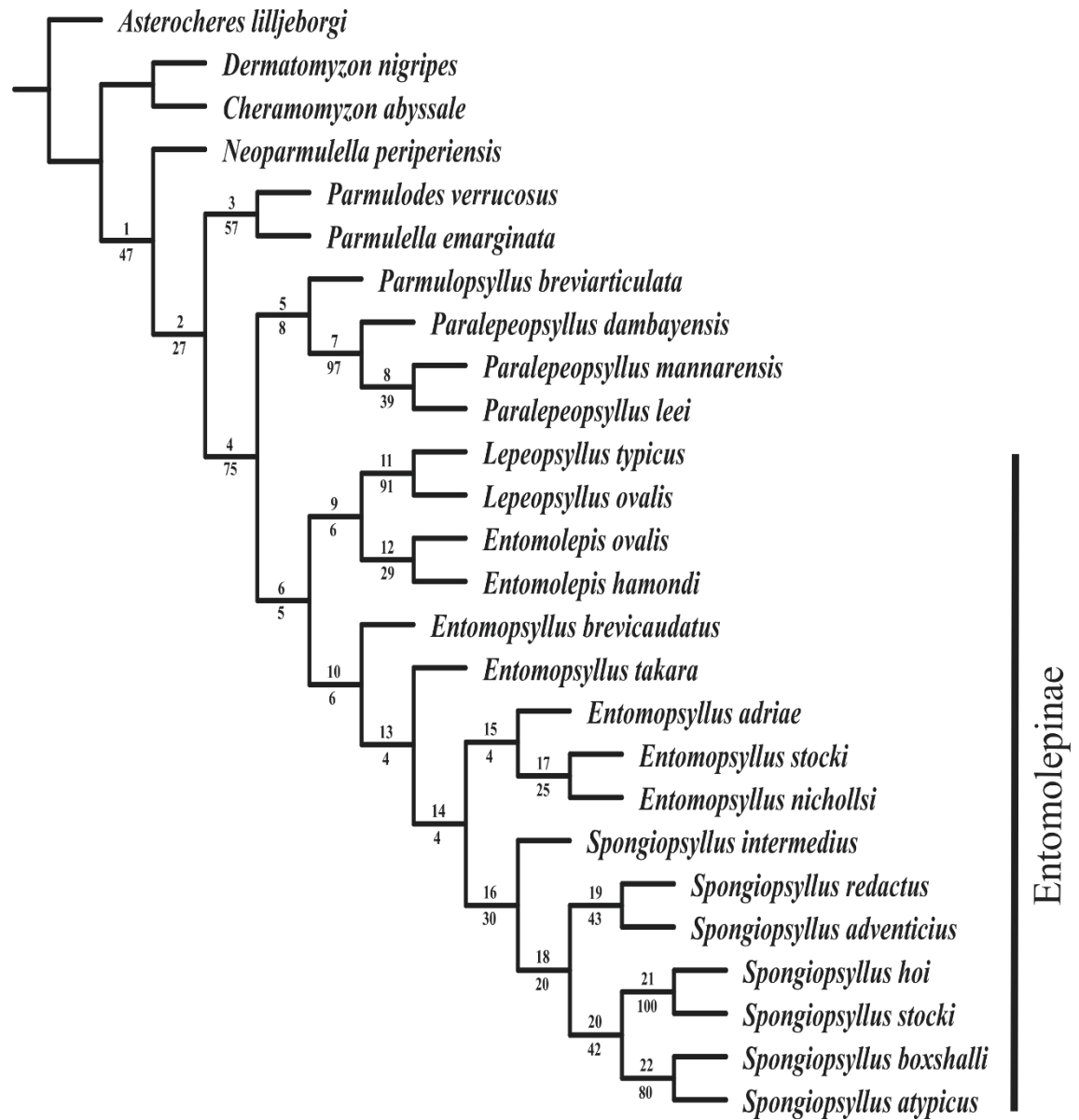
**FIGURE 2.** A, Most Parsimonious Tree, length 372, consistence index = 0.42, retention index = 0.55, numbers above the branches indicate Relative Bremer supports. B, Frequencies differences (CG) of Symmetric resampling ( $p = 33$ ).

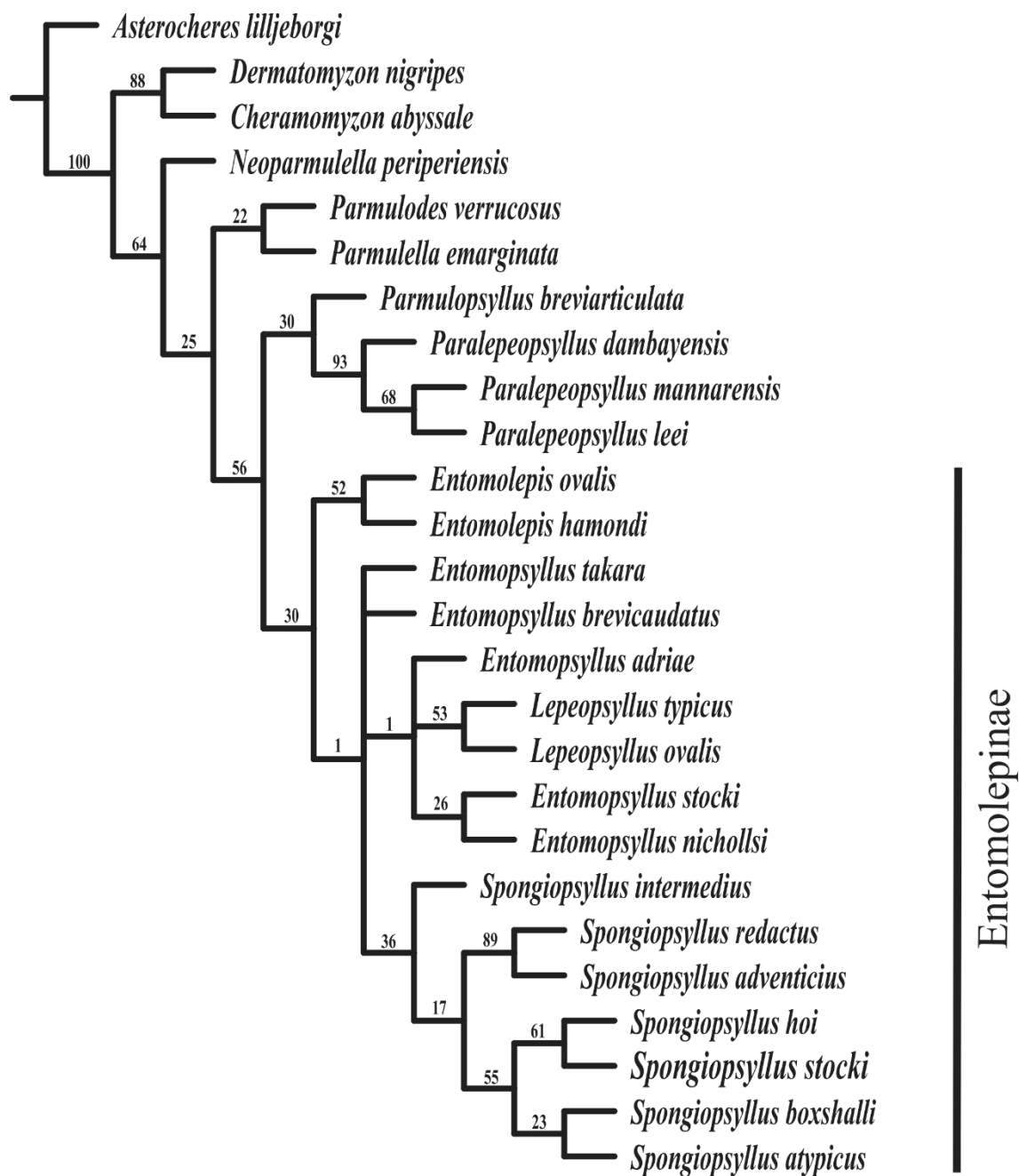
**FIGURE 3.** Most Parsimonious Tree of Implied weighting analysis, length 56.77659, consistence index = 0.40, retention index = 0.52, numbers above branches indicate clade numbers; numbers below branches indicate Relative Bremer supports.

**FIGURE 4.** Symetric Resampling ( $p = 33$ ) of Implied weighting analysis. The numbers represent the Frequencies differences (CG) of clades.









## Appendix

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	
<i>Asterocheres lilljeborgi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Cheramomyzon abyssale</i>	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0	0	0	0	0	1	0	0
<i>Dermatomyzon nigripes</i>	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	2	0	0
<i>Entomolepis hamondi</i>	1	0	0	1	1	0	1	1	1	1	1	0	0	1	0	1	0	1	0	1	0	1	?	?	1	0	0	0	0	1	1	1	1	0	?
<i>Entomolepis ovalis</i>	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	1	1	1	1	1	0	?
<i>Entomopsyllus adriae</i>	0	0	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	1	0	0	1	5	1	0	0	
<i>Entomopsyllus brevicaudatus</i>	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	0	0	0	0	1	1	0	0
<i>Entomopsyllus nichollsi</i>	0	0	1	1	0	1	0	1	1	1	1	0	0	1	0	0	0	1	0	1	0	1	2	1	1	0	0	1	0	1	2	1	0	1	
<i>Entomopsyllus stocki</i>	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	0	0	0	1	1	0	0	
<i>Entomopsyllus takara</i>	?	?	?	?	0	0	1	1	1	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	3	1	0	0
<i>Lepeopsyllus ovalis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	0	1	0	?	1	1	?	
<i>Lepeopsyllus typicus</i>	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0	1	0	1	?	1	1	?	
<i>Neoparmulella periperiensis</i>	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	?	?	0	1	0	1	0	0	0	0	1	0	0
<i>Paralepeopsyllus dambayensis</i>	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Paralepeopsyllus leei</i>	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Paralepeopsyllus mannarensis</i>	0	0	1	1	0	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	0	1	0	0	1	0	2	0	0	
<i>Parmulella emarginata</i>	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1	?	?	1	0	0	1	0	0	2	1	0	0	
<i>Parmulodes verrucosus</i>	0	0	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	2	1	0	0	
<i>Parmulopsyllus breviarticulata</i>	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	1	0	0	4	2	0	0	
<i>Spongiopsyllus adventicius</i>	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	3	1	0	0	
<i>Spongiopsyllus redactus</i>	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0	1	3	0	0	0	
<i>Spongiopsyllus atypicus</i>	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	4	1	0	0	
<i>Spongiopsyllus stocki</i>	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	0	0	4	1	0	0	
<i>Spongiopsyllus boxshalli</i>	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	3	1	0	0	

<i>Spongiopsyllus hoi</i>	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	0	0	1	5	1	0	0
<i>Spongiopsyllus intermedius</i>	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	0	1	0	0	3	1	0	0
	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
<i>Asterocheres lilljeborgi</i>	1	1	0	3	2	1	-	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	
<i>Cheramomyzon abyssale</i>	1	1	0	3	2	1	-	0	0	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Dermatomyzon nigripes</i>	1	1	1	3	2	1	-	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Entomolepis hamondi</i>	?	?	0	3	2	1	-	1	0	1	2	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Entomolepis ovalis</i>	?	?	0	3	2	1	-	1	1	2	1	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0
<i>Entomopsyllus adriae</i>	3	2	0	3	0	1	-	1	0	2	1	2	0	1	1	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0
<i>Entomopsyllus brevicaudatus</i>	3	1	0	3	2	1	-	1	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0	1
<i>Entomopsyllus nichollsi</i>	-	2	0	3	2	1	-	1	0	2	2	1	0	0	1	1	0	1	1	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0
<i>Entomopsyllus stocki</i>	3	1	0	3	2	1	-	1	0	2	1	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0
<i>Entomopsyllus takara</i>	3	1	0	3	1	1	-	1	0	2	2	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0
<i>Lepeopsyllus ovalis</i>	?	?	?	?	?	?	?	?	0	2	1	2	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lepeopsyllus typicus</i>	?	?	?	?	?	?	?	?	0	2	1	2	1	0	0	?	?	?	1	0	1	1	0	?	?	0	1	0	1	0	0	1	0	0
<i>Neoparmulella periperiensis</i>	2	1	0	3	2	1	-	1	0	2	3	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Paralepeopsyllus dambayensis</i>	1	1	1	3	2	1	-	1	0	2	2	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Paralepeopsyllus leei</i>	1	1	1	3	2	1	-	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Paralepeopsyllus mannarensis</i>	2	0	0	3	2	0	1	1	1	2	?	2	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Parmulella emarginata</i>	2	1	0	2	2	0	0	1	0	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Parmulodes verrucosus</i>	2	1	0	3	2	1	-	1	1	2	2	2	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
<i>Parmulopsyllus breviarticulata</i>	2	1	0	3	2	1	-	1	1	1	?	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Spongiopsyllus adventicius</i>	3	2	0	3	2	1	-	1	0	2	2	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1
<i>Spongiopsyllus redactus</i>	3	2	0	3	2	1	-	1	0	2	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Spongiopsyllus atypicus</i>	2	1	0	3	2	1	-	1	0	2	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1
<i>Spongiopsyllus stocki</i>	3	1	0	3	1	1	-	1	0	2	2	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1



<i>Spongiopsyllus boxshalli</i>	2	1	0	3	2	1	-	1	1	2	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
<i>Spongiopsyllus hoi</i>	3	1	0	3	2	1	-	1	1	2	2	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
<i>Spongiopsyllus intermedius</i>	4	2	0	3	2	0	0	1	1	2	2	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127
<i>Asterocheres lilljeborgi</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	
<i>Cheramomyzon abyssale</i>	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Dermatomyzon nigripes</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Entomolepis hamondi</i>	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	-	-	-	-	-	-	-
<i>Entomolepis ovalis</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	-	-	-	-	-	-	-	-
<i>Entomopsyllus adriae</i>	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0
<i>Entomopsyllus brevicaudatus</i>	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	1	1	0	1	0	0	
<i>Entomopsyllus nichollsi</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0
<i>Entomopsyllus stocki</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	1	0	0	
<i>Entomopsyllus takara</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0	
<i>Lepeopsyllus ovalis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	0	0	0	1	0	?	0	0	
<i>Lepeopsyllus typicus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	0	0	0	?	?	?	0	0	
<i>Neoparmulella periperiensis</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	0	0	0	0	0	0	1	1	1	0	0
<i>Paralepeopsyllus dambayensis</i>	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Paralepeopsyllus leei</i>	0	1	0	1	1	1	1	1	1	1	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Paralepeopsyllus mannarensis</i>	0	1	0	1	0	1	0	1	1	0	?	0	1	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Parmulella emarginata</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	0	0	0	0	1	-	-	-	-	-	-
<i>Parmulodes verrucosus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	-	-	-	-	-	-
<i>Parmulopsyllus breviarticulata</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	-	-	-	-	-	-	-
<i>Spongiopsyllus adventicius</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	0	1	1	?	0	0
<i>Spongiopsyllus redactus</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	0	1	1	?	0	0
<i>Spongiopsyllus atypicus</i>	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0

<i>Spongiopsyllus stocki</i>	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	0
<i>Spongiopsyllus boxshalli</i>	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	0
<i>Spongiopsyllus hoi</i>	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	0
<i>Spongiopsyllus intermedius</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	-	0	1	1	0	0	0	1	0	1	0	0

	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156
<i>Asterocheres lilljeborgi</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	2
<i>Cheramomyzon abyssale</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	-	0	0	0	0	0	1	1	?
<i>Dermatomyzon nigripes</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	-	0	0	0	0	0	1	0	?
<i>Entomolepis hamondi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	4	-
<i>Entomolepis ovalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	4	2
<i>Entomopsyllus adriae</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	2
<i>Entomopsyllus brevicaudatus</i>	0	0	1	0	0	0	0	0	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	2	?
<i>Entomopsyllus nicholli</i>	0	0	1	0	0	0	0	0	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	2
<i>Entomopsyllus stocki</i>	0	0	1	0	0	0	0	0	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	2	-
<i>Entomopsyllus takara</i>	0	0	0	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	?	2
<i>Lepeopsyllus ovalis</i>	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	2	-
<i>Lepeopsyllus typicus</i>	0	0	1	0	0	0	0	0	0	0	1	0	0	-	-	-	-	-	-	-	-	-	-	?	?	?	?	?	-
<i>Neoparmulella periperiensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	2	2
<i>Paralepeopsyllus dambayensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	?
<i>Paralepeopsyllus leei</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	?
<i>Paralepeopsyllus mannarensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-
<i>Parmulella emarginata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	2	2
<i>Parmulodes verrucosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	2	2
<i>Parmulopsyllus breviarticulata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	3	?
<i>Spongiopsyllus adventicius</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	2
<i>Spongiopsyllus redactus</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	-

<i>Spongiopsyllus atypicus</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	2
<i>Spongiopsyllus stocki</i>	0	1	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	?
<i>Spongiopsyllus boxshalli</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	2
<i>Spongiopsyllus hoi</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	2	?
<i>Spongiopsyllus intermedius</i>	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	2	?

## Conclusões

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Estudos recentes tem revelado novos táxons de Entomolepididae no litoral brasileiro (Borges *et al.*, em prep.; Farias *et al.*, em prep.). Em consonância, este estudo apresenta quatro novas espécies do gênero *Spongiopsyllus* (*S. atypicus*, *S. stocki*, *S. boxshalli* e *S. hoi*) associadas à esponja *Aplysina cauliformis* coletadas na Baía de Todos-os-Santos, Bahia. Os novos registros somam-se as espécies já descritas, ampliando a diversidade de Entomolepididae para 9 gêneros e 23 espécies. O maior incremento é observado para o Atlântico Sul, o qual apresenta, até o momento, nove espécies conhecidas da família.

Esta tese representa o primeiro estudo que teve por objetivo realizar a investigação das relações filogenéticas internas de Entomolepididae. Ateriormente, a tese de Johnsson (2003) representa o único estudo filogenético que incluiu representantes de Entomolepididae, tendo como foco investigar as relações entre as famílias de Siphonostomatoida associadas a invertebrados. Contudo, o autor não adentrou nas relações internas da família, além de não ter publicado seus dados. Assim, os resultados obtidos no capítulo 3 revelam dados inéditos e relevantes sobre as relações filogenéticas entre os gêneros e espécies de Entomolepididae.

Apesar de prática e facilmente identificável, pois considera o número de segmentos pedígeros presentes no prossomo, a divisão de Entomolepididae em duas subfamílias proposta por Eiselt (1959) não reflete uma organização filogenética. Os resultados aqui alcançados demonstram a condição não monofilética de Parmulodinae. Em contraste, a presença do terceiro e quarto segmentos pedígeros livres é sinapomórfica para Entomolepinae. Em consequência, é proposta uma nova designação para este clado, renomeado como Neoentomolepididae, a fim de

desvincular o cenário filogenético construído nesta tese com a classificação prévia de Eiselt (1959).

A evolução de Entomolepididade é amplamente influenciada por caracteres homoplásticos e seus clados são definidos por poucos caracteres não ambíguos. Dentre seus gêneros, apenas *Entomopsyllus* não representa uma unidade monofilética. *Entomopsyllus* está proximamente relacionado à *Spongiopsyllus* e é provável que ambos representem apenas um gênero. Entretanto, os baixos valores de suporte não permitem incluir, indubitavelmente, *Spongiopsyllus* em *Entomopsyllus*, sendo necessários mais dados morfológicos e/ou moleculares para esclarecer precisamente esta questão. A inclusão de autapomorfias não homoplásticas nas diagnoses pode facilitar a identificação dos limites genéricos e permitir a delimitação mais precisa entre os gêneros.

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## Resumo

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Entomolepididae é uma família de sifonostomatóides com distribuição cosmopolita. Até o momento, é composta por 9 gêneros e 19 espécies, com maior diversidade no Indo-Pacífico. Entomolepididae encontra-se dividida em duas subfamílias que diferem, basicamente, pelo número de segmentos pedígeros entre o cefalotórax e o escudo terminal – Parmulodinae apresenta apenas um segmento enquanto que Entomolepinae possui dois segmentos. Assim como nas subfamílias, é comum encontrar sobreposições nas diagnoses do gênero. Apesar de ser um grupo relativamente antigo, não há na literatura dados acerca das relações entre as espécies de Entomolepididae. Assim, esta tese teve por objetivo realizar uma revisão taxonômica e um estudo filogenético da família Entomolepididae. Ao estudar os espécimes tipos de *Parmulodes verrucosus* e *Entomopsyllus stocki*, foi possível identificar inconsistências que levaram à redescrição da primeira e a adição de notas na descrição da segunda espécie. O estudo da fauna associada à esponjas do gênero *Aplysina* permitiu a identificação de 4 novas espécies de *Spongiopsyllus*: *S. atypicus*, *S. stocki*, *S. boxshalli* e *S. hoi*. O estudo filogenético incluiu as 23 espécies de Entomolepididae, conhecidas até então, além de 3 espécies de Asterocheridae como grupos-externos, e como resultado, foi obtida apenas 1 árvore maximamente parcimoniosa. Apenas a subfamília Entomolepinae foi recuperada como grupo monofilético. Dentre os gêneros de Entomolepididae, apenas *Entomopsyllus* não é monofilético. *Spongiopsyllus* mostrou-se um clado próximo à *Entomopsyllus*. A evolução de Entomolepididae envolveu

muitos caracteres homoplásticos, tornado difícil o reconhecimento de padrões.

## Abstract

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Entomolepididae is a cosmopolitan siphonostomatoid family. Until now, the family is composed by 9 genera and 19 species with major diversity on Indo-Pacific Ocean. Entomolepididae has two subfamilies which differs basically by the number of pedigerous segments between the cephalotorax and the terminal shield – Parmulodinae show one segment instead Entomolepinae has two segments. As in the subfamilies, is common to find overlaps in genera diagnosis. Despite its ancient characteristics, do not have in the literature data concerning the relationships among Entomolepididae species. Thus, this thesis aimed to make a taxonomic revision and a phylogenetic study of Entomolepididae. The analyze of *Parmulodes verrucosus* and *Entomopsyllus stocki* type specimens allowed the identification of incongruences that led to the redescription of the first and to the descriptive notes of the second species. The study of associated fauna of *Aplysina* sponges allow the identification of 4 new *Spongiopsyllus* species: *S. atypicus*, *S. stocki*, *S. boxshalli* and *S. hoi*. The phylogenetic study include all 23 known Entomolepididae species, in addition to 3 Asterocheridae species as outgroups, resulting in 1 most parsimonious tree. Only the subfamily Entomolepinae was recovered as monophyletic. Among the genera, just *Entomopsyllus* was non-monophyletic. *Spongiopsyllus* is a clade close to *Entomopsyllus*. The Entomolepididae evolution involved many homoplastic characters which become difficult the identification of patterns.

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## Referências Bibliográficas

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- Ahyoung, S.T., Lowry, J.K., Alonso, M., Bamber, R.N., Boxshall, G.A., Castro, P., Gerken, S., Karaman, G.S., Goy, J.W., Jones, D.S., Meland, K., Rogers, D.C. & Svavarsson, J. (2011) Subphylum Crustacea Brünnich, 1772. *In*: Zhang, Z.Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Magnolia Press, Auckland, 165–192.
- Brady, G.S. (1899) On the marine Copepoda of New Zealand. Transactions of the Zoological Society of London, 15, 31–54.
- Borges, C., Neves, E.G. & Johnsson, R. (em preparação) A new Entomolepididae genus and a new species of *Spongiopsyllus* associated with sponges in Todos-os-Santos Bay, Bahia, Brazil.
- Boxshall, G.A. & Halsey, S.H. (2004) An Introduction to Copepod Diversity. The Ray Society, London, 966pp.
- Canário, R., Neves, E. & Johnsson, R. (2012). *Spongiopsyllus redactus*, a new species of Entomolepididae (Copepoda, Siphonostomatoida) associated with a scleractinian coral in Brazil. Zoosymposia, 8, 49–55.
- Eiselt, J. (1959) *Entomolepis adriae*, ein Beitrag zur Kenntnis der kaum bekannten Gattungen siphonostomer Cyclopoiden: *Entomolepis*, *Lepeopsyllus* und *Parmulodes* (Copepoda, Crust.) Sitzber. Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, 168, 643–660.
- Eyun, S. (2017) Phylogenomic analysis of Copepoda (Arthropoda, Crustacea) reveals unexpected similarities with earlier proposed morphological phylogenies. Evolutionary Biology, 17(23), 1–12.

- Farias, A., Neves, E.G. & Johnsson, R. (em preparação) A new species and genus of Entomolepididae Brady, 1899 (Copepoda Siphonostomatoida) associated with the endemic octocoral *Phyllogorgia dilatata* (Esper, 1900) (Cnidaria, Octocorallia) from Northeastern Brazil.
- Huys, R. & Boxshall, G.A. (1991) Copepod Evolution. The Ray Society, London, 468pp.
- Johnsson, R. (2000) *Spongiopsyllus adventicius* new species and genus of Entomolepididae (Copepoda: Siphonostomatoida) associated with sponges in Brazil. *Hydrobiologia*, 417, 115–119.
- Johnsson, R. (2003) Filogenia das famílias de Siphonostomatoida (Copepoda) associadas a invertebrados marinhos, com ênfase em Asterocheridae. Universidade de São Paulo, Tese, 415pp.
- Kim, I.H. (2004) Two new species of siphonostomatoid copepods (Crustacea) associated with the stoloniferan coral *Tubipora musica* (Linnaeus) from Madagascar. *Korean Journal of Biological Sciences*, 8, 187–196.
- Khodami, S., McArthur, J.V., Blanco-Bercial, L. & Arbizu1, P.M. (2017) Molecular Phylogeny and Revision of Copepod Orders (Crustacea: Copepoda). *Scientific Reports*, 7(9164), 2–11.
- Mckinnon, A.D. (1988) A revision of Entomolepididae (Copepoda: Siphonostomatoida) with Descriptions of Two New Species from Australia, and Comments on *Entomolepis ovalis* Brady. *Australian Journals of Science Research*, 2, 995–1012.
- Stock, J.H. (1992) Entomolepididae (Copepoda: Siphonostomatoida) from the Antilles. *Studies on the Natural History of the Caribbean Region*, 71, 53–68.

- Thompson, I.C. & Scott, A. (1903) Report on the Copepoda collected by Prof. Herdman, at Ceylon, in 1902. Ceylon Pearl Oyster Fish. Gulf of Manaar, Supplementary Reports, 7, 227–307. pls. 1–20.
- Ummerkutty, A.N.P. (1960) Studies on indian copepods I. *Paralepeopsyllus mannarensis*, a new genus and species of Cyclopoid Copepod from the Gulf of Mannar. Journal of Marine Biology, 2, 105–114.
- Uyeno, D. & Johnsson, R. (in preparation) Two new species of Siphonostomatoida (Copepoda) found on cnidarians in Tokara Islands, Southern Japan.
- Wilson, C.B. (1944) Parasitic copepods in the United States National Museum. Proceedings of the United States National Museum, 94, 529–582.
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## Anexos

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### Normas de formatação para submissão de trabalhos à Zootaxa

#### Preparation of manuscripts

1) *General*. All papers must be in English. Authors whose native language is not English are encouraged to have their manuscripts read by a native English-speaking colleague before submission. Nomenclature must be in agreement with the *International Code of Zoological Nomenclature* (4th edition 1999), which came into force on 1 January 2000. Author(s) of species name must be provided when the scientific name of any animal species is first mentioned (the year of publication needs not be given; if you give it, then provide a full reference of this in the reference list). Authors of plant species names need not be given. Metric systems should be used. If possible, use the common font Times New Roman and use as little formatting as possible (use only **bold** and *italics* where necessary and indentions of paragraphs except the first). Special symbols (e.g. male or female sign) should be avoided because they are likely to be altered when files are read on different machines (Mac versus PC with different language systems). You can code them as m# and f#, which can be replaced during page setting. The style of each author is generally respected but they must follow the following general guidelines.

2) The **title** should be concise and informative. The higher taxa containing the taxa dealt with in the paper should be indicated in parentheses: e.g. A taxonomic revision of the genus *Aus* (Order: family).

3) The **name(s) of all authors** of the paper must be given and should be typed in the upper case (e.g. ADAM SMITH, BRIAN SMITH & CAROL SMITH). The address of each author should be given in *italics* each starting a separate line. E-mail address(es) should be provided if available.

4) The **abstract** should be concise and informative. Any new names or new combinations proposed in the paper should be mentioned. Abstracts in other languages may also be included in addition to English abstract. The abstract should be followed by a list of **key words** that are not present in the title. Abstract and key words are not needed in short correspondence.

5) The arrangement of the **main text** varies with different types of papers (a taxonomic revision, an analysis of characters and phylogeny, a catalogue etc.), but should usually start with an **introduction** and end with a list of **references**. References should be cited in the text as Smith (1999), Smith & Smith (2000) or Smith *et al.* (2001) (3 or more authors), or alternatively in a parenthesis (Smith 1999; Smith & Smith 2000; Smith *et al.* 2001). All literature cited in the text must be listed in the references in the following format (see a [sample page here](#) in PDF).

#### A) **Journal paper:**

Smith, A. (1999) Title of the paper. *Title of the journal in full*, volume number, page range.

#### B) **Book chapter:**

Smith, A. & Smith, B. (2000) Title of the Chapter. *In*: Smith, A, Smith, B. & Smith, C. (Eds), *Title of Book*. Publisher name and location, pp. x–y.

#### C) **Book:**

Smith, A., Smith, B. & Smith, C. (2001) *Title of Book*. Publisher name and location, xyz pp.

#### D) **Internet resources**

Author (2002) Title of website, database or other resources, Publisher name and location (if indicated), number of pages (if known). Available from: <http://xxx.xxx.xxx/> (Date of access).

Dissertations resulting from graduate studies and non-serial proceedings of conferences/symposia are to be treated as books and cited as such. Papers not cited must not be listed in the references.

Please note that:

- (1) **journal titles must be written in full (not abbreviated)**
- (2) **journal titles and volume numbers are followed by a ", "**
- (3) **page ranges are connected by "n dash", not hyphen "-", which is used to connect two words.**

For websites, it is important to include the last date when you see that site, as it can be moved or deleted from that address in the future.

On the use of dashes: (1) Hyphens are used to link words such as personal names, some prefixes and compound adjectives (the last of which vary depending on the style manual in use). (2) En-dash or en-rule (the length of an 'n') is used to link spans. In the context of our journal that means numerals mainly, most frequently sizes, dates and page numbers (e.g. 1977–1981; figs 5–7) and also geographic or name associations (Murray–Darling River; a Federal–State agreement). (3) Em-dash or em-rule (the length of an 'm') are used far more infrequently, and are used for breaks in the text or subject, often used much as we used parentheses. In contrast to parentheses an em-dash can be used alone; e.g. What could these results mean—that Niel had discovered the meaning of life? En-dashes and em-dashes should not be spaced.

6) Legends of **illustrations** should be listed after the list of references. Small illustrations should be grouped into plates. When preparing illustrations, authors should bear in mind that the journal has a matter size of 25 cm by 17 cm and is printed on A4 paper. For species illustration, line drawings are preferred, although good quality B&W or colour photographs are also acceptable. See a guide [here](#) for detailed information on preparing plates for publication.

7) **Tables**, if any, should be given at the end of the manuscript. Please use the table function in your word processor to build tables so that the cells, rows and columns can remain aligned when font size and width of the table are changed. Please do not use Tab key or space bar to type tables.

8) **Keys** are not easy to typeset. In a typical dichotomous key, each lead of a couplet should be typed simply as a paragraph as in the box below:

```
1 Seven setae present on tarsus I ; four setae present on tibia I; leg I longer than the body;
legs black in color ... Genus A
- Six setae present on tarsus I; three setae present on tibia I; leg I shorter than the body; legs
brown in color ... 2
2 Leg II longer than leg I ... Genus B
- Leg II shorter than leg I ... Genus C
```

Our typesetters can easily convert this to a proper format as in this [PDF file](#).